RESPONSES OF CAT'S PULVINAR NEURONS TO MOVING VISUAL STIMULI

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Abstract. Visually-driven pulvinar neurons were investigated by moving visual stimuli. Of a total of 256 observed neurons 25% were not sensitive to the movement of light spots, but revealed a vigorous activity during the movement of black objects. According to the response pattern elicited by the motion of objects through receptive fields, neurons were classified as follows: (a) directionally non-selective — 41%, (b) directionally selective — 28%, (c) multimodal — 29%, (d) suppressed-by-contrast type — 2%. Background illumination exerts different types of influences on the movement-evoked spike responses in the pulvinar neurons. Eighteen percent of the neurons were not affected by background illumination. Eight percent of the neurons were transformed from directionally non-selective into the directionally-selective ones, some of which reversed their preferred directions during background illumination (5%). Activity of 15% of the neurons was facilitated and of 21% was suppressed during various levels of background illumination. Twenty three percent of the neurons lost their spike activity when the background illumination was switched on.

INTRODUCTION

On the basis of neuroanatomical data (1, 31) it is well known that axons running from the mid-brain visual centers (Superior Colliculus, Pretectum) to the visual cortex pass via the posterior thalamic nuclei while making synaptic contacts with the thalamic neurons. This is the main eptrogeniculate pathway to the cortex. Recently Berman and Jones (5) have presented data according to which the cat's retina sends afferents to the pulvinar nucleus of the posterior thalamus. However,
these fibers are sparse, so that the main visual inputs to the posterior thalamic nuclei originate from the mid-brain centers.

Investigations carried out by several authors (11–13, 23, 31–34) in the mid-brain visual centers have established that neurons of these centers display a prominent sensitivity to moving visual stimuli.

Godfraind et al. (9), Veraart et al. (35) and more recently Chalupa and Fish (7) have described functional properties of the pulvinar-LP complex neurons of the cat's thalamus. These are the most comprehensive experiments dealing with the problem of functional significance of the pulvinar and related nuclei in the analysis of visual information. The data presented by the above mentioned authors have demonstrated a sensitivity of the posterior thalamic neurons to moving visual patterns. In this sense they appear to be similar to the mid-brain visually-driven neurons.

Although Godfrained et al. (9), Veraart et al. (35) and Chalupa and Fish (7) have carried out precise investigations on the response properties of neurons in the posterior thalamic nuclear group they made no attempt to study the activity of neurons under different environmental conditions, i.e. at different levels of background illumination. It is well known from (Granit's (10) work that background illumination can reliably modify the responses of retinal ganglion cells by changing the receptive field structure. Further data have been accumulated on the effect of background illumination on neuronal activity of the higher visual centers (15, 24, 29, 30). We therefore set out to compare the neuronal responses of the pulvinar-LP complex to moving stimuli during dark adaptation and at different level of background illumination. Such an approach could facilitate a study of the dynamic properties of thalamic neurons engaged in the analysis of visual information.

METHODS

Seventy six adult cats were used in two series of experiments. Tracheotomy, fixation in stereotaxic apparatus and pretrigeminal section of the brain stem (36) were performed under ether anesthesia. The animals were then paralysed with Flaxedil (Gallamine triethiodide, 20 mg/h) or with Ditiline (Diiodide dicholin ester of succinic acid) 7 mg/kg every hour and artificially ventilated (21 strokes/min). The stroke volume (20 ml/kg) was adjusted so that no hyper (or hypo-) ventilation occurred, as tested by EEG recording. Blood pressure was measured using a mercury manometer connected to a femoral artery and was maintained between 90–120 mm Hg. Body temperature was
kept at 37–38°C with a heating pad. The heart activity was controlled by ECG. The level of pretrigeminal section was examined after each experiment. A trephine hole in the skull was filled with a soft bone wax to avoid brain pulsations. The eyes were covered by contact lenses of "0" dioptic power which helped to keep corneas transparent.

