

THE STRUCTURE OF VISUAL RECEPTIVE FIELDS OF CAT'S PULVINAR NEURONS

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Abstract. Receptive fields of 382 neurons in the pulvinar were investigated. The observed receptive fields were classified according to the neurons' responses to stationary flashing light spots positioned in different parts of the receptive field. New receptive field types with multiple discharge centers were observed. Neurons with these receptive fields generally responded with multimodal discharges to moving visual stimuli. The background illumination resulted in a decrease of the number of *on-off* and *off* receptive fields whereas the number of the *on* receptive fields became higher. In a majority of cases the receptive fields with multiple discharge centers lost their responsiveness during background illumination. The changes in the receptive field sizes measured by light spot in dark and light adapted conditions were attributed mainly to scattered light. The sizes measured by black stimuli under the same conditions remained constant.

INTRODUCTION

It has been established by several authors (9, 13, 21, 32, 42) that more than 30% of cells in posterior thalamic nuclei of the cat respond to various kinds of visual stimuli. These findings agree well with the morphological data (1, 11, 14, 20, 29) according to which there exist well — organized afferent and efferent connections of the pulvinar with

the structures in the brain well known for functional significance in the central visual processing. These are superior colliculus, pretectum, lateral geniculate nucleus, visual cortex and the retina itself. Hence the pulvinar nucleus of the posterior thalamus is situated in a crucial point for visual messages from the retina through the extrageniculate pathway to the visual cortical centers.

From this point of view it is interesting to investigate the functional role of the pulvinar in the analysis of visual information. A comprehensive study of the problem has been made recently by Godfraind et al. (13), Veraart et al. (42), Chalupe and Fish (9). The response patterns of neurons in posterior thalamic nuclei to different visual stimuli were investigated in detail and some characteristics of the structure of their receptive fields were described. After the fundamental works of Hartline (16) numerous experiments were conducted in the visual structures other than pulvinar to establish a detailed structure of the receptive fields of visually driven neurons. The retinal ganglion cells and neurons of the lateral geniculate nucleus have mainly concentric types of receptive fields (15, 23, 24, 31, 36), the neurons of visual cortex have complex and hypercomplex receptive fields along with simple fields (25, 26). Superior colliculus and pretectum contain visually sensitive neurons with homogeneous structures of their receptive fields (17, 18, 33, 40, 41). In the present paper we proceed from this point to describe the detailed organization of receptive fields of the pulvinar neurons. We believe that this organization underlies the mechanisms of response patterns of the visually driven pulvinar neurons.

To demonstrate the dynamics properties of the receptive field organization in the cells under investigation, we have tested the effects of background illumination, well known for its modulatory influence on the responses of visual neurons.

METHODS

Seventy six cats 2.5-3.5 kg of body weight were used for our experiments. They were anesthetized with ether for initial surgical preparation. After tracheotomy, cannulation of the cephalic vein and of the femoral artery, the brain stem was transected at the pretrigeminal level (4, 43). The head of the animal was fixed in a Horsley-Clarke stereotaxic apparatus modified for visual research. Small craniotomy was made above the projection area of the posterior thalamic region. The hole in the skull was then filled with soft wax to avoid brain

pulsations. The animal was artificially ventilated (21 strokes/min). Stroke volume was 20 ml/kg of body weight. Arterial blood pressure was 90–120 mm Hg. The heart activity was continuously monitored and the brain activity was tested by EEG recording. The body temperature was maintained between 37.5–38.5° by a heating pad. The nictitating membrane was retracted by neosynephrine, the pupils were dilated by a 0.1% solution of atropine sulfate and the corneas were covered by contact lenses of a “0” dioptric power. The eye immobilization was achieved by intravenous injection of Flaxedil (Gallamine triethiodide) in an initial dose of 80 mg followed by an infusion at the rate of 40 mg/h, or Ditiline (Diiodid dicholin ester of succinic acid) was injected intramuscularly at 7 mg/kg of body weight every hour.

The recording of single unit activity usually began 3 h after the ether anesthesia was discontinued.

Methods of recording. Tungsten microelectrodes (22) were used for recording the single unit activity. They were electrolytically sharpened and coated with a vinyl varnish. Their tip diameter was 1–5 μm and their resistance was 40–50 $\text{M}\Omega$. An identification of the action potentials was performed prior to the recording in orders to establish whether they originated from the neuronal soma or the axon (5, 24). Only the soma spikes were considered for analysis. Spikes were converted into standart pulses using a level-discriminating circuit. The level of triggering was adjusted only for the unit under investigation and was continuously checked using an oscilloscope. Standart pulses were fed into an interspike interval analyser (10, 27). Its output was displayed on another oscilloscope screen as a dot pattern distribution. The abscissa corresponded to the time of stimulation and ordinate, to the logarithmic scale of successive interspike intervals. Each dot corresponded to an individual spike interval. A superposition of 15–30 responses was made on stationary film. This was the main averaging method used in our experiments. The number of dots was counted for each averaged response.

