ANALYSIS OF VISUALLY EVOKED ACTIVITY IN THE PRETECTAL REGION OF THE CAT

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The present paper deals with the functional organization of the pretectal region of the cat. Together with other data reported by us in the previous paper (Harutiunian-Kozak et al. 1968a) it completes our concept of the functional role of the pretectal region in the processes of vision.

Several authors localized in the pretectum the main center of the pupillary light reflex (Keller and Stewart 1932, Magoun 1935, Magoun and Ranson 1935, Singleton and Peele 1965, Cavaggioni et al. 1968, Smith et al. 1968). Obviously, this is the reason why the majority of investigators have been involved in studying the functional properties of the pretectal region from the point of view of its role as the pupillary light reflex center.

However, later investigations have suggested that the pretectal area may subserve not only the modulation of the pupillary light reflex, but is also concerned with learning of visual discrimination habits (Thompson and Massopust 1960, Thompson and Rich 1961, Thompson et al. 1963, Fishman and Meikle 1965, Thompson et al. 1967).

Urbaitis and Meikle (1968) have demonstrated that learning of intensity discrimination in the cat may remain after lesions in the superior colliculi and in the visual cortex. According to the same authors this function is compensated by the undamaged pretectal area. Thompson and Massopust (1960) have presented data showing that in the conditioned reflex experiments (black-white discrimination habit) a strong retention-deficit was observed in rats with lesions in the pretectal areas. Further, Thompson et al. (1963) have demonstrated that bilateral lesions of the pretectal area in rats and cats have resulted in a dissociation between the

visual and auditory avoidance conditioned responses, that is, the lesions did not affect the auditory avoidance reflexes while the visual avoidance has been strongly impaired. These authors have tried to find in the pretectum some crucial points responsible for the visual avoidance reflex. The critical region concerned with the visual behavior has been localized in the antero-medial pretectum in the rat and in the postero-lateral pretectum in the cat (Thompson and Rich 1961, Thompson et al. 1963).

According to anatomical data, there are direct projections from the retina to the pretectal region, so the latter one receives the primary visual input information (Bishop and Clare 1955, Singleton and Peele 1965, Laties and Sprague 1966, Garey and Powell 1968). Studies of the optic nerve fibre degeneration in the cat have shown many degenerated terminals in the pretectum, especially in the region of the nucleus of the optic tract (Singleton and Peele 1965, Laties and Sprague 1966, Garey and Powell 1968). It is highly probable that, owing to these connections and due to the connections with midbrain structures especially with the Edinger–Westphal nucleus, the pretectum can modulate the pupillary light reflex. However, the experiments done by Thompson and others, and also our experiments (Harutiunian-Kozak et al. 1968b), have suggested that the cat's pretectum is also involved in another kind of analysis of visual information, that is, it may subserve visual perception on a level comparable perhaps to that of the visual cortex.

The method of single unit analysis, as well, as the recording of compound potentials have been used to explore some functional characteristics in the pretectal area. Considerable attention has been paid to different modalities of neurones and their discharge patterns in response to visual stimuli.

Since relatively few investigations have been carried out on the pretectal region as one of the primary subcortical visual centres, we hope that the data presented in this paper will contribute to a better understanding of the functional properties of this area.

METHODS

Analysis of single unit responses and of compound evoked potentials was performed using ANOPS analyzer (Jankowski 1957).

Forty cats with midpontine pretrigeminal section (Żernicki 1964) were used, and 122 units were examined. The coordinates of the pretectal area and in particular of the optic tract nucleus were found according to the stereotaxic atlas of Jasper and Ajmone-Marsan (1960).

The stimuli employed were similar to those used in our experiments with the superior colliculus except that an additional stimulus was applied it was an edge

moving across the receptive field in various direction (Fig. 1). For the details of the method see the preceding paper (Harutiunian-Kozak et al. 1970).

All the brains were histologically examined. In most cases the electrode trace was localized in the lateral pretectum.
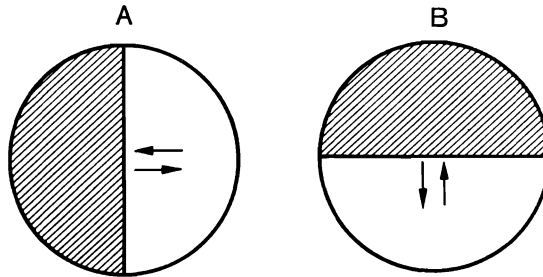

Fig. 1. The edges and their direction of movement.

RESULTS

Most investigations of the single unit activity in the cat's pretectum have utilized diffuse light flashes as stimuli (Cavaggioni et al. 1968, Smith et al. 1968). In our experiments, in addition to light flashes, moving stimuli were used. They enabled us to find new categories of neurons apart of those revealed by diffuse light stimuli.

Attempts were made to classify neurons in the pretectum according to their firing patterns in response to different visual stimuli. The neurons were divided into the following subgroups.

1. Directionally insensitive neurons (non-DS). These neurons responded vigorously to objects moving across their receptive fields, regardless of the direction of movement (symmetrical responses).

2. Direction-sensitive (DS) neurons responding vigorously to stimuli moving in one direction through their receptive fields and not responding at all, or weakly, to stimuli moving in the opposite direction (asymmetrical responses).

3. Orientation-sensitive neurons responding intensely when objects moved along one orientation (e.g. vertical), whereas their response to movement in the perpendicular orientation was weak.

4. Neurons which suppressed their spontaneous activity when light spot entered into their receptive fields.

5. Neurons which suppressed their activity during the period of changing the intensity of illumination from light to dark (negative off neurons).

6. Neurons not responding to changes in diffuse illumination of the receptive field, but only to the movement of an object in the field.

7. Neurons responding only to changes in intensity of illumination and not to objects moving across their receptive fields.

8. Non-visual neurons.

All of these kinds of the neurons, except for classes 6 and 8 responded to light flashes. A majority of their responses were diphasic ("on-off"), but responses exclusively to "on" and exclusively to "off" were also observed.

A great majority of neurons responded vigorously to the objects moving in their receptive fields.

Directionally insensitive neurons (non-DS)

Forty-four of the 122 cells examined belong to this group (36%).

The firing patterns of such cells were characterized by strong responses to the objects moving in their receptive fields with nearly equal number of spikes for two opposite directions of movement. These neurones lack the ability to detect the direction of movement. The post-stimulus time histograms of these neurons had a form of two symmetrical columns; we shall call their reactions — "symmetrical responses".

Figure 2ABEF shows post-stimulus. time histogram (PSTH) of a neuron driven by a photic stimulus; a light spot, 8° in diameter, is moving across the receptive field in various directions. The ordinate presents the number of spikes per address while the abscissa indicates the time after the start of movement from the left or from above. There were 127 repetitions of the stimuli applied, so that highly averaged discharge patterns of the neuron are presented.

It is seen from this figure that the neuron responds in a similar way to different directions of movement. In general, the PST-histograms are symmetrical.

It was possible to record the compound responses to moving stimuli from the same point by using the same lead (Fig. 2CDGH). This is an advantage of the method used, and makes it possible to observe the activation of a number of neurons by the same stimuli. Thus one has a clear picture of the background activity in the part of the pretectum from which the single unit is recorded. The temporal relations, as well as correlation between single unit responses and mass activity, were thus determined. The shapes of evoked potentials in Fig. 2 suggest that, in this point of the pretectum, the majority of cells respond equally well to movements in all directions.

Figure 3 represent post-stimulus time histograms of another non-DS unit. This neuron responded also to changes in diffuse illumination. In this case, however, there existed a discrepancy between the firing pattern
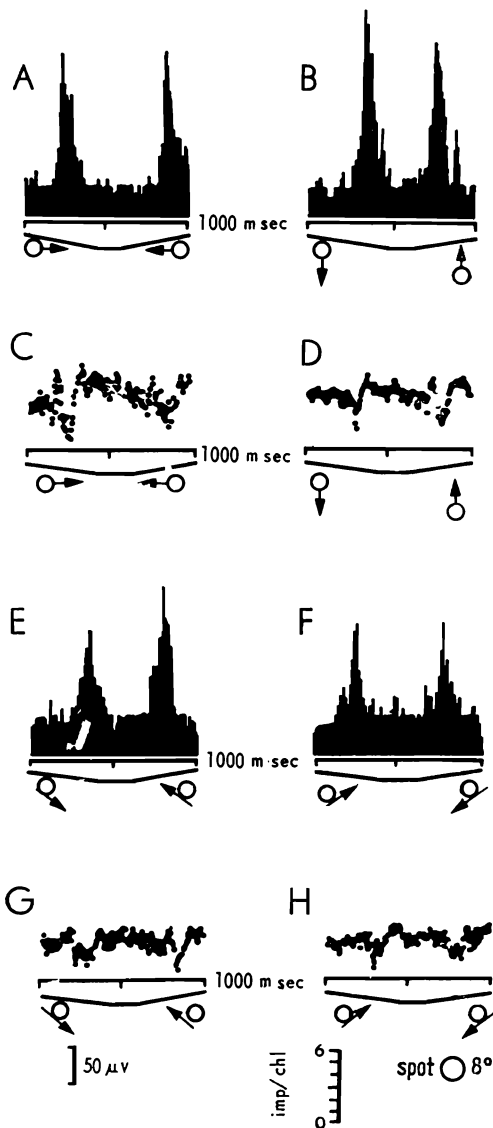
Fig. 2. Responses of directionally non-sensitive single cell and evoked potentials to the moving light spot. A, PST-histogram of the cell response to the movement in the horizontal plane (symmetrical histogram). B, PST-histogram of the same cell during the stimulus movement in vertical plane. C, D, Evoked potentials from the same point where neuron responses were recorded to the same kind of stimulus. E, F, PST-histograms during the movement of the disk in oblique directions at 45° of angle. G, H, Evoked potentials to the oblique movements at 45° of angle. Arrows shows the direction of movement. 64 repetitions of stimuli. On the abscissa were given the time after the stimulus onset, on the ordinates the number of spikes per channel for PSTH, and averaged amplitude of potentials for evoked responses.

