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VISUALLY EVOKED POTENTIALS AND SINGLE UNIT ACTIVITY IN THE SUPERIOR COLLICULUS OF THE CAT

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In contemporary investigations of visual information processing the focus of interest has been shifted from the lateral geniculate nucleus (LGN), toward the tectum and pretectum. It has turned out that neurons of the cat's tectum and pretectum are more sensitive to moving stimuli than to changes in diffuse illumination (Straschill and Taghavy 1967, McIllwain and Buser 1968, Sprague et al. 1968, Harutiunian-Kozak et al. 1968ab, Sterling and Wickelgren 1969).

Further observations demonstrated that there is a basic difference in the structure of receptive fields of cells in the visual centers mentioned above: the fields of tectal cells appeared to be homogeneous, i.e. stimulation of each part of receptive field evoked approximately the same responses (Harutiunian-Kozak et. al. 1968a); there is no classical concentric arrangement of the field consisting of a central area and an antagonistic periphery so typical for the cells in the retina and the LGN (Kuffler 1953, Hubel 1960, Wiesel 1960, Kozak et al. 1965).

More recent investigations have shown that most neurons in the superior colliculus were direction-sensitive, i.e. they responded with increasing rate of their action potentials to stimuli moving in one preferred direction and their activity was suppressed when the stimuli moved in the opposite direction (the null direction — Barlow and Levick 1965).

This phenomenon has been described by many authors in many species: in the frog's retina (Maturana et al. 1960), in the rabbit's retina and LGN (Barlow et al. 1964, Arden 1963), in the pigeon's retina (Maturana and Frenk 1963), in the cat's tectum and in the visual cortex (Baumgartner et al. 1964, Hubel and Wiesel 1965, Marchiafava and Pepeu 1966, Stras-

chill and Taghavy 1967, McIllwain and Buser 1968, Sprague et al. 1968), and in the monkey visual cortex (Hubel and Wiesel 1968).

However, possible mechanisms underlying this phenomenon are still unclear. Barlow and Levick (1965) suggested that directional sensitivity of ganglion cells in the rabbit retina is a result of inhibition which occurs when a stimulus moves in the null direction. In their opinion, the outer plexiform layer of the retina was the site of this inhibition. This layer contains synaptic contacts between the receptor cells and expansions of the bipolar and horizontal cells. The horizontal cells are supposed to convey the inhibition between the receptors and bipolar cells.

Straschill and Taghavy (1967) explained directional sensitivity in the cat in a similar way.

Recently Wickelgren and Sterling (1969) demonstrated that ablation of the visual cortex could drastically affect the properties of directional sensitivity of the collicular cells. After the cortical ablations the directionally sensitive neurons in the superior colliculus did not respond selectively to one specific direction.

It is possible that the mechanism of directional sensitivity in the cat has a different basis that in the rabbit.

Directional sensitivity is not the only way of analysing the incoming information in the superior colliculus. There exist some other types of cell activity which are equally interesting and obviously have their role in the integration processes of the superior colliculus.

This investigation is a continuation of our previous experiments on the possible role of the superior colliculus in the analysis of visual information (Harutiunian-Kozak et al. 1968a). Special attention was paid to proper differentiation and classification of the possible modes of responses of the collicular cells and also to the analysis of compound evoked responses to different visual stimuli.

METHODS

Twenty-nine adult cats were used in the experiments. 83 cells were investigated. All the cats were intially anaesthetized with ether and then the trachea and the radial vein in the forpaw were cannulated. The head was fixed in a stereotaxic instrument and the mid-pontine pretrigeminal section was performed (Żernicki 1964). Artificial respiration with the frequency of 16 to 20 strokes per minute and stroke volume of 20 ml/kg body weight was applied. A rectangular piece of bone 6×10 mm, together with the underlaying dura was removed from the skull. This opening made above the superior colliculus was covered with warm soft wax which after hardening prevented brain pulsations. Tungsten electrodes held in a manipulator were inserted according to coordinates of the superior colliculus (Jasper and Ajmone-Marsan 1960) to the position of about 1–2 mm above the superior colliculus. Then the electrode was lowered slowly using a micromanipulator in steps of 20–30 μ.

When the tip of the electrode reached the surface of the superior colliculus it was left there for 5 to 10 min to rest. To immobilize the preparation fully, Flaxedil was administered intravenously at rates of 20 mg/hr. The pupils were dilated with 0.1% atropine sulfate. The corneae were prevented from drying by instilling physiological saline solution every 5 min. Throughout the experiment both corneae were transparent and moist.

At the beginning of all experiments stimuli moved by hand (Fig. 1) were applied in order to estimate borders of a receptive field, the kind of a neural response and its stability. During recording the stimuli were usually moved mechanically by a servo-mechanism (Kozak and Katrycz, unpublished). A light disk, mostly of 8° in diameter, was projected on a perimeter screen at 75 cm distance in front of the cat eyes. The screen was white, concave of about 63° in diameter.

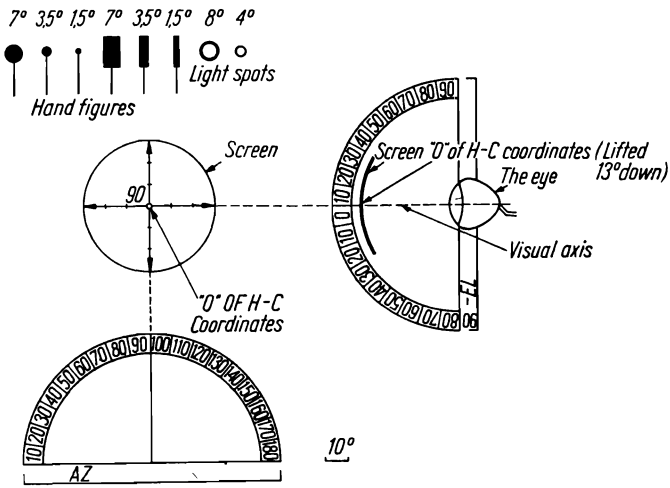

Fig. 1. The design of perimeter and examples of visual stimuli. Right, view from side, showing the scale of elevation. Lower left, view from above, showing the scale of azimuth.

It could readily be shifted horizontally and vertically so that the center of the receptive field of the unit examined could be in the center of the screen. The screen could be positioned anywhere in the visual field of the cat. We used the spherical polar system of coordinates of the visual field, consisting of angles of azimuth and elevation, as described by Bishop et al. 1962a.

The tungsten electrodes (Hubel 1957) were sharpened electrolytically, so that their tip diameters were about 2–5 μ, and they were then covered, except for tips by the Pearl clear vinyl lacquer.

Action potentials (spikes) of single neurons and compound field potentials were picked up by the same electrode. The potentials were fed into a Grass cathode follower, Grass amplifiers P6 and P5, connected in series to Tektronix 502 oscilloscope for a visual display and, parallelly amplified spikes were used to trigger a pulse generator (the Schmitt Trigger) giving standard pulses. The pulses were fed into a analyzer (ANOPS) (Jankowski 1967) to obtain the post-stimulus time (PSTH) recordings (Fig. 2).

