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ANALYSIS OF VISUAL INFORMATION IN MIDBRAIN CENTERS

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Abstract. The role of pretectum and colliculus superior in the analysis of visual information was studied. Single unit responses to visual stimuli were recorded. Several types of responses were observed, including "suppressed by contrast", "direction non-sensitive" and "direction sensitive" responses. An attempt was made to define the place and mechanism of direction-sensitivity of the cell. The conclusion is put forward that horizontal cells in the first layers of retina are not responsible for direction-sensitivity. Detailed analysis of receptive field structure revealed "homogeneous" and "heterogeneous" types of receptive fields as shown by response patterns of the neuron to a flashing light spot positioned in different parts of the receptive field. Study of latency distributions also revealed both complex "heterolatent" and more simple "homolatent" organizations of receptive fields. The effect of the intensity of background illumination was investigated. Results show that changing of the background illumination can influence the response pattern of a cell, and sometimes can influence the direction-sensitivity.

Most investigations presented in this Symposium are concerned with behavior of the animal. In contrast, we are endeavoring to analyse the behavior of single nerve cells. However, since the animal's behavior is a direct outcome of the behavior of its nerve cells, our presentation may still be of interest to those engaged in research on the higher integrative processes of the nervous system.

The main problem explored during several years in our laboratory has been the mechanisms of modulation of incoming afferent information by the cells in specific visual nuclei. We wanted to find out how these cells modify the input from the receptors to produce the response which is transferred elsewhere into the nervous system. The problem

is complicated. To simplify it we tried first to find a group of cells situated not far from the receptors. Secondly, it was necessary to provide natural excitation of the receptors and to study the natural information coding in afferent paths in order to be sure that the modulation performed by the cell actually occurs in the animal.

The experiments were performed on acute pretrigeminal cats thus eliminating the influence of anesthetics. Single cell responses were recorded from the midbrain with tungsten microelectrodes (see 6) with tip diameter of 3–5 μ and resistance about 50 megaohms. Recording and analysing methods are shown on Fig. 1 (5). The responses of single cells were averaged using an "ANOPS" analyser in the poststimulus time histogram mode, as described by Gerstein and Kiang (2).

Excitation of the retinal photoreceptors was achieved by the use of different patterns of stimuli projected onto a white screen located 70 cm in front of the cat's eyes (Fig. 1). The pupils were maximally dilated by atropine and neosynephrine, and the corneas were protected by contact lenses.

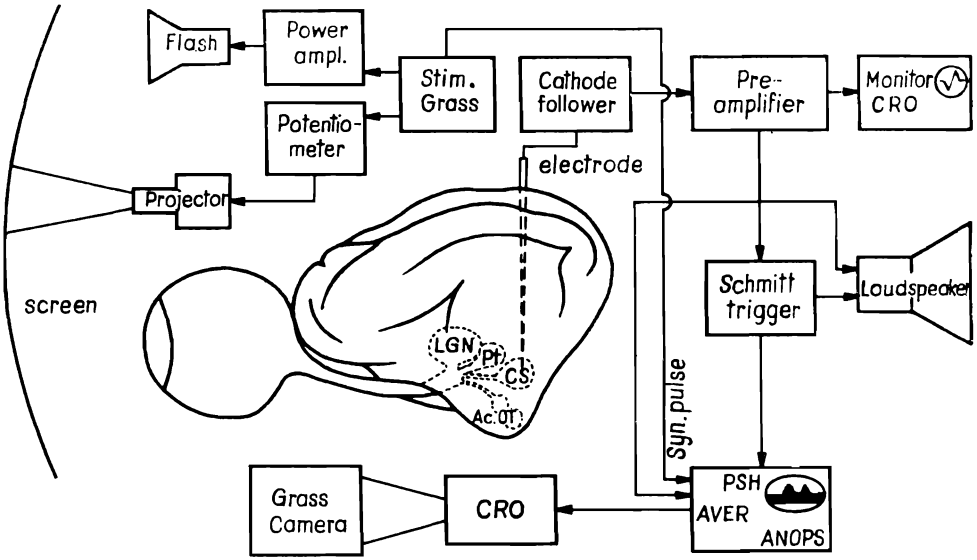

Fig. 1. Diagram of stimulating, recording and analysing apparatus.

In the first series of experiments, the general characteristics of the cells were investigated. A detailed classification of observed responses was made and has been presented in our previous papers (4, 5). The present paper uses some of these observations to demonstrate of what kind of modulation of incoming information the cells in the midbrain

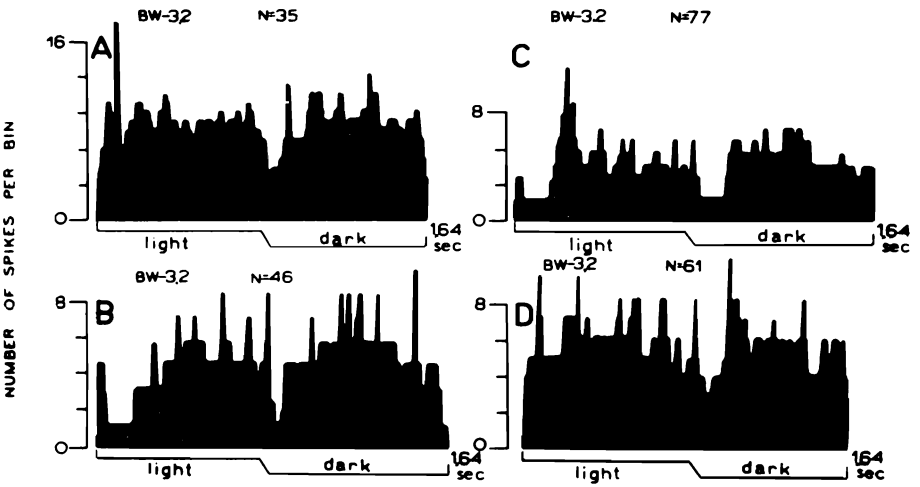

Fig. 2. Inhibitory responses to a change of the intensity of illumination. *A* and *C*: Post-stimulus time histograms (PSTH) of responses to flashing diffuse light of two neurons in colliculus superior; *B* and *D*: PSTH of responses of two neurons in pretectum. In all cases the rate of flashing light was 0.8/sec, and the intensity 8 cd/m². N, number of repetitions; BW, bin width in milliseconds.

are capable of performing. Figure 2 presents PST histograms of responses of two cells in the superior colliculus (*A* and *C*) and two cells in the pretectum (*B and D*). Change from light to dark is characterized by an inhibition of the spontaneous activity. Generally, such cells display fast, irregular spontaneous spike discharges. The modulation they perform consists of inhibition of maintained activity for about 100 msec after reduction of illumination or, in some cases (Fig. 2*BC*), following an increase in light intensity. Another group of cells is characterized by increasing their discharges in response to changes in intensity of diffuse illumination (Fig. 3*A–C*) and by a weak, or essentially no response to movements of light spots across their receptive fields (Fig. 3*D–F*). The third group, on the contrary, responds very well to moving stimuli (Fig. 4*AC*) and hardly reacts to changes of diffuse illumination (Fig. *4BD*).

