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# THE EFFECT OF BACKGROUND ILLUMINATION ON THE RESPONSES OF THE NEURONS OF THE CAT'S SUPERIOR COLLICULUS TO MOVING STIMULI

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*Abstract.* The influence of background illumination on unitary neuronal responses of cat's superior colliculus to moving stimuli were investigated. Diverse types of neurons responding to background illumination were observed: Neurons which did not change their activity during background illumination; neurons in which the response to moving stimuli during background light was facilitated; cells in which the spatio-temporal dispersion of the peak of evoked response was narrowed with light adaptation; cells in which activity was suppressed during background illumination; and neurons in which the specific response was changed to an unspecific one (and vice versa) during background illumination. The background illumination itself did not evoke any response in the cell, and the suggestion was put forward that subthreshold influences could modulate the evoked activity of the neuron.

## INTRODUCTION

It is known from psychophysical experiments (6) that a low background illumination facilitates pattern perception in man. More recently Suzuki et al. (13, 14) and Nunokawa (11) presented data concerning the influences of the background illumination on visually evoked potentials and receptive field organization of neurons in striate cortex. One can presume that the influence of background illumination at the cortical level is partly dependent upon the changes which have already taken place in the retina and lower visual centers. Thus Barlow et al. (1, 2) in their early experiments demonstrated clearly that there is a modulation of unit responses in the retina, evoked by peripheral stimulation during different levels of light and dark adaptation. Our previous investigations, carried out on the visual centers of the cat's midbrain showed that at this subcortical level the background illumination is also capable of modulating the visually evoked activity of neurons (3, 5). We observed that a low intensity diffuse illumination of the background, which was in itself subthreshold for evoking any activity in the cell, could still significantly modulate its visually evoked responses.

In this paper we present the first part of our results concerning the role of background illumination in the modulation of visually evoked responses of the neurons in superior colliculus. Special attention was paid to the problem of the responses to moving patterns and their relation to the background illumination.

## METHODS

Sixty two cats were used for experiments. Animal preparation and recording techniques have been described elsewhere (3). However, the main points are briefly given here.

The animals were tracheotomized under ether anesthesia and a pretrigeminal section was performed. Experiments began 2 hrs later in order to allow time for the ether anesthesia to subside. Flaxedil (60 mg/hr, given intravenously) was used to immobilize the animals and artificial respiration was given (stroke volume 20 ml/kg). The pupils were fully dilated by 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.

Moving visual stimuli: circular spots, usually 5° in diameter, and slits of light were projected onto a perimeter-like device. The arrangement of the perimeter enables one to position the screen anywhere in the visual field at a constant distance from the cat's eyes (70 cm), and thus permits an exploration of the whole retina.

In each experiment the intensity of background illumination and that of the spot was measured using a SEI photometer.

Single unit activity was recorded extracellularly. Tungsten wire microelectrodes (7) with tip diameter 2–3$\mu$m were used; the electrode tip resistance after insulation of the shaft with a vinyl varnish was 30–50 MΩ. The microelectrode was connected to a high-input impedance cathode follower and to an amplifier with a high-pass filter (Grass P-6). A Schmitt-trigger circuit detected the action potentials and produced standard pulses. These pulses were fed to the input of an ANOPS-1 digital analyzer (10), which was used for compiling of histograms of average responses.

After each experiment electrolytic lesions were made by passing 0.5 ma current for 30 sec, the microelectrode being positive. After perfusion with physiological solution and with 10% formalin solution, 30 $\mu$m thick histological sections of the brain were cut and stained by the Nissl method. The electrode tracks in each experiment were identified.