Visual stimuli and receptive field plotting. A perimetric device with a circular concave screen with the ρ 0.95, subtending 100° of the visual angle was used for plotting of the receptive fields and for projection of the visual stimuli. The screen center was at a distance of 78 cm from the anterior nodal points of the cat's eyes. Estimations of the position of the area centralis were made using a narrow beam reversible ophthalmoscope (6, 30). The receptive field of each eye was plotted with the other eye covered a black shield. Manually held wands with black figures were used (squares and disks of different sizes, covered with black velvet to plot out the boundaries of each receptive

field on the perimetric screen. After determination of the receptive field boundaries and of the optimal stimuli for triggering the cell, automatic stimuli were delivered from a projector system with a galvanometric device to which a mirror was attached. The whole system was controlled by a low-frequency generator. The stationary flashing spots were positioned in different parts of the receptive field along its horizontal and vertical axes. Stimulation was performed with a frequency of 1/s (500 ms *on* and 500 ms *off*, the risetime for the onset of the light flash was 80 ms, and the decay-time was equal to 70 ms). The averaged response patterns for each point of stimulation were analyzed quantitatively and pattern diagrams were plotted.

The background illumination was 0.05–20 lx and the intensities of the spot illumination, 0.5–50 lx. The ratio of illuminances of the stimulus spot to the background was maintained under 10 except in some cases of dark adaptation. The measurements of the receptive field size using black stimuli were more reliable than those using light spots because of the absence of scattered light effects.

A stereotaxic atlas of Jasper and Ajmone-Marsan (28) was used for determination of the pulvīnar coordinates. After each experiment an electrolytic lesion was made via the recording microelectrode (0.5 mA during 60 s). The brain was then perfused with saline solution (0.9%) followed by 10% formaline solution. After a week's fixation 30 μ m sections were cut and the localization of the electrode tip was checked histologically.

RESULTS

A total of 382 visually-sensitive neurons in the cat's pulvīnar were investigated, which constituted one-third of all neurons observed. Of the visual neurons 27% responded only to the movement of black objects and no discharges could be elicited in these neurons by light stimuli. Thirteen percent of the neurons could be activated only by movements of visual stimuli and did not respond to stationary light spots. The present study deals only with the neurons responding to the stationary flashing spots. Thus the receptive field characteristics were investigated in 262 neurons, which responded clearly to stationary light spots and to those moving through their receptive field.

Upon isolation of a single unit at first the estimation of its receptive field was done manually with black stimuli. Afterwards the receptive field was investigated by stationary light spot positioned in different sections, generally along the horizontal and vertical axes of the receptive field.

Figure 1 illustrates the distribution of the centers of the receptive fields for left-side pulvinar neurons in the visual field. White circles in the figure represent the centers of receptive fields of monocularly driven contralateral neurons. Black circles show the centers of contralateral receptive fields of binocularly driven neurons. As is seen from Fig. 1, most receptive fields of pulvinar neurons are situated in the lower temporal part of the visual field.

A majority of investigated neurons (48%) had receptive fields with the longitudinal axis oriented horizontally. Twenty three percent of the neurons had vertically oriented receptive fields and 26% had a circular arrangement of their receptive fields. A small number of neurons (3%) had receptive fields with boundaries which were impossible to determine.

The structure of the receptive fields in dark adaptation. In the first series of experiments the receptive fields were investigated in semidarkness. Light spots of 5° in diameter were used with an illumination of 5 lx against an almost dark background (0.05 lx).

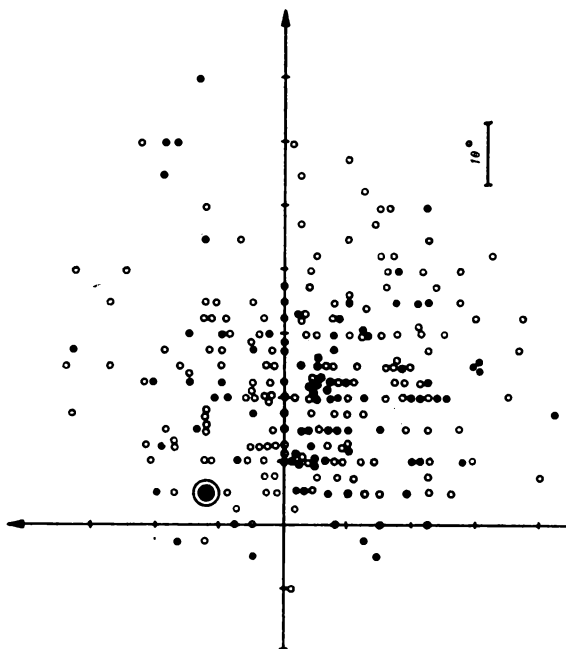


Fig. 1. Distribution of the receptive field centers of the left pulvinar neurons in the visual field. Open circles represent contralaterally driven monocular receptive fields, filled circles are contralaterally driven binocular receptive fields. The position of area centralis in this and all consecutive figures is marked by semi-filled circle.