Some cells in the midbrain respond more specifically. For example, they can differentiate between various directions of movement. In Fig. 5 two cells having this feature are presented, as is particularly obvious in the PST histograms of the cell shown in *A*, *B*, and *C*. In *B* and *C* the horizontal and vertical movements of a 5° light spot evoked unequal responses for different directions of movement.

Special attention was paid to this kind of cell as an example of neurons capable of modifying incoming information in a specific way.

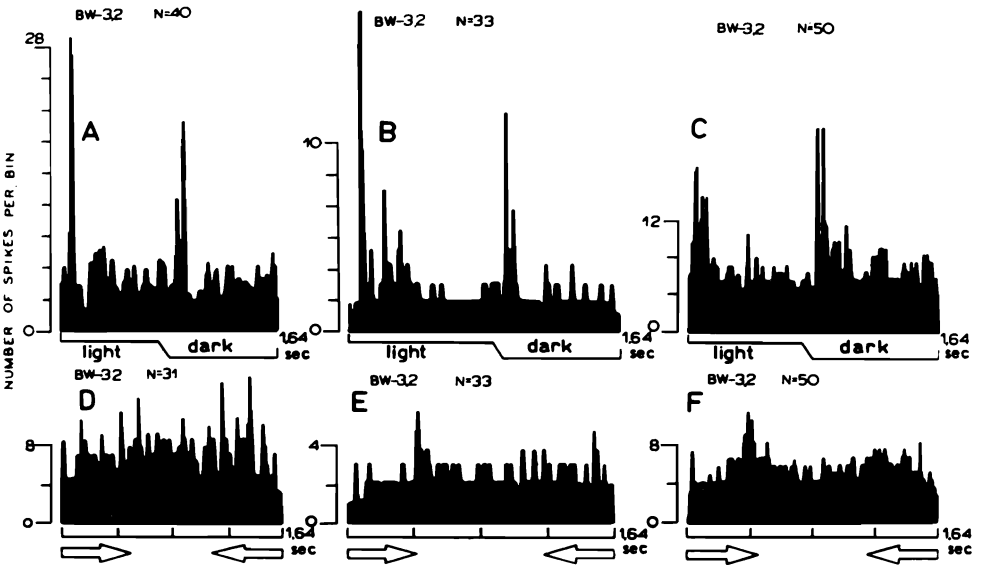

Fig. 3. Neurons in colliculus superior responding intensively to change in illumination and weakly to moving stimuli. *A–C*: PSTH of responses of three neurons to a flashing diffuse light. The rate of flashing, 0.8/sec. Note the prominent "on–off" reaction. D–F: PSTH response of the same cells to moving 8° light disc with 6 cd/m² intensity of illumination. The speed of movement was 90°/sec. Note the weak reaction of each cell.

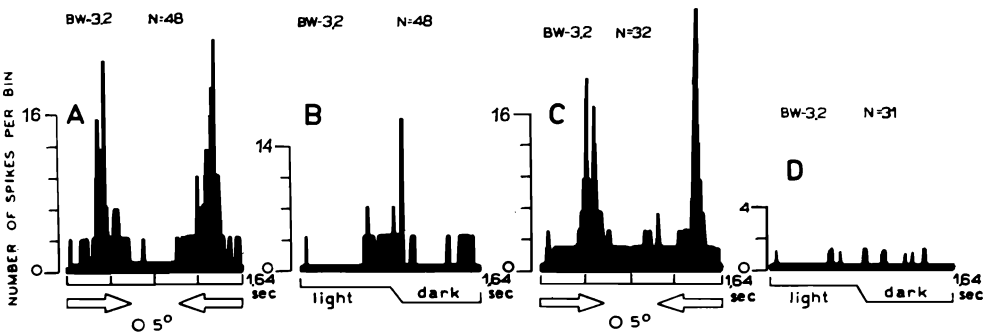

Fig. 4. Responses of two neurons in colliculus superior sensitive to a moving pattern. *A*: PSTH of responses of the cell to movement of a 5° light spot. Note the clear reaction to the movement. *B:* The response of the same cell to a flashing light. Note the weak "off" reaction. *C*: PSTH of another cell to the movement of a 5° light spot. The cell responds vigorously to the movement. *D*: Lack of response of the same cell to a flashing diffuse light.