## RESULTS

A total of 184 neurons were investigated. Preliminary experiments, in which spots of light were moved on a diffusely illuminated screen, have indicated that the effect of background illumination differed from cell to cell. Thus, as the first step, we determined the types of influence of background illumination on the neuronal responses evoked by the

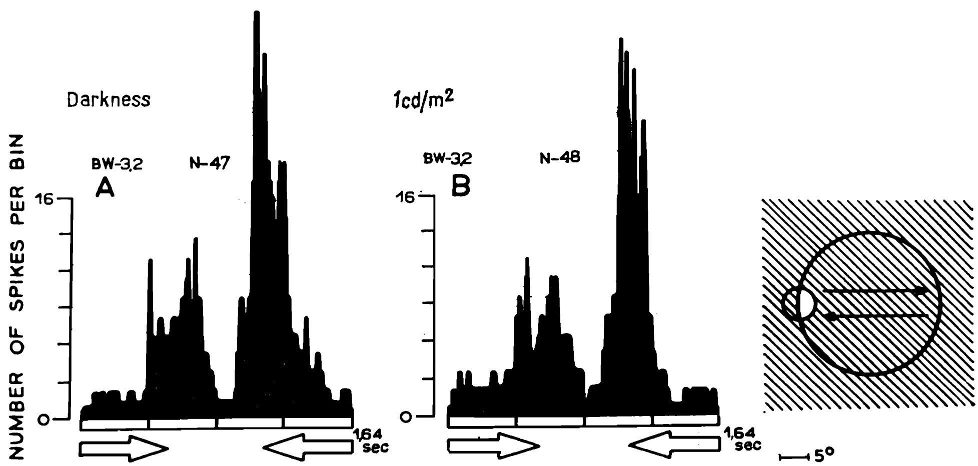


Fig. 1. Responses of a neuron in the superior colliculus which did not change the pattern of its averaged response during background illumination. *A*: PST-histogram of responses of the cell to the movement of a 5° light spot in the receptive field. The response is direction sensitive. Background illumination 0.02 cd/m². *B*: PSTH of responses of the same neuron to the same stimulus during background illumination of 1 cd/m². The intensity of the illumination of light spot is 6.2 cd/m². BW: bin width in milliseconds, N: number of repetitions.

movement of visual stimuli in the cell receptive field. None of the neurons described in the present paper responded to the switching "on" and "off" of background illumination alone. It will be shown that even such a low intensity diffuse illumination of the whole retina is sufficient to significantly modulate the evoked response pattern of the neurons. Only 16% of cells studied failed to show any changes in their evoked activity when the background was illuminated.

Figure 1 presents the PST histograms of responses of such a neuron. In Fig. 1*A* the response of the cell to the movement of a 5° light spot (6.2 cd/m² luminance) is presented. The light spot was moving through the entire receptive field. Figure 1*B* illustrates the response of the same neuron to the same stimulus during low-level background illumination (1 cd/m²). The background light was switched "on" 30 min before the Fig. 1*B* histogram was compiled. No significant differences between response patterns could be observed in these histograms. However, 84% of neurons in the superior colliculus showed "subthreshold influences" of the background illumination upon their responses to moving stimuli.

Many cells (40%) reacted most intensely when an optimal level of background illumination was introduced. For most neurons this optimum was close to 1 cd/m². Figure 2 shows one of the neurons which reacted best during background illumination of 1 cd/m² (Fig. 2*B*) and decreased the amplitude of its response histogram when the level of background

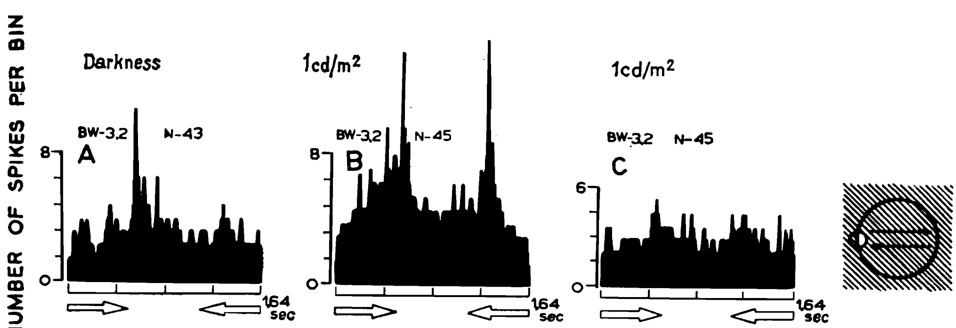


Fig. 2. Illustration of the optimal degree of background illumination for the organization of unitary responses in colliculus superior to moving stimuli. *A*: PST-histogram of responses of the neuron to the movement of 5° light spot in darkness. Direction sensitivity exists. *B*: PSTH of responses of the same cell to the same stimulus during a background illumination of 1 cd/m². Note the facilitated responsiveness and also the changing of the pattern of responses from direction sensitive to non-directionally sensitive. *C*: PSTH of the same neuron during background illumination of 3 cd/m². The responses are suppressed. The intensity of the illumination of the spot, 6 cd/m².

