ACTA NEUROBIOLOGIAE EXPERIMENTALIS

Acta Neurobiol. Exp. 1994, 54: 321-333

Spatial summation processes in visually driven neurones of cat's pretectal region

Gayane G. Grigorian, Bella A. Harutiunian-Kozak, Anahit L. Kazarian, Armenui A. Hekimian, Tigran M. Markarian and **Julius A. Kozak**

Laboratory of Physiology of Sensory Systems, Institute of Applied Problems of Physics, National Academy of Sciences of Armenia, 25 Nersesian St., 375014 Erevan, Armenia

Abstract. The spatial summation processes of single neurones of cat's pretectal region were investigated with moving and stationary visual stimuli. The results indicate that the majority of the investigated neurones changed their responses essentially at the gradual increase of size of the applied stimuli (i.e. showed negative or positive summation). Particularly, direction non-sensitive neurones showed symmetrical changes of spatial summation curves in response to two opposite directions of movement. By contrast, in some direction sensitive neurones different characteristics of responses for the two opposite directions of movement were observed. Thus the number of discharges in the responses to the preferred direction could increase or decrease at the gradual increase of the moving stimulus size, while the responses to the null direction could remain stable or *vice versa*. The same was observed for the "ON" and "OFF" responses in the ON-OFF neurones. Thus, it appears that the pattern of responses of a given neurone to different directions of movement and to the "on" and "off" periods of stationary stimulation are shaped by independent mechanisms.

Key words: pretectal region, cat, visually driven neurones, receptive field, moving and stationary visual stimuli, summation processes

INTRODUCTION

Since the time of pioneer investigations of Magoun and Ranson (1935) on the functional significance of cat's pretectal region in the pupillary light reflex a considerable amount of data has been accumulated showing that the pretectal neurones are involved in central processing of visual information incoming to the nuclear complex directly from retina as well as from the visual cortex (Laties and Sprague 1966, Kanaseki and Sprague 1974, Kawamura et al. 1974, Schoppmann 1981). Further behavioral experiments established that the pretectal region participates to some extent in visually guided behaviour and learning (Thompson and Massopust 1960, Thompson and Rich 1961, Less and Rich 1963, Łukaszewska et al. 1967, Urbaitis and Meikle 1968, Sprague 1972, Sprague et al. 1973, Wintercorn 1975). Deficits of attentional control of the gaze shift are probably the main result of pretectal lesions (Fishman and Meikle 1965, Berlucchi et al. 1972, Sprague 1972, Wintercorn 1975, Pinchoff and Wintercorn 1979).

Researchers investigating properties of visually driven neurones in the pretectal area emphasised their sensitivity to moving visual stimuli and contrasts (Harutiunian-Kozak et al. 1968, 1970, 1974, Straschill and Hoffmann 1969, Sprague et al. 1973, Schoppmann 1985, Schweigart and Hoffmann 1992). However, our knowledge of the receptive field properties of pretectal neurones is far from being complete, with only fragmentary information on the structure of their receptive fields and spatial summation (Collewijn 1975, Hoffmann and Schoppmann 1981, Hoffmann and Distler 1989, Ibbotson and Mark 1994). Those properties are important for understanding the integrative functions of pretectal neurones.

In the previous report (Grigorian et al. 1993) we described some characteristics of summation processes in the receptive fields of visually driven pretectal neurones. In this study we present results of further investigations of the spatial organization of receptive fields of the neurones, and their mechanisms of spatial summation.

METHODS

Details of animal preparation and the recording techniques have been described in several earlier papers (e.g. Harutiunian-Kozak et al. 1970). The experiments were carried out on 40 adult cats. The tracheotomy, fixation of the animal in a stereotaxic frame and pretrigeminal brain stem transection were performed under ether anaesthesia (Żernicki 1968). Unilateral craniotomy was made and the part of the bone overlying the pretectal region was removed. After insertion of a recording electrode the craniotomy was filled with soft wax to prevent pulsations of the brain. The animals were immobilized with the i.m. injection of ditiline (diiodide dicholine ester of succinic acid, 7 mg/kg per hour) and artificially ventilated with a pulmonary pump at the rate of 19/min. The functional state of the animal was constantly monitored: EEG and ECG were recorded continuously, blood pressure was 90-100 mm Hg and the heating pad kept the temperature within the limits of 37.5^{o}-38.0^{o}.

Single unit activity was recorded with tungsten wire microelectrodes (Hubel 1957) covered with vinyl varnish except for the uninsulated tip of 2-5 μm size. Microelectrodes were inserted into the pretectal region according to its stereotaxic coordinates (Jasper and Ajmone-Marsan 1954, Avendano et al. 1980). Neuronal spikes amplified with conventional amplifiers and transformed into standard pulses with a Schmidt trigger were fed to an interspike interval analyser (Huxley and Pascoe 1963, Chung et al. 1974). Each action potential was displayed on the oscilloscope screen as light dot. The synchronization of the trapezoid wave generator (used for stimulation) with the cathode ray sweep made the light dots (each showing at the moment of occurrence of a spike) to appear on the oscilloscope screen in direct relation to the time of presentation of the visual stimuli. The cycle of stimulation was repeated 10 to 15 times per analysis. In each photograph all the spikes occurring during the analysis are registered. In such photographs the ordinates indicate the length of interspike interval, abscissae - the time of stimulation (first ON phase - 500 ms and

then OFF phase - 500 ms; correspondingly for moving stimuli - first 500 ms movement rightward and then 500 ms movement leftward). The spikes generated for each phase of stimulation were counted from the photographs (Fig. 1). To avoid errors in the counting procedure, when dense accumulation of dots was visible during repetitive stimulation, responses of the neurone were registered with a series of photographs, each documenting 3 or 5 sequences of stimulations. Afterwards, the partial results were summed up. However, in a few cases the dense superpositions of dots formed even after single sweeps of stimulation. These cases were discarded. The ANOPS digital analyser was used to compute peristimulus time histograms (PSTH) to outline qualitatively the pattern of discharge distribution during stimulation time. Neuronal spike responses to 15-30 repetitions of stimuli were averaged in time domain.

Visual stimuli were projected on a concave screen (90 cm in diameter) situated 1 m from the nodal points of the eyes and moved by a mechanical device which could shift the position of the screen both horizontally and vertically along the perimeter of the hemicircle of 1 m radius. This way the whole visual field was accessible for analysis. Bright spots of different diameters were used as one type of stimuli. Illumination of the spots was 8 lx against a 2 lx background. Another type, the dark stimuli were round shadows of 2 lx illumination against an 8 lx background. Thus, the stimulus *vs.* background contrast was kept constant throughout the experiment.