According to the pattern of responses to the stationary spot flash, the receptive fields were classified as follows: *on* (15%), *off* (30%), *on-off* (38%), simple (2%), the receptive fields with multiple discharge centers named "multicenter" (12%) and concentric receptive fields (3%).

Figure 2 represents the distribution of responses of the first two groups of neurons, *off* (A) and *on* (C) to the flashing light spot positioned along the longitudinal (horizontal) axis of the receptive field. Figure 2B, D shows the corresponding latency distribution of the responses. As can be seen from Fig. 2, both *off* and *on* neurons exhibit, sharp differences in the response amplitudes from the central zone of the field and from the periphery. As a rule, the light spot flashing in the central part of the receptive field yielded vigorous responses of the cell. Latency distribution corresponded well to the response patterns of the cells displaying shorter latencies in the central part of the receptive fields (Fig. 2B, D) and longer — on the periphery.

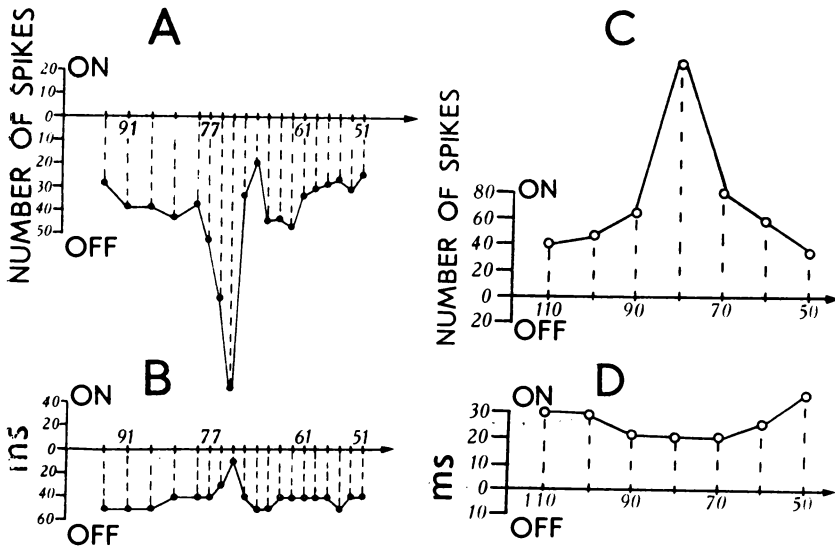


Fig. 2. Distribution of the evoked discharges and latencies of responses to flashing light spot in receptive fields of an *off* (A, B) and *on* (C, D) neuron. A, distribution of discharges along the horizontal axis of the receptive field of an *off* neuron; B distribution of latencies of each response obtained along horizontal axis of the receptive field described in A. C, distribution of discharges evoked by a flashing light spot in an *on* receptive field along its horizontal axis; D, latency distribution in the receptive field described in C. On the abscissa the horizontal axis of receptive fields are presented in degrees. Ordinates in A and C indicate the number of spikes during 15 repetitions of stimuli at each examined area of the receptive field. Ordinates in B and D indicate the latency of the averaged response in ms. Denotations are the same for all subsequent figures.

An *on-off* receptive field which represents the third group is illustrated in Fig. 3A. In every point of the field *on-off* responses were elicited by the flashing light spot. Although quantitatively the responses to light *on* and *off* are nearly equal, the latency distribution is quite different, showing three times longer latencies to light *off* than to *on*.