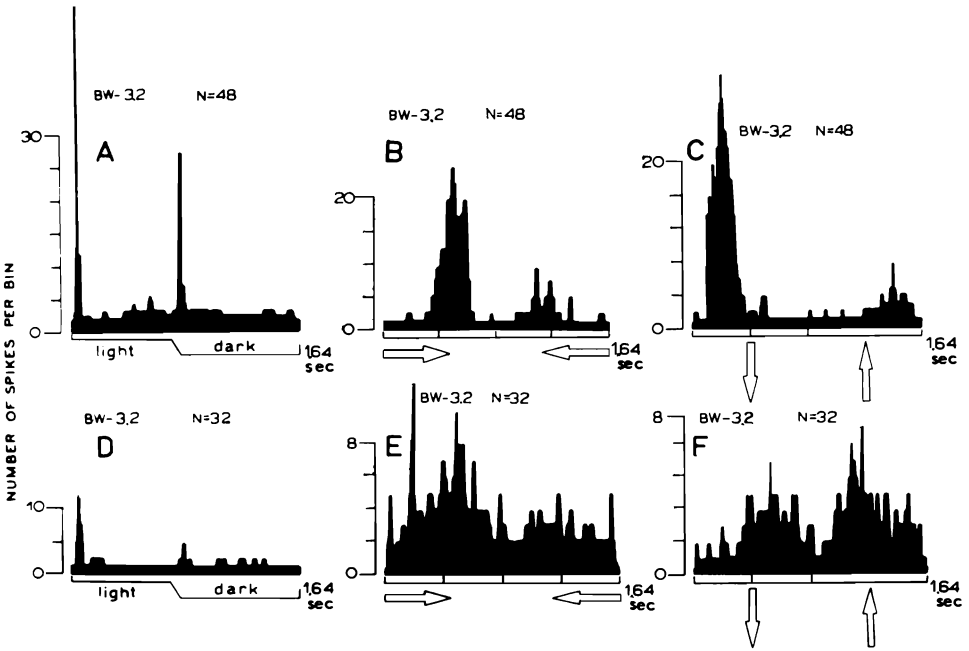

Fig. 5. Direction sensitive neurons in colliculus superior. *A*: PSTH of responses of a neuron to a flashing diffuse light. Note a clear "on-off" response. *B*: Responses of the same neuron to 5° moving light spot. There exists asymmetry of responses with a preference in the left-to-right direction. *C*: Responses of the above, described cell to vertical movement of a 5° light spot. Again asymmetry is apparent, preferred direction being from up downwards. *D*: Responses of another cell in colliculus superior to flashing light. Note a weak "on" response. *E* and *F*: Responses of the same cell to horizontal (*E*) and vertical (*F*) movement of a 5° light disc.

The first problem to be resolved is what mechanism can produce such a feature as directional selectivity. An explanation was provided by Barlow and Levick (1), working on the rabbit, whose retina is different from that of the cat. They located the main mechanism of directional sensitivity in the outer retinal layers and explained it by the functioning of horizontal cells. It is quite possible that in the rabbit the mechanism of directional sensitivity is organized in this way, but in the cat it seems to be different. First, direction-sensitive cells have not been observed in the cat retina, besides the one cells reported by Stone and Fabian (9). In order to get more data about this problem, we designed the following experiment. The positions of the receptive fields of the collicular neurons were determined in each penetration of a microelectrode. Then the response characteristics and receptive field locations of neurons were compared. It became clear that, in some cases, neurons having quite different

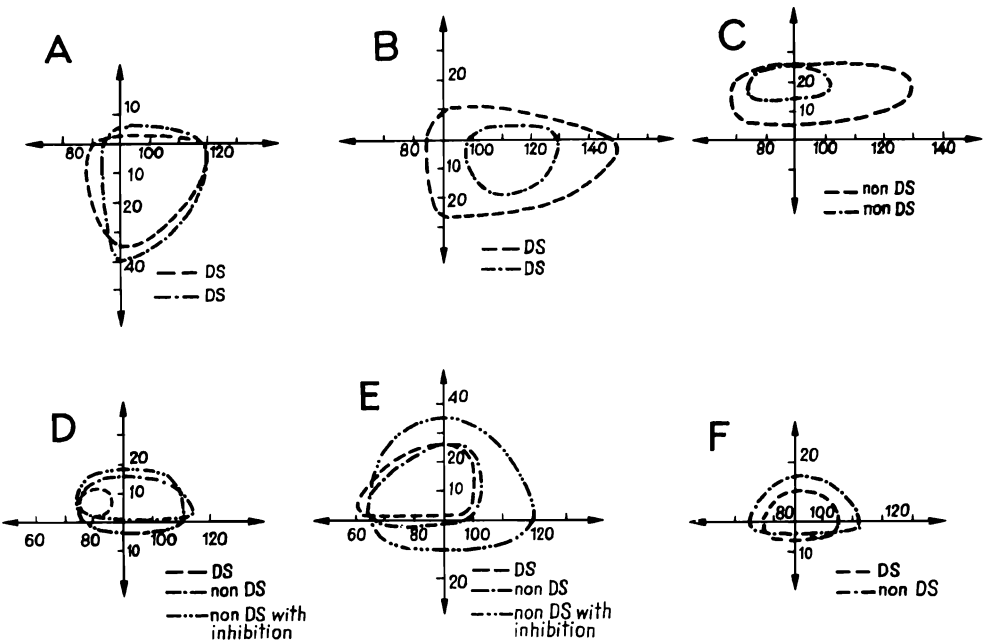

Fig. 6. Overlap of receptive fields of neurons with different characteristics of responses to a moving light spot. *A–F*: Different penetrations of the electrode in the lateral pretectal region.

response characteristics had their inputs from the same part of the retina (Fig. 6*D–F*). It is difficult to assume that the same part of the retina (at least the outer layers) could serve three different mechanisms of the neuronal responses. So we came to the conclusion that the mechanism of directional sensitivity is situated more centrally.

During that study the columnar organization of neuronal groups in the superior colliculus was confirmed (Fig. 7 and 8). 70% of the collicular neurons investigated were organized in vertical columns. This means that all the cells recorded from one penetration of the microelectrode had one or two response features in common although they could differ in other characteristics. In Fig. 7 three vertical penetrations in the lateral part of superior colliculus are presented. In Fig. 7*A* all nine neurons recorded from one penetration were directionally non-sensitive, but they differed in their reactions to diffuse flashing light. Some of them responded with an "on" reaction, two of them had "on–off" responses and the rest did not respond to the flashing light at all. The receptive fields of these neurons overlapped to a considerable extent. In 10% of the penetrations we found a perfect organization and all neurons in such a column had identical response features. One such column is represented in Fig. 8*B*.