Receptive fields of the visually driven neurones and their positions in the visual field were determined on the perimeter screen. The lengths of the horizontal and vertical axes of each receptive field were determined with hand held visual stimuli, then the geometrical centre of the receptive field was defined and its position in the visual field drawn and recorded with an accuracy of $\pm 1^{\circ}$. The receptive fields were then analysed with automatically applied stationary and moving visual stimuli of sizes subtending from 1° to 19° of visual angle. The plots of neuronal responses were made according to the number of discharges against the stimulus size.

At the end of each experiment the recording site was coagulated with the electric current of 0.6 mA applied through the recording electrode for 30 s. The brain was then perfused with 10% formalin and postfixed for about two weeks. The site of the recording was checked on coronal sections cut at 40 μm on the freezing microtome and counterstained with the Nissl stain.

RESULTS

General characteristics of neuronal responses

The activity of 223 visually driven neurones in the pretectal region was investigated. According to

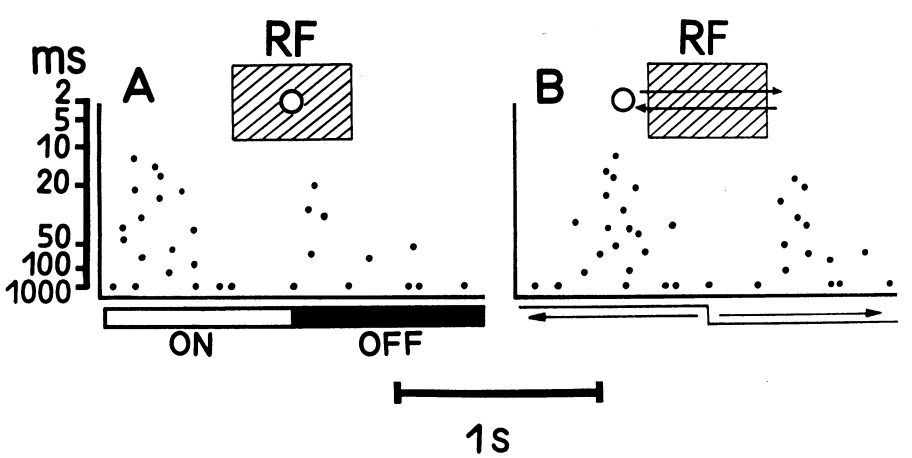

Fig. 1. Responses of a pretectal neurone recorded with the interspike interval analyser. A, distribution of spikes generated during three cycles of stimulation with flashing bright spot (5°) positioned in the centre of the receptive field. Light strip shows ON period, dark strip - OFF period of stimulation. B, distribution of spikes evoked by 5° spot moving along the horizontal axis of the receptive field. Arrows indicate the directions of motion. Three repetitions of stimulation were performed.

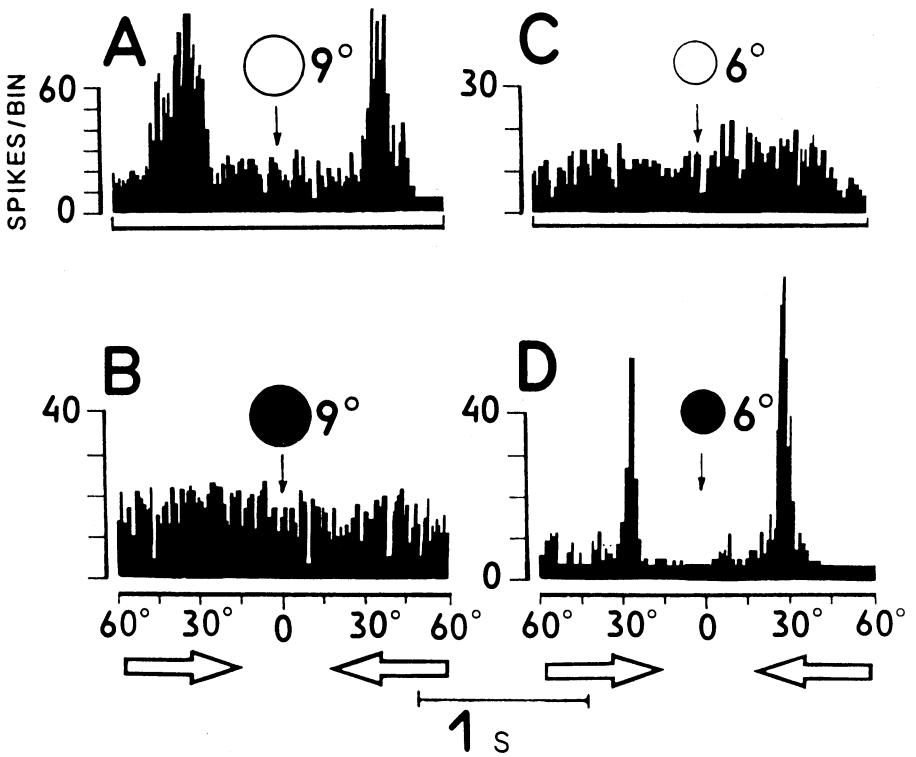

Fig. 2. Response characteristics of two pretectal neurones to the movements of bright and dark stimuli along the horizontal axis of their receptive fields. A, PSTH of neuronal responses to the movement of bright spot (9^{o}). B, PSTH of the same neurone to the movement of a dark spot (9^{o}). C, PSTH of responses of another pretectal neurone to the movement of a bright spot (6^{o}). D, PSTH of responses of the same neurone to the movement of a dark spot (6^{o}). The arrows indicate the directions of spot movement across the receptive field. Abscissae in each histogram indicate the time of stimulation. Small vertical arrows indicate the turning point of directions of motion. Ordinates indicate the number of spikes per bin in each histogram. Averaging achieved by 30 repetitions of stimuli. Explanations are the same for Fig. 3.

the histological verification the majority of neurones were recorded in the posterior pretectal nucleus and the nucleus of the optic tract. In some cases of recordings made very close to the surface of brainstem, on the border of pretectum and superior colliculus it was hard to decide from which structure the recording was made. These neurones were not included in the present study. No differences were noted between neurones of the investigated pretectal nuclei as concerning the properties of spatial summation processes, so in this study they are all presented as "pretectal" neurones.

The majority of neurones (76%) showed spontaneous activity of a moderate frequency (5-10 imp/s) in the absence of defined visual stimuli. Of the remaining cells 18% lacked it and 6% demonstrated relatively high frequency spontaneous spike discharges of about 20-30 imp/s. The well-defined responses to stationary stimulation of receptive fields were observed in 83% of neurones. The remaining 17% of neurones either did not respond to stationary stimuli at all, or exhibited weak responses which enabled us to estimate the site of their receptive fields.