illumination increased to 3 cd/m² (Fig. 2C). These results will be presented in more detail in the following paper.

Forty four per cent of neurons suppressed their evoked activity during background illumination. Figure 3 shows two histograms of the averaged responses of a neuron to the movement of a 5° light spot in its receptive field. Figure 3*A* represents the response of the cell in complete darkness, and the histogram B shows the response to the stimulus during 1 cd/m² illumination of the background. The averaged responses to the moving

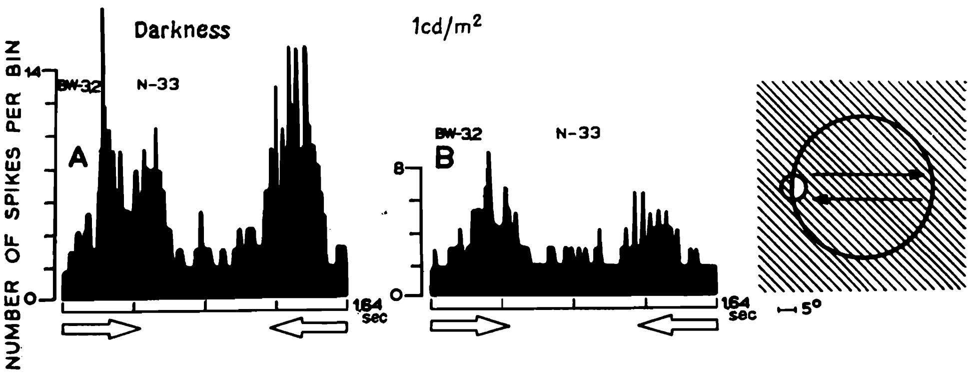


Fig. 3. Responses of a neuron in which activity was suppressed during background illumination. *A*: PST-histogram of responses of the cell to the movement of a light spot 6.5 cd/m² through its receptive field in darkness. *B*: PST-histogram of responses of the same cell during background illumination of 1 cd/m².

spot were suppressed when the diffuse background light was projected over the whole surface of the screen. Suppression of the response occurred mainly at the peaks of the histograms but the level of the spontaneous activity between peaks was not changed. In later experiments this fact was confirmed. Some neurons changed their stimulus-evoked activity during background illumination but maintained an approximately steady level of spontaneous discharges.

In the next group (75⁰/₀ of the entire population) we included neurons which changed their activity during background illumination so that the peak response was narrowed. Figure 4 shows the PST-histogram of averaged discharges of a neuron to the movement of the 5° light spot: before (*A*) and during (*B*) background illumination. It can be clearly seen from this Figure that there was a slight suppression of the entire activity of the neuron and a narrowing of the distribution of the peak responses. The receptive fields of such neurons shrink significantly during background illumination, and probably this is one of the possible explanations for the changes of their response patterns.