Evoked potentials differentiated with 50 msec time constant were fed directly into the ANOPS analyzer working in Averaging (AV) mode. The averaging technique left out all potential fluctuations not concerned with a response to a given stimulus and, thus, the response were obtained in a more filtered form. Periods of analysis of the computer were synchronized by impulses coming from a Grass

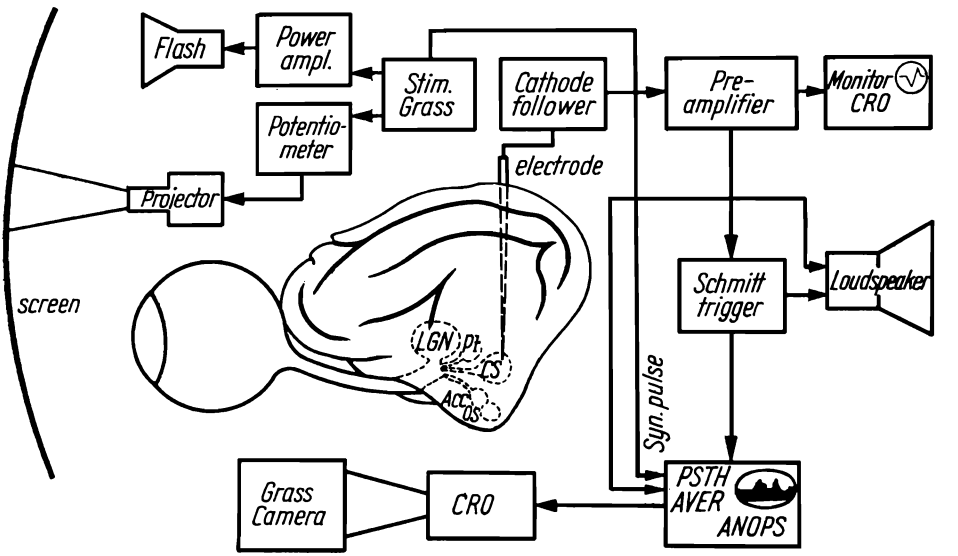

Fig. 2. Block diagram of stimulating, recording and analysing apparatus.

stimulator, which in turn controlled the movement of stimuli. The averaged responses (PSTH and AV modes) were displayed on another Tektronix 502 oscilloscope and subsequently photographed by a Grass kymograph camera (Fig. 2).

As was already mentioned the averaged responses were obtained by an adequate number of repetitions of the stimuli. This stressed the real properties of the cell responses. Since a majority of cells tended to habituate after many repetitions, number of impulses per address of memory were rather small, but this had no influence on modes of responses. The latter conclusion was obviously of primary importance for our experiments.

The receptive fields were specified according to the H-C coordinate system. 90° on the azimuth scale and 0° on elevation scale of the perimeter corresponded to the intersection of the Horsley–Clarke parasagittal and horizontal planes through the eye center (Fig. 1).

Analysis of single unit activity could be conducted for a sufficiently long period of time of the order of 4–5 hr.

After the experiments, brains were taken out for histological examination. Some of the brains were perfused with saline and 10% formaline, taken out and fixed for few days in the 10% formaline solution. Then brains were frozen and sectioned at 30–50μ. In the second series of experiments, when an experimental session was over, the microelectrode was withdrawn and replaced by a macroelectrode inserted according to the same coordinates. The macroelectrode placed in the site of recording was left untill next morning. The brain was then removed

and fixed in formaline and sectioned at 30–50 μ. The latter way of marking appeared to be as effective as electrocoagulation.

Luminance of the screen illuminated by the flash was 15 cd/m^2. Luminance of the moving spots subtending 8° and 4° was 2 and 8 cd/m^2 respectively.

RESULTS

Evoked potentials. The multi-neuronal responses to the stimuli rhythmically moving in front of the cat's eyes could easily be heard as a "swish" in the loudspeaker when the electrode tip penetrated through the layers of the superior colliculus. Similar responses have already been described in the lateral geniculate nucleus (LGN) by other investigators (Bishop et al. 1962b). The visual centers having marked input from retina have well defined mass responses to various visual stimulations. This

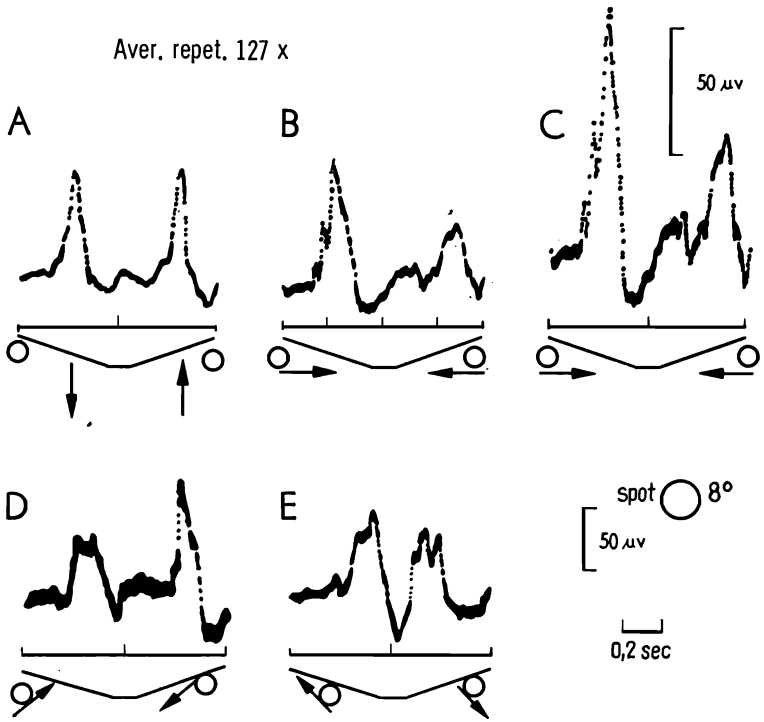

Fig. 3. Averaged evoked potentials in the superior colliculus in response to a moving stimulus (light disk). A, Compound evoked response to the movement of stimulus in the vertical orientation. The amplitude of response is equal for both directions. Symmetry is evident. B, Evoked potentials at the same recording point, as above. The stimulus is moving in the horizontal plane. Clear directionality in response is evident. The preferred direction from left to right. C, The same as "B" with the higher amplification. D, E, Compound evoked responses to the movements of light disk (8°) in oblique directions. Negativity upward.

is an important indication of the position of the electrode, the kind of functional identification. The swish reaction, being the compound response of many cells responding to given visual stimuli in suitable conditions (high amplification and averaging) may be recorded as evoked potentials. The tungsten electrodes, which were used by us were quite suitable for recording such compound potentials. The main advantage of this method lies in that same electrode may be used to recording either the evoked field potentials or the spikes of single neurons.

