ACTA NEUROBIOL. EXP. 1973, 33: 563-573

THE ORGANIZATION OF VISUAL RECEPTIVE FIELDS OF NEURONS IN THE CAT COLLICULUS SUPERIOR

Bella HARUTIUNIAN-KOZAK, Krystyna DEC, and Andrzej WRÓBEL

Department of Neurophysiology, Nencki Institute of Experimental Biology
Warszawa, Poland

Abstract. The receptive field organization of neurons in the superior colliculus of the cat was investigated. Extracellular recordings from single units were made during the stimulation of their receptive fields by flashing light-spots and diffuse light illumination. According to the differences in their organizations receptive fields were classified as "homogeneous", if the response pattern to flashing spot was the same in every point of the receptive field; and "heterogeneous", if the pattern of response of the cell changed irregularly as a function of a change in the location of the flashing spot. Receptive fields were also classified according to the latency distribution throughout the receptive field. The latency of the "on" response evoked by a flashing light-spot was measured. Two types of receptive fields were observed: homolatent, if there were no significant differences in the latencies between neighboring points in the receptive field; and heterolatent, if the latencies of responses were irregularly distributed and significant differences in latencies between neighboring points existed. It is concluded that the receptive fields in the cat's colliculus superior have granular structure.

INTRODUCTION

The concept of visual receptive field was first formulized by Hartline (1), who defined it as a region of the retina whose illumination elicits a response in a certain cell. Response patterns of ganglion cells evoked by retinal stimulation by light were characterized as "on", when the cell responds to the onset of light; as an "off"-response, when evoked by cessation of light; and "on-off" when the cell responds to both. Using stationary flashing light-spots, the detailed structure of receptive fields of neurons in different levels of the visual pathway has been explored. It is established now that the ganglion cells of the retina and that of the lateral geniculate body have concentric receptive fields. This means that

the central part of the receptive field, when stimulated, evoked an "on" or "off" response in the cell and that the circular surround evoked a response opposite to that of the center (5, 9).

The receptive field organization differs at each level of the central nervous system. At higher levels the organization of receptive fields becomes more complicated. The neurons of visual cortex, for example, possess simple, complex and hyper-complex types of receptive fields according to the classification of Hubel and Wiesel (6, 7).

Receptive fields of midbrain neurons have a rather homogeneous structure in comparison with the receptive fields of retinal ganglion cells (2, 11). A spot of light flashing in such a receptive field evoked more or less the same pattern of response, regardless of its localization. Generally it was a phasic "on–off" response.

We think that additional information is needed to describe fully the visual receptive fields in the midbrain. Measurements of latencies of neuronal responses at successive positions of a flashing light spot along a path through the receptive field and investigation of patterns of responses from different parts of the receptive field are necessary.

In this study some new properties of visual receptive fields will be described. The response patterns to visual stimuli of neurons in colliculus superior were investigated, and measurements of latencies were done. The evidence obtained in this way indicated that, the majority of receptive fields were not homogeneous, but have a mozaically organized heterogeneous structure.

METHODS

Fifty six adult cats were used. Under ether anesthesia a pretrigeminal midpotine transection was performed. Experiments began 2 hr later in order to allow time for the ether anesthesia to subside. The animals were immobilized by Flaxedil. To keep the eyes in a fixed position, high doses of Flaxedil were used (60 mg/hr, given intravenously). Completely paralyzed animals were artificially ventilated, using a Palmer constant-volume pump; the stroke volume was 20 ml and the respiratory rate, 18–19/min. The pupils were fully dilated with 1% atropine sulfate, and the nictitating membrane was fully retracted by instilling 10% neosynephrine (phenylephrine hydrochloride). Contact lenses of 0 diopters were used to prevent the corneal surfaces from drying and becoming cloudy. A clinical ophthalmoscope was used for viewing the retina and checking the transparency of the cornea.

