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INFLUENCE OF ADAPTATION LEVEL ON RESPONSE PATTERN AND SENSITIVITY OF GANGLION CELLS IN THE CAT'S RETINA

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SUMMARY

1. The effect of background illumination on response pattern is correlated with its effect on visual sensitivity by analysing post-stimulus time-histograms obtained from single ganglion cells in the cat's retina at various levels of background illumination between zero and 2×10^6 photons (wave-length 523 nm).sec^{-1}.deg^{-2} (via 5·7 mm^2 pupil).

2. If background illumination did not exceed a critical value, about 10^3 photons (523 nm).sec^{-1}.deg^{-2} (via 5·7 mm^2 pupil), stimulation of the centre of a receptive field resulted in either sustained excitation (i.e. increase in discharge rate) during 'on' and cessation of the excitation at 'off' (on-centre unit), or sustained inhibition (i.e. decrease in discharge rate) during 'on' and cessation of the inhibition at 'off' (off-centre unit). Within this low adaptational level, a ganglion cell maintained its maximum sensitivity regardless of whether the weak background light was presented or not.

3. When background level exceeded the critical value up to 2×10^6 photons (523 nm).sec^{-1}.deg^{-2}, however, the simple, sustained responses changed into compound responses with two transient components of opposite polarities, either excitation at 'on' and inhibition at 'off' (on-centre unit), or inhibition at 'on' and excitation at 'off' (off-centre unit), and also the sensitivity began to decrease as the background increased, approximately obeying Weber's law.

4. It is suggested that a ganglion cell gives simple-sustained response when its gain control mechanism remains inactive at a low background illumination below a critical level, whereas it gives compound-transient response when its gain control mechanism becomes active as background illumination exceeds the critical value.

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INTRODUCTION

An interesting feature of cat retinal ganglion cells is variability of their response patterns under different stimulation conditions. Response patterns of visual neurones have been described in three types (Adrian & Matthews, 1927; Hartline, 1938; Granit, 1944; Kuffler, 1953): (1) 'on' response, that is, discharging after the onset of illumination; (2) 'off' response, discharging after its cessation; and (3) 'on-off' response, discharging after both its onset and cessation. In the light adapted cat's retina (within the photopic range) all three types of responses, 'on', 'off' and 'on-off' can be elicited from a single ganglion cell, depending on the location and extent of retinal area which is stimulated within its receptive field (Kuffler, 1953), on stimulus intensity (Granit, 1944; Donner & Willmer, 1950), and on background illumination (Granit & Therman, 1935; Kuffler, 1953). In dark adapted state, however, Barlow, FitzHugh & Kuffler (1957) observed 'pure on' or 'pure off' units which gave additional discharge only at 'on' or only at 'off' and inhibition of the resting discharge at the opposite phase of the stimulus wherever they were stimulated within their receptive fields.

The present work reports a detail of response patterns and their reversible changes with background illumination below the photopic range. A functional correlation between the effect of background illumination on response pattern and that on visual sensitivity of a given ganglion cell is discussed in line with a possible neural mechanism of the retina. A brief account of the result was presented (Yoon, 1969).

METHODS

Post-stimulus time histograms of impulse occurrences during 'on' and 'off' periods of a stationary light stimulus were obtained from single ganglion cells in the cat's retina *in situ* by the methods which have been fully described by Barlow & Levick (1969*a*). The cat was anaesthetized by a continuous intravenous infusion of ethyl carbamate (19 mg/kg.hr) and α-chloralose (0·63 mg/kg.hr) and was also paralysed by infusion of D-tubocurarine chloride (0·5 mg/kg.hr) and gallamine triethiodide (5 mg/kg.hr). All units were isolated from the retinal area within 20° of the area centralis. A diagram of the light input system is sketched in Fig. 1. An arm with a pointer was attached to the movable test stimulus light box (TS) such that the tip of the pointer was in symmetry with respect to a pivot (P), which determined the location of the test stimulus in the cat's visual field. Both the test stimulus and the background light (BG) passed a narrow band interference filter (IF) and a correcting lens (L), and entered the cat's eye via a 5·7 mm^2 artificial pupil. After proper optical alignments the whole optical system and the experimental animal were shielded from stray light with a blackout device. The position of the centre of the test spot was specified by its symmetric position on the two-dimensional Cartesian co-ordinates of the receptive field mapping board (RFMB) indicated by the pointer of the arm. This symmetric device made it possible to map out the detail of receptive

fields even in complete darkness. Method of radiometric calibrations of the light sources is described elsewhere (Barlow, Levick & Yoon, 1972).

Thresholds were determined subjectively by listening to the sequence of impulse discharges monitored by a loudspeaker and also by observing an oscilloscope screen which displayed action potentials. In the majority of cases these subjective estimates of threshold agreed with the corresponding objective thresholds calculated by the methods of Barlow & Levick (1969*a*) within a factor of two.