Analysis of the evoked responses in the superior colliculus to movements demonstrated that, in some cases, their amplitude depends upon directions of the movements. This means that directional sensitivity may also be demonstrated in the compound evoked potentials which reflect total responses of many cells. Recently Sprague et al. (1968) have stressed that the mass reaction of cells in the superior colliculus did not exhibit directional sensitivity. The reason of this conclusion may be that in their experiments they did not record the compound potentials. Their statement was based on listening to the swish in the loudspeaker, when it is somehow difficult to estimate the strength of the responses.

Figure 3 illustrates the averaged potentials in the superior colliculus in response to a visual stimulus (a light disk, 8° in diameter), moving in different directions. Figure 3A shows the evoked response to a stimulus moving in the vertical plane. Symmetry of this figure suggests that the responses to upward and downward movements are equal. However, responses to movements in the horizontal plane are asymmetrical, as can be seen in Fig. 3BC. The stimulus movement from the left to the right evoked much greater amplitude of the potential than the movement in the opposite direction. There is also some asymmetry of responses to the oblique movements at the angle of 45° (Fig. 3D).

If we assume that evoked potentials are the algebraic sum of postsynaptic potentials of many cells in close vicinity of the electrode tip, then, obviously, we may expect that in this case neurons responding to the movement from the left to the right predominate in a given population and that their activity is synchronous. As a sum of postsynaptic potentials, the evoked potentials form a background activity of neurons in a certain area. So a comparison of a single cell activity with the evoked potentials will tell us whether a cell examined is typical for the population of cells in a given area.

Types of cells in the superior colliculus

We tried to classify the various cells in the superior colliculus according to the character of their responses to visual stimuli.

1. Units directionally insensitive (non-DS). Neurons responding vigorously to moving stimuli, equally well to all directions of movements (symmetrical responses).

2. Direction-sensitive (DS) units. Neurons responding strongly to a movement in one direction and not responding to movements in the opposite direction (asymmetrical responses).

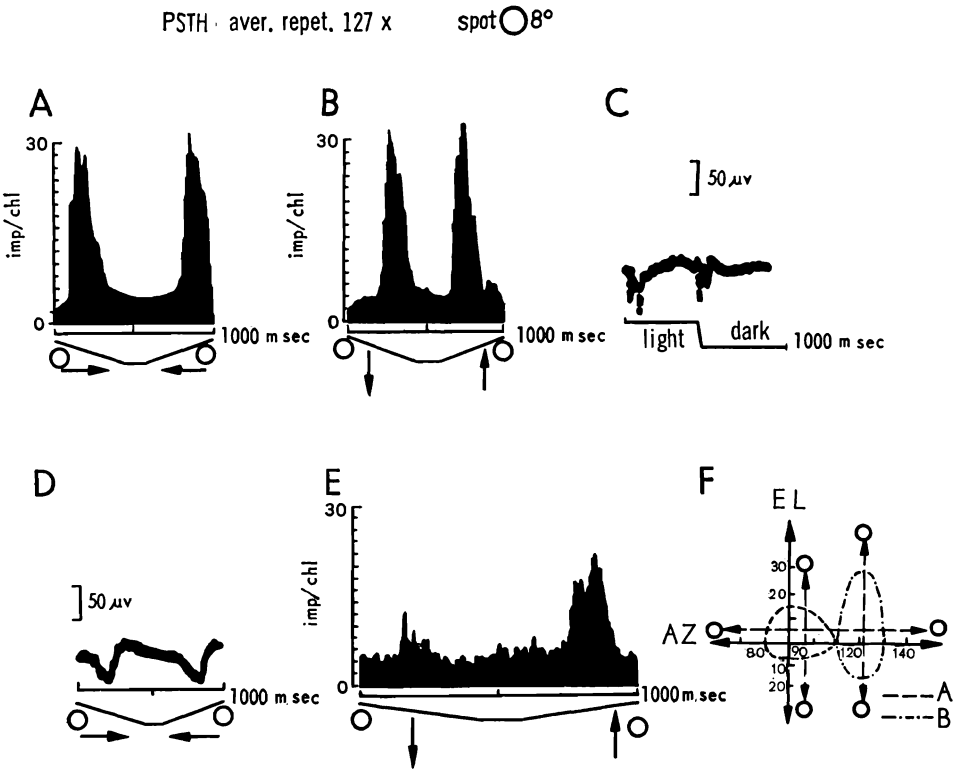

Fig. 4. Direction non-sensitive neuron in superior colliculus. A, Post-stimulus time histogram of spike responses of the neuron to movements of a light disk in the horizontal plane. The histogram is symmetrical. B, Responses of the same neuron to the movement in the vertical plane. The number of spikes is nearly the same in both directions. C, Evoked potential to the flash recorded at the same point where single unit is recorded. D, Evoked potential to the movement of stimulus in the horizontal plane. There exists well defined correlation between responses of cell and background activity. Compare "A" and "D". E, Post-stimulus histogram of responses of a neuron in close vicinity of previous one. Responses to the movement of stimulus in the vertical plane are asymmetrical. The neuron is direction-sensitive. F, Receptive fields of the two neurons described above. A: Cell with histograms A and B, B: Cell with histogram E.

3. Orientation-sensitive units, responding strongly to movements along one meridian, e.g. vertical, and responding weakly to movements along the perpendicular meridian, e.g. horizontal.

4. Neurons in which the spontaneous activity was inhibited when a white stimulus entered into their receptive field.

5. Neurons respoding only to changes in diffuse illumination and not responding to moving objects.

6. Neurons responding only to moving stimuli and not responding to changes in diffuse illumination.

7. Non-visual neurons.

Directionally insensitive neurons (non-DS)

These neurons formed the most numerous group, 45% of the cells examined. A typical response for cells in this group is shown in Fig. 4. Such a cell is excited i.e. its spike frequency is increased when white object enters and moves across its receptive field. The responses to movements in any direction are similar and therefore both histograms shown in Fig. 4AB are symmetrical. The cell represented in Fig. 4 exhibited "on-off" responses within all parts of its receptive field. Fig. 4CD show field potentials recorded at the same point. It will readily be seen that the form of the averaged compound potential is also symmetrical. We may conclude that near the point of recording a majority of neurons have the type of response which is shown in Fig. 4A. Such a fact may be significant for the analysis of incoming information by the superior colliculus.

About 100 μ beneath this cell there was another cell exhibiting pronounced directional sensitivity (Fig. 4E) their receptive fields being situated close to each other (Fig. 4F).

Direction-sensitive neurons (DS)

Neurons of this kind have already been described in the superior colliculus of the cat (Marchiafava and Pepeu 1966, Straschill and Taghavy 1967, Sprague et al. 1968, McIllwain and Buser 1968, Wickelgren and Sterling 1969, Harutiunian-Kozak et al. 1968a). Most authors have found that a high percentage or even a majority of collicular cells were directionally sensitive. In our experiments such cells constituted only 30% of the cell population examined, and formed the second most numerous group.