All the examined neurones reacted well to stimuli moving across their receptive fields. The most striking feature of these neurones was their differential sensitivity to the light or dark stimuli. In Figure 2 the PSTHs of two neurones to moving light and dark spots are presented. Both neurones are direction non-sensitive as indicated by the fact that their responses to the opposite directions of motion are almost symmetrical. Figure 2A and B illustrates responses of a light-sensitive pretectal neurone to the movement of 9^{o} bright and dark spots. As it is apparent from the figure there are clear-cut responses to the movement of the bright spot (Fig. 2A) and the absence of any reaction to the movement of the dark spot (Fig. 2B). The neurone whose responses are presented on Fig. 2C and D responds well to the motion of 6^{o} dark spot (Fig. 2D) whereas the movement of the bright spot did not elicit any response (Fig. 2C). This is an exemple of a dark-sensitive neurone.

The majority of pretectal neurones responded preferentially to moving objects. These neurones were classified according to their responses to the directions of motion. Three groups of neurones

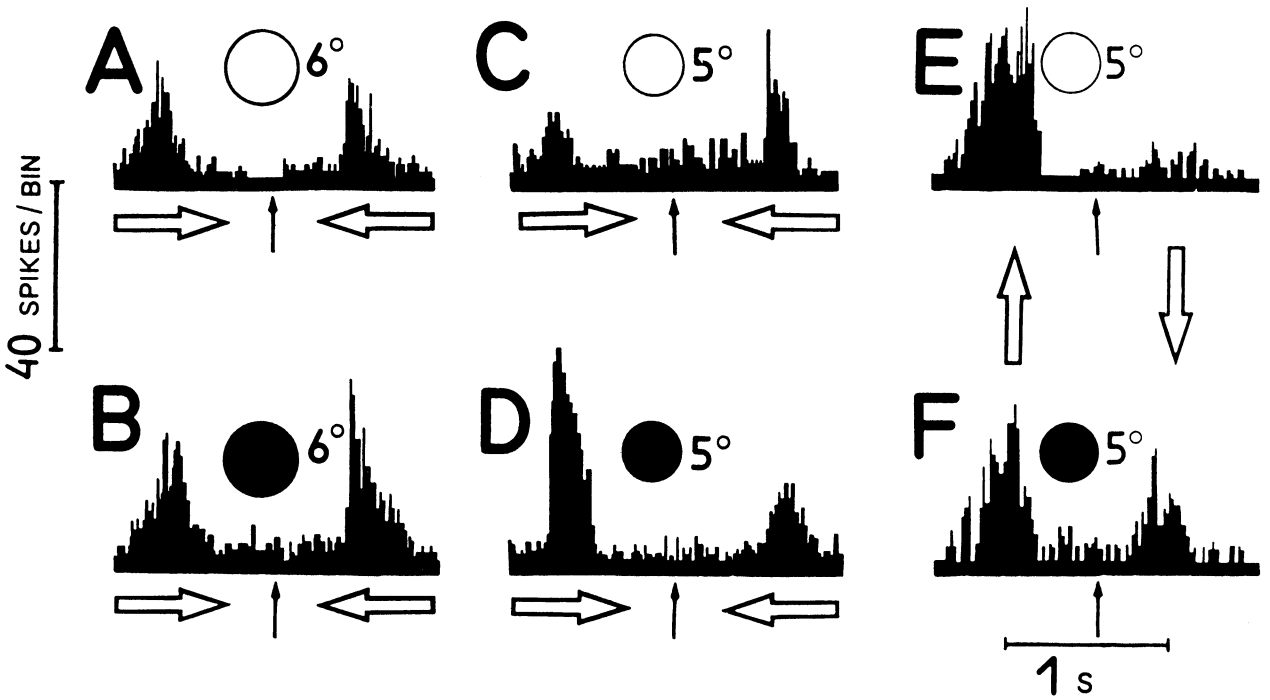

Fig. 3. Response patterns of three pretectal neurones to the opposite directions of movement of bright and dark spots. A and B, PSTH of responses of a direction non-sensitive neurone. C and D, PSTH of responses of direction-sensitive neurone. E and F, PSTH of responses of a direction-selective neurone.

were distinguished: group I - direction non-sensitive neurones, which responded with nearly equal numbers of discharges to the two opposite directions of movement irrespective of the polarity of contrast between the stimulus and background (Fig. 3A and B); group II - direction sensitive neurones, responding to the stimulus movement in a certain (preferred) direction with the optimal response and to the movement in the opposite (null) direction with minimal or no reactions, but changing their response patttern when the polarity of contrast of the stimulus was reversed (Fig. 3C and D); neurones of the group III were characterized as direction selective. They did not change their preferred direction when the polarity of contrast of the moving stimuli was reversed (Fig. 3E and F).

After defining the response characteristics of neurones to moving visual stimuli, a series of spots of increasing sizes moving across the horizontal axis of the receptive field or stationary in the centre of the field was applied. The number of discharges elicited by the stimulus was counted against the stimulus size, and the plot of the dependence defined the spatial summation properties of the neurone.

Spatial summation in the direction non-sensitive neurones

Our results showed that in about 11% (25 out of 223) of the direction non-sensitive neurones (group Ia) no essential change of responses was observed when the size of the moving stimulus changed. This suggests that the responses of these neurones are shaped by a spatial summation process. Figure 4A presents the response plot of one such neurone. As is seen from the figure the number of discharges (ordinate) has remained essentially unchanged when the moving stimulus size was increased from 3° (the first point on the abscissa) up to 18°. These neurones had generally small receptive field dimensions (between 1 and 4 deg. square) although two neurones of this type had large receptive fields.