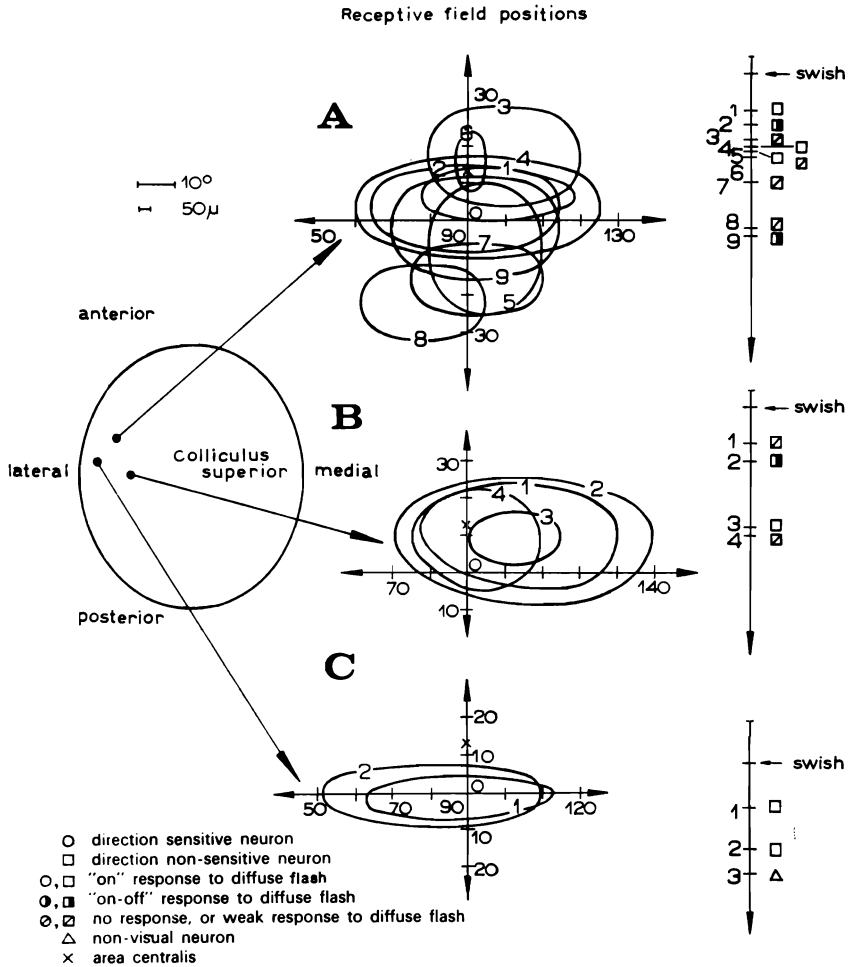

Fig. 7. Columnar organization of neurons in colliculus superior. On the left, the surface of colliculus superior is shown with the points of microelectrode penetration. *A–C*: position of receptive fields of neurons observed during consecutive penetrations. On the right, microelectrode track for each penetration. The numbers show the order of the neurons.

Although the columnar organization of visually driven neurons in the midbrain gives some information about the interneuronal connections required for complex analysis of afferent information, it provides no answer as to how the specific response of the cell is organized. The mechanisms of the modulation of incoming information still remain obscure.

The next step to come closer to this main problem was done by investigating in detail the structure of the receptive field of neurons responding to visual stimuli. In the first series of experiments we studied

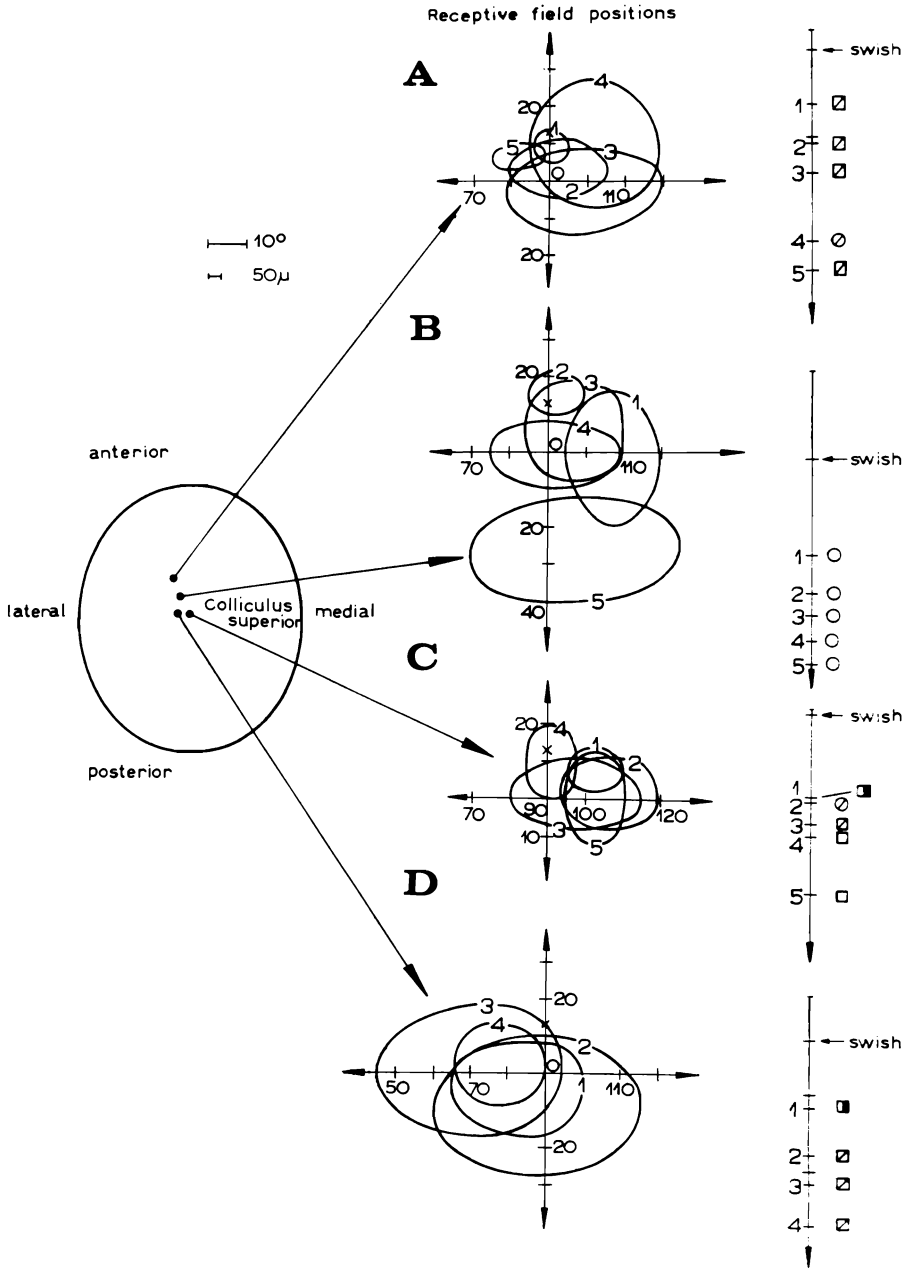

Fig. 8. An example of a perfect columnar organization of neurons in colliculus superior. Explanations as in Fig. 7.

the pattern of responses to a flashing spot placed in different parts of the receptive field. Two types of receptive fields were observed. The first type we called homogeneous, i.e., the same pattern of response could be recorded from every point of the field (Fig. 9). In the second type the field was heterogeneous, i.e., different response patterns were pro-