In each experiment the coordinates of the blind spot were mapped with a narrow-beam reversible ophthalmoscope (the beam width was 1°),

and then the center point of area centralis was calculated (12). Thus all the receptive fields measured could be mapped in relation to the area centralis.

For the measurement of visual receptive fields a perimeter-like device with white semi-concave screen was used. The screen subtended 60° of visual angle, and the animals' eyes were at a distance of 70 cm from the perimeter screen. The arrangement of the perimeter enables the screen to be placed anywhere in the visual field at a constant distance from the cat's eyes, and thus permits an exploration of the whole retina.

As visual stimuli, diffuse light flashes and circular light spots were used (1.5°, 2.25° and 5° in diameter). They were projected on the screen by a slide projector. The parameters of flashing and spot movements were controlled by a Grass stimulator, using a servo-mechanism.

In each experiment the intensity of background illumination and that of the light-spot was measured using a SEI photometer. It ranged between 0.2 cd/m² for background illumination and 4–6 cd/m² for light-spots. The intensity of illumination by diffuse light flashes was 8 cd/m². Generally experiments were done in scotopic light conditions.

Single unit activity was recorded extracellularly. Tungsten wire electrodes (0.1 mm in diameter) were electropolished in a saturated solution of $NaNO_2$ using 7–9 v a–c (4). The tip diameter of the electrodes was from 1.5 to 3 μ; the resistance after covering by vinyl varnish was 30–50 MΩ. The microelectrode was connected to a high-input impedance cathode follower and then to an amplifier with high-pass filter (Grass P-6). A Schmitt-trigger circuit detected the action potentials producing standard pulses. These pulses were fed into an ANOPS-1 digital analyzer (8), which was used to compute histograms of average responses. Each histogram was a sum of unit responses to 20–30 repetitions of stimuli, distributed in 512 analyzer bins.

After experiments electrolytic lesions were made by passing 0.5 ma d–c for 30 sec, the brain electrode being positive. After perfusion with physiological solution and 10% formalin solution, 30 μ-thick histological sections of the brain were made and stained by the Nissl method. The electrode tracks in each experiment were identified.

RESULTS

Receptive fields were mapped for 78 single units. The data presented in this paper were gathered on the basis of responses from neurons observed for periods of 2 to 4 hr. This time was necessary for adequate analysis of response patterns of single units when different types of testing stimuli were used.

After an identification of the cell as visually sensitive (using figures moved by hand) and after determination of its spike shape as a somato-dendritic response, detailed exploration of the entire receptive field of the neuron was done.

First, a stimulus consisting of a diffuse illumination of the retina by 0.8/sec flashes was applied. A minority of cells studied had tonic responses lasting for the duration of either light or dark periods of the stimulus cycle. A majority of neurons observed phasic "on–off" responses to the diffuse flashing light, i.e., a burst of spikes at the onset and cessation of light.