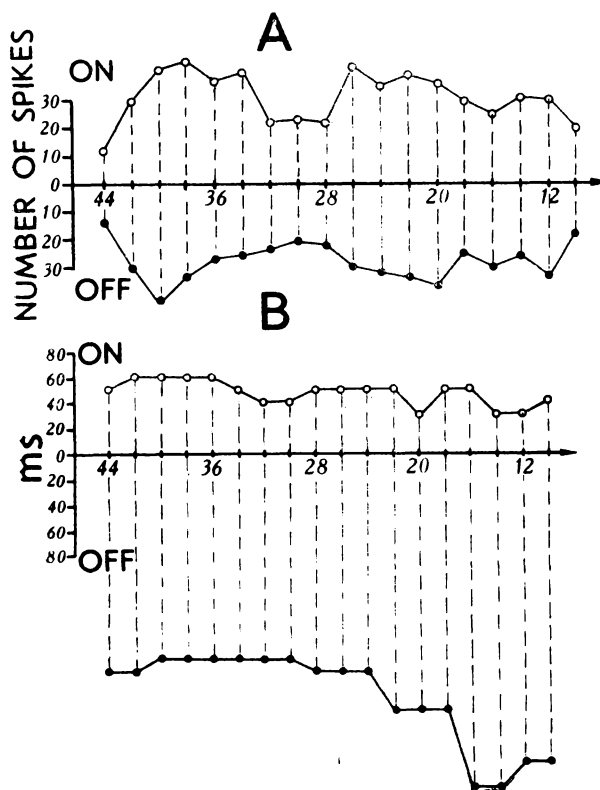


Fig. 3. A, distribution of discharges evoked by the flashing light spot in an *on-off* receptive field. B, distribution of latencies for *on* and *off* responses in the same receptive field.

The fourth group was so-called "simple" type of the receptive field (2%). We called them "simple" because of their resemblance to the simple fields in the visual cortex (25). These receptive fields were composed of two quantitatively different parts (*on* and *off*) although the boundaries between them were not as clear as in the case with the receptive fields of the visual cortical neurons. They were rarely observed in the pulvina.

The most interesting group of receptive fields seems to be the

receptive fields with multiple discharge centers (12%). This group was characterized by a non-uniform distribution of sensitivity to the flashing light over the receptive field surface. Silent zones were observed intermingled with the regions having well-defined responses to light on or off. The unequal distribution of sensitivity to light is shown in the receptive field presented in Fig. 4A. The neuron demonstrated in this figure had a receptive field with unequal distribution of sensitivity to light off. As is seen from Fig. 4, there were small regions in the receptive field having on discharges intermingled with silent zones. On the other hand, off discharges could be evoked from every explored area of the field. In Fig. 4B the latency distribution in the same receptive field is presented.

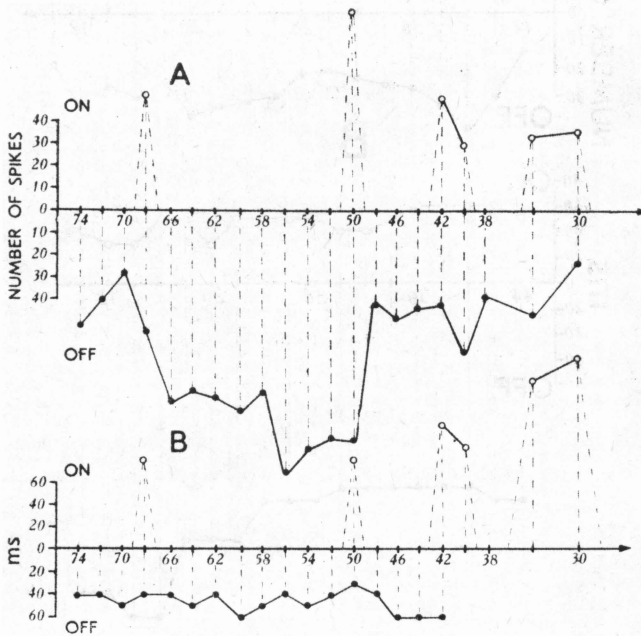


Fig. 4. A, different distribution of intensity of responses to on and off. B, latency distribution in the same receptive field.

The central zone of the receptive field presented in Fig. 5A did not evoke any discharges to the flashing spot, whereas the peripheral zones revealed a well-defined sensitivity to stationary visual stimuli. The same is true for the receptive field of another neuron shown in Fig. 5B, C, which represents the number of discharges of the cell to a spot light on and off along the horizontal (B) and vertical (C) receptive field axes. The central zone of the receptive field revealed poor responses to the flashing spot light.

In an earlier study (21) we have described neurons which responded to the motion of a light spot through their receptive fields by multimodal distributions of spike discharges. Most of these neurons had receptive fields of a multicenter type.