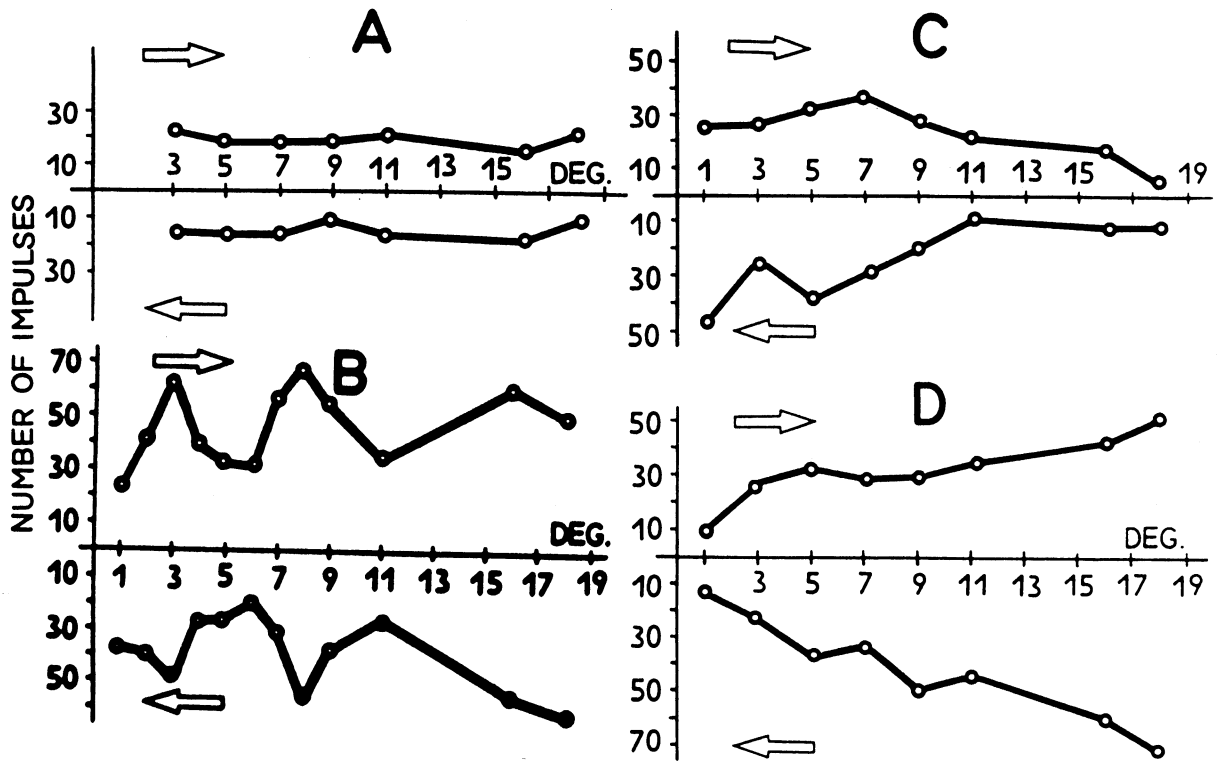

Fig. 4. Spatial summation plots of four direction non-sensitive neurones. A, response plots of a neurone which does not show summation of responses with increasing the stimulus size. B, spatial summation plot of a neurone with periodic and symmetrical response characteristics for each direction of motion. C, response plot of a neurone showing a negative spatial summation. D, response plots of a neurone revealing a positive summation. Moving bright spots are shown with open circles. Abscissae indicate the size of moving stimuli in degrees, ordinates indicate the number of discharges (the sum of all spikes in the response). Arrows show the directions of motion across the horizontal axis of the receptive field. Explanations are the same for Figures 4 through 9.

The next group (Ib) was formed by those direction non-sensitive neurones (23 units, about 10%), which reacted to the gradual increase of moving stimulus size with the clear decrease of response, i.e., they showed the negative spatial summation (Figure 4D). The configurations of the plots of neurones of this group suggest that their receptive fields are organized concentrically, the centre of the field being excitatory with the inhibitory surround. Thus, increasing the size of stimulus resulted in decreasing the number of discharges evoked from the centre.

The third group (Ic) encompassed those directionally non-sensitive neurones (65 units, about 29%) which showed positive spatial summation, i.e., gradual increase of the stimulus size resulted in corresponding enhancement of responses of the neurone. Figure 4D presents the spatial summation plot of a neurone of this group. As it is seen from the figure the 18^{o} stimulus evoked response four times stronger than the 1^{o} stimulus. Thus, in contrast to the previously described receptive fields the surround of this receptive field is not inhibitory in respect to the centre of the field.

The fourth group (Id) of the direction non-sensitive neurones was characterized by the waxing-waning course of the spatial summation (6 neurones, about 3%). Responses of such a neurone exhibiting three response maxima (to the 3^{o}, 8^{o} and 16^{o} light spots) are presented in the Fig. 4B. We think that receptive fields of such neurones are organized nonuniformly, having many excitatory and inhibitory zones around the centre of the receptive field. As it is also seen in the Fig. 4B the responses

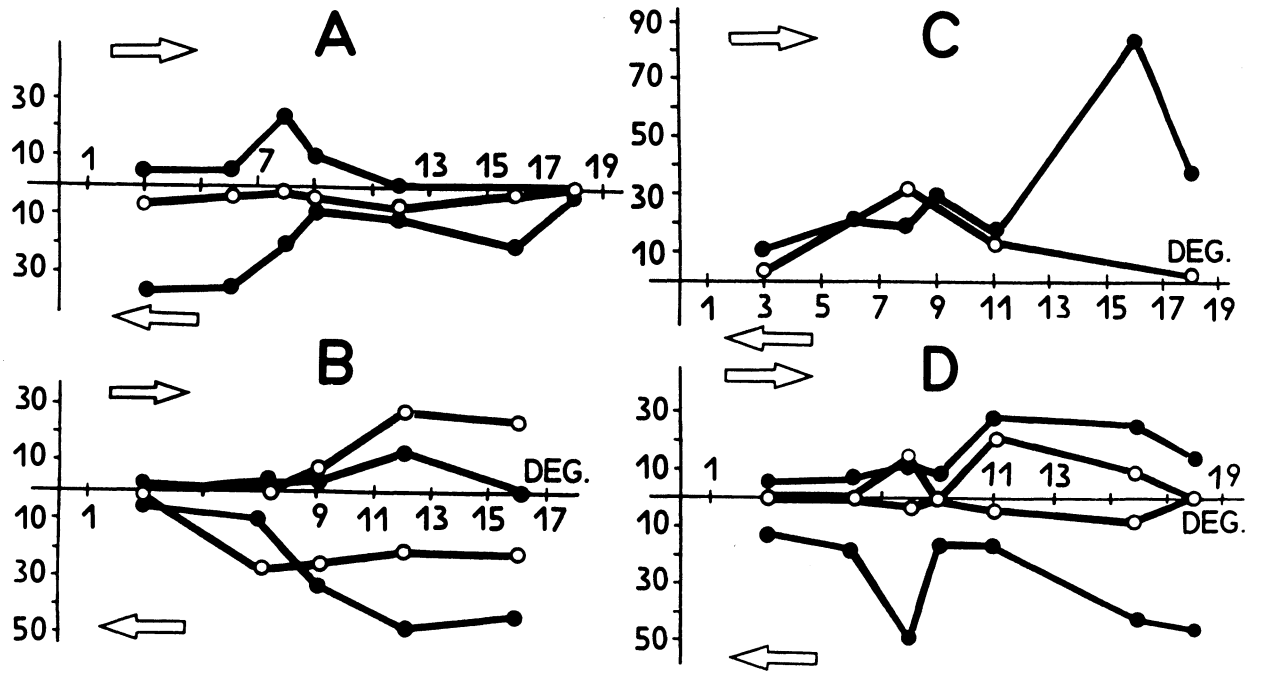

Fig. 5. Spatial summation in the direction-sensitive neurones. A, negative spatial summation curve of a direction-sensitive neurone. B, positive spatial summation curve of a direction-sensitive neurone. C, spatial summation curve of a direction-selective neurone. The bright spot movement shows a negative summation (open circles); the dark spot movement (filled circles) results in a positive summation. D, spatial summation curve of a neurone that displays a reversal of the preferred direction for a dark moving stimulus (filled circles) and a stable preferred direction for a bright moving stimulus (open circles).

of these neurones most of the time were almost symmetrical in respect to the two directions of movement. However, in a few neurones they differed considerably in respect to either direction of movement or polarity of contrast of the stimulus.