After this procedure, responses to a small spot of light, generally 5°

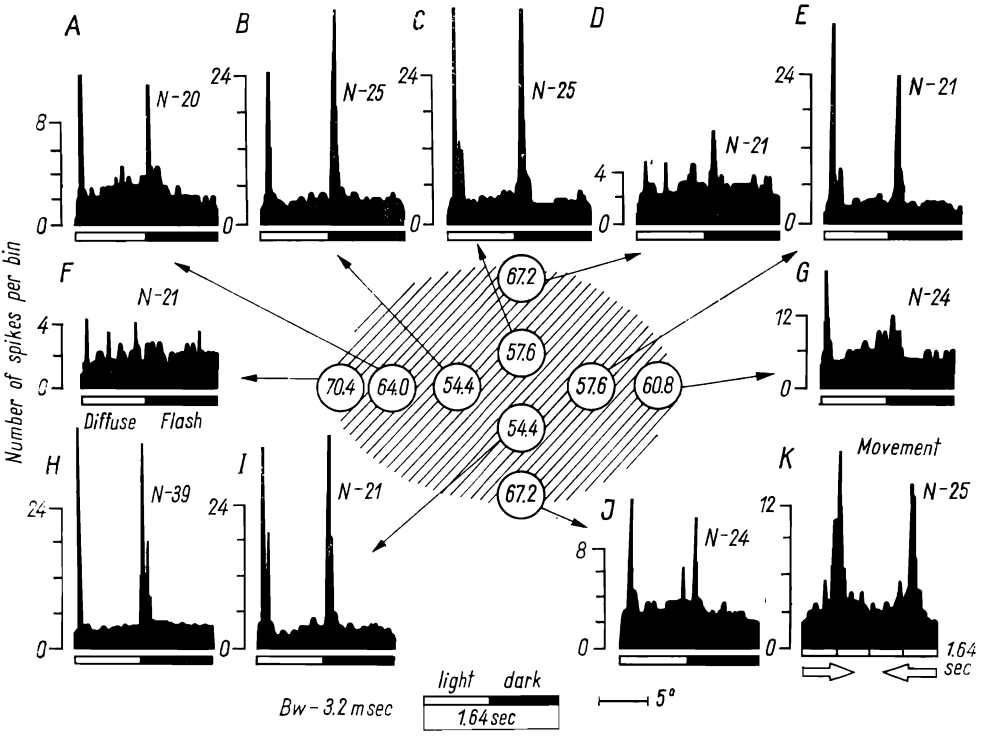

Fig. 1. Heterogenous receptive field of a neuron in the superior colliculus. *A–G*, *I* and *J*: Post stimulus-time (PST) histograms of responses to a spot 5° in diameter, flashing in different parts of the receptive field. *H* and *K*: PSTH of responses to diffuse light flash and moving spot, respectively. Circles show the location of light-spot. Arrows point to corresponding response patterns. The numbers in the circles show the latency of the "on" response in msec. In all figures the rate of flashing light was 0,8/sec and illumination of light-spot 4 cd/m². N, number of repetitions; Bw, bin width.

in diameter, flashing at the same rate (0.8/sec) were tested. The light spot was then placed in different parts of the receptive field, and response patterns of the cell were studied using the averaged post-stimulus-time histogram method (PSTH).

In the present experiments we were interested not only in the general pattern of response, but also in how they were altered as a function of spot localization. Thus we paid special attention to the proportions of "on" and "off" components of the general response. Then it became clear, that most of the visual receptive fields described by us as "homogeneous" (2) really were not so.

Fifty two per cent of the receptive fields had a more complicated structure. The proportions of "on" and "off" components changed in these receptive fields when the localization of the light-spot was changed. We called these receptive fields "heterogeneous". For example, the receptive field shown in Fig. 1 could be interpreted as homogeneous, but this is only a first impression. When analysed in more detail, certain differences in response patterns of the cell to the stimulation of different points of its receptive field could be found. Although sometimes minute, the differences clearly existed. Comparing the histograms *B* and *E* of Fig. 1, one can see in both histograms that there were "on–off" responses; but in *B* the "off" component prevailed; and in *E* the "on" component dominated. Actually, there were no two histograms of responses of the cell represented in Fig 1 which were identical.

Nearly 43% of receptive fields of neurons in the colliculus superior of the cat had a purely "homogeneous" structure. In these receptive fields the proportions of "on" and "off" components were not changed by changing the localization of the flashing light-spot (Fig. 2).

A small percentage (5%) of receptive fields had a narrow surrounding strip with a response pattern opposite to that of the center. One such neuron, with a more or less concentrically organized structure of the receptive field, is presented in Fig. 3. The histograms show a post-stimulus-time analysis of the frequency of responses of the cell to moving stimuli. When the light rectangle was less than 2°x3°, the cell responded vigorously to its movement (Fig. 3*A*). In this situation the stimuli excited the center of the receptive field, and surround inhibition was not detectable. When the size of the stimulus was increased (up to 20°), inhibition of response occurred when the spot moved across the receptive field (Fig. 3*BC*), and exite the inhibitory surrounding.