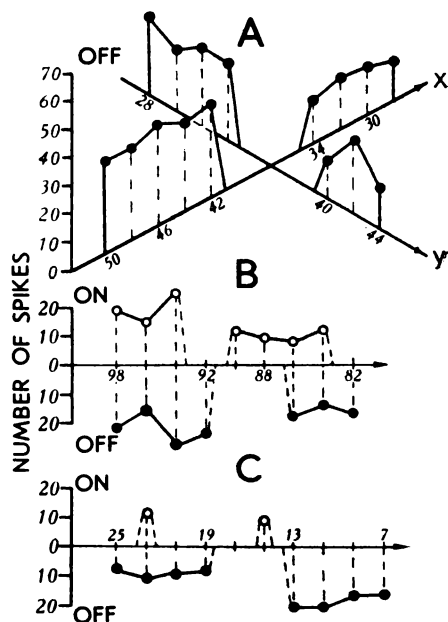


Fig. 5. The off (A) and on-off (B, C) receptive fields with silent central zones. A, the receptive field of an off-neuron where the central zone remains non-responsive to stationary flashing light spot while the surrounding zone gives prominent off-response. B, C, distribution of discharges on horizontal and vertical axis of an on-off receptive field with silent zones existing both as in on and off responses.

A small percentage of neurons (3%) constituted the sixth group having receptive fields of a concentric type. Generally, these fields revealed on-off responses from their central part and on or off responses from the surrounding area, or vice versa.

The effects of background illumination on the receptive field structure. The second series of our experiments concerned the modulatory effects of background illumination on the receptive fields in single pulvinar neurons and the dynamic properties of these receptive fields.

One hundred five neurons were investigated at different levels of light adaptation. At first the characteristics of the neuronal responses to flashing stationary light spot were determined in semi darkness. The percentage of the on-off neurons was highest (40%), the off neurons constituted 32% and on neurons 14%. Neurons with multicenter receptive fields constituted 14%.

Under light-adapted conditions the percentage of the on-off neurons sharply decreased and became 13%, off neurons constituted 26% and

the *on* neurons reached 30%. The multicenter receptive fields were transformed into homogeneous *on* or *off*, or became almost completely unresponsive to light flashes. 31% of the neurons under study displayed a complete suppression of the evoked activity during light adaptation.

The receptive field dimensions were estimated using flashing light spots and moving black objects in semi-darkness and at different levels of background illumination. The data presented here suggest that cats can see black objects even in semi-darkness, when illumination of the perimeter screen is as low as 0.05 lx. Measurements of the receptive fields were performed under the same conditions using light spot stimuli. The main purpose of employing black objects as stimuli was to avoid the effect of the scattered light, which is inevitable when using light spots. All receptive fields studied during dark adaptation had larger sizes when measured by light stimuli in comparison with the dimensions estimated by black stimuli. This fact points to the role of scattered light in this type of measurements.

The data presented below show the effects of background illumination upon the apparent receptive field sizes (measured by light spot and black stimuli) and upon the patterns of cell responses.

Figure 6 illustrates a receptive field of an *on* neuron. The number of spike discharges evoked by a flashing light spot in semidarkness and during a background illumination of 1.5 lx and 5.25 lx is presented (Fig. 6A1, A2, A3). The intensity of the *on* response increased during background illumination (A2 vs. A1) but the size of the area yielding the spike responses was smaller. When measured by a flashing light spot, the boundaries of the receptive fields were larger in semi-darkness (B1) than during light adaptation (B2, B3). Meanwhile estimations of field sizes by black stimuli (Fig. 6C) did not reveal any changes in the receptive field size in semi-darkness and during the illumination of the background (C1, C2, C3). During light adaptation, the area of the receptive field sensitive to light stimuli appears to be smaller (Fig. 6B3) than that responsive to black stimuli (Fig. 6C3).

Figure 7 shows the changes in the response patterns and receptive field sizes of an *off* neuron measured in semi-darkness and at different levels of light adaptation. A slight decrease in the intensity of the response occurred after switching the background illumination *on* (A1 vs. A2-4). The receptive field size shrank after the illumination of the background (Fig. 7B1 vs. Fig. 7B2-4) when tested by light stimuli. The receptive field sizes as measured by black stimuli (Fig. 7C1-4) stayed constant and were comparable to those measured by light stimuli on the illuminated background.

Figure 8 illustrates the responses of an *on-off* neuron and changes of its receptive field dimensions during background illumination. The *on-off* responses recorded in semi-darkness were transformed into a weak *on* response during light adaptation (A1, 2). The receptive field measured by light stimuli had larger sizes in semi-darkness (Fig. 8B1) as compared with those for black stimuli (Fig. 8C1). After light adaptation only a small area in the visual field gave light induced