Spatial summation in the direction sensitive neurones

Of the whole population of investigated neurones about 32% (71 out of 223) were direction sensitive, i.e., they changed their preferred direction of movement when the polarity of contrast of the stimulus was changed. The direction sensitive neurones showed both simple forms of spatial summation (positive or negative) and the complex courses of summation. Figure 5A presents responses of a neurone showing negative summation. The neurone is direction selective and it did not change its generally preferred direction (right to left) after changing the polarity of stimulus contrast, though the response was significantly diminished. Nevertheless, during the gradual increase of stimulus size to 8° the neurone became direction non-sensitive (filled circles), and at the stimulus size of 9° the preferred direction (right to left) for dark spots was changed to the direction opposite to that for the smaller stimuli (left to right). Apart from small fluctuations the gradual increase of size of the moving stimulus resulted in gradual decrease of the number of spike discharges in the response (negative summation). Figure 5B presents responses of a neurone with characteristics opposite to those shown in Fig. 5A. In this neurone the increase of size of the moving stimulus resulted in the increase of its spike discharge frequency, i.e., in a positive spatial summation. These were were rather simple forms of summation, very similar to those found in the non-directional neurones.

Spatial summation in the direction selective neurones

Direction selective neurones (i.e., neurones that did not change the pattern of their responses when stimuli of the opposite contrast polarity were applied) constituted about 15% of the investigated population (33 out of 223). The neurone whose responses are presented in the Fig. 5C has somewhat different spatial summation characteristics compared to the characteristics of the direction sensitive neurones presented in the Fig. 5A and B. There is a positive spatial summation at the gradual increase of stimulus size when the dark spots are applied. By contrast, responses to the moving bright spots after some enhancement at the 7^{o}-9^{o} range decay to null with further increase of the stimulus size. Some of these neurones demonstrated even more complicated changes of response at the gradual increase of stimulus size. For example, the preferred direction of the neurone whose responses are illustrated in the Fig. 5D varied with stimulus size. As it is seen from the figure it is a dark sensitive neurone that reacted more intensely to the movement of dark spots (filled circles). The dark spot of 6^{o} elicited responses of the neurone when it moved from right to left, but at the stimulus size of 11^{o} the preferred direction was changed into left to right. Further increase of the size of moving dark spot to 16^{o} resulted in the preferred direction being restored to the right to left direction. The same neurone did not change its preferred direction when the bright spots (empty circles) were presented.

Figure 6A presents responses of a neurone showing negative summation in the preferred direction,

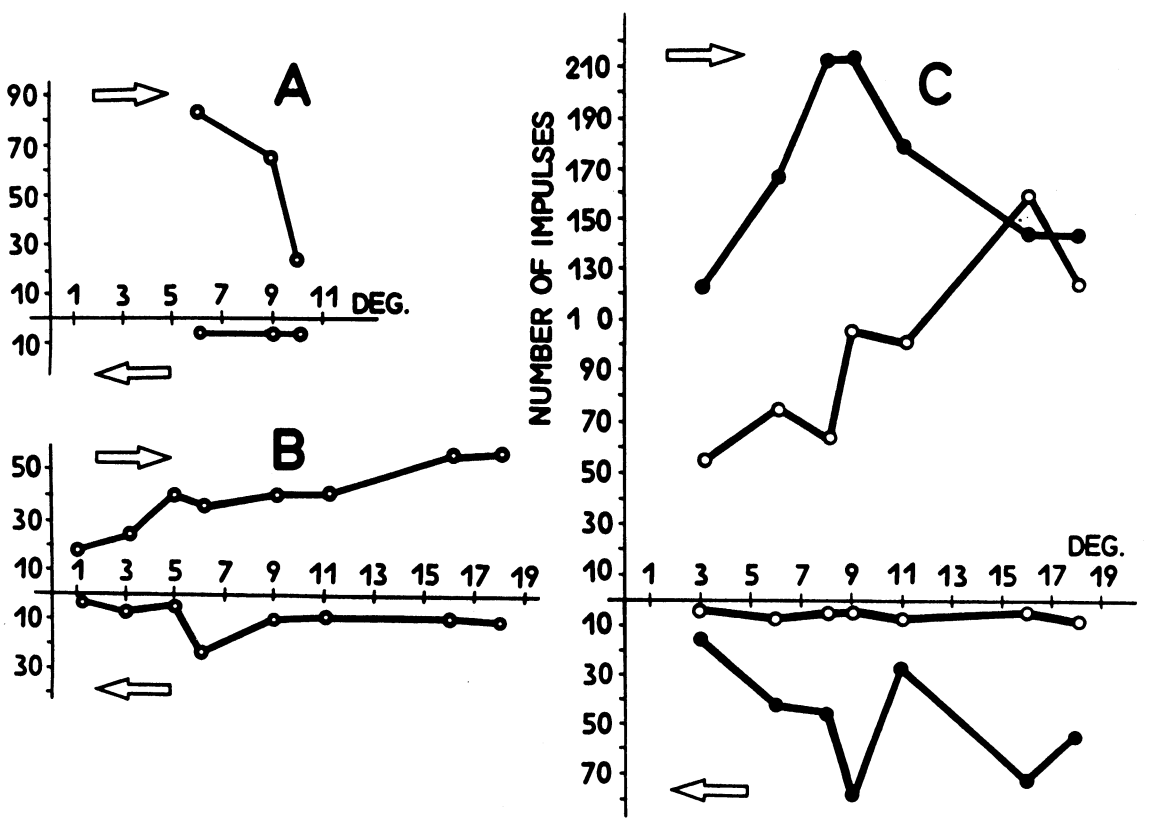

Fig. 6. Spatial summation in direction selective neurones. A, spatial summation curve of responses of a direction selective neurone that shows negative summation in the preferred direction, while in the null direction the summation of responses is absent. B, responses of another direction selective neurone showing positive spatial summation for preferred direction and stability of responses in the null direction. C, spatial summation plots for a direction selective neurone. The neurone was tested with bright (open circles) and dark (filled circles) moving stimuli. Response for the bright stimuli moving in null direction stays stable, whereas all other responses changed with changing sizes of the applied stimuli.

whereas the change of stimulus size did not result in any changes of the response for the opposite direction of movement (the null direction). The next neurone whose responses are presented in Fig. 6B showed positive spatial summation for preferred direction, whereas responses to the movement in the null direction stayed almost unchanged, except for a small fluctuation when the 6° stimulus was applied. Plots of spatial summation of another directionally selective neurone are presented in Fig. 6C. It is apparent that the responses to the preferred direction undergo dramatic changes when the size of the applied stimulus is increased for both light and dark stimuli, while responses to the bright stimuli moving in the null direction stay unchanged.