of the single cell and the mass activity of background cells. The evoked potentials are small and unclear (Fig. 3FG) whereas the cell response is very intense (Fig. 3AE). This is even more obvious in the case of responses to moving stimuli. There is only a weak correlation between single unit and background neuron activity. Such observations may indicate that the cell picked up by our microelectrode is not typical for the cell population in its vicinity.
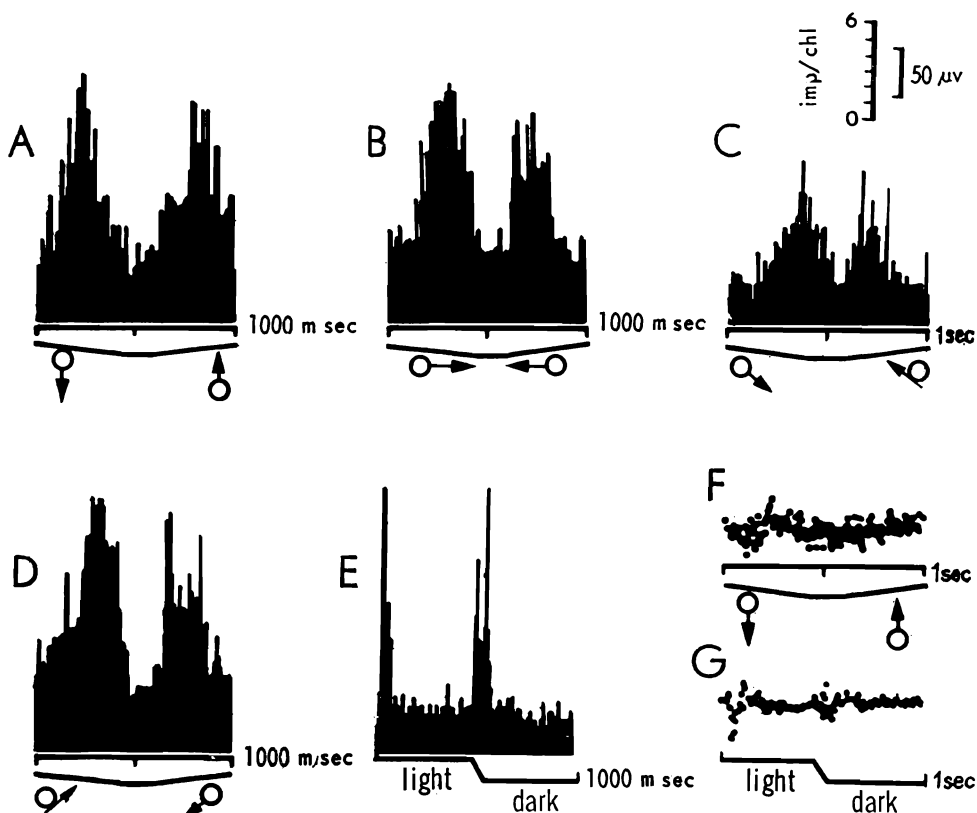

Fig. 3. Directionally non-sensitive cell response. A, B, PST-histograms of responses to the movements in the vertical and horizontal orientations. C, D, PST-histograms of responses to the oblique movements (45° of angle). E, PST-histogram of the same cell to the changing of diffuse light at the rate 1/sec. F, G, Evoked potentials from the same point to the movements in the vertical orientation and to the changes of diffuse light. 64 repetitions of stimuli for the PSTH and evoked potentials.

Direction-sensitive neurons

Among 122 cells examined 36 (29%) cells exhibited sensitivity to one direction of movement. These neurons responded by increasing their

firing rate during the movement of an object in a certain direction across the receptive field, called the preferred direction, and responded weakly, if at all, during the movement in the opposite direction, called the null direction (Barlow and Levick 1965). PST-histograms, of spike firing of such a neuron showed the maximum number of spikes in the preferred direction and only a few spikes in the null direction. Thus, the whole histogram was asymmetrical.

As a rule, direction-sensitive neurons became readily habituated by the repetition of stimuli. Their sensitivity to the changes of diffuse light is generally very low, although some of them may be very sensitive to flashing light. An example of a cat's pretectal neuron responding in this way is shown in Fig. 4ABC. Responses to a white spot moving in
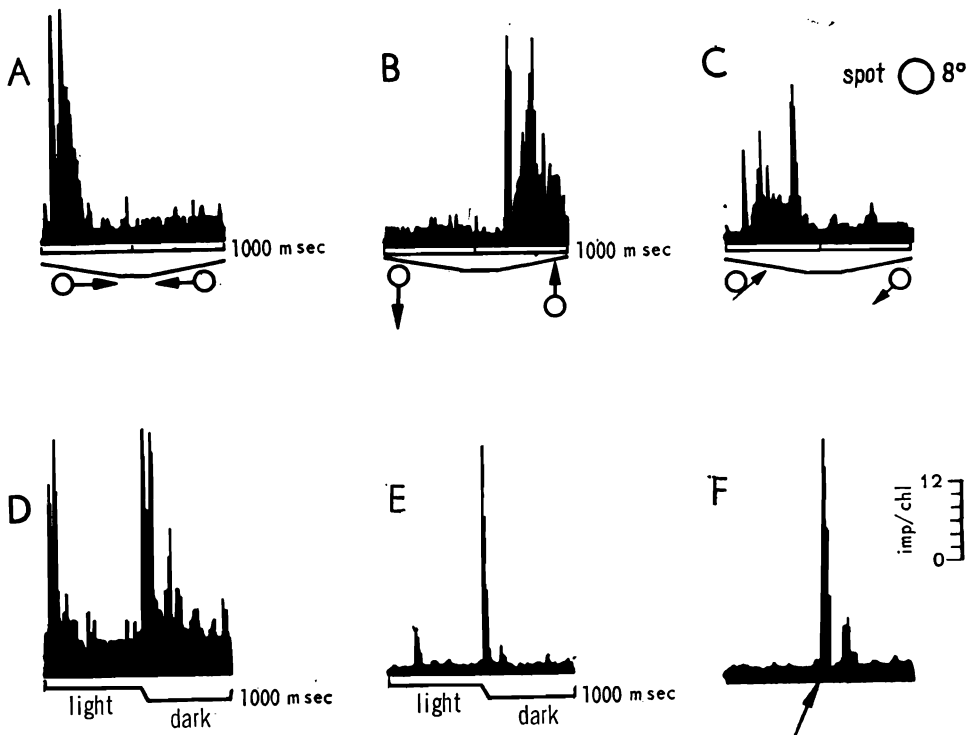

Fig. 4. PST-histograms of direction-sensitive neuron in the pretectum. A, B, PST-histograms of responses to the moving stimulus in the receptive field in the horizontal and vertical orientations. There is an asymmetrical type of PSH. The preferred directions are from left to right, and from down to up. C, PSTH of responses to the oblique movements (45° of angle). D, PSTH of responses to flashing diffuse light 1/sec. E, PSTH of responses to flashing light spot 8° in diameter. F, Short-term dimming of the illumination of receptive field. The arrow shows the moment of darkening of the field. Before and after arrow the illumination was steady. 127 repetitions of stimuli.

preferred directions are quite strong, as indicated in Fig. 4 by the number of spikes, while during the movement in the opposite direction the neuron is almost silent.

Figure 4DEF demonstrated the effect of a change in diffuse illumination on the responses of the same cell. There is an "on-off" response with the stronger "off" reaction (Fig. 4D). In Fig. 4E, the responses to flashing light spot (4° in diameter) in the center of the receptive field are presented. The response is mainly "off" with weak "on" reaction. Figure 4F shows the average discharge pattern of the cell to a sudden dimming of the illumination of its receptive field. The cell reacts strongly to the decrease in diffuse illumination. Such cells, having double modality (direction-sensitivity and sensitivity to changes of illumination) were found mainly in anterior parts of pretectal area.

The receptive fields of all direction-sensitive neurons have homogeneous structure (Fig. 15) and differed from such in LGN and retina, where the concentric type of receptive field prevails. The same mode of direction-sensitivity was observed in every part of the receptive field.