Directional sensitivity of the collicular neurons was tested with stimuli moving in various directions and orientations (vertically and hori-

zontally) and in two oblique directions at 45° angles. The speed of the movements in most cases was 63°/sec. In some cases slower movements, of 13°/sec were used.

Figure 5ABCD, shows the post-stimulus time histograms of a direction sensitive neuron.

When the stimulus entered into the receptive field the neuron responded with an increase in its discharges represented by maxima in the PSTH. It will readily be seen in Fig. 5 that the maxima for some directions of movements are higher than those for the opposite directions. This neuron showed preference to two directions upward and from right to left. The movements in the opposite directions elicited much smaller number of spikes. This indicates that some kind of inhibition must influence the cell activity during the movement in the null direction.

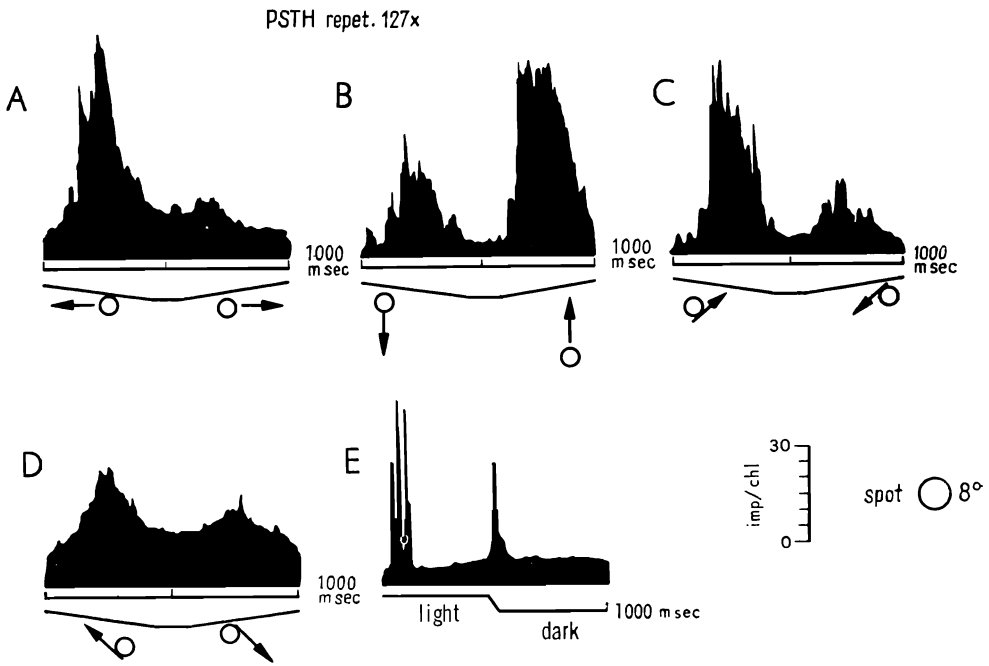

Fig. 5. Responses of a direction-sensitive cell to the movements of a light disk and to a light flash. A, Post-stimulus histogram of responses of the cell to the movement of stimulus in the horizontal plane. Preferred direction is from right to left. B, Responses of the same cell to the movements in vertical plane. Preferred direction is upward. C, D, Responses to the movements in oblique directions (45° of angle). E, Post-stimulus histogram of responses of the direction-sensitive cell to the changing of diffuse light (1/sec).

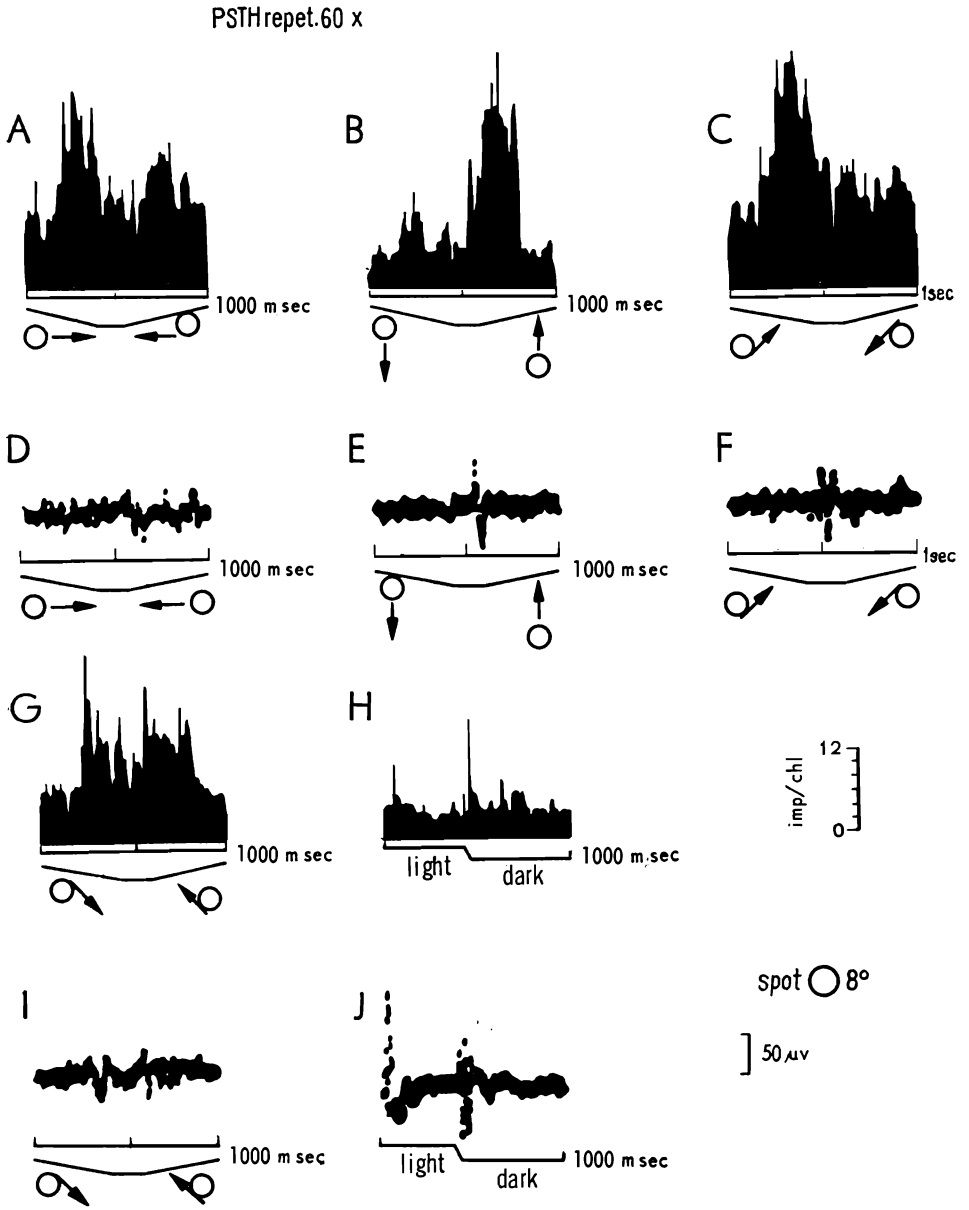

Fig. 6. Responses of a single cell and evoked potentials to the movements of a light disk and to a light flash. A, B, Post-stimulus time histograms of responses of a direction-sensitive neuron to the movement of stimulus in horizontal and vertical planes. Preferred directions from left to right, and upward. C, G, Post-stimulus histograms of responses of the same cell to the movements in oblique directions. H, Responses of the direction-sensitive cell to diffuse light flashes. A very weak reaction to the diffuse light is evident. D, E, F, I, J, Compound evoked potentials (mass responses of background activity) corresponding to each histogram of the cell, evoked by the same kind of stimuli. There is little correlation between the background activity and individual cell response.