The next step in the detailed examination of receptive field organization of neurons in the superior colliculus was the investigation of latencies of responses.

The highly complicated nature of the receptive field organization

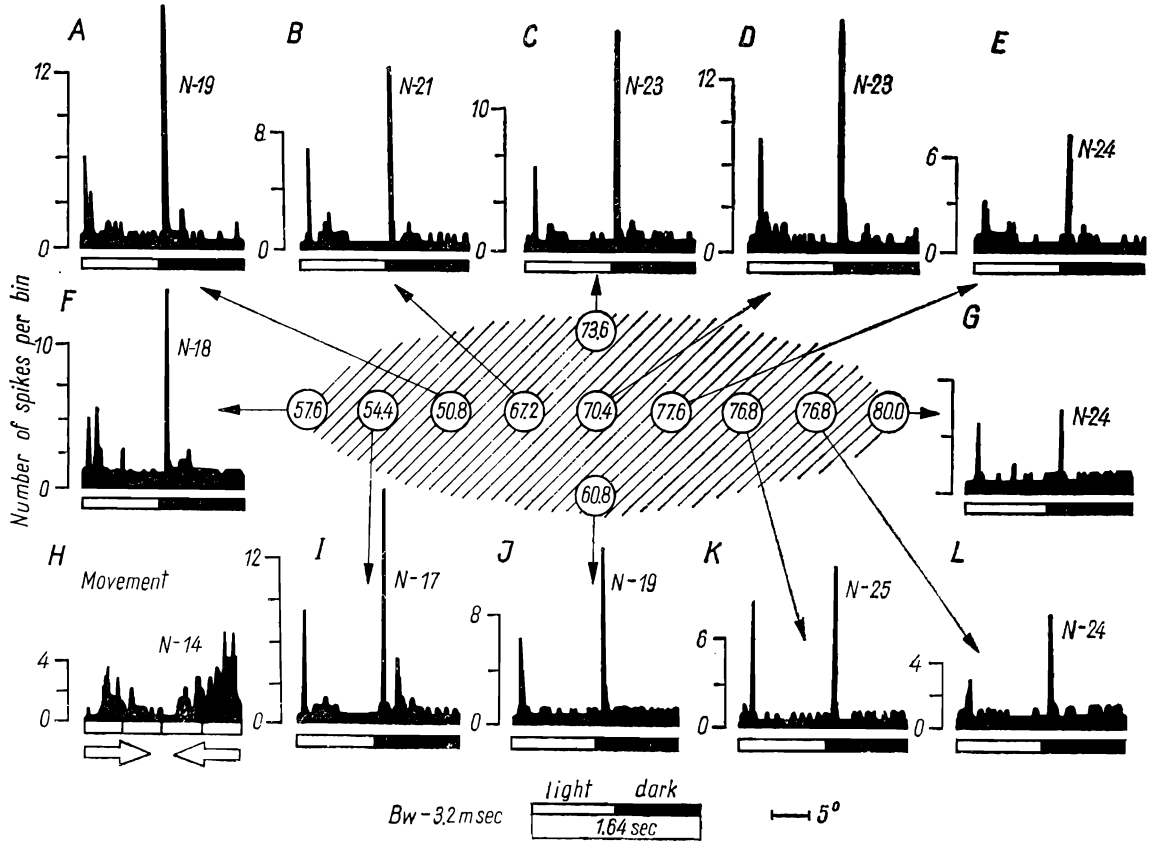

Fig. 2. Homogeneous receptive field. There were no significant differences between the "on" and "off" components of response of the cell to changing of the location of the flashing spot.
Explanations as in Fig. 1.