The orientation sensitive neurons

Visual cells of this type are similar in their functional characteristics to the direction-sensitive neurons. These neurons also reacted selectively to movements in some directions but only in terms of orientations. It means that they responded intensely to stimulus moving in one orientation, for example vertical, and did not react during their movement in the perpendicular direction (e.g. horizontal). The firing pattern during the optimal orientation of movement may be either symmetrical or asymmetrical in respect to the two opposite directions. Thus, sensitivity to directions can be noticed only by using perpendicular orientations of movements. This kind of a unit is shown in Fig. 5B which illustrates the cell response to a stimulus moving along the horizontal orientation. Neuron discharge in this case is strong and independent of the direction of the movement, i.e. symmetrical. The response of the same cell to the stimulus moving vertically is much weaker (Fig. 5C).

The corresponding evoked potentials are shown in Fig. 5DEF. There seems to be only a weak correlation between PS histograms of the cell and evoked averaged potentials from the same point. The character of evoked potentials in E indicates that, in the vicinity of the recording cell, a majority of neurons have the properties of direction sensitivity described in the preceding chapter.

Another cell, represented in Fig. 6, shows the optimal firing pattern to movements of a light disk in vertical orientation, having little directional sensitivity within this orientation (Fig. 6B). Meanwhile, the same
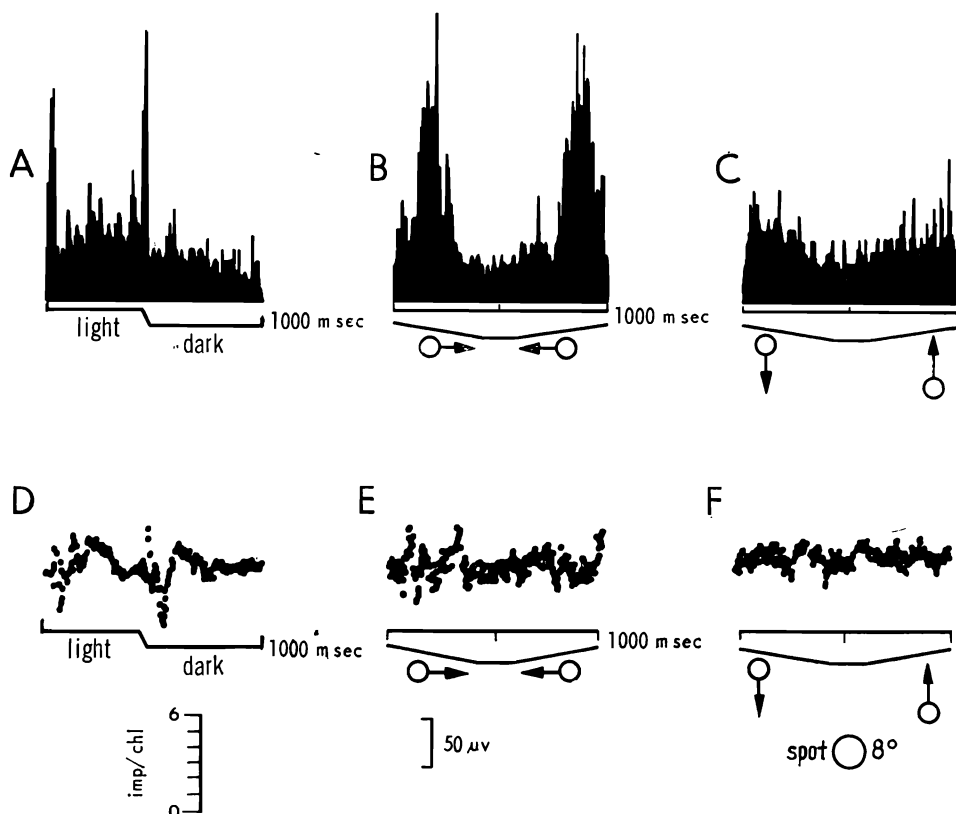
Fig. 5. PSTH of non-DS orientation-sensitive neuron, and evoked potentials from the same point. A, PST-histogram of responses to light flashes (1/sec) "on-off" response with intense activity in light, is observed here. B, Movement of a light disk in the horizontal orientation (preferred orientation). C, Responses to the movement of the same disk in vertical orientation (null orientation). D, E, F, Corresponding evoked potentials from the same point. 64 repetitions of stimuli.

light disk moving horizontally has no effect upon the cell firing (Fig. 6C). Responses are relatively weak during the movements in oblique orientations, at the angle of 45° (Fig. 6GH). The corresponding evoked potentials to the same stimuli are shown in Fig. 6DEF. There exist some degree of correlation between PST-histograms and compound evoked potentials.

The orientation-sensitive neuron which is represented in Fig. 7 was a unique one. The spontaneous activity of that cell was suppressed by stimuli (light disks) entering their receptive fields. Fig. 7BC illustrates the orientation sensitive properties of that cell. The typical suppression effect of the moving light stimuli on spontaneous discharges of the neuron
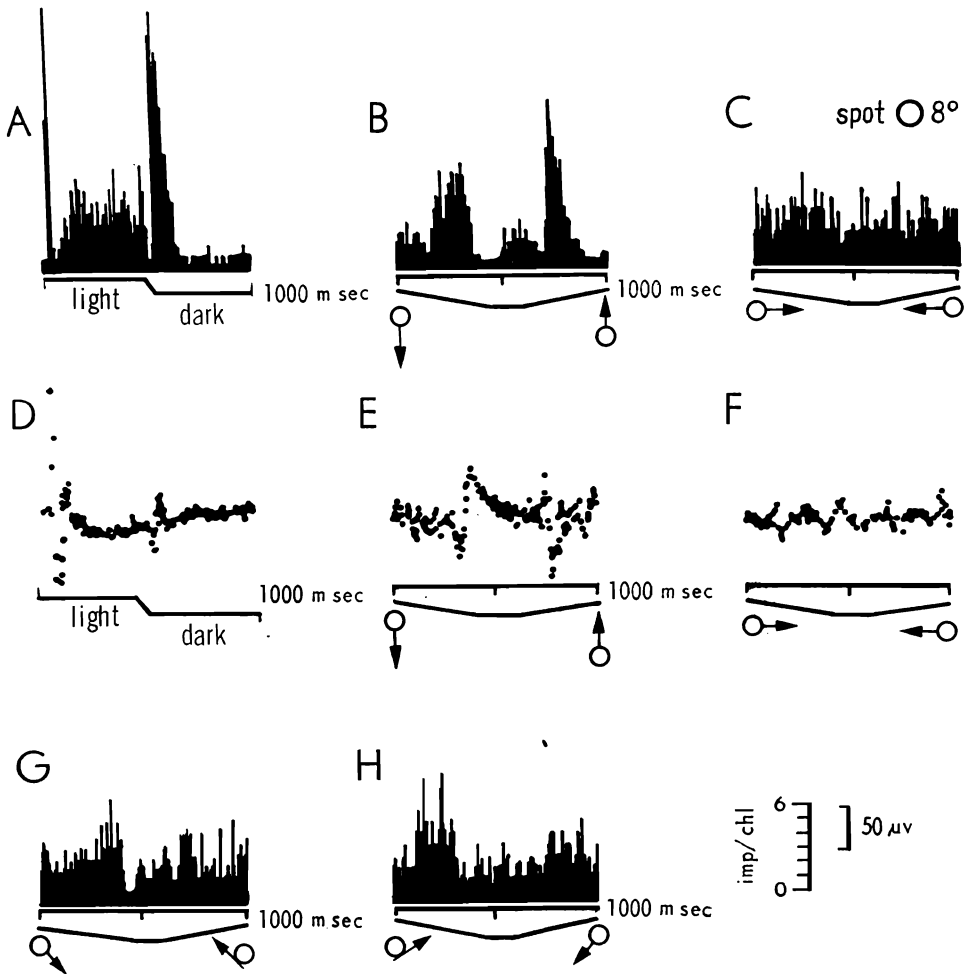
Fig. 6. PST-histograms of DS orientational sensitive neuron. A, Response to the flashing diffuse light (1/sec). B, Movements of light spot in vertical orientation (preferred orientation). C, Movements of the same stimuli in horizontal orientation (null orientation). D, E, F, Corresponding evoked potentials from the same point. G, H, Responses of the cell to the movements of light spot in oblique directions 45° of angle. 127 repetitions of stimuli.

occurs during horizontal movements (Fig. 7B), and is virtually absent during vertical movements (Fig. 7C). Some correlation between unit responses and the background activity is evident here.