Spatial summation of the stationary visual stimuli

Of 185 neurones sensitive to stationary visual stimulation 102 neurones which exhibited clear-cut excitatory responses to the stationary stimuli were tested with flashing light spots of gradually increasing sizes (from 1° to 18°) centred at the centre of their receptive fields. The data were analysed by plotting the number of neuronal spike potentials (cordinate) against the sizes of applied stimuli (abscissa). For each neuron the responses to the ON and OFF periods of stimulation were considered and counted separately.

SPATIAL SUMMATION IN ON-OFF NEURONES

Neurones of this type constituted 39% of the population responsive to the stationary stimuli. They could be divided into three groups. Fourteen percent of the investigated neurones did not show any spatial summation when the stationary visual stimuli were applied, i.e., changing the size of the flashing light spot did not result in any significant changes in the ON or OFF responses of the neurone (Fig. 7A). Nearly 16% of the neurones showed positive summation, i.e., the intensity of their responses increased with the increase of the size of flashing bright spot. Figure 7B demonstrates the summation

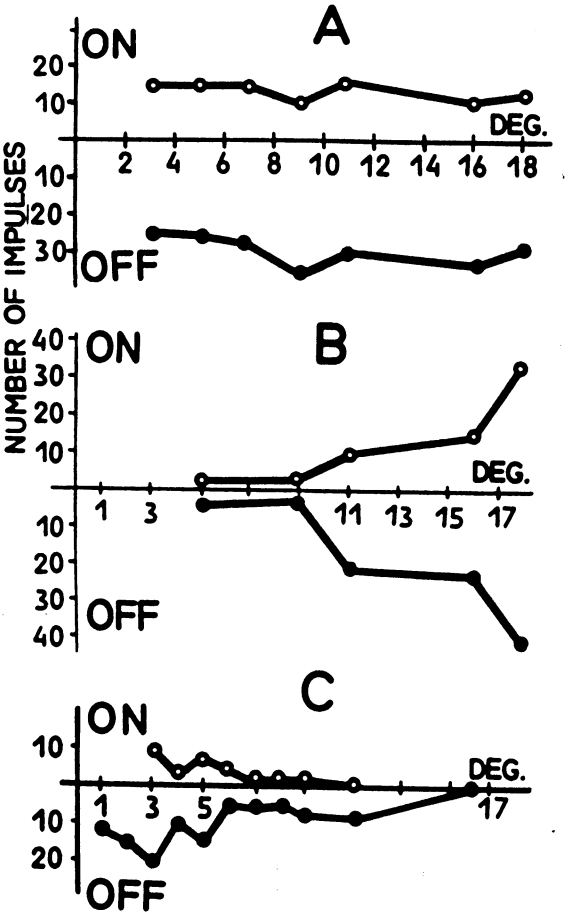

Fig. 7. Spatial summation plots of neurones tested with stationary visual stimuli. A, an ON-OFF neurone, which lacks the spatial summation. Increasing the sizes of stationary flashing light did not change the intensity of responses of the neurone. B, an ON-OFF neurone which briskly enhanced its response when the flashing bright spot reached the size of 11°, showing positive summation. C, responses of an ON-OFF neurone showing negative spatial summation. In all responses the number of discharges decreases at the increasing of dimensions of the flashing bright spot.

curve of one such neurone. As it could be seen from the figure, starting from the stimulus size of 11° the number of discharges in the response has briskly increased to both light "ON" and "OFF" phases of stimuli. Nine percent of the neurones exhibited a negative summation, i.e., a gradual increase of the flashing spot size resulted in a gradual decrease of the number of discharges in the response of the neurone (Fig. 7C).

Generally, ON and OFF responses of the ON-OFF neurones showed parallel changes when the stimulus sizes were changed. Thus, the plots are nearly symmetrical as is shown in the Fig. 8A and B. However, in some ON-OFF neurones differences between ON and OFF responses could change independently, sometimes even in the opposite direction. For example, the neurone whose responses are illustrated in Fig. 8C showed summation of the ON responses to the gradual increase of size of the stationary stimulus, but the same neurone almost did not change the magnitude of its responses when the light spot was switched OFF (Fig. 8C). In some neurones the OFF response could increase with the increasing size of stimulus, while the ON response could stay almost unchanged or decrease (Fig. 8D).

SPATIAL SUMMATION IN OFF NEURONES

The OFF neurones (constituting 59% of the population responsive to the stationary stimuli) exhibited almost the same properties of spatial summation as the other types of neurones observed in the pretectal region. Some of those neurones reacted to the increase of flashing spot size with a decrement in the number of discharges, showing the negative spatial summation (Fig. 9A). The gradual increase of size of flashing light spot in the next group of OFF neurones resulted in an increase of the number of discharges in the response (Fig. 9B). Some pretectal neurones revealed a periodicity of spatial summation with the waxing and waning sequence in the response row. Figure 9C presents the course of summation of such a neurone. Our impression