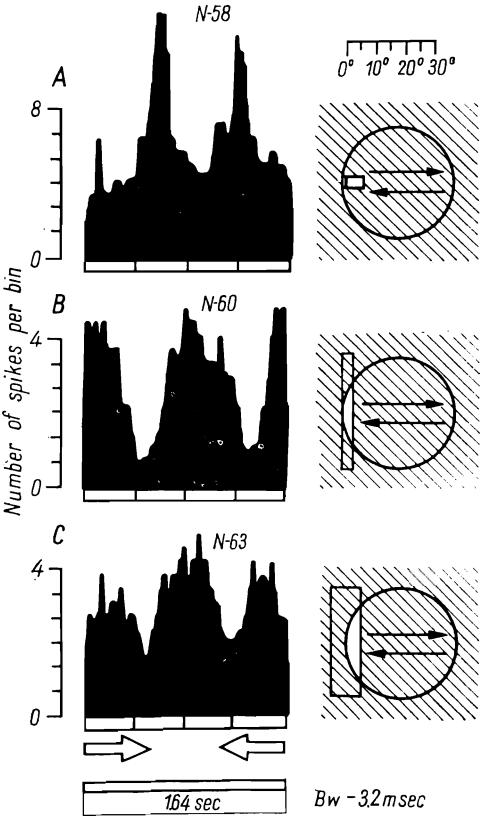

Fig. 3. Responses of the neuron to moving stimuli when the receptive field had an inhibitory surround. *A*: PST histogram of responses to horizontal movement of a square (5° × 6°) through the central part of the receptive field. *B*: PST histogram of responses to movement of a 2° × 40° strip of light through the entire receptive field. Inhibition of the responses occurs. *C*: PST histogram of responses to the movement of light square 10° × 38°. Inhibition of the responses is apparent.

became more obvious when latencies of responses to the flashing spot were measured. There were three types of latency distribution in the receptive fields.

The *first type* was characterized by minimal differences in latencies

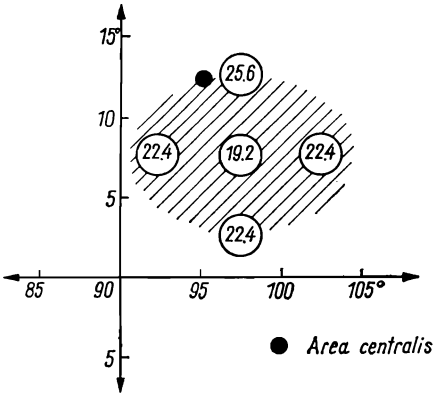

Fig. 4. Latency distribution in a homolatent receptive field. Circles represent the location of the flashing light-spot. Numbers in circles show the latency of the "on" response (in msec).

of responses evoked from the central and peripheral parts of receptive fields respectively. Figure 4, represent such a receptive field. There were almost no differences in the latencies of responses to the light-spot flashing in different parts of the receptive field.

The *second type* of receptive fields have the well-known differences in the latency of responses elicited from the central and peripheral parts of the receptive field. Responses evoked by the excitation of the central part, as a rule, have shorter latencies in comparison with the peripherally evoked responses. One example of such receptive field is shown in Fig. 5.

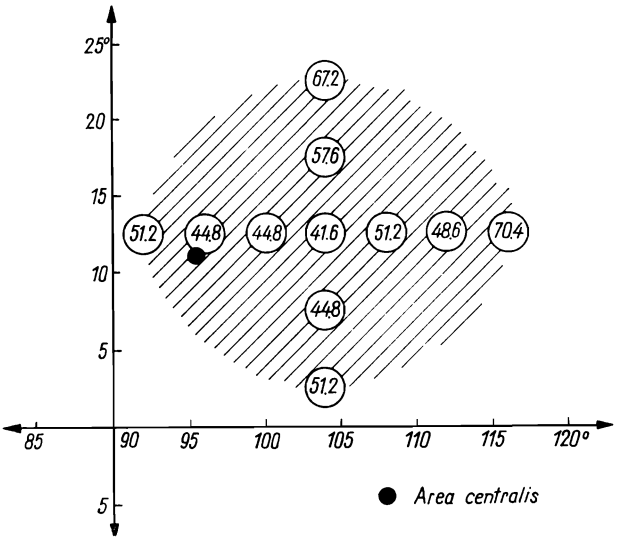

Fig. 5. A receptive field with regular distribution of latencies. Central part of the field has shorter latencies. Explanations as in Fig. 4.