All three types of orientation-sensitive units responded phasically "on-off" to the changes of diffuse light.
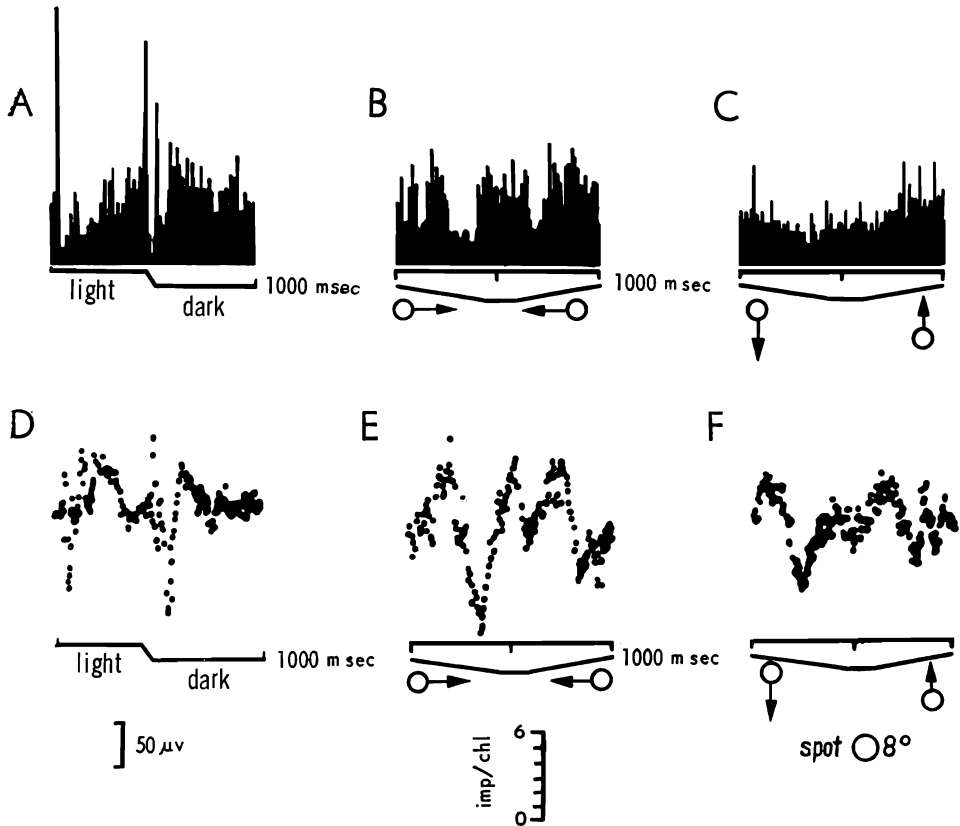
Fig. 7. Responses of a "suppress by contrast" orientation sensitive neuron. A, PST-histogram of the responses to the flashing light (l/sec). B, Typical response of this kind of the cell to the movements of light spot in the receptive field (Horizontal orientation is preferred). There are marked suppressions of spontaneous activity when the stimulus is entering into the field. C, Movements of light spot in vertical orientation. The characteristic response of the cell is absent. D, E, F, Evoked responses in the same point to respective stimuli.

Neurons suppressed by white stimuli entering their receptive fields

The cells of this group were characterized by a high degree of spontaneous activity. They exhibited the usual phasic responses to changes of diffuse light, i.e. "on-off" responses. The receptive field appeared to be homogeneous and from every point of the field one could get the same type of response of the cell. The most interesting feature of these cells was the abrupt change of the intense spontanous activity at the moment when the moving stimuli entered into their receptive fields. Ganglion cells of this kind have been found in the retina by Rodieck (1967) and called "suppressed-by-contrast" cells. We have

observed similar cells in cat's superior colliculus (Harutiunian-Kozak et al. 1970). However, one must emphasize that the number of such cells is very small. Only five cells were observed by us among 122 units studied. The interesting mode of information transfer by these cells is worthwhile to be analyzed.

Figure 8 illustrates the firing pattern of one of the above-mentioned cells. The pronounced spontaneous activity of this cell was markedly reduced by entering of a moving light spot into its receptive field. The suppressing effect persisted as long as the light spot remained within the receptive field (Fig. 8ABCD).
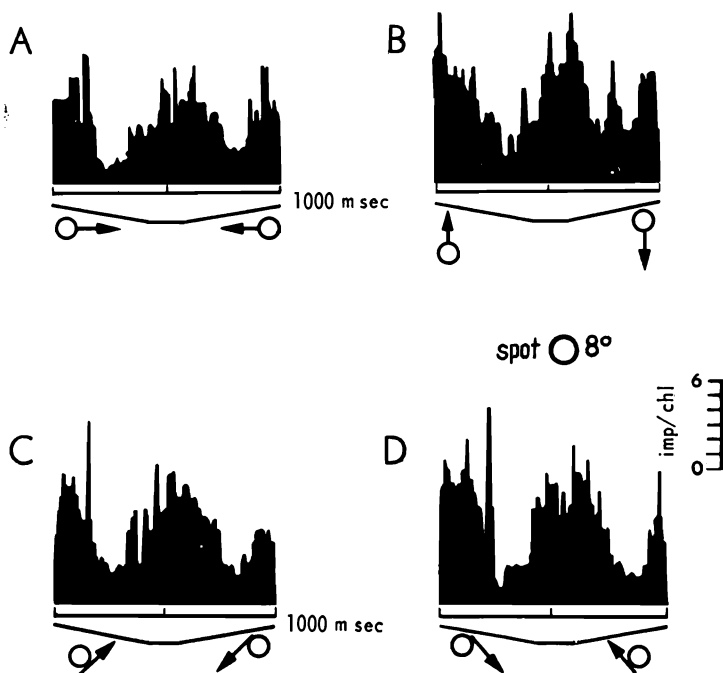

Fig. 8. "Suppressed by contrast" type unit. A, B, Responses to the movements of stimuli in the horizontal and vertical orientations. The suppression of the spontaneous activity is evident. C, D, Responses to the oblique movements (45° of angle). The type of response was not changed. 64 repetitions of stimuli.

Neurons responding with short-term suppression to changes of diffuse light

Three neurons of this kind were found. Since they exhibited very pronounced spontaneous activity and an extremely brief response, it was difficult to notice their reactions while listening to a loudspeaker. For the same reasons it was difficult to define their receptive fields accurately. It was possible to obtain only rough estimates of their field sizes.

However, the kind of responses of these cells may clearly be seen when recording PST-histograms, as shown in Fig. 9 where "A" demonstrates the mode of information transfer about changes of diffuse light from light to dark. Instead of increasing its firing rate (usual "off" response in other unit types) the cell reduced the frequency of its spikes when the light was switched off. The same cell responded only weakly to movements of an object in its receptive field. (Fig. 9B).
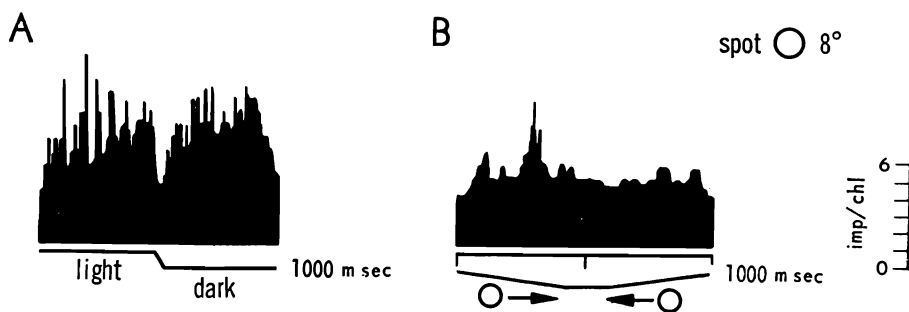

Fig. 9. PSTH of "negative off" neuron. A, Responses of the cell to the flashing light. There are short-term inhibition of activity at the moment of changing the diffuse illumination from light to dark. B, Responses of the same cell to the stimuli moving in horizontal plane. There are light directionality. 64 repetitions of stimuli.

Neurons sensitive only to the movements of a stimulus

We observed eight neurons of this modality. Their general feature is that they respond vigorously to movements of objects in their receptive fields, but the changes of diffuse illumination do not influence their activity.

Neurons sensitive only to the changes of diffuse illumination

In the preliminary experiments on the pretectum we expected that a majority of the pretectal cells would have such properties. This suggestion was based on the well known role of the pretectum in the mediation of the pupillary light reflex. However, our experimental results indicated that relatively very few neurons responded exclusively to changes in diffuse illumination, including the phasic responses, as well as tonic ones only three out of 122 cells observed. It is possible that more units of this sort would have been found have we used very fine microelectrodes to record from small pretectal cells.

Non-visual neurons

In the course of electrode penetration through the pretectum we observed some neurons whose activity could not be influenced by the visual stimuli applied. The number of such non-visual units may be quite marked, and could reach 23–25%. The existence of such "non-visual" neurons may indicate that the pretectal visual center contains cells of the other sensory modalities. It is however, possible that some of the neurons would have responde to more sophisticated visual stimuli.