Tungsten microelectrodes (17) of 2–5 μm tip diameter and resistances of 40–50 MΩ were used. The responses of single cells were averaged for 15 to 30 repetitions of stimuli using an interspike interval analyser (8, 19). Upon isolation of a single unit a judgement was frist formed of whether the recording had been made from a fiber or the soma, only somaspike being accounted for (18). Generally 2–4 h were required for a full investigation of response characteristics of each visually sensitive single unit.

A diagram of the stimulating, recording and analyzing apparatus is presented in Fig. 1. A large concave screen of a paerimetric device whose center was 78 cm distant from the nodal points of cat's eyes was diffusely illuminated at 0.05 lx during dark adaptation and 1.5–5.25 lx during light adaptation. The low illuminations were measured by a photomultiplier FEU-36 and higher illuminations by luxmeter YU-16. Light spots of different sizes (1–20°) and different intensities (3.75–12.75 lx) were projected onto the screen from a conventional slide projector. The movements of the light spots were achieved by a mirror galvanometer connected to a low frequency generator. A large
range of movement velocities (5–200°/s) was tested in the first series of experiments. A majority of the pulvinar neurons showed maximal responses to the movement velocities above 100°/s. The most reliable responses were obtained using the 180°/s velocity, in good agreement with the results of Chalupa (7) and Mason (22). In our experiments the speed of 180°/s was used.

Movements in the horizontal, vertical and oblique planes (45° to the horizontal) were applied. 80% of the neurons under investigation displayed maximal responses to the horizontal movements, generally along the longitudinal axis of the receptive field. In our figures, we show the neuronal responses to horizontal movements only.

The period at dark adaptation was 40 min and that of light adaptation was 15 min.

Recording area was limited by the following coordinates: A5–A8; L5–L7; H(-4)–H(-8) according to stereotaxic atlas of Jasper and Ajmone-Marsan (20).

Following each experiment, an electrolytic lesion was made at the recording point using the recording microelectrode. A 0.5 mA current was applied for 60 s. The brain was perfused by saline solution (0.9%) followed by 10% formaline. After a week of fixation, 30μm sections were made and the electrode tip position was checked histologically.

RESULTS

A total of 265 visually driven pulvinar neurons were investigated, which constituted 35% of all observed neurons. The remaining 65% were non-visual. Occasionally recordings were made from the lateral posterior (LP) nucleus (20 neurons) and the posterior (P) nucleus of the thalamus (15 neurons). No differences were found between the response characteristics of the LP and P neurons and those of pulvinar. In all figures the response patterns of the pulvinar neurons were presented as the most typical for the posterior thalamic nuclei. By advancing the recording electrode by micrometer control, the characteristic swish response to visual stimulation was observed when the electrode entered the nucleus under study. From this multineuronal reaction a single neuron was picked up by a careful microelectrode adjustment. The cell thus isolated was investigated using different tests.

Most cells (70%) showed a spontaneous activity of 5–35 imp/s. Of the visually driven neurons 25% were not sensitive to the moving or stationary flashing light spots, but revealed vigorous reactions to the movement of black objects. Seventy five percent of the cells were
equally sensitive to the movement of both black and light spots. Two percent of cells responded only to the stationary flashing light spots and 6% — only to the moving objects in the receptive field.

According to the response patterns evoked by moving visual stimuli, the pulvinar neurons were classified as follows: (i) directionally non-selective (41%), (ii) directionally selective (28%), (iii) multimodal (28%), (iv) suppressed by contrast type (2%).

Directionally non-selective neurons. The cells of this group responded to the movement of light spot in two opposite directions with equal number of discharges. Figure 2 shows the responses of two pulvinar neurons (A and B) having such characteristics. The moving stimulus was a 5° light spot with the intensity of illumination 5 lx against a background of 0.05 lx. The neuron presented in Fig. 2A has a large receptive field of a 30–40° diameter and its discharge evoked by the moving light spot continues during the passage of the light spot across the receptive field. This fact indicates that the receptive field has a homogeneous distribution of excitability all over its surface. The neuron of Fig. 2B has a small receptive field size (5°).