We referred to the *two* types of receptive fields described above as homolatent, in contrast to the *heterolatent* receptive fields where considerable, and also irregular differences existed in the latency distribution within the receptive field. An example of such a latency distribution is presented in Fig. 6. The spot flashing in the very center of the receptive field elicited a response with longer latency than the spot flashing in the peripheral parts (compare 70.4 msec in the center with 57.6 msec in the periphery). There existed an irregular distribution of latencies over the entire receptive field presented in Fig. 6. Sometimes the differences in latencies between nearby points reached values of 20 msec. Probably this complicated irregular distribution of latencies

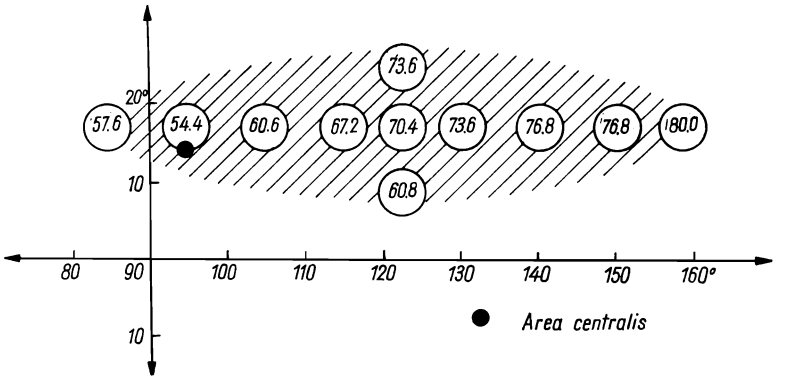

Fig. 6. A heterolatent receptive field. Distribution of latencies is irregular. The central part has a longer latencies. There were significant differences in latencies between neighboring points. Explanations as in Fig. 4.

throughout the receptive field has an important meaning in the analysis of visual information in the midbrain.

We tried to find a correlation between the pattern of responses and the latency distribution measured for the same receptive field. We were unable to find any correlation between them. The homogeneous receptive fields had either a heterolatent or homolatent organization. Attempts to find some correlation between the responses to moving stimuli and latency distribution in the receptive field were also made. Initially we expected that the cells with more specific responses, i.e. direction sensitive, should have a more complicated heterogeneous and heterolatent structure of their receptive fields. But the experimental data did not bear out this expectation. The direction-sensitive neurons could possess homogeneous, homolatent receptive fields as well as heterolatent and heterogeneous receptive fields. The same was true for direction-nonsensitive neurons.

DISCUSSION

It is well-known from anatomical and physiological data that visual information, before reaching the cortical level, is received by neurons of the primary visual subcortical structures: lateral geniculate body, pretectum, superior colliculi and accessory optic nuclei. Recent data of Sprague, Berlucchi and Di Berardino (10) have emphasized the role of midbrain centers in the performance of visual discrimination tasks. Probably the midbrain visual centers of the cat are engaged, in the analyses of visual information concerned to the patterned stimuli. We consider the detailed structure of receptive fields in midbrain centers as the basic

problem to be investigated in the way of exploration of the mechanisms uderlying these analytical processes in the midbrain.