Responses to edges moving across the receptive fields

An attempt was made to observe the discharge neuron properties of pretectal cells when applying two different kinds of moving objects. Moving light disks (4–8° in diameter) and moving edges were used as stimuli. In the latter case the whole visual field was initially illuminated and moving edge produced a gradual darkening of the field, or a gradual increase of illumination when withdrawing from the field. So it is somehow difficult to give an appropriate interpretation of the data observed: was it the changing diffuse light which influenced the firing pattern of the cell, or the moving edge itself?
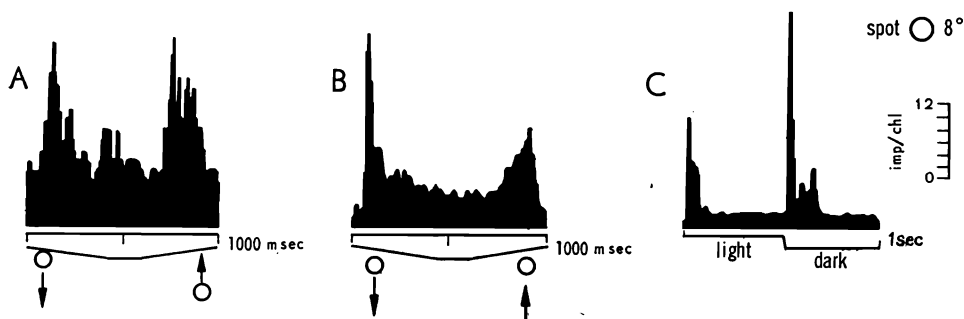
Fig. 10. Different responses of the pretectal neuron to the movements of light spot and the edge. A, PST-histogram of responses to the movement of the light spot in vertical plane. The response is non-DS, the histogram is symmetrical. B, Responses of the same cell to the movement of the edge across receptive field. The response is DS, the histogram is asymmetrical. C, Responses of the cell to the flashing light. Note marked "off" response, and a weaker "on" reaction. 127 repetitions of stimuli.

Our results are illustrated in Fig. 10 and 11. It is evident that the cell responded with approximately the same number of spikes to a light disk moving in both vertical directions across the receptive field (Fig. 10A). The PST-histogram was here symmetrical. The same cell fired asymmetrically when a horizontal edge was moving vertically across its
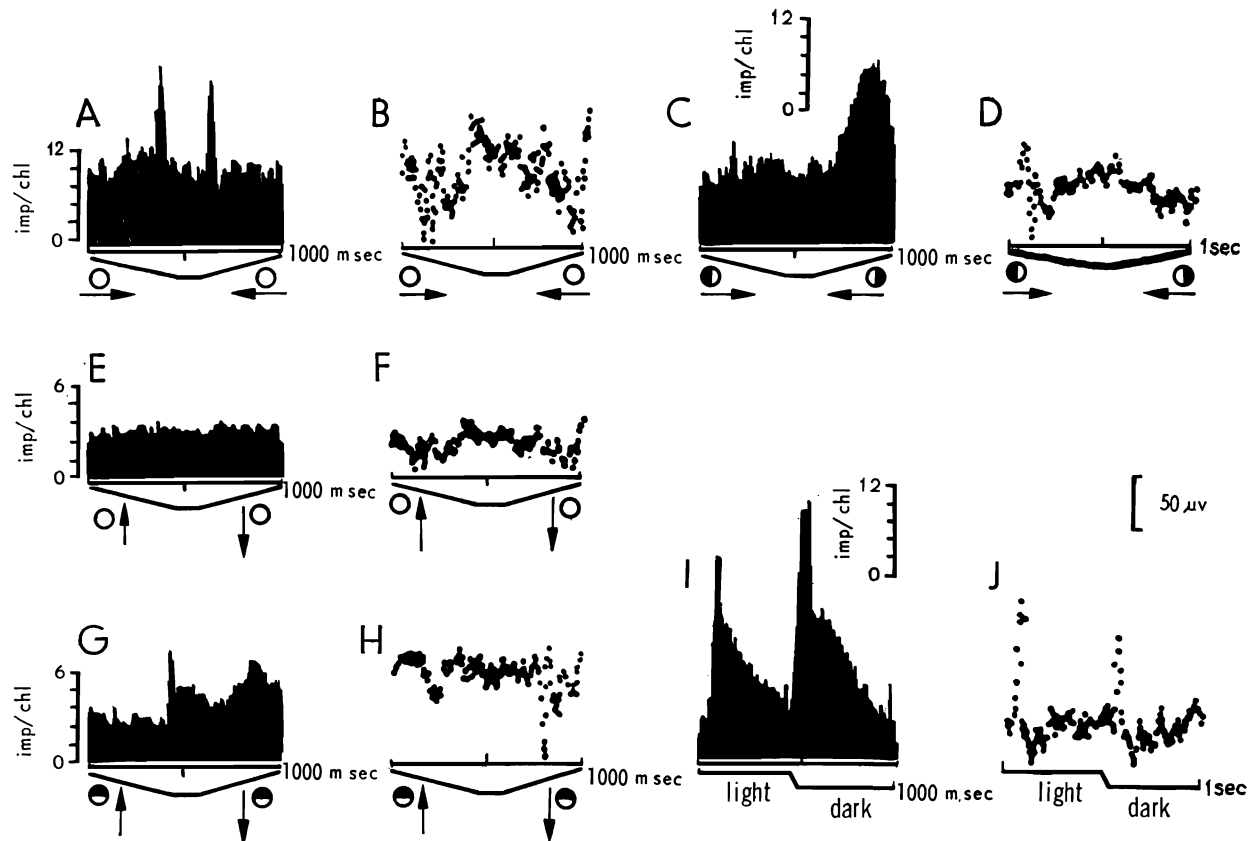
Fig. 11. Responses of single cell and evoked potentials to the movement of the light spot and the edge. A, Responses of the cell to the movement of light spot (8°) in horizontal plane. Symmetrical, non-DS response. B, Corresponding to "A" evoked potential. Amplitudes of the potential shifts is equal in both directions. C, Responses of the same cell to the movement of an edge. Asymmetrical DS-like response is evident. Preferred direction from right to left. D, Corresponding to "C" evoked potential. There are unequal amplitudes of potentials. Preferred direction from left to right. E, F, PST-histogram of the cell response and evoked potential from the same point to the movement of the light spot in vertical plane. G, H, Responses of the same cell and evoked potentials to the movement of the edge in the receptive field. I, J, PST-histogram of cell response and evoked potentials to the light flash l/sec. Repetitions of stimulus in A, B, C, D, I, J, — 127 ✕. and in E, F, G, H — 64 ✕.

receptive field (Fig. 10B). Figure 10C shows the response of the same cell to changes of diffuse illumination.

Figure 11 demonstrates another observation upon a cell, which exhibited similar characteristics. The response of this cell to the moving light disk, is directionally insensitive the PST-histogram is symmetrical and there exists a correlation between the firing patterns of single cell and the compound evoked activity (Fig. 11AB).

The picture was changed when the edge was moving. The response became very asymmetrical and more pronounced. There was a marked increase of number of spikes during the movement of the edge in the direction from right to the left, and only a steady background activity when the edge moved in the opposite direction (Fig. 11C). It was interesting that the compound potential showed asymmetry too, although in opposite manner (Fig. 11D). Vertical movements of the disk did not change the spontaneous activity of the cell at all (Fig. 11E). The edge moving vertically, can produce intense firing of the neuron, when moving downward in the field (Fig. 11G). There was a marked correspondence between single cell responses and compound evoked potentials (Fig. 11EFGH). Thus, the background activity in this part of the pretectum was similar to the activity of the neuron studied.

As mentioned above, the moving edge might be supposed in some way to be equivalent to a change in diffuse illumination. Therefore, the next step was to examine the influence of light flash on the activity of such cell. The response to the flash is demonstrated in Fig. 11I. There were very strong "on-off" responses. One can suppose, that if the movement of the edge in the receptive field had something in common with the changing of diffuse light, then the response to the edge generally should be similar to the responses to the flash. Since it was evidently not so, one must try to find some other explanation for the difference between these two responses.

It is quite possible that the cell responds symmetrically. i.e. it is direction non-sensitive to the movement of small objects, and asymmetrically, i.e. direction-sensitive to the movements of edges of objects covering the whole surface receptive field. If this suggestion is right, then it is obvious that pretectum subserves a rather high degree of analysis of the incoming visual information.

Responses to flashing light

Figure 12 is composed of responses to flashing light of single cells recorded in various experiments. Each PST-histogram is accompanied by the corresponding averaged evoked potential recorded at the same