![Fig. 2. Responses of two directionally non-selective neurons (A and B) to the motion of a light spot through their receptive fields. Spot size, 5°; illumination of the light spot, 3.75 lx; illumination of the background, 0.05 lx. The dots represent individual spikes. Abscissa represent the time of stimulation (500 ms to rightward and 500 ms to leftward motion). Ordinates indicate interspike intervals in ms. Arrows show the direction of motion. The responses to 15 repetitions of stimuli are accumulated. Denotations are the same for all figures.](image)

Responses to motion were also investigated using the scanning method, i.e. stimulating along different horizontal paths through the receptive field at 5° vertical intervals. There were no qualitative differences in the response patterns, i.e. directionally non-selective responses were recorded everywhere in the field. However, the responses recorded from the field's periphery were feeble.

The directionally non-selective neurons showed a response summation with increasing the size of the moving stimulus. An example of such neuron is presented in Fig. 3. The neuron increased the number of its discharges with increase of the stimulus size. The responses did not increase any more for stimuli sizes in excess of 11°.
A more interesting phenomenon was observed in the neuron represented in Fig. 4. With the increase of the stimulus size from 1° to 20°, a non-directional response of the cell was transformed into a directional one with the preferred direction from left to right.

Fig. 3. Summation of the responses of a directionally non-selective neuron to the movement of light spots of increasing diameters (4°-11°). The numbers in the middle of each frame indicate the sizes of moving stimuli in degrees of the visual angle. The increase in the number of discharges with the increasing size of the stimulus is evident.

Directionally-selective neurons. This type is characterized by an asymmetrical distribution of discharges elicited by the movement of visual stimuli through the receptive field (4). In one direction (called the preferred direction) the cell gives vigorous discharges, whereas a motion in the reverse direction elicits almost no response. There exist a great deal of variations in the response patterns of the neuron of this kind. Figure 5 illustrates four examples typical for the neurons described. In Fig. 5A a directionally selective neuron is presented revealing vigorous discharges during the left-to-right stimulus movement and completely inhibiting its activity during the reverse direction of the light spot motion. In Fig. 5B the neuronal responses having an opposite preferred direction are presented. Most neurons showed preferences to the movement from left to right. The neuronal responses presented in Fig. 5C differ substantially from those described above.
Fig. 4. Transformation of a directionally non-selective response into a directionally-selective one by increasing the size of a moving light spot. A, B, C, responses to the motion of a light spot 1°, 2° and 3° (degrees) in diameter, respectively. Directionally non-selective responses are evident. D, E, F, responses to the motion of light stimuli of 16°, 18° and 20° diameters. Directionally selective response is evident with the rightward preferred direction.

Fig. 5. Types of directionally selective responses in four different cells. A, B, responses of two neurons with rightward and leftward preferred directions. C, responses of a cell with a bimodal distribution of discharges in the preferred direction and a monomodal one — in the null direction. D, discrimination of motion direction by different distributions of interspike intervals.
This neuron reveals monomodal discharges in one direction of stimulus motion (right to left) and a bimodal distribution of discharges in the opposite direction of motion. We suggest that this quality could also be regarded as a discriminating factor for the perception of the direction of motion. The last neuron (Fig. 5D), on the other hand, possesses quite a different way of analysing the direction of movement. The movement from right to left yields discharges with long interspike intervals, whereas in the opposite direction short intervals prevail.

The summation processes are less prominent in the directionally-selective neurons. In most cases no summation was observed with the increasing stimulus size. Figure 6 illustrates responses of a directionally-sensitive neuron to the motion of light spot of different sizes (5 to 20°). As seen from Fig. 6, no essential differences could be observed.

![Figure 6](image)

Fig. 6. Responses of a directionally-selective neuron to the motion of a light spot with progressively increasing diameters. Note the absence of summation.
between the responses to the motion of 5° stimulus and that of 20°. A small percentage (5%) of directionally selective cells exhibit a summation with increasing spot size up to 11°. For greater stimulus diameters the response was either slightly suppressed or remained unchanged.