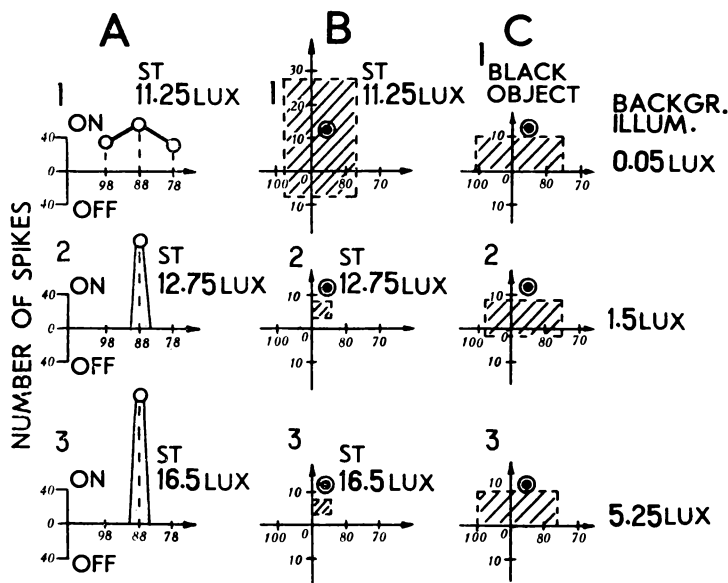


Fig. 6. Effects of background illumination in an *on* receptive field. **A**, distribution of discharges evoked by flashing light spot positioned at 5° intervals along horizontal axis of the receptive field in the dark (A1) and different levels of background illumination (A2,3). **B**, the sizes of the receptive field of the same neuron measured by light spot in the dark (B1) and different levels of background illumination (B2,3). **C**, the same receptive field measured by black stimulus in the dark (C1) and different levels of background illumination (C2,3). The numbers on the right edge of the figure indicate the level of background illumination. ST, the intensity of illumination of the light spot. Denotations are the same for subsequent figures.

responses (Fig. 8B2), whereas the black stimuli elicited responses over the same area as in the semi-darkness (Fig. 8C2). Again we were confronted with the fact that light-sensitive region in the receptive field is of a smaller size than the region sensitive to black stimuli and is situated nearly in the center of the black field (compare Fig. 8B2 with Fig. 8C2).

Some neurons which responded well to a flashing spot in semi-darkness lost their activity during light adaptation. The cell whose

responses are presented in Fig. 9 demonstrates this property. As seen in A1, the cell responded by on-off discharges to the flashing light spot all over the receptive field. Only the narrow central region failed to respond to light on. After the illumination of the background by 1.5 lx, the responses of the cell had completely disappeared. Hence it was impossible to form any judgement about the receptive field size

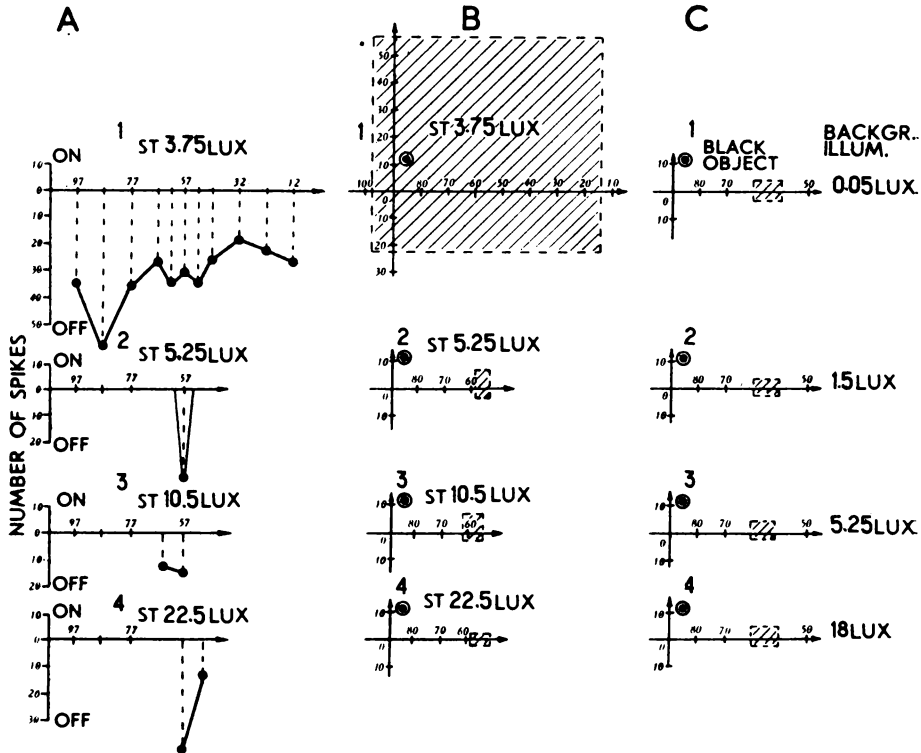


Fig. 7. Effects of background illumination in an off receptive field. A, distribution of evoked discharges in the dark (A1) and different levels of background illumination (A2-4). B, sizes of the receptive field measured by a light spot in dark (B1) and different levels of background illumination (B2-4). C, sizes of the receptive field measured by a black stimulus in the dark (C1) and at different levels of background illumination (C2-4).

when tested by light spot, during light adaptation while the same light spot yielded responses over a large area of the visual field in semi-darkness (Fig. 9B). The receptive field of the same neuron tested by lack stimuli had the same dimensions in semi-darkness (Fig. 9C1) as under the light adapted conditions (C2, 3).