place in the pretectum where single unit is recorded. The data presented in this figure, together with other data enable us to conclude that there are some pretectal visual cells which do not respond to the changes of diffuse light (Fig. 12I), but, as far as our observations are concerned the evoked potentials were always influenced by the flashing light (Fig. 12).
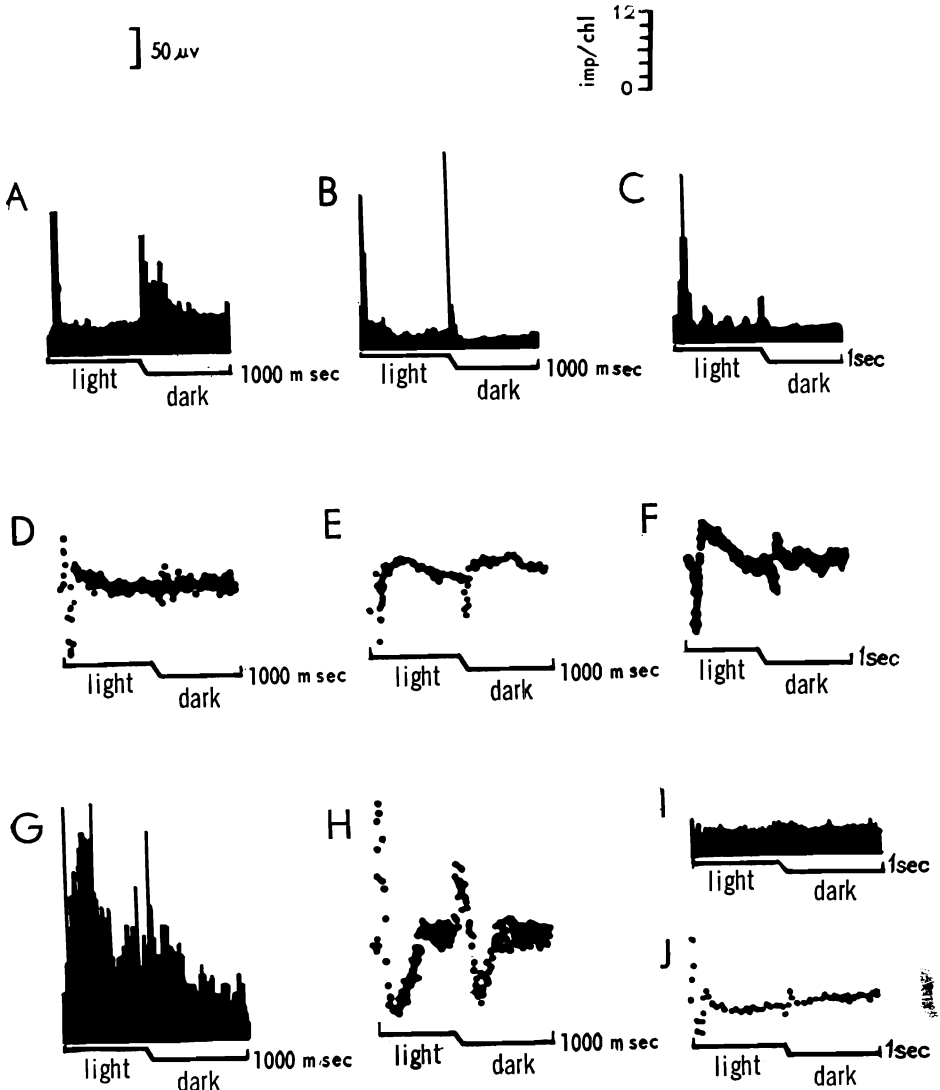

Fig. 12. Responses of different cells from different points to the flashing light (l/sec). Each histogram is accompanied by the corresponding evoked potential recorded from the same point. A and D; B and E; C and F; G and H; I and J. 127 repetitions of stimuli.
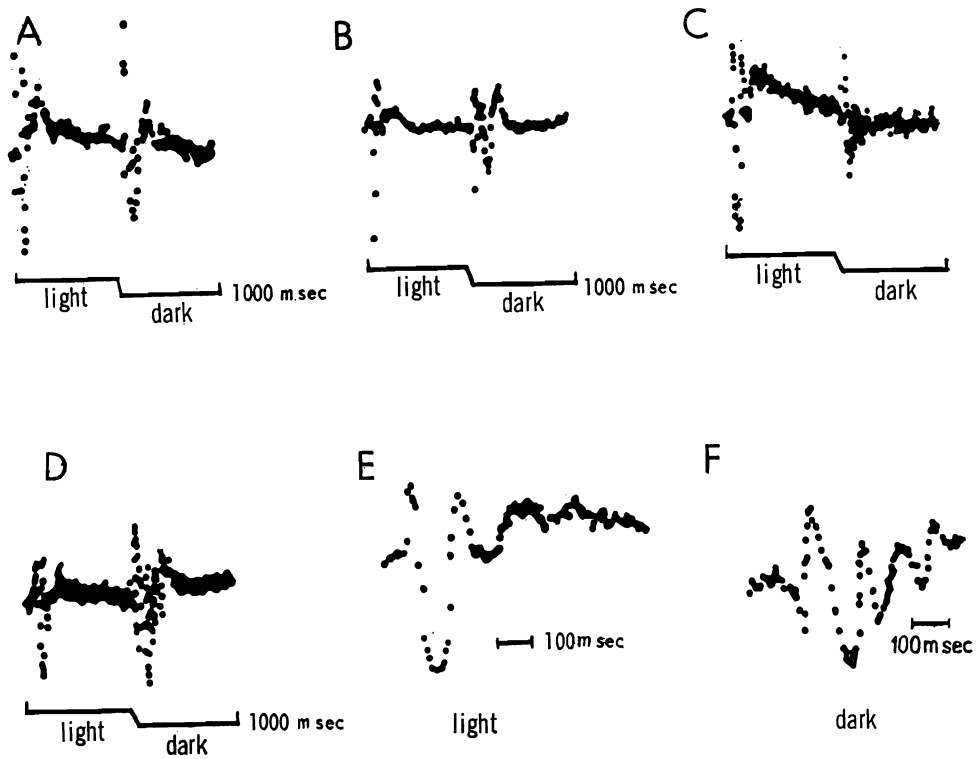
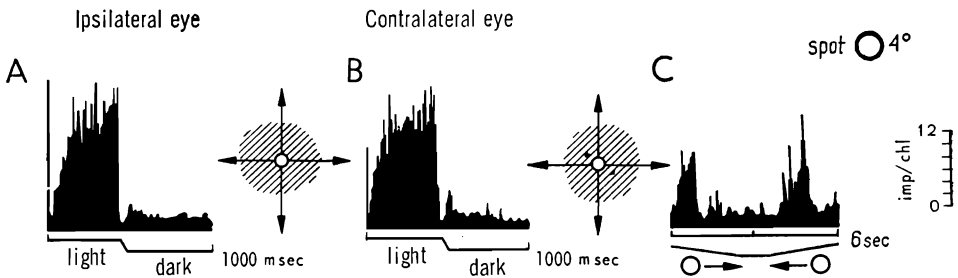Fig. 13. Oscilatory potentials in four pretectal sites evoked by diffuse flashing light.

Fig. 14. Responses of a binocular neuron to the spot-flash and moving stimuli. C, The response of the cell to the same spot moving horizontally. Both eyes open. 127 repetitions of stimuli.

Moreover, among the different types of evoked potentials very interesting mode of activity were observed, as shown in Fig. 13. In some cases fine oscillations of evoked potentials when occurring as the response to the changes of light were observed. These oscillations may occur at the beginning of the light phase, and/or at the onset of the darkness. The rate of oscillations is nearly 10/sec. There were put forward a suggestion that these oscillations looked like to the cortical alpha rhythm.
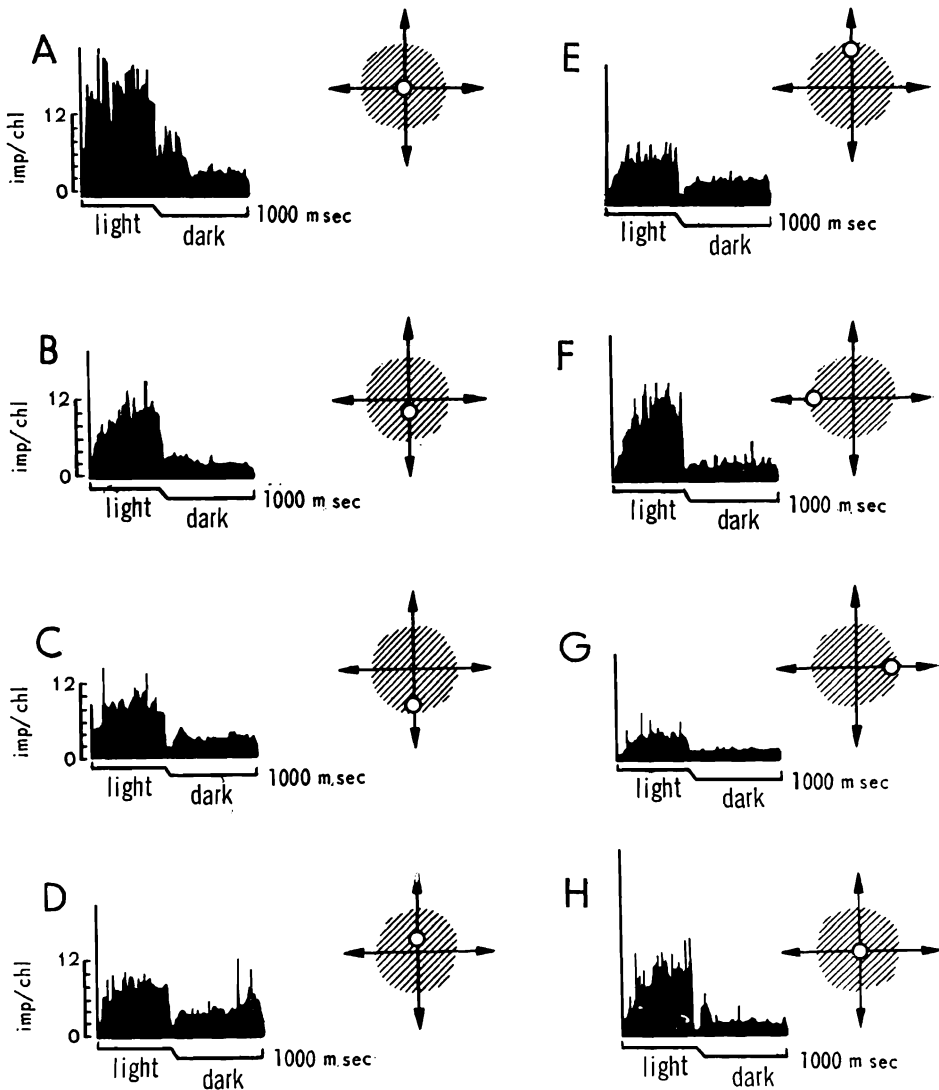

Fig. 15. Responses of single cell to the flashing of the spot in different parts of the receptive field (the same cell from Fig. 14). On the right of each histogram are presented positions of the spot in receptive field. 127 repetitions of stimuli.