The receptive field of the direction-sensitive neurons appeared to be homogeneous, i.e. similar responses to light flashes were obtained in each part of the field.

Figure 6 also shows responses of a DS unit. This neuron responds very weakly to a diffuse light flash (Fig. 6H). The preferred directions of this neuron were upward and from the left to the right. Responses to the oblique directions of movement differed less, especially in Fig. 6G. Figure 6 shows also the evoked potentials recorded at the same point, wherefrom the neuron spikes were recorded. It will be seen that the horizontal movements do not produce evoked potentials, while responses to the vertical movements are asymmetrical and are correlated more or less with the preferred — direction maxima in the PSTH. In all other

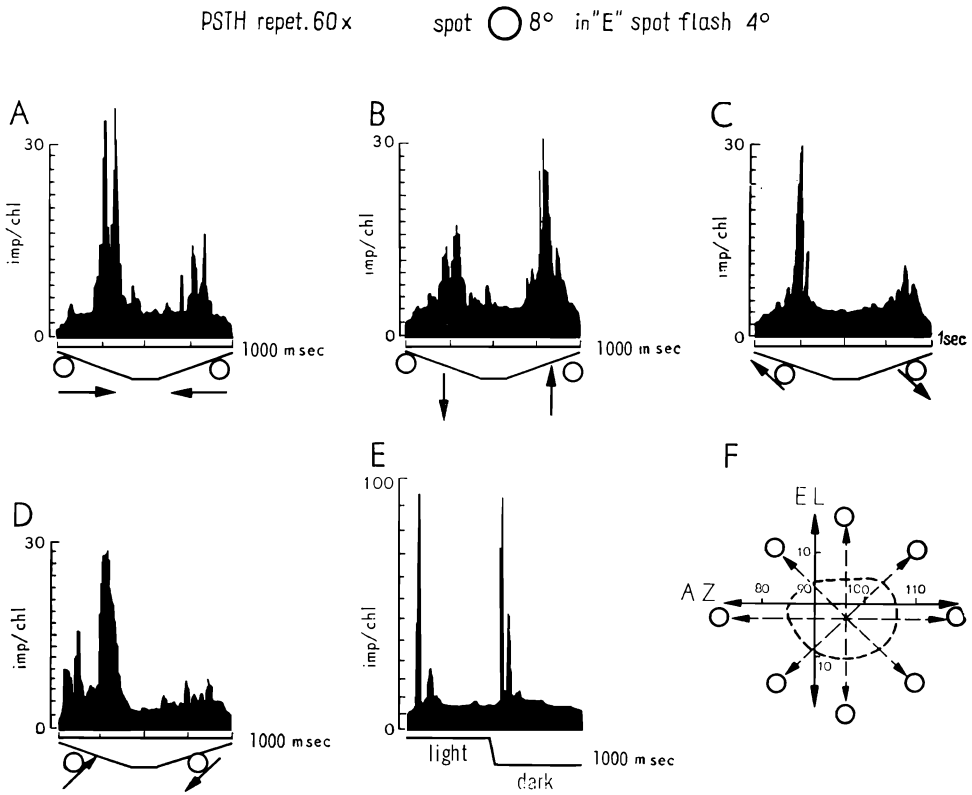

Fig. 7. Direction-sensitive neuron with a prominent reaction to the light flash. A, Post-stimulus histogram of responses of the neuron to the movements in a horizontal plane. Preferred direction is from left to right. B, PSTH — of responses to the movements in vertical plane. Preferred direction upward. C, D, PSTH — of responses to the movements in oblique directions. Again directional sensitivity is evident. E, Strong "on-off" response of the same cell to the flashing light spot (1/sec, 4°). F, The position of the receptive field of the neuron.

cases such correspondence does not take place. We often observed such discrepancies between maximum responses of the PSH and of the evoked potentials. There were rare cases in which a full coincidence of time courses of both responses could be observed. This provides further evidence for a complex nature of the cell representation.

Figure 6J illustrates the "on-off" evoked response to flashing light. Judging by the size of the responses the majority of cells in this place respond briskly to diffuse light. Thus, the cell examined is not typical for this population of cells as its "on-off" response to light is very weak (Fig. 6H). It is probable that the microelectrode picked up large cells, and that the evoked responses were made up of a large number of small cells.

The situation described above may be reversed. Although some of the DS cells did not respond to diffuse light, some other cells among them exhibited brisk responses to light changes in addition to quite pronounced directional specificity. An example of such a neuron is illustrated in Fig. 7. This cell responds briskly to light "on" and "off" (Fig. 7E). As will be seen this neuron exhibits directional sensitivity for all orientations. Figure 7F shows a map of its receptive field together with arrows showing directions of stimuli.

Orientation sensitive neurons

Neurons belonging to this group show brisk responses to movements in one orientation, e.g. horizontal and very weak reactions to movement in another orientation, e.g. vertical. Responses of such an orientation--sensitive cell are shown in Fig. 8. The vertical movements hardly elicit any response (Fig. 8C) while responses to horizontal movements are well pronounced (Fig. 8AB). This neuron is also slightly direction-sensitive.

Neurons suppressed by white stimuli entering their receptive fields

Neurons of a similar kind have been described in the cat's retina by Rodieck (1967), who called them "suppressed-by-contrast" units. The number of such cells found by us in the superior colliculus was very small, only 3%. Maybe the fibres of the retinal cells described by Rodieck (1967) converge on these units. This notion would be supported by the fact that the collicular receptive fields measuring from 10 to 40° in diameter are larger than the retinal receptive fields of such cells described by Rodieck (1967) (2.5° in diameter).