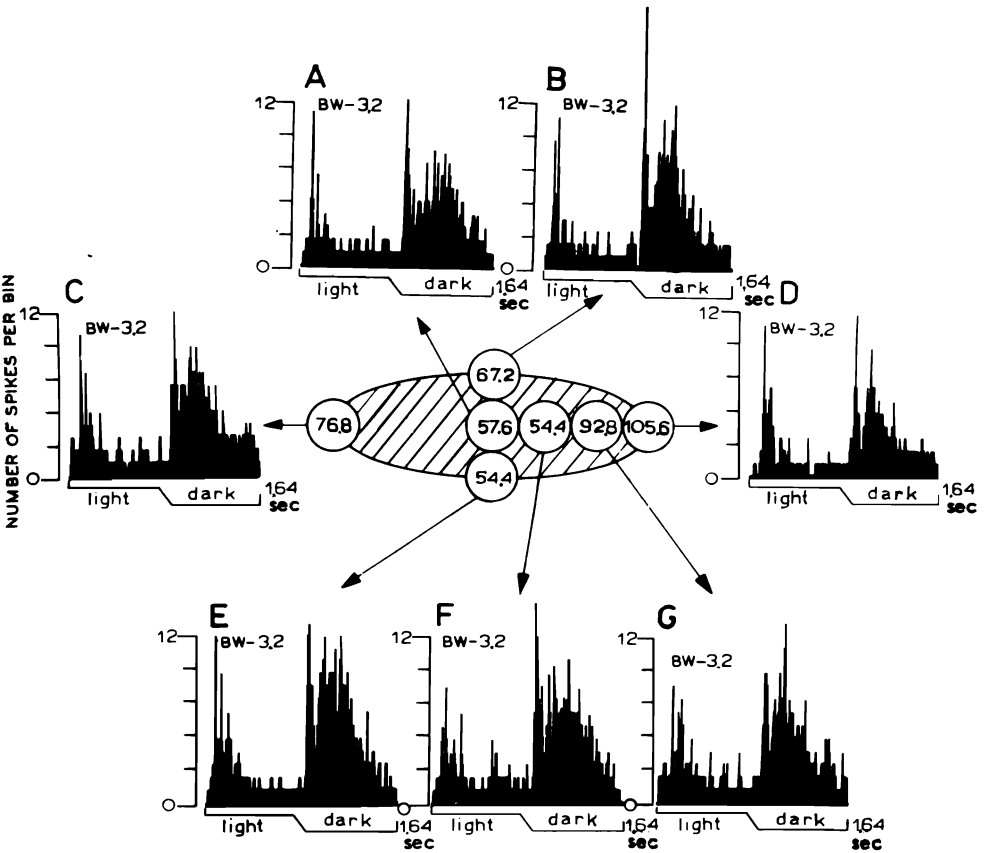

Fig. 9. Homogeneous receptive field of a neuron in colliculus superior. *A–G*: PSTH of responses to a 5° spot flashing in different parts of the receptive field. Circles show the localization of the light spot in the receptive field. Arrows point to corresponding response patterns. The numbers in the circles indicate the latency of the "on" response in msec. In all figures the rate of flashing was 0.8/sec and illumination of the light spot 4 cd/m². N, number of repetitions; BW, bin width in milliseconds.

duced from different points of the field for the same flashing spot (Fig. 10). Although "on–off" responses could be elicited from every point of the receptive field, the proportion of "on" and "off" response components were different with different locations of the flashing spot, e.g., the

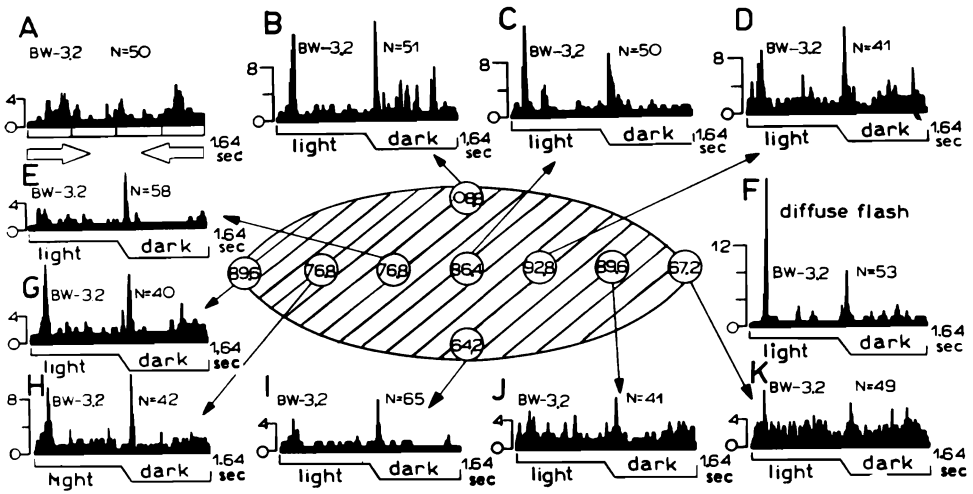

Fig. 10. Heterogenous receptive field of a neuron in the pretectum. There were differences among the components of the response of the cell to changing of the location of the flashing spot. *A* and *F*, PSTH of responses to moving spot and diffuse light flash respectively. B–E, and G–K, PSTH of responses to a spot 5° in diameter flashing in different parts of the receptive field. Explanations as in Fig. 9.

pattern of responses in *C*, with the "on" component prevailing differed from that in *D* where the "off" component was dominant (Fig. 10). Such detailed exploration of the visual receptive fields revealed that many fields were not homogeneous.

Surprising results were obtained when the latencies of the responses were measured. Three distinct groups of receptive fields were found. In a minority of the fields latencies of responses to a flashing spot were equal from different points of the field. We called these fields "homolatent". For instance the "on" responses in Fig. 11 have latencies close to 22.4 msec in every point of the receptive field. The second group of receptive fields have well-known differences in latencies between the periphery and the center of field. As a rule, centrally evoked responses have shorter latencies than those from the periphery (Fig. 12). The most interesting was the third group where no regularity could be observed in the latency distribution over the receptive field. The latencies of responses from neighboring points differed by 10–20 msec without any obvious pattern (Fig. 13). We call these receptive fields "heterolatent".