Multimodal neurons. Neurons of this type generally had no spontaneous activity. They responded with multimodal discharges during the stimulus movement through their receptive fields. Figure 7 represents responses of two such neurons in the pulvinar. Figure 7A illustrates neuronal responses which had two modes of discharge in each direction of the movement. The impression was that discharges were evoked at the border zones of the receptive field. This leads us to the conclusion that a nonuniform distribution of excitability exists over the receptive field, the border zones being more sensitive to moving visual stimuli. Furthermore, some neurons of this type differentiate the directions of movement by different distributions of modes of discharges. One of such neurons is represented in Fig. 7B. In one direction of movement (right to left) a new, intermediate mode of discharge appears, whereas in the opposite direction only two modes of discharge persist.

Suppressed by contrast type. These neurons were rare in the cat's pulvinar. Their typical features include a high level of spontaneous activity which is interrupted by a moving stimulus entering their receptive fields. As can be seen from the Fig. 7C, slight increases in discharges occurred when the stimulus crossed the receptive field borders. The central zone of the receptive field did not yield any discharges. Similar neurons were described by Rodieck and Stone (26) in the cat's retina and classified as the "suppressed by contrast" type neurons.

The effect of background illumination on the responses of pulvinar
neurons to moving stimuli. The influence of background illumination on the discharge patterns of pulvinar neurons in response to movement was studied in 155 cells of a total of 265 cells. The neurons investigated were classified into six types depending on their responsiveness to background illumination: suppressed, totally losing activity, facilitated, direction reversed and direction developing, losing multimodality, ineffective.

Suppressed type. Suppression of activity was found in 21% of cells when the level of background illumination was increased. The suppression effect was observed in all types of neurons except in the "suppressed by contrast type" where it has mainly a facilitating effect. A typical example of the suppressing effect of background illumination is presented in Fig. 8. Responses of a directionally non-selective neuron are presented in Fig. 8A, B where the background illumination results in a suppression of activity (Fig. 8A, vs. Fig. 8B). A shortening of the duration of the response to a moving stimulus was observed after the increase in background illumination. This could be explained by the effect of stray light which is the case in semi-darkness. Our next paper will deal with this problem in more detail.

Total suppression of activity. A total loss of activity was observed

![Fig. 8. The suppressing effect of background illumination on the responses evoked by moving stimuli of two neurons (A, B and C, D). A, responses of a neuron to moving light spot in semi-darkness. B, suppression effect of background illumination on the spike responses of the same neuron. C, responses of another neuron to a moving light spot in semi-darkness, D, complete disappearance of evoked responses after a 1.5 lx illumination of the background. The background illumination is indicated on the right border of the figure. In the middle of each frame the intensity of spot illumination is shown. Denotations are the same for all following figures.]
in 23% of neurons when the background illumination was switched on (Fig. 8C, D). Background illuminance of 1.5 lx intensity was sufficient to produce a complete disappearance of the cell spike responses (Fig. 8D). Rarely, a ten-fold rise in the illumination of the light spot would evoke a feeble response from a small area in the center of the receptive field.

**Facilitated type.** Figure 9 illustrates responses obtained from a cell belonging to the suppressed by contrast type. In Fig. 9A the responses during dark adaptation are shown. There was a clear-cut inhibition of activity when the light spot crossed the receptive field center. This inhibition gradually decreased when the background was illuminated (Fig. 9B). By further increasing the background illumination (Fig. 9C) the inhibitory effect evoked by the stimulation of receptive field center could be reversed into an excitatory one. Facilitatory effects of the background illumination have been also observed by us in other types of neurons forming a total of 15% of all observed effects of background illumination.