Figure 9 shows post-stimulus histograms of responses of such a neuron to diffuse illumination and to moving stimuli. Figure 9BCDE shows the post-stimulus histograms of responses to 8° light disk moving

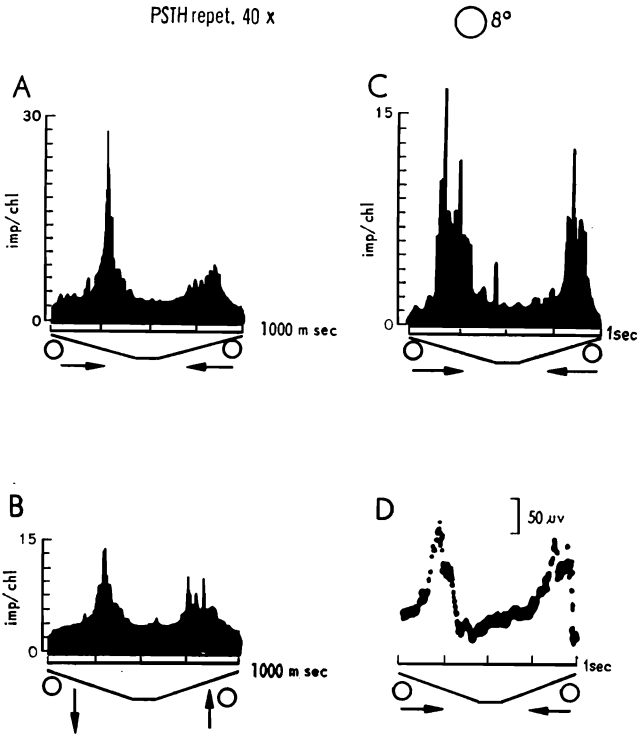

Fig. 8. Post-stimulus histogram — of responses of orientation-sensitive cells. A, Post-stimulus histogram of the orientation-sensitive neuron in response to the movements in horizontal plane. The response is direction-sensitive with preferred direction from left to right. B, PST histogram of responses of the same cell to the movements in the vertical plane. The response is rather weak and directional sensitivity not so pronounced. C, Responses of a neighbourinal cell to disk movements in a horizontal plane. There is some degree of directional sensitivity, but not pronounced. Preferred direction from left to right. D, Compound evoked potentials recorded at the same point in response to the movements of the stimulus in the horizontal plane.

across the receptive field of this cell. Directions of movements are marked by arrows.

It is clearly seen that the spontaneous activity is suppressed when the stimulus crosses the receptive field. It will also be seen that the responses resumed soon after the stimulus crossed the field, without any rebound-like reaction. The receptive field of this neuron also appeared to be homogeneous. Similar "on-off" responses were obtained in all parts of the field and no antagonistic surround was found. Figure 9A illustrates the response to the flash which consists of the weak "on"-response and the strong "off"-response. This type of coding, seems to occur in the superior colliculus rarely.

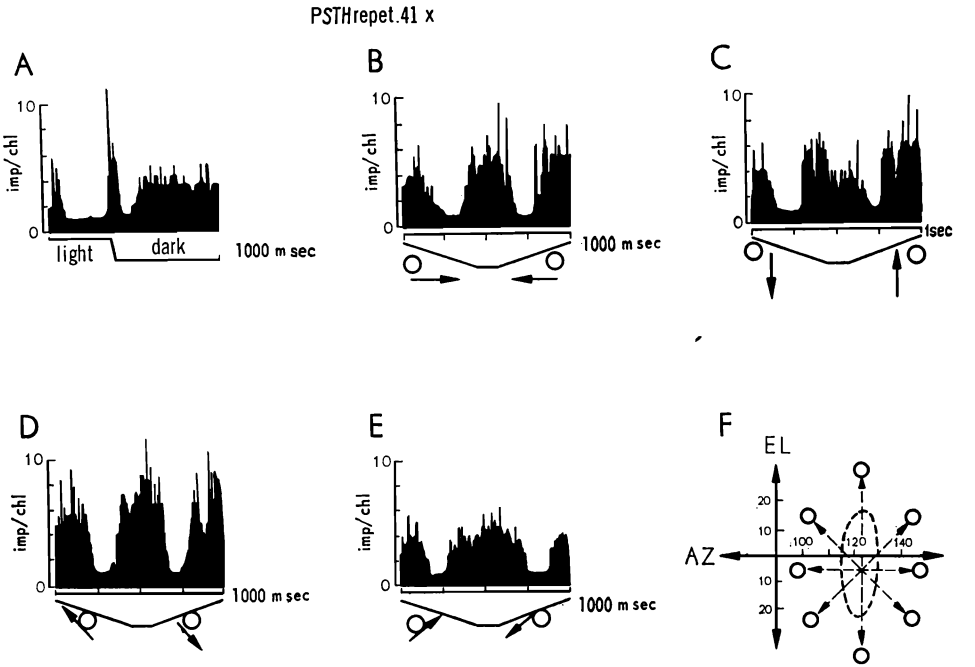

Fig. 9. Responses of a "suppressed-by-contrast" type unit. A, Post-stimulus histogram of responses to the diffuse flashing light (l/sec). B, Responses to the horizontal movement of the stimulus (light disk). There is characteristic inhibition of spontaneous activity when stimulus enter into the receptive field of the cell. C, PST-histogram of responses to the movements in the vertical plane. D, E, The same type of reaction to the movements in oblique directions (45° of angle). F, The position of the receptive field of the neuron.

Neurons responding exclusively, to changes in illumination and not responding to moving objects

These neurons form the smallest group of cells examined in the superior colliculus, only 2%.

Neurons responding only to movements of objects and not responding to diffuse light

They made up 7% of all cells and were included to the group of the DS and non-DS cells previously described.

Non-visual neurons

Apart of neurons responding in some way to visual stimuli, there were others which did not respond to any stimuli used in this investigation. Such cells were quite numerous making up 20% of all cells examined.

As it is known, the superior colliculus receives many fibres from the retina. Apart of this main input there are also inputs from the somatic afferents along the spino-tectal tract (Jassik-Gerschenfeld 1965), from the visual cortex (Altman 1962), etc. It is quite possible that the neurons classified by us as non visual are connected with the above mentioned afferents and take part in other kinds of information processing. It is also possible, however, that these neurons could be highly specialized and that they would require more specific stimuli to be excited.

Receptive fields

All the receptive fields examined by us were homogeneous without any antagonistic center-surround structure. Thus, the structure of the collicular receptive fields is quite dfferent from the structure of fields in the retina and in the lateral geniculate nucleus. Kuffler (1953) in his original work described a classical type of a receptive field of retinal ganglion cell. This field consisted of a central area and a concentric surround responding to light in opposite ways.

Since then retinal receptive fields of other kinds have been described (Stone and Fabian 1966, Rodieck 1967, Spinelli 1967). It is very probable that ganglion cells of these kinds send their axons to the superior colliculus. We could not find any narrow antagonistic surround within the collicular receptive fields as it was found by McIllwain and Buser (1968). Only in one case we found some parts of a receptive field on one side of the field from which responses opposite with respect to the whole field reaction were elicited.