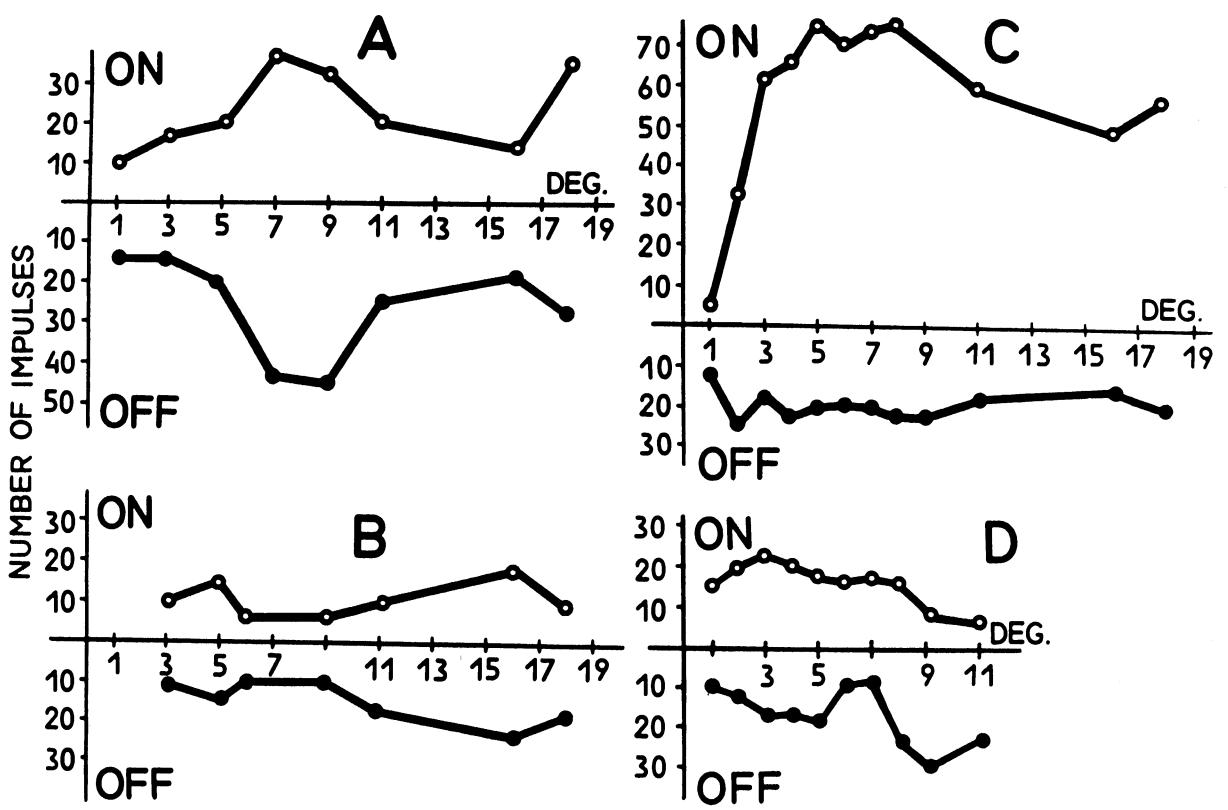

Fig. 8. Spatial summation plots of the ON-OFF neurones. A, B, responses of two neurones which show symmetrical changes in ON and OFF responses to the increasing size of the flashing bright spot. C, responses of an ON-OFF neurone with the differentiated reaction to the increase of flashing spot size. The ON response was enhanced (positive summation) whereas the OFF response underwent negligible changes. D, responses of an ON-OFF neurone which showed opposite changes in ON and OFF reactions to the increase of the flashing spot size. The ON response decreased (negative summation), the OFF response become enhanced (positive summation).

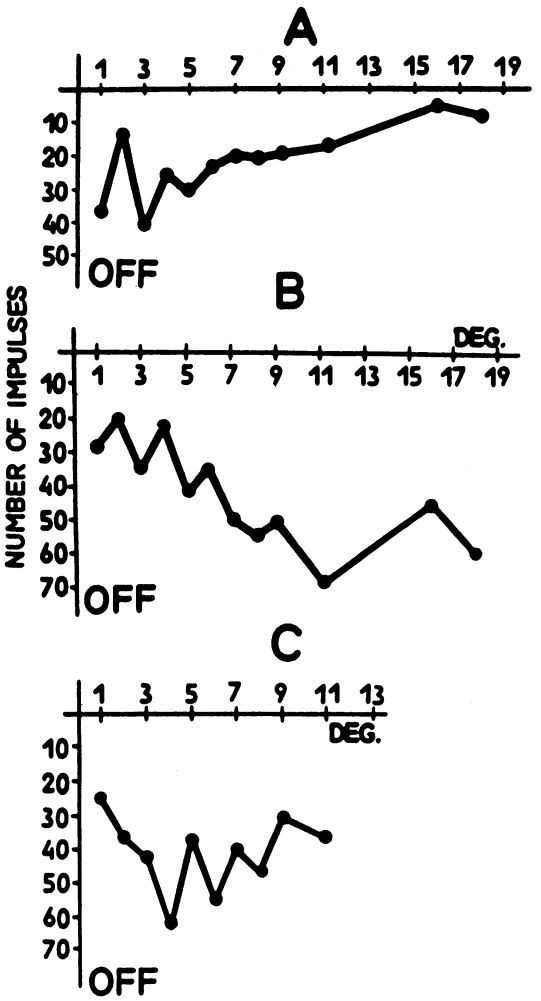

Fig. 9. Spatial summation in the OFF neurones. A, an OFF neurone displaying negative spatial summation. B, an OFF neurone showing positive spatial summation. C, an OFF neurone with periodical course of spatial summation to a gradual increase of the flashing bright spot sizes.

is that periodic excitatory and inhibitory effects follow each other in the responses of these neurones.

The neurones with pure ON responses were very rare in the pretectal region (2%). Therefore we were able to investigate only two ON neurones, and both of them showed negative spatial summation, i.e., gradual increase of the flashing spot size led to a decrease of the intensity of responses. Thus, it seems that receptive fields that have a homogeneous structure (consisting of only OFF or only ON elements) have nevertheless intrinsic mechanisms able to regulate the intensity of neuronal responses inrelation to the size of visual stimuli.

DISCUSSION

The results presented in this study show that the majority of the pretectal neurones show spatial summation, sometimes a complex one. We confirmed previous data about higher sensitivity of pretectal neurones to the moving stimuli than to the stationary ones (Harutiunian-Kozak et al. 1968, 1970, Strashill and Hoffman 1969, Sprague et al. 1973, Schoppmann 1985, Schweigart and Hoffmann 1992).

Only a relatively small percentage of neurones (15% of the whole population and 11% of the direction non-sensitive neurones) did not show any summation effects in their responses and therefore the gradual increase of the stimulus size did not affect their response intensity. The remaining 85% of neurones showed a marked spatial summation of responses. The course of spatial summation in the direction non-sensitive neurones was symmetrical, i.e., there were similar changes (quantitatively and qualitatively) in neuronal responses to the two opposite directions of movement of the visual stimuli. It is interesting to note that such symmetry existed even when the spatial summation showed periodicity.

In the group of the direction sensitive neurones, apart from the neurones exhibiting symmetrical course of summation for both directions of movement, there were neurones that exhibited differences in reactions for two opposite directions of motion. For example, the responses of a neurone to the preferred direction of stimulus movement could be inhibited or facilitated by the increase of stimulus size, but the responses to the null direction of motion could remain stable or *vice versa*. This suggests that the neurone integrates the incoming information on different directions of movement in a different way. In some cases the gradual change of the size of visual stimulus could result in dramatic changes of response, so the preferred direction could be transformed into the null direction.