After such a detailed exploration of the receptive fields, we tried to find some correlation between the pattern of responses of a cell to the moving stimuli and the structure of its receptive field. At first, one would presume that such a specific modulation of incoming information

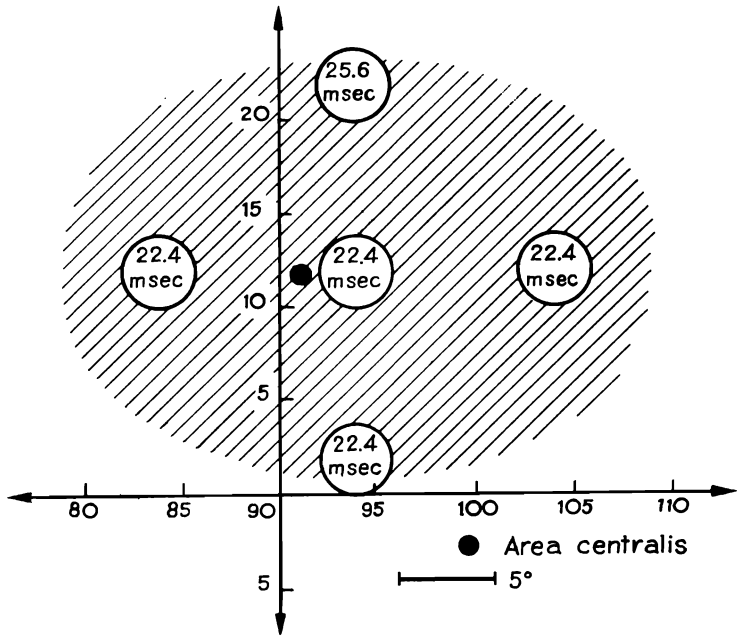

Fig. 11. Latency distribution in a homolatent receptive field (a neuron in the pretectum). Circles represent the location of the flashing light-spot. Numbers in circles show the latency of the "on" response in msec.

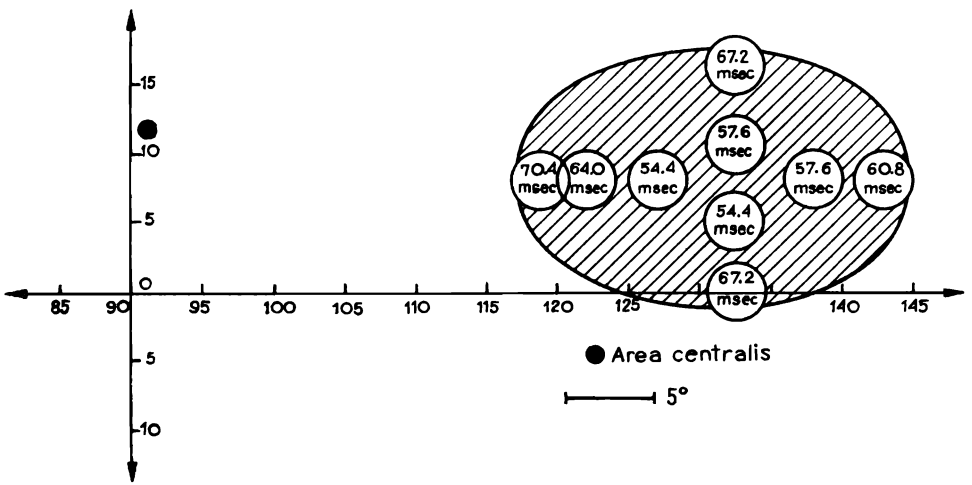

Fig. 12. A receptive field of a neuron in the pretectum with a regular distribution of latencies. Central part of the receptive field has shorter latencies. Explanations as in Fig. 11.

as directional sensitivity needs a more specific and complex structure of the receptive field. Unfortunately, this proved to be untrue. No correlation could be found between the responses of the cell to moving stimuli and the structure of its receptive field as revealed by the response latencies to flashing spots. Simply organized, homogeneous receptive fields could display highly specific direction-sensitive responses, and more complex "heterogeneous" fields could have simple, directionally-insensitive responses. Thus, the mechanism of directional sensitivity still remains inexplicable.

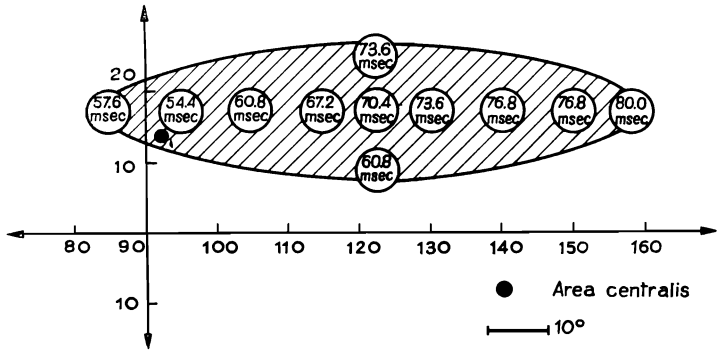

Fig. 13. A heterolatent receptive field of a neuron in colliculus superior. Distribution of latencies is irregular. The central part has longer latencies. There were significant differences in latencies between neighboring points. Explanations as in Fig. 11.

After the above-described series of experiments, performed during several years, we came to the conclusion that it would be very difficult to solve this problem directly. Thus we tried to change, in some way, the design of the experiments and decided to find some factors which would effectively influence the modulation processes in the cell. The aim of such experiments was the following: if there were some experimental factor which would influence the mechanism under study and the kind of changes it would produces in the neuron were known, we would be able to come closer to understanding the processes influenced by that factor. Our efforts in this direction were met with some success as shown in Fig. 14, the first of this series of experiments. This Figure presents post-stimulus time histograms of one cell in the superior colliculus of the cat in response to the movement of an 8° light spot (6 cd/m² illumination) in the vertical and horizontal directions through its receptive field (Fig. 14*AC*), the contrast between background and the moving stimuli being maximal (movement of a light spot in complete darkness). Figure 14*BD*, on the other hand, demonstrates responses to the same