An attempt was made to determine the area wherefrom swish reaction could be elicited. It was interesting to observe whether there was any correlation between spatial positions of receptive fields of individual units and the swish reaction from the same point. Figure 10 demonstrated the receptive fields of a single neuron and swish reaction in the same point of the electrode track. In the majority of cases the two fields overlap. It would be then difficult to explain the observed discrepancies between the patterns of unit firing and of evoked potentials by the spatial non-coincidence of the receptive fields of the neuron and of the mass reaction.

Columnar structure

Apart of observations of properties of collicular units it was of interest to examine also the anatomical organization of these units expecially whether they are organized in columns or not. In our investigations, we compared single unit responses in a single vertical penetration and corresponding receptive fields of these units.

Figure 11 shows an example of such a study. Figure 10ABC, show the post-stimulus histograms of three different cells responding to the vertical movements. The distance between successive cells was of an order of 50–100 μ. As will be seen, all the three cells respond in different ways. The neuron represented in Fig. 11A exhibits a directional sensitivity with the preferred direction downward; the neuron in Fig. 11B is also direction-sensitive but its preferred direction is just opposite — upward; the cell in Fig. 11C does not show directional sensitivity at all, its responses are almost symmetrical. Figure 11F shows maps of the

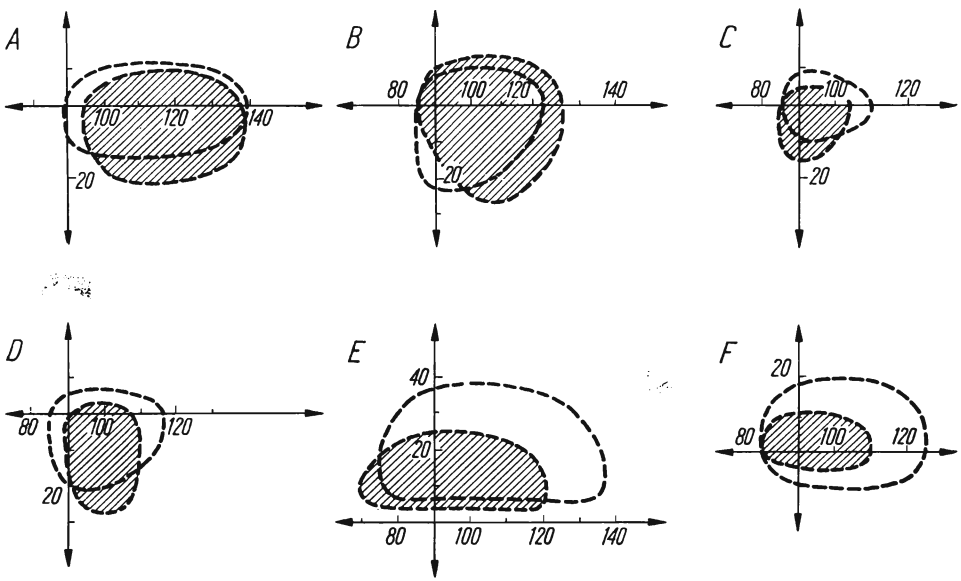

Fig. 10. Unit-fields and swish-fields. A-F, Six different locations of the electrod tip. For each location two areas in the visual field were outlined: the diagonal line shading corresponds to the receptive field of a single unit (unit-field). The other outlined surface corresponds to the area from which swish reaction could be obtained recorded from same electrode location (swish-field).

receptive fields of these three neurons. A considerable degree of overlap is clearly seen from the plot. Thus, neurons of quite different properties may be subserved by the same part of the retina. This was found in many cases one of which is demonstrated in Fig. 12 where results of different experiments are shown. All the plots are maps of receptive fields of pairs of neighbouring neurons in the same electrode penetrations. In some cases neighbouring neurons show similar modes of action (Fig. 12ABC), and similar positions of receptive fields and this might

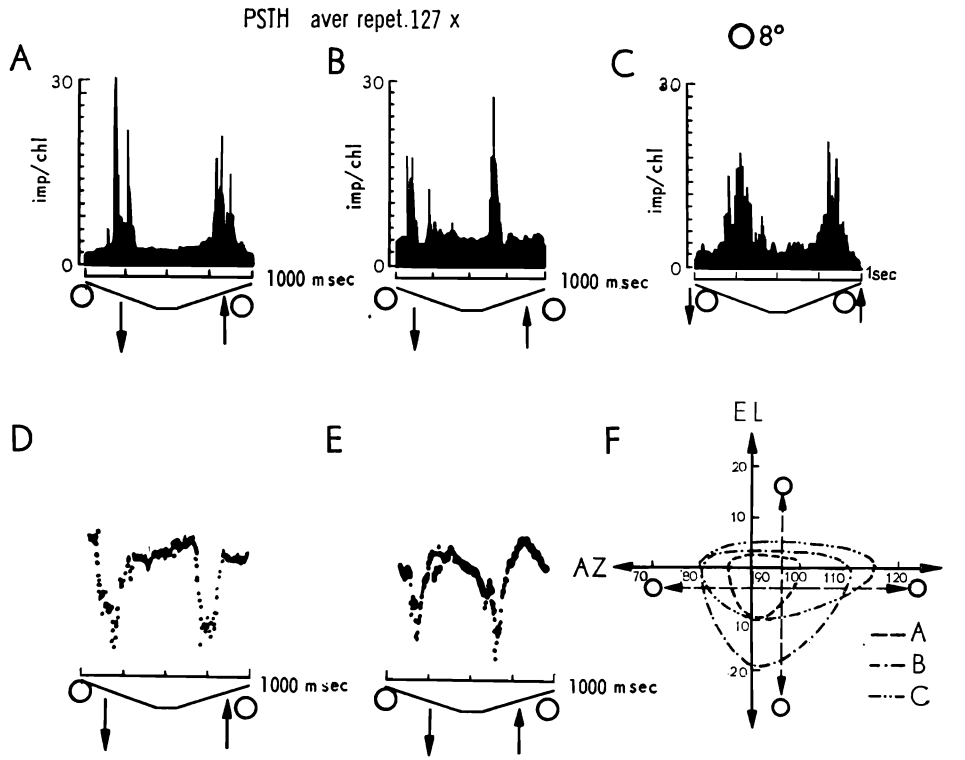

Fig. 11. Responses to moving stimuli (light disk) of three successive neurons in one penetration. A, PST-histogram of responses of a direction-sensitive cell to the movement in a vertical plane. Preferred direction — downward. B, PST-histogram of responses to the vertical movement of another direction-sensitive unit in close vicinity to the previous cell. Preferred direction — upward. C, PST-histogram of responses of the third cell in the same penetration. This unit responded in a similar way to the movement of stimulus in different directions. D, E, Averaged evoked potentials corresponding to "A" and "B". There is some correlation between responses of an individual cell and of the background activity. F, Positions of receptive fields of above mentioned neurons. Note a marked overlap.

suggest the existence of a columnar organization. However, there are also neighbouring neurons (Fig. 12DE) exhibiting quite different response properties which contradict the principle of the columnar organization, at least from the point of view of their functional characteristics. However, this draws attention to the fact that direction-sensitive and direction non-sensitive neurons may have receptive fields with a high degree of overlap (Fig. 12DE).