To clarify the role played by scattered light in the estimation of apparent dimensions of the receptive field in semidarkness and under

different levels of background illumination, a control series of experiments has been conducted. The aim of these experiments was to maintain a constant level of light spot intensity against the lighting intensity of the background by their proportional modification. This method allows one to sustain a constant amount of scattered light for different levels of background illumination. The results are shown on

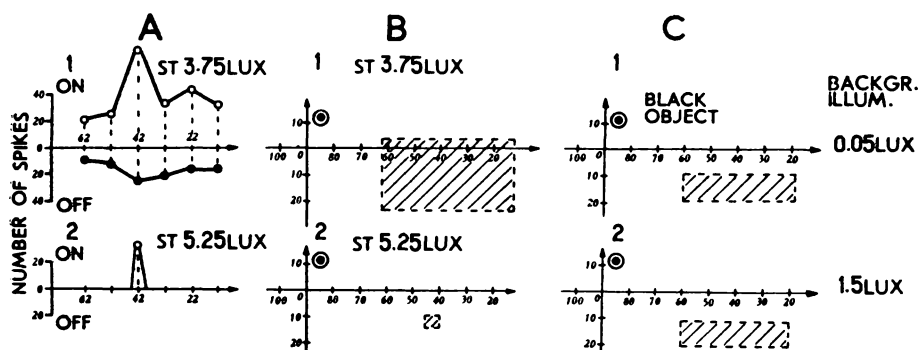


Fig. 8. Effects of background illumination on an on-off receptive field. A1, 2, change of an on-off response to a weak on response during light adaptation. B, the receptive field size measured by light stimuli in semi-darkness (1), and after light adaptation (2). C, the receptive field size measured by black stimuli.

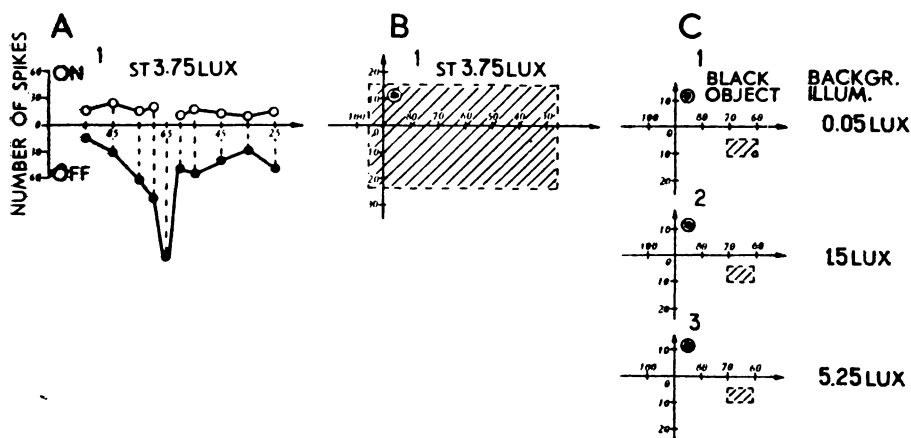


Fig. 9. Disappearance of the responses evoked by flashing light spot during background illumination. A, the on-off responses evoked by light spot flashing through the receptive field. B, size of the receptive field as measured by light spot in darkness. C, size of the receptive field as measured by black stimulus in semi-darkness (C1) and at different levels of background illumination (C2, 3).

Fig. 10. It is clearly seen from this figure that no changes in the receptive field dimensions were observed while varying the illumination of the background.