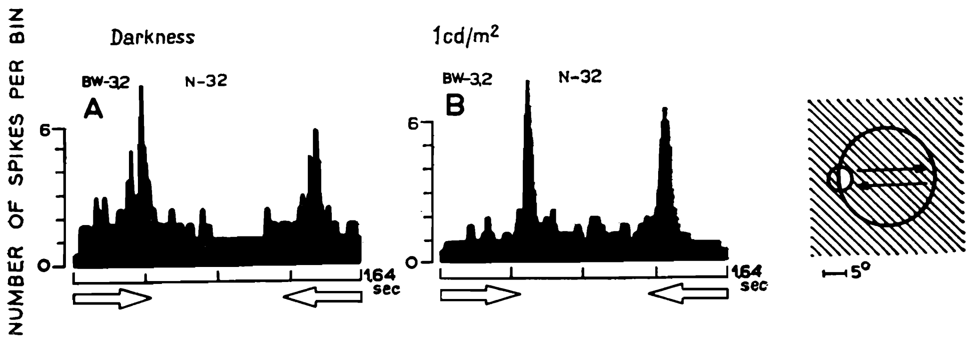


Fig. 4. Responses of a neuron which changed the spatio-temporal distribution of its discharges during background illumination. *A*: PST-histogram of responses of the neuron to moving stimuli in darkness. *B*: PSTH of responses of the same neuron during background illumination of 1 cd/m². Note the remarkable narrowing of the peak response.

Figure 5 illustrates PST-histograms of averaged responses of a neuron which were obtained in darkness (Fig. 5*A*) and during low-intensity background illumination (Fig. 5*B*). This Figure shows that the movement of a 3° x 17° light rectangle in the receptive field of the neuron in darkness evoked a weak response (Fig. 5*A*) with a slight directional sensitivity,

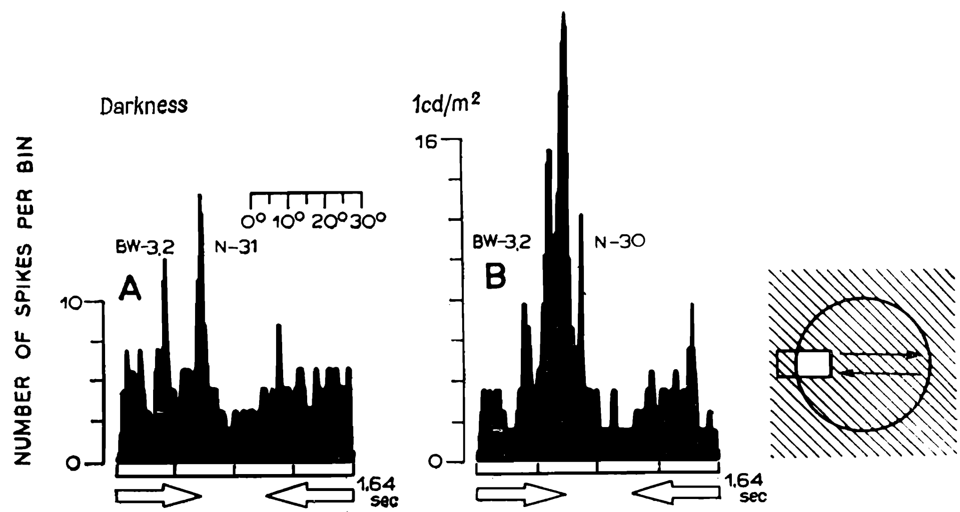


Fig. 5. Activity of a neuron which increased its response after illumination of the background. *A*: PTS-histogram of responses of a neuron in darkness. Note the weak response when the rectangle was moved from left to right. *B*: PST-histogram of the same neuron during background illumination of 1 cd/m². One can see the more prominent direction-sensitivity.

the prefered direction being from left to right. When the diffuse background illumination was switched on 1 cd/m², the cell's reaction to the movement became stronger and with a more prominent directional sensitivity. The movement from left to right was much more accentuated. Nunokawa (11), who observed similar effects of background illumination on the activity of neurons in the visual cortex, designated them as the "facilitated type". Twenty nine per cent of the directionally sensitive neurons were included in this group.