Overlapping of receptive fields in general was very often observed in the superior colliculus. For example, Fig. 13 shows maps of receptive

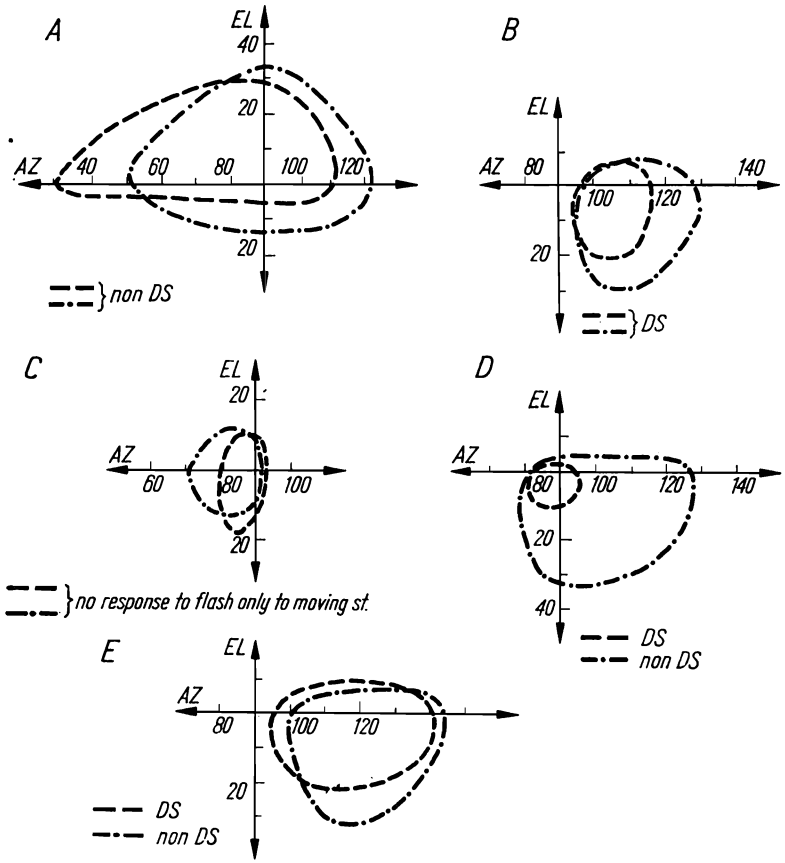

Fig. 12. A–E, Positions of receptive fields of pairs of neighbouring neurons and their functional characteristics in five different penetrations.

fields of four neighbouring neurons in one penetration. All these fields overlap one another. One may suppose that some mode of spatial distribution of receptive fields of single neurons exist in superior colliculus in columnar manner.

Thus, we failed to find the classical columnar organization of the collicular units which was described by Sprague et al. (1968). The possible reason of our failure may be the way of investigations, inadequate to this task, e.g. distances between neighbouring neurons from 50 to 100 μ seemed to be too long. It is quite possible that closely neighbouring neurons exhibit properties transitional from one cell to the other. Since our results are far from being conclusive this problem needs further detailed investigations.

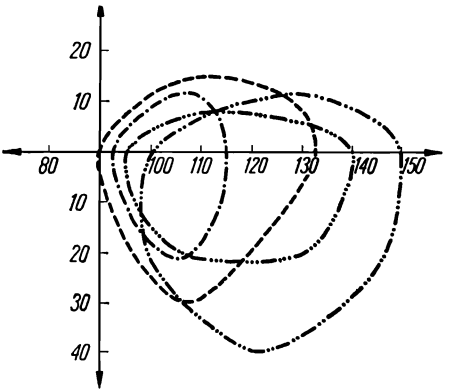

Fig. 13. The positions of receptive fields of four neurons in one penetration. The fields are partially overlapping.

DISCUSSION

Summing up, we may conclude that the types of neurons described above characterize cells in the superior colliculus. A rather high percentage of the direction sensitive neurons is worthwhile to be emphasized. Unfortunately, without a special histological study, we are unable to provide any morphological description of distribution of the direction-sensitive cells (according to their preferred directions) in various layers and parts of the superior colliculus as it was done by Straschill and Hoffman (1969).

Mechanisms underlying directional sensitivity are still a controversial problem. Stone and Fabian (1966) have described only one direction-sensitive neuron in the cat retina and since then no other results like that have been published.

Barlow and Levick (1965) localized the directionally sensitive mechanism of the rabbit ganglion cells in the outer plexiform layer. They suggested that the horizontal cells could play some inhibitory part in suppressing responses to movements in the null directions. Of course, it could be so in the rabbit retina. Recently, Wickelgren and Sterling (1969) described experiments which suggest that the mechanism of directional sensitivity has its site in the visual cortex. As far as collicular neurons are concerned we assume that in the cat this mechanism originates from outside of the retina.

As was demonstrated in our investigations of receptive fields, the collicular neurons of quite different properties may have overlapping receptive fields (Fig. 12). This means that a direction-sensitive neuron may have its receptive field in a similar part of the retina as the direction non-sensitive cell. Thus, a considerable part of the retina must be common to both these neurons. It would seem a little strange if we assumed that the same part of the retina may subserve at the same time DS and non-DS neurons providing different mechanisms. If we took for granted that the retina is the site of the directional sensitivity mechanism we would rather except that neurons being subserved by almost identical parts of the retina should exhibit response properties, more or less alike. Otherwise one must suggest very complicated mosaic structure of retina. Besides that it is quite possible that collicular neurons of the cat have different mechanism underlying this phenomenon.

Some authors suggested that the high degree of specialization of the collicular cells is connected with their role in the oculomotor reflex (McIllwain and Buser 1968). Undoubtedly, there must be some connection like that (Dreher et al. 1965). However, we cannot restrict the role of the tectum only to this function. The highly specialized functions as the direction-sensitivity, orientation-sensitivity, etc. may subserve the visual information analysis in rather high level. It is possible that the colliculus superior plays some part in complex processes of analysis of visual perception.

SUMMARY

1. Responses of neurons in the superior colliculus to movements of light disk and to changes in diffuse illumination were examined.

2. Neurons were classified into the following groups: (i) Direction non-sensitive neurons. (ii) Direction-sensitive neurons. (iii) Orientation--sensitive neurons. (iv) "Suppressed by contrast" neurons. (v) Neurons responding only to changes of diffuse light. (vi) Neurons responding only to moving stimuli but not to diffuse light. (vii) Non-visual neurons.

3. A considerable degree of overlap among receptive fields of the neurons were observed.

4. It was suggested that the mechanism of directional sensitivity originates from outside of the retina, probably in the visual cortex or in the superior colliculus itself.

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Pages 211-232, Fig. 4-9 and Fig. 11

and

Pages 233-262, Fig. 2-15

instead of 1000 msec should be 1640 msec