**Fig. 9.** The facilitating effect of background illumination on the responses of a "suppressed by contrast" type neuron. A, responses to the motion in semi-darkness. B, C, responses during background illumination of 1.5 lx (B) and 5.25 lx (C).
**Direction-reversed and direction-developing types.** Some directionally non-selective cells become directionally selective (8%) with the increasing background illumination. Figure 10 shows typical responses of such neuron. The neuron which was directionally non-selective in darkness (Fig. 10A) was transformed into a directionally-selective one by an increased background illumination (Fig. 10B). In Fig. 10C, D the averaged responses of a direction-reversed type neuron were presented (5%). In Fig. 10C the directional response to the movement of light spot in the dark had a rightward preference. The same neuron responded with a leftward preference (Fig. 10D) when the background was illuminated (1.5 lx).

![Figure 10](image)

Fig. 10. Transformation of a directionally non-selective response into a directionally-selective one (A, B) and reversal of preferred direction (C, D) by a 1.5 lx background illumination.

**Losing multimodality.** Some neurons which had a multimodal type of spike discharges to the movement of a light spot in darkness lost their characteristic response-pattern during background illumination (10%) and were transformed into a more common, monomodal, directionally non-sensitive type (Fig. 11A, B and C). Some neurons of this type lost their multimodal response pattern at a weak illumination of the background (1.5 lx), whereas others did so at a higher (3.5 lx) level of background illumination.

**Non-effective.** 18% of neurons were not responsive to the changes in background illumination.
Fig. 11. Transformation of a multimodal responses into a monomodal type by illumination of the background. A, multimodal responses evoked by moving light spot in semi-darkness. B, responses of the same neuron to the spot motion against an illuminated background of 1.5 lx. C, the same neuron responding by monomodal distributions of discharges when the background is illuminated by 5.25 lx.

DISCUSSION

Our results confirm the data obtained by Godfraind et al. (9) and Veraart et al. (35), showing that about 35% of neurons in the pulvinar-LP complex of the thalamus exhibit a visual sensitivity. Chalupa and Fish (7) found a somewhat higher percentage (42%) of the visually sensitive neurons. Probably this difference is due to a different animal preparation used by us and by Godfraind et al. (9) and Veraart et al. (35), and that used by Chalupa and Fish (7). The pretrigeminal cats were convenient for our purpose because of a low-level spontaneous activity of their neurons. They helped us to obtain clear-cut responses to visual stimuli and made it possible to study the characteristic patterns of the neuronal responses in more detail.
On the basis of response patterns of the cells investigated in the pulvinar, nucleus lateralis posterior (LP) and nucleus posterior (P), a conclusion was reached that there are no differences between these regions. The same observations were made by Chalupa and Fish (7) and they found it rather puzzling, because it was shown anatomically that the pulvinar receives its main visual input from the pretectal region, whereas the LP afferent fibers originate in the superior colliculus. We do not think that there is anything puzzling in these results. Our earlier investigations (11-13) on the pretectal region and the superior colliculus have established a great similarity between single-unit responses evoked by visual stimuli in the pretectal region and superior colliculus. One should not therefore expect to find any differences at the final points of their efferents either.

In general, our results resemble those of Godfraind et al. (9), Veraart et al. (35). The visual input to the pulvinar-LP complex of the thalamus is well-organized and a rather high-level visual processing occurs there in. The most interesting result was the observation of cells with multimodal responses which have not been described by the above-mentioned authors. These cells are analogous to those described by Bishop et al. (6) and Pettigrew et al. (25) in visual cortex. It seems likely that multiple discharge centers exist in such receptive fields and that these centers are situated in the border zones of the receptive field.

Recently experimental data were accumulated showing that the background illumination essentially modifies the visually evoked responses of the retinal and cortical cells (21, 24, 27-30) and those of the visually-sensitive neurons in the midbrain (15).

The observations reported here seem to corroborate the results obtained by Nunokawa (24) who found similar effects of the background illumination on the responses of visual cortical cells evoked by moving stimuli. The reversal of the preferred direction and the transformation of a non-directional response into a directional one in our experiments demonstrate an efficient response modulation at subcortical levels by altering the background illumination. It can be concluded that light adaptation causes the modulation in the sensory processing at nearly all levels of brain structures engaged in the central visual processing.

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