Binocular neurons

The problem of binocular interaction is beyond the scope of present investigation. However some observations are worthwhile to present.

Sixty seven cells out of 122 were found to be binocularely driven (55%).

Figure 14 illustrates an example of a cell which could be activated from both eyes similarly. Responses to spot-flashes presented to either eye are nearly identical (Fig. 14AB). Figure 15 shows firing pattern of the cell when both eyes are stimulated. No serious difference can be noticed. Figure 14C shows the responses of the above mentioned binocular cell to the movement of light disk in horizontal plane.

Some binocular cells are influenced differently by stimuli presented to the left or right eye. There may be a domination of the ipsilateral or contralateral eye.

Eighteen cells could be activated exclusively from the contralateral eye. The cells influenced only from the ipsilateral eye were very rare, only two of them were observed.

Latencies of responses to light flashes of single-unit spike discharges and of evoked potentials

Attempts were made to measure the latencies of evoked potentials and of single unit responses to flashing diffuse light (1/sec) and flashing light spot 4° in diameter (1/sec). The light spot was, as a rule, placed in the center of the receptive field. Table I and II shows latent periods measured from summated records of the ANOPS analyzer.

Table I

The latency of the cell response and evoked potentials
from the same point

Cell no.	PSTH diffuse flash (in msec)	PSTH spot-flash (in msec)	AV diffuse flash (in msec)
1	96	105.2	
2	96	104.8	
3	28.8	44.8	9.6
4	120		51.6
5	36		19.2
6	76.8		
7	54.4		

It was found that the latency of single unit responses to the diffuse light flash were shorter (between 28.2 msec and 120 msec) in comparison with the latency of the same cells to the flashing spot light (between 44.8 msec and 204.8 msec) (Table I). Latent periods of visually evoked potentials to diffuse flashes were always shorter (9.6 msec to 51.2 msec), than to the spot-flash (19.2 msec to 54.4 msec) (Table II). As a rule,

Table II

The latency of evoked potentials

Coordinates	AV diffuse flash (in msec)	AV spot-flash (in msec)
A=6, L=3, H=15.1	12.8	19.2
A=5, L=2.7, H=15.4	28.8	54.4
A=7, L=3, H=15.7	12.8	16.0
A=7, L=2.5, H=15	19.2	32.0

responses to small spot flashing in the center of the receptive field have longer latencies, than responses to diffuse flash light, recorded from the same point (Table II). Confusing was the fact, that despite the longer latency, the responses to a small spot flashing in the center of the field may cause prominent responses of the cell, as compared with the diffuse light. This is very unusual when the receptive fields are homogeneous. One more peculiarity of the observed data: the single unit responses are always more delayed than the corresponding evoked potentials, recorded at the same points. It is rather difficult to explain also the very short latencies of evoked potentials measuring 9.6 msec.

The structure of the receptive fields

The organization of the receptive fields of the pretectal visual neurons differed considerably from those of the retinal and LGN cells. In the pretectum the fields were homogeneous, that is, they had no obvious antagonistic parts (center-surround). As is well known, the antagonistic structure of receptive fields is typical for retinal ganglion cells (Kuffler 1953, Wiesel 1960), cells in the LGN (Hubel and Wiesel 1961, Bishop et al. 1962) and some cells in the visual cortex (Hubel and Wiesel 1959, 1962, 1965).

Figure 15 shows the PST–histograms of responses of a cell to a small spot of light (4° in diameter) flashing in various parts of its receptive field. There are "on" — responses to the spot-flash in the center of the receptive field (Fig. 15AH). Changes in the position of the flashing spot toward the receptive field periphery along the vertical or horizontal orientations do not change the general shape of responses (Fig. 15BCD EF). There seem to be only quantitative differences between responses in the center of the field and in points close to its periphery that is there are the strongest response is in the center (Fig. 15A).
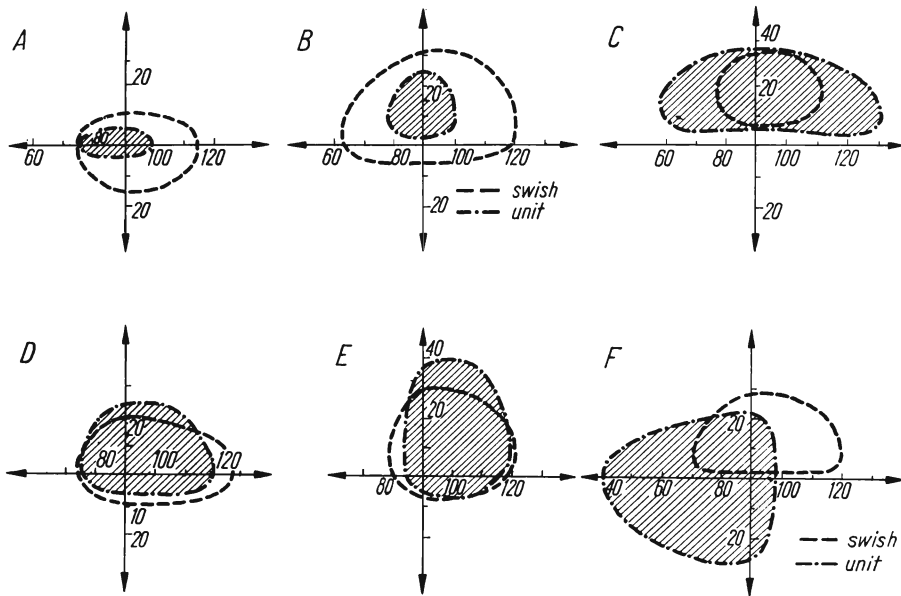

Fig. 16. The receptive field of single units (crossed areas) and swish responses from the same points. Note marked discrepancies betwen the positions of unit receptive field and area from which the swish response could be driven (C, F).

In the course of our observations on single unit responses we often investigated the background activity of surrounding cells: "swish" response. The swish response to a visual stimulus is the summed response of a group of cells close to the electrode tip (Bishop et al. 1962); it can be heard from loudspeaker connected to the preamplifier. This synchronous response of many cells is the basis of the generation of compound evoked potentials investigated. As mentioned above, we tried to find the relationship between the activity of a single cell and that of its background. It seems useful then to compare sizes and positions of receptive fields of single units with fields from which compound responses, i.e. the swish reaction could be elicited. The data obtained showed that

in the majority of cases single unit receptive fields lay within the areas from which swish responses were obtained (Fig. 16AB). However, there were also cases of some discrepancies as well (Fig. 16DEF), or sometimes the swish area could be smaller than the unitary receptive field (Fig. 16C). Figure 16F shows a unitary receptive field which is situated quite differently than the swish area.

These discrepancies in the mutual position of unitary receptive fields and swish areas cannot fully explain the observed discrepancies between the firing paterns of single cells and the evoked potentials.

Columnar structure

The question of possible columnar structure has attracted our attention when studying the superior colliculus and it will be covered in this study, too. Unfortunately our histological verification was not precise enough to give full support for the study on the columnar structure in the pretectum, and our conclusions are based mainly on the functional properties of cells examined together with the locations of their receptive fields. The electrode tip was initially placed on the surface of the pretectum, often in the nucleus of the optic tract (where we could find the visual neurons with ease), and then lowered slowly using a micromanipulator; various cell responses were recorded along such electrode track. The average distance from one cell to another was within the range of 50–100 μ. Unfortunately this distance is rather large, and this makes our analysis of the columnar structure only an approximate one. Figure 17 depicts sets of receptive fields of two or three cells in one track.

In almost half of the cases examined the responses of the neighbouring cells to the same stimuli were similar. For example, Fig. 17ABC shows that two neighbouring cells with overlapping receptive fields exhibited also similar modes of responses. In Fig. 17AB the cells were direction-sensitive. Figure 17C shows receptive fields of two cells in another track, these cells were direction non-sensitive. It seems that this functional arrangement of cells may indicate some kind of a columnar structure which has been described in the central nervous system, especially in the somatosensory cortex (Mountcastle 1957), among binocular cells in the visual cortex (Hubel and Wiesel 1969), and among the visual cells in superior colliculus (Sprague et al. 1968).