In 45% of directionally sensitive cells, background illumination caused the directional preference to become weaker, and differences in the intensity of responses for the two opposite directions less prominent

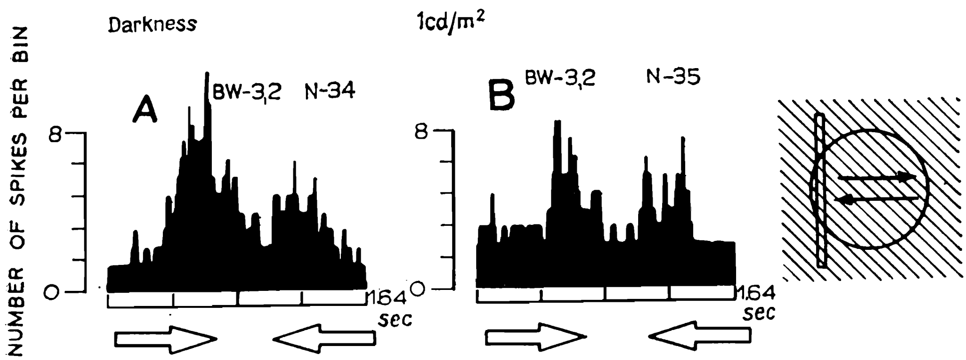


Fig. 6. Responses of a neuron in which direction-sensitive response to moving stimuli changed into a non-directionally sensitive one during background illumination. *A*: PST-histogram of responses of a cell to a moving slit 1.5° × 40°, in darkness. Observe the direction-sensitive response with prefered direction from left to right. *B*: PSTH of responses of the same cell to the movement of the same stimulus during background illumination of 1 cd/m². Note the smaller difference in response intensity between prefered and null direction.

(Fig. 6*B*). So the background illumination is capable of modulating the cell's response even when it is a discriminative, direction-sensitive response. The remaining (26%) direction-sensitive neurons showed no significant change with alteration of the background illumination.

## DISCUSSION

These experiments have shown that background illumination can influence the neuronal responses in diverse ways: (i) suppresses the activity of some neurons; (ii) facilitates evoked responses of other neurons; (iii) narrows the spatio-temporal dispersion of the peak of evoked response; (iv) reduces the differences between the preferred and null directions in direction-sensitive cells (and vice versa). Only in small percent of cases does not affect the cell's spontaneous activity significantly.

Any patterned visual stimulus when perceived subjectively, is perceived not only as a certain intensity of illumination of a particular part of the receptive field, but also as a patch illuminated more or less intensely than the neighboring region (2). Thus, logically, one can assume that the background light must play an important role in the mechanisms of perception. Confirmation for such an assumption has been provided by the psychophysical data of Hecht (6), who showed that a weak illumination of background heightened the acuity of vision. In neurophysiological experiments Barlow obtained data, concerning the background influences and receptive field structure of ganglion cells of the cat's retina (2). However, Hubel and Wiesel (8, 9) presented data showing that background light failed to affect unit activities of neurons in the visual cortex of the cat. On the other hand, Suzuki and Jacobson (13), Sasaki et al. (12) and Nunokawa (11) recently found that both the unitary responses and the evoked potential activity in the visual cortex, were altered by background illumination.

In the present experiments, evoked responses of some midbrain neurons were significantly modulated by the illumination of the background. In 40% of the cases a facilitation of unit responses to moving stimuli was observed during illumination of the background. This type of neurons could be the neurophysiological correlate of the psychophysical phenomenon of facilitation of pattern perception during low-intensity background illumination (6). Quite interesting were those types of influences of background light on the cell activity in which a modulation of specific responses occurred, for example, a change of the response of a direction-sensitive neuron into a non-directionally sensitive one. If one bears in mind that the background illumination itself did not evoke any response in the cell, then one could put forward a suggestion that subthreshold influences could modulate the evoked activity of the neuron. We think that the problem of the role of subthreshold influences on cell membrane is worth further investigation.

Another conclusion which can be made on the basis of our data concerns the organization of the connections between the retina and neuron in the midbrain. It seems that, apart of the existence of a strictly delimited space in the retina called the receptive field, and directly connected with the neuron, there are extensive parts of retina outside of the receptive field, which also have connections with the neuron in this visual center. Probably these connections are indirect and thus, their action on the cell is weaker. The response of the neuron to a visual stimulus would be an integrated sum of the informational input impinging on it by direct, as well as by indirect pathways. And this indirect, weak input could sometimes became the main modulation factor in the determination of the final, precise response of the neuron.

Thus the observations presented above allow us to conclude that small, subthreshold influences on the neuron could be very important in the modulation of information processes.

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