Furthermore, in some cases one of the applied contrasts evoked well-defined summation (positive or negative) of the responses while the opposite po-

larity of contrast of the stimulus did not change the responses of the same neuron. Such independence of the ON and OFF phases of responses was observed in the ON-OFF neurones, where the magnitude of the ON response of the ON-OFF neurone could change with the change of size of the flashing bright spot, while the OFF response of the same neurone stayed stable. Therefore, one could argue that there are independent mechanisms shaping the ON and OFF responses of the visual sensitive pretectal neurones. The same appears to be true in relation to the responses to stimuli moving in the opposite direction in the direction sensitive neurones. The receptive fields of some of these neurones showed a periodic course of spatial summation, for both moving and stationary visual stimuli. Receptive fields of these neurones may have complex structure and appear to contain many excitatory and inhibitory zones surrounding the receptive field center.

Complex organization of receptive fields of some pretectal neurones can determine nonlinear modulations of responses of these neurones when additional segments of their receptive fields are involved with larger stimulus. These properties of the pretectal neurones may be important in central processing of visual information related to the perception of sizes and directions of objects moving in the visual field.

REFERENCES

Avendano C., Juretschke M.A. (1980) The pretectal region of the cat: a structural and topographical study with stereotaxic coordinates. J. Comp. Neurol. 193: 69-88.

Berlucchi G., Sprague J.M., Levy J., Di Berardino A.C. (1972) Pretectum and superior colliculus in visually quided behavior and in flux and form discrimination in the cat. J. Comp. Physiol. Psychol. 78: 123-172.

Chung S.H., Lettvin G.Y., Raymonds S.A. (1974) The CLOOGE: a simple device for interspike interval analysis. J. Physiol. 239: 63P-66P.

Collewijn H. (1975) Direction-selective units in the rabbit's nucleus of the optic tract. Brain Res. 100: 489-508.

Fishman M.W., Meikle T.H. (1965) Visual intensity discrimination in cats after serial tectal and cortical lesions. J. Comp. Physiol.Psychol. 59: 193-201.

Grigorian G.G., Harutiunian-Kozak B.A., Afrikian M.B., Markarian T.M. (1993) Spatial summation processes in visually driven neurons of cat's pretectal region. Neurophysiology 1: 376-382.

Harutiunian-Kozak B., Dec K., Wróbel A. (1974) Analysis of visual information in midbrain centers. Acta Neurobiol. Exp. 34: 127-143.

Harutiunian-Kozak B., Kozak W., Dec K. (1968) Single unit activity in the pretectal region of the cat. Acta Biol. Exp. 28: 333-343.

Harutiunian-Kozak B., Kozak W., Dec K. (1970) Analysis of visually evoked activity in the pretectal region of the cat. Acta Neurobiol. Exp. 30: 233-262.

Hoffmann K.-P., Distler C. (1989) Quantitative analysis of visual receptive fields of neurons in nucleus of the optic tract and dorsal terminal nucleus of the accessory optic tract in macaque monkey. J. Neurophysiol. 62: 416-428.

Hubel D.H. (1957) Tungsten microelectrodes for recording from single units. Science 125: 549-550.

Huxley A.F., Pascoe J.E. (1963) Reciprocal time-interval display unit. J. Physiol. 167: 40P-42P.

Ibbotson M.R., Mark R. F. (1994) Wide field nondirectional visual units in the pretectum: do they suppress ocular following of saccade-induced visual stimulation. J. Neurophysiol. 72: 1448-1450.

Jasper H., Ajmone-Marsan C.A. (1954) A stereotaxic atlas of the diencephalon of the cat. Canadian National Res. Council, Ottawa.

Kanaseki T., Sprague J.M. (1974) Anatomical organization of pretectal nuclei and collicular laminae in the cat. J. Comp. Neurol. 158: 319-338.

Kawamura S., Sprague J.M., Niimi K. (1974) Corticofugal projections from the visual cortices to the thalamus, pretectum and superior colliculus in the cat. J. Comp. Neurol. 158: 339-362.

Laties A.M., Sprague J.M. (1966) The projection of optic fibers to visual centers of the cat. J. Comp. Neurol. 127: 35-70.

Less H., Rich I. (1963) Dissociation of visual and auditory habits following pretectal lesions in rats and cats. J. Comp. Neurol. 121: 161-172.

Łukaszewska I., Schweigerdt A., McNew J.J. (1967) Retention of visual and kinesthetic discrimination in rats following pretecto-diencephalic and ventral mesencephalic damage. J. Comp. Physiol. Psychol. 63: 458-468.

Magoun H.W., Ranson S.W. (1935) The afferent path of the light reflex. A review of the literature. Arch. Ophthalmol. 13: 862-874.

Pinchoff B.S., Wintercorn J.M.S. (1979) Deficits in luminous flux discrimination by cats with lesions of the superior colliculus - pretectum. Brain Res. 173: 217-224.

Schoppmann A. (1881) Projections from areas 17 and 18 of the visual cortex to the nucleus of the optic tract. Brain Res. 223: 1-17.

Schoppmann A. (1985) A developmental study of retinal afferents and visual responses in the cat pretectum. Exp. Brain Res. 60: 350-362.

Schweigart G., Hoffmann K.-P. (1992) Pretectal jerk neuron activity during saccadic eye movements and visual stimulations in the cat. Exp. Brain Res. 91: 273-283.

Sprague J.M. (1972) The superior colliculus and pretectum in visual behavior. Invest. Ophthalmol. 11: 473-482.

Sprague J.M., Berlucchi G., Rizzolatti G. (1973) The role of the superior colliculus and pretectum in vision and visually guided behavior. In: Handbook of sensory physiology (Ed: R. Jung). Springer-Verlag, Berlin, VII/3: 27-102.

Strashill M., Hoffmann K.-P. (1969) Response characteristics of movement-detecting neurons in pretectal region of the cat. Exp. Neurol. 25: 165-176.

Thompson R., Massopust L.C. (1960) The effect of subcortical lesions on retention of brightness discrimination in rats. J. Comp. Physiol. Psychol. 53: 488-496.

Thompson R., Rich I. (1961) A discrete diencephalic pretectal area critical for retenation of visual habits in the rat. Exp. Neurol. 4: 436-443.

Urbaitis J.C., Meikle T.H. (1968) Relearning and dark - light discrimination by cats after cortical and collicular lesions. Exp. Neurol. 20: 295-311.

Wintercorn J. M. S. (1975) Visual discrimination between spatially separated stimuli by cats with lesions of the superior colliculus - pretectum. Brain Res. 100: 523-533.

Żernicki B. (1968) Pretrigeminal cat: a review. Brain Res. 9: 1-14.

Received 25 May 1994, accepted 20 October 1994