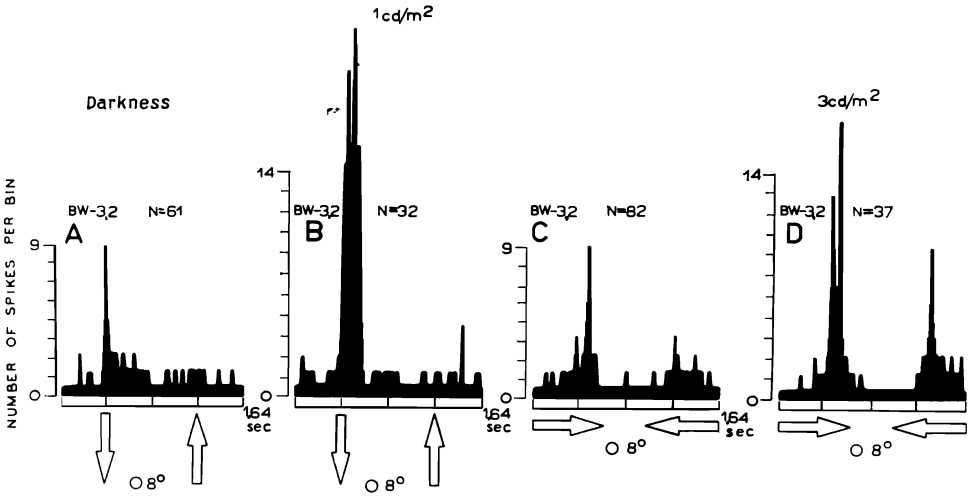

Fig. 14. The effect of background illumination on the responses of a cell in colliculus superior. *A* and *C*: PSTH of responses to vertical and horizontal movements of an 8° light spot across the receptive field, in darkness. *B* and *D*: PSTH of responses of the same neuron to the moving stimuli after increasing the background illumination to 1 cd/m² (*B*) and 3 cd/m² (*D*). Light spot illumination, 6 cd/m²; speed of the movement, 90°/sec.

moving spot with a background illumination of 1 cd/m² and 3 cd/m² respectively. As can be clearly seen (Fig. 14), the cell which has a weak response in complete darkness (see the number of repetitions), reveals a great intensity of response when the background is slightly illuminated. In further experiments we tried to determine the optimal degree of background illumination with which the most prominent response could be evoked by moving stimuli. In Fig. 15 the post-stimulus time histograms of six cells were presented. The first column represents responses evoked in complete darkness, second and third columns represent responses to the same stimuli with a background illumination of 1 cd/m² and 3 cd/m², respectively. The optimal degree of background illumination is 1 cd/m², a more intense illumination depresses the response.

In further experiments we investigated the effects of background illumination on the direction-sensitive characteristics of the cells in the midbrain. Nearly 40% of the investigated neurons were influenced by background illumination in a very definite way. For example, the neuron which responds specifically (with a direction sensitive reaction) to movement of a light spot in its receptive field, changes its response to a less specific one, i.e., it responds non-preferentially when the background is illuminated with 1 cd/m² (Fig. 16A–D). In Fig. 17 post-stimulus time histogram of four neurons are presented, which reveal the same

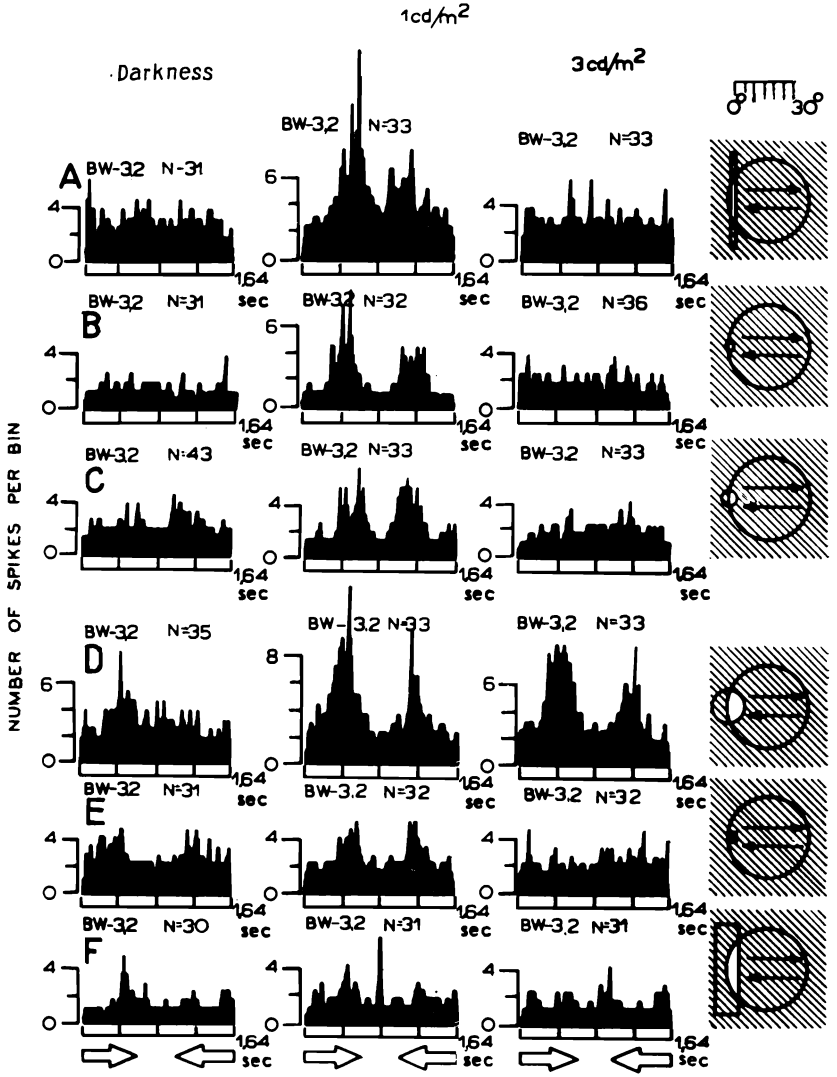

Fig. 15. Illustration of optimal background illumination for the organization of the responses of cells in colliculus superior to a moving stimulus. PSTH of responses of six different neurons (*A–F*). Left column shows the responses in darkness; middle and right columns, the responses during background illumination of 1 cd/m² and 3 cd/m², respectively.

type of influence of the background illumination. In the first column (*A–D*) PST histograms of responses of four neurons to the moving stimuli in full darkness are presented. The second column represents responses of the same cells to the same stimuli with a 1 cd/m² back-