However, examples described should be supplemented with others shown in Fig. 17DEF. Here again the receptive fields of neighbouring neurons found in different penetrations are presented. These fields also exhibit a considerable amount of overlap, but, as will be seen, the proper-
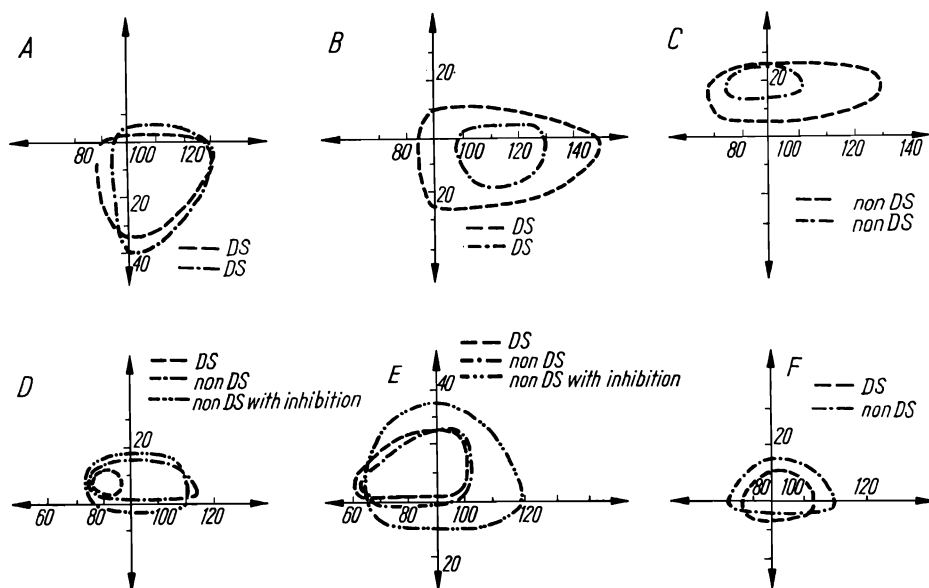
Fig. 17. Demonstration of receptive field positions of neighbouring cells during the penetration of the microelectrode through the pretectum. Each plot represents one track of electrode. Note correlations in first three tracks between neighbouring cells (A, B, C) (as functional as well as positional). D, E, F — show marked discrepancies.

ties of the cells are different. For example, Fig. 17D shows receptive fields of three neighbouring neurons in one penetration. One of the cells is direction-sensitive, the second is direction non-sensitive, while the third cell, has a rear mode of activity, its activation being suppressed by light spots entering into the receptive field Fig. 17EF shows more of such mixed tracts.

This phenomenon which has been observed by us in the superior colliculus shows clearly that the neurons with highly overlapping receptive fields can have quite different properties. When taking into account only the locations of receptive fields, one finds some kind of columnar structure in the pretectum.

DISCUSSION

It was interesting to find similar results in the experiments on the superior colliculus and on the pretectum. Apparently, both subcortical visual centers have much in common, and they are, as a whole different from the lateral geniculate nucleus. This fact was mentioned in the preceding papers (Harutiunian-Kozak et al. 1968ab) and was confirmed in this investigation.

It should be stressed that we carefully looked for functional differences between the superior colliculus and the pretectum, while expecting to find in the anterior pretectum some cells of very high sensitivity to changes in diffuse illumination. The general impression is that, functionally these both centers are like each other.

It is quite possible that cells closely connected with the transfer of information about diffuse illumination exist in the pretectum. Such cells could form a basis for the role played by the pretectum in the pupillary light reflex as was assumed by some authors (Magoun and Ranson 1935, Shakhnovich and Shakhnovich 1964, Cavaggioni et al. 1968, Smith et al. 1968). However, our data suggest that the cat's pretectum is generally involved also in some processes concerned with pattern vision. To some extent our results support data of the previous authors who suggested some role of the pretectum in the acquisition of conditioned-reflexes to visual stimuli in cats and rats (Thompson and Massopust 1960, Thompson and Rich 1961, Thompson et al. 1963, Fishman and Meikle 1965, Urbaitis and Meikle 1968).

One of arguments against restricting the function of the pretectum to that of a pupillary reflex center is that within this structure there exist many direction- and orientation-sensitive cells and cells which do not respond at all to diffuse illumination, but only to objects moving within their receptive fields. The properties of all the three kinds of cells are consistent with the analysis of information in visual perceptual processes rather than for mediation of the pupillary reflex.

Moreover, the cells exibited very specific reactions to stimuli. For example, a cell responded to "on-off" changes in diffuse light, and its firing was suppressed when a stimulus entered its receptive field. Such a specific reaction seems to have little in common with the light reflex, as the latter would presumably require a steady response to illumination.

The example mentioned may be supplemented by our data on responses to moving-edges (though not numerous) and to moving spots which demonstrate that the same cell may respond very specifically to each kind of stimulus. The two sets of examples mentioned above suggest that the level of analysis of visual information in the pretectum is comparable with that in the visual cortex.

The pretectal neuron responses were quickly habituated. This fact, which has been pointed out in our preceding paper (Harutiunian-Kozak et al. 1969), does not support the notion about possible participation of the pretectal cells in the puppilar reflex, because the latter does not habituate.

The data on the latent periods are difficult to interpret. There was

a difference between the latencies of the evoked potentials and those of single-unit responses, the former was always much shorter than the latter. For example, an evoked potential latency may be 9.6 msec while a cell response recorded at the same point exhibits a latency of not less than 28.8 msec. Latent periods of single-unit responses may be as long as 120 msec. According to Cavaggioni et al. (1968) the latencies of cell responses in pretectum are within the range of 30–90 msec. Our results showed a wider range of estimates. Such a difference in latencies of responses of various cells to the same stimulus indicates that either these cells are innervated by long-latency retinal ganglion cells or that obviously not all visual cells have direct retinal inputs. It may be further speculated that neurons with longer latencies receive signals from the retina either by the very thin fibres or through a very long polysynaptic pathways possibly by loops through the visual cortex. In future experiments a possible correlation between the discharge pattern of a cell and its response latency will be examined.

Furthermore, Table I shows a considerable difference in latencies of responses of a cell to diffuse illumination and a spot-flash. It might be explained by summation processes in the retina, but this problem requires further investigation.

The most difficult for interpretation are the data showing extra-short latencies of evoked potentials to changing of diffuse light (9.6 msec). As is known from the study of Bishop and Clare (1955) the pretectum receives rather thin fibers, but the magnocellular part of the optic tract nucleus receives also a small number of thick fibers. The total number of fibres going from the retina to the pretectum is greater than the number of such fibers going to the superior colliculus (Singleton and Peele 1965).

Attempts were made to find a columnar arrangement of cells in the pretectum. The results obtained are not conclusive enough to suggest a columnar organization of the pretectum cells in the classical meaning of this term (Mountcastle 1957, Sprague et al. 1968). Our results merely demonstrate that sometimes neighbouring neurons located one above the other may have similar response characteristics and a similar spatial localization of their receptive fields (Fig. 17ABC). But sometimes the cells which exhibited quite different modes of firing patterns had similar spatial distribution of fields and this fact does not support the columnar structure concept. However, in most cases we found vertical columns of cells having more or less similar spatial localization of their receptive fields. The observations show that there is a considerable overlap of receptive fields of neighbouring neurons. It is interesting that in this respect the pretectum again resembles to the superior colliculus.

Neurons exhibiting quite different types of responses may have a common part of the retina. If the mechanism of the directional sensitivity were placed in the outer layers of the retina, it would be rather difficult to explain the functional differences between cells having nearly the same retinal locus.

To fit the experimental results, we would have to assume a very strange retinal-mosaic arrangement or we might expect that the mechanism of directional sensitivity has its site outside of the retina. This, in turn, may take place in the pretectum or possibly in the visual cortex as demonstrated by Wickelgren and Sterling (1969) in the superior colliculus.

Another finding concerned with the directional sensitivity mechanism seems paradoxical. A stimulus moving at high speeds throughout a receptive field of a direction-sensitive neuron produces an intensification of the direction-sensitive effect (i.e. the response to stimuli in the null direction is more suppressed and the firing in preferred direction more accentuated). A similar phenomenon was observed by McIllwain and Buser (1968) in the superior colliculus. As is known, the retinal synaptic processes are rather slow. Thus, the slow-speed movements should be more efficient especially in inducing the suppression effect (when stimuli move in the null direction).

SUMMARY

1. Single unit activity was recorded from the cat's pretectal region using various visual stimuli (diffuse flash, spot-flash, moving stimuli).

2. The pretectal neurons were divided to eight groups: (i) directionally insensitive neurons, (ii) direction-sensitive neurons, (iii) orientation-sensitive neurons, (iv) suppressed-by-contrast neurons, (v) "negative off neurons", (vi) neurons responding only to movements, (vii) neurons responding only to changes of illumination, and (viii) non-visual neurons.

3. There is a striking resemblance between functional characteristics of the pretectal region and the superior colliculus concerning visual responses.

4. The existence of directionally selective, orientationally selective and other neurons proved the suggestion, that pretectal region take a part in higher level analysis of incoming visual information.

5. A small minority of neurons, observed in anterior pretectum, having high sensitivity to the changes of light intensity, are probably concerned with the pupillary light reflex.

6. It seems likely that the mechanism of directional sensitivity of pretectal neurons lies behind the retina, either in the pretectum itself or in the higher levels, including the visual cortex

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