The comparison of our data with the well-known facts on the structure of the lateral geniculate and ganglion cell receptive fields enable us to attempt some generalizations. First, there are clear-cut differences in the organization of receptive fields at the subcortical level. For example, the geniculate neurons have circular, concentric types of receptive fields. The organization of these fields is characterized by antagonistic center-surround portions, so they are classified as "off" center and "on" center, respectively. The sizes of these receptive fields are rather small, on the average 10° in diameter. On the contrary, in the majority of cases the midbrain visual receptive fields are not circular but are rather larger (30–40° in average) and irregular in shape, and a small percentage of them have antagonistic surrounds.

Our data have added some information about the structure of the midbrain visual receptive fields. By investigating systematically the entire receptive field we found a heterogeneity in their substructure. It was revealed that the latency of responses from each point of the field could differ and that these differences could be up to 20 msec for neighboring points. These findings suggest that there exist a kind of granular organization within the visual receptive field, which is probably adequate for detecting patterned stimuli.

On the basis of our results it is difficult to determine what the function of the superior colliculus is. However, one can assume that such complicated structure of receptive fields serves for more than the well known role of superior colliculus in the organization of oculomotor reactions. Obviously, such an intricate mozaic structure of receptive fields is rather suitable for the perception of contrast patterns. As a consequence, one can suggest that there is some distribution of functional analysis of visual information on the level of subcortex, as we mentioned in the previous paper (3). The information about movements and pattern vision would be analysed partly in the midbrain centers. Then elaborated to a certain degree, it reaches the visual cortex. Such a multilevel system would be reliable in a complete analysis of visual information.

This investigation was supported by Project 09.4.1 of the Polish Academy of Sciences and by Foreign Research Agreement 05.275.2 of the U.S. Department of Health, Education and Welfare under PL 480.

REFERENCES

1. HARTLINE, H. K. 1940. The receptive fields of optic nerve fibres. Amer. J. Physiol. 130: 690–699.
2. HARUTIUNIAN-KOZAK, B., KOZAK, W. and DEC, K. 1970. Visually evoked potentials and single unit activity in the superior colliculus of the cat. Acta Neurobiol. Exp. 30: 211–234.
3. HARUTIUNIAN-KOZAK, B. 1972. The role of tecto-pretectal region in the analysis of visual information (in Polish). Acta Physiol. Pol. 24: 1–17.
4. HUBEL, D. H. 1957. Tungsten microelectrode for recording from single units. Science 125: 549–550.
5. HUBEL, D. H. and WIESEL, T. N. 1961. Integrative action in the cat's lateral geniculate body. J. Physiol. 155: 385–398.
6. HUBEL, D. H. and WIESEL, T. N. 1962. Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. J. Physiol. 160: 106–154.
7. HUBEL, D. and WIESEL, T. 1965. Receptive fields and functional architecture in two non-striate visual areas (18 and 19) of the cat. J. Neurophysiol. 28: 229–289.
8. JANKOWSKI, T. 1967. ANOPS, organization and construction (in Polish). Przegl. Telekom. 5: 141.
9. KUFFLER, S. W. 1953. Discharge patterns and functional organization of mammalian retina. J. Neurophysiol. 16: 37–68.
10. SPRAGUE, J. M., BERLUCCHI, G. and Di BERARDINO, A. 1970. The superior colliculus and pretectum in visually guided behavior and visual discrimination in the cat. Brain, Behav. Evol. 3: 285–294.
11. SPRAGUE, J. M., MARCHIAFAVA, P. L. and RIZZOLATTI, G. 1968. Unit responses to visual stimuli in the superior colliculus of the unanesthetized mid-pontine cat.
12. VAKKUR, G. J., BISHOP, P. O. and KOZAK, W. 1963. Visual optics in the cat, including posterior nodal distance and retinal landmarks. Vision Res. mid-pontined cat. Arch. Ital. Biol. 106: 169–193.
3: 289–314.

Received 13 December 1972

Bella HARUTIUNIAN-KOZAK, Krystyna DEC and Andrzej WRÓBEL, Department of Neurophysiology, Nencki Institute of Experimental Biology, Pasteura 3, 00-973 Warszawa, Poland.