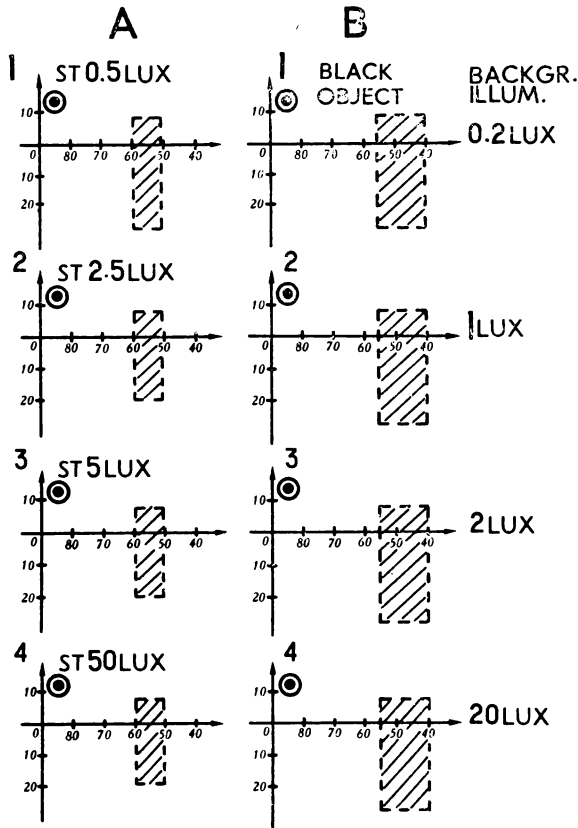


Fig. 10. The sizes of the receptive field of a neuron as measured by light (A1-4) and black (B1-4) stimuli. The illuminance ratios of the light spot to the background remained constant for 1 through 4.

The size of the receptive field measured by light stimuli in semi-darkness and during background illumination did not change at all (Fig. 10A 1-4). The same is true for measurements with black stimuli. The results of these control experiments have confirmed our assumption that the changes in the sizes of receptive fields as measured by light stimuli for different levels of light adaptation are mainly due to the presence of scattered light.

DISCUSSION

An attempt has been made in this study to classify individual neuronal receptive fields in the pulvinar. The first three groups of receptive fields have structure resembling those of the tecto-pretectal region (17, 18, 33, 41, 42). The receptive fields of the fourth group are similar to the simple receptive fields of visual cortex neurons as described by Hubel and Wiesel (25, 26). The most interesting are the receptive fields of the fifth group. These receptive fields are mosaically organized into excitable subunits interspersed with silent zones. One could compare these fields with the receptive fields as described by Bishop et al. (7, 8) and Pettigrew et al. (35) who suggest the existence of the visual receptive fields with multiple discharge centers. According to the assumptions of these authors such a structure plays an important role in the perception of dark and light boundaries of visual stimuli. From the functional point of view our earlier observations have induced us to put forward a suggestion that the receptive fields with multiple discharge centers are specialized in the perception of the velocity and size of the visual stimuli. The sixth group is characterized by a resemblance to the concentric type of receptive fields as described for the lateral geniculate neurons (15, 24). There exists a central region in these fields giving a discharge pattern opposite to the one obtained on the periphery. The center is predominantly *on-off* with *on* or *off* responses from the surround.

The second series of experiments dealing with the influences of background illumination on the receptive field structure of neurons in the pulvinar showed that the state of adaptation significantly modified the cell's response patterns to the light stimuli.

Kuffler (31) in his early experiments had emphasized that the receptive field size of the retinal ganglion cells depended on the stimulus intensity, the size of the exploring spot and the state of dark adaptation. Numerous experiments performed in the retina (2, 3, 12), and at subcortical (15, 19) and cortical (34, 37-39) levels indicated the modulatory effects of light adaptation on the functional characteristics and receptive field size of visually sensitive neurons. The main result obtained showed that under dark adapted conditions the receptive field size was much greater than that measured under light adaptation. Hypotheses were put forward (12, 39) on the role of inhibitory processes underlying the mechanisms of changes in the receptive field size.

The results presented in this study show that the receptive field measured in semi-darkness using light or black stimuli have different

size; the former generally being larger. Under light adaptation this difference is reversed and the light — sensitive area becomes smaller than that measured by a black stimulus. The observed discrepancies are probably caused by the presence of scattered light. In the dark, evidently, a strong scattered light is present around a light spot, whereas the black stimuli are deprived of it. So the dimension of the receptive field for light spot become greater than those measured by black stimuli. Illumination of the background produces a sharp decrease in the amount of scattered light, resulting in the reduction of the size of the receptive field. The black stimuli serve as a good control for the scattered light effects. Experiments with simultaneous proportional changes of the luminancies of the flashing light spot and the background showed no changes in the dimensions of the receptive field due to a transition from dark to the light adapted conditions. It seems that modulatory effects of background illumination concerned mainly the patterns of neuron responses and did not affect its receptive field dimensions. A conclusion could be drawn that the changes in the sizes of receptive fields described by other authors (12, 39) were conditioned mainly by scattered light.

The next problem to deal with is the differences in sizes of the receptive fields measured by light and black stimuli during background illumination. In a majority of cases the receptive field for the light stimulus is smaller than that measured by black stimulus. On the basis of the observation the suggestion has been put forward that the receptive fields of visually sensitive neurons in the pulvinar possess discrete regions sensitive to different types of stimuli. It seems that a greater part of the receptive field is specialized in the perception of black objects, while a small area mostly in the center of the black field has a high sensitivity to light. However, any suggestions about specific channels for the perception of light and black stimuli would be partly speculative and simplified and need further studies.

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