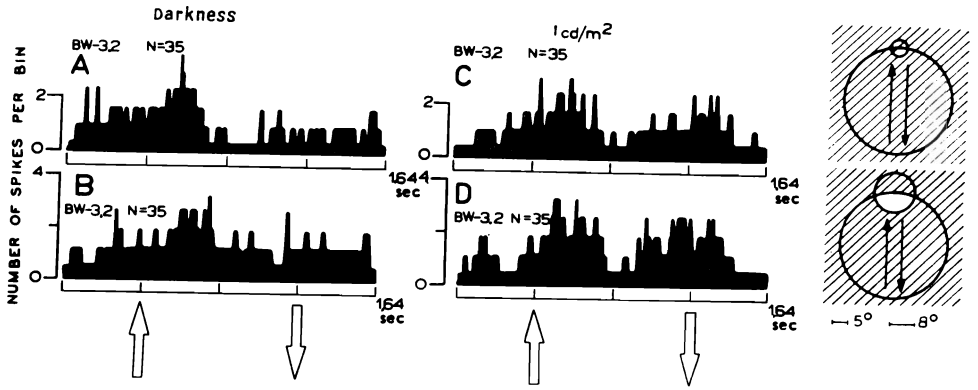

Fig. 16. Effect of the background illumination on the direction-sensitive response of a neuron in the colliculus superior. *A* and *B*, PSTH of responses to two moving stimuli (5° and 8° light spots, respectively) in darkness. *C* and *D*, responses of the same cell when background illumination was increased to 1 cd/m². Note the lack of directional sensitivity under background illumination of 1 cd/m².

ground illumination of the fields. The influence of background illumination is obvious. The responses become less specific. Other types of influence of background illumination were also observed and will be described in a subsequent publication.

Thus, after many unsuccessful experiments, it became possible to find a factor which could influence the mechanism subserving the specific function of certain neurons.

What kind of changes could such diffuse illumination of the background induce? One point is clear, that whereas the moving stimuli excite only the receptors of a restricted part of the retina (the receptive field) having most direct connections with the cell investigated, the diffuse background illumination excites the entire retina including its peripheral parts. It is quite possible that peripheral retina also has connections with the cell being studied, but rather indirect or through more numerous synapses. Thus, weak illumination of those parts of the retina also induces a weak subthreshold influence on the neuron studied. Such a subthreshold synaptic bombardment is not sufficient to elicit spike activity in the cell, but it could be adequate to produce subthreshold changes in the resting membrane polarization. We have no direct data as to whether these changes might be depolarizing or hyperpolarizing. Probably the former is more probable. The evoked small, displacement of the resting membrane potential seems to be sufficient to change the cell response to stimulation of its receptive field. It is probable that the level of membrane potential from which the cell starts its evoked action has determining properties not only in relation to the intensity

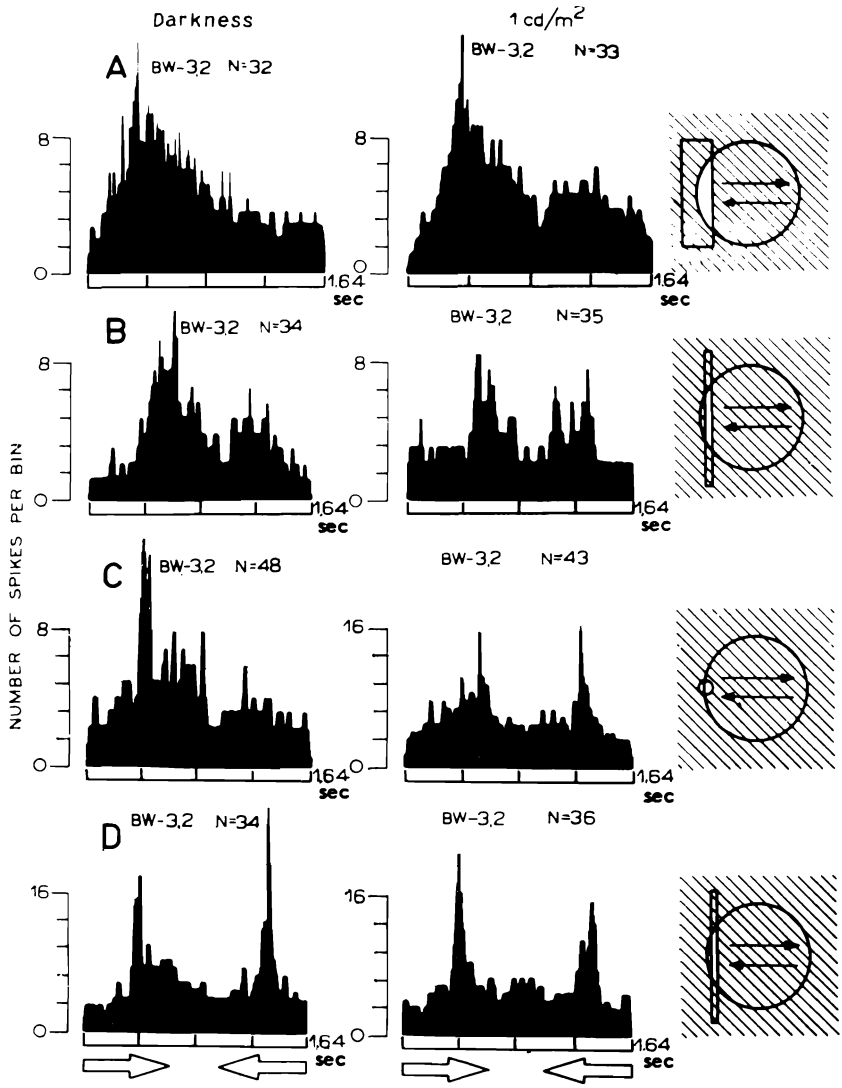

Fig. 17. Effect of the background illumination on the direction sensitive response in a few different cells (*A–D*) in colliculus superior. Explanations as in Fig. 16.

of discharge, but even determines qualitative changes, in the form of interval distribution of neuronal discharges.

Thus, on the basis of the above described data, one can draw some conclusions. First, the advanced averaging methods in physiology are necessary to observe all forms of information carried by the nerve cells. For example, the kind of information presented by the neurons of Fig. 2 would be impossible to observe without the use of averaging

methods. Second, the detailed exploration of the visual receptive fields of midbrain neurons reveals that the classification of visually-driven cells as found in the early works of Hartline (3), Kuffler (8), and Hubel and Wiesel (7) was not adequate to describe all types of responses, especially when latency distribution is measured. On the basis of the above data one can conclude that there exists a granular organization in some receptive fields, which must be more adequate in the perception of patterned processes. We also suggest that, for the qualitative organization of a cell response, subthreshold changes of the level of membrane potential are important.

The analysis of the data presented in this paper allows us to draw one more conclusion, i.e., that the specific response of neurons is not static nor permanent, but is related, to a great extent, to the conditions in which the cell exists. As far as these conditions are varable and change with different factors, the specific response of the cell also will change as a function of these variables.

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