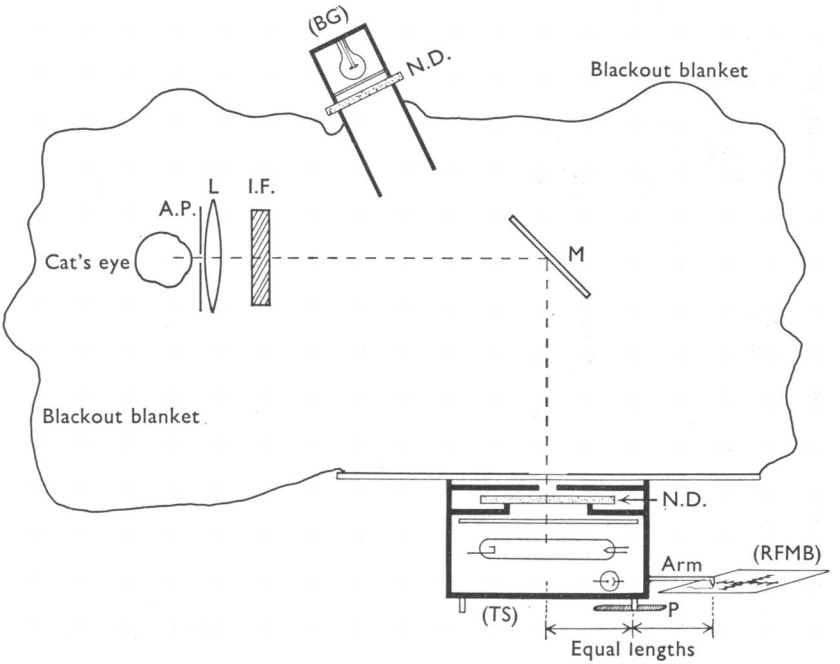

Fig. 1. Diagram of light input system. The test stimulus light spot (TS) scans the visual field by rotations at the pivot (P) and by linear motions of the pivot along a straight-line groove. The position of the centre of the test spot is specified by its symmetric position on Cartesian co-ordinates of the receptive field mapping board (RFMB), indicated by the pointer of the arm. This symmetric device makes it possible to map out the detail of receptive fields even in complete darkness. A.P.: 5·7 mm² artificial pupil. I.F.: narrow band interference filter with peak wave-length of 521 nm. L: spectacle lens. M: from surface mirror. N.D.: neutral filters of various densities.

RESULTS

Change of response patterns with adaptational level

Discharge patterns of single ganglion cells were displayed by post-stimulus time-histograms as shown in Fig. 2, for an on-centre unit (YZ:2).

When the unit was adapted to a background illumination of 2×10^6 photons (wave-length 523 nm).sec^{-1}.deg^{-2} (via 5·7 mm^2 artificial pupil) in the mesopic range, stimulation of the centre of the receptive field with a small light spot (0·48° in diameter) elicited a compound response showing transitory excitation (i.e. increase in discharge rate) at on-phase

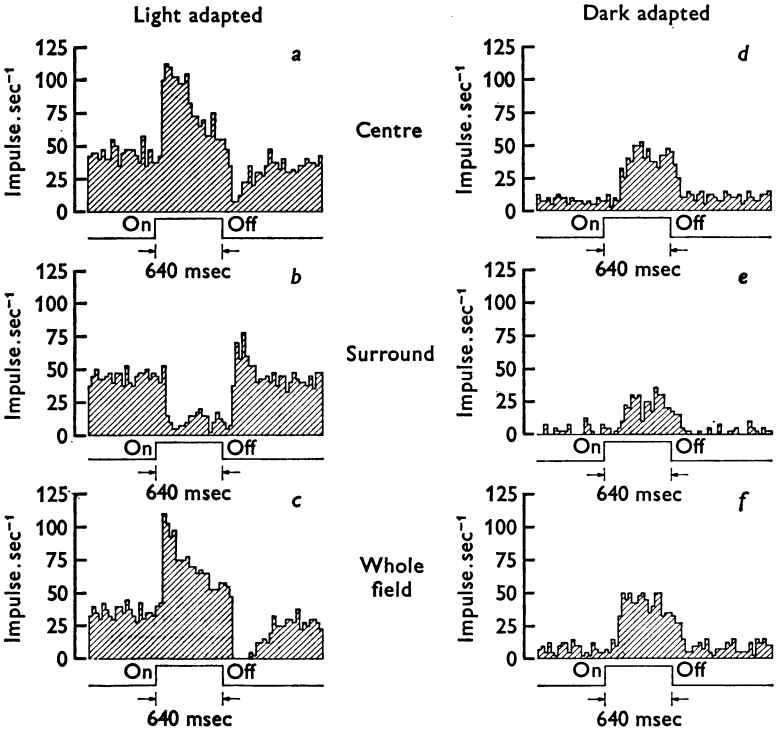

Fig. 2. Post-stimulus time histograms of an on-centre unit (YZ: 2). *a*, *b* and *c* were collected at background illumination of 2×10^6 photons (523 nm).sec^{-1}.deg^{-2} (via 5·7 mm^2 pupil). *d*, *e* and *f* were obtained in darkness. The size of test spot was 0·48° in diameter for both the centre and the surround, and that for the whole field was 4·5° × 4·5° square. The duration of test stimulus was 640 msec.

and inhibition (i.e. decrease in discharge rate) at off-phase of the stationary light stimulus (Fig. 2*a*). In darkness, however, the compound transitory response of the centre changed to a simpler pattern showing sustained excitation during 'on' and cessation of the excitation at 'off' (Fig. 2*d*). The response evoked from the antagonistic surrounding zone of the on-centre unit showed a similar change as the adaptational level varied in agreement with Barlow & Levick (1969*b*). At the mesopic background

level, the response of the surround showed transitory inhibition at 'on' and excitation at 'off', whereas it showed excitation during 'on' and cessation of the excitation at 'off' in darkness (Fig. 2*e*). Since the antagonistic surround disappears in darkness (Barlow *et al.* 1957) the latter excitatory response in darkness (Fig. 2*e*) was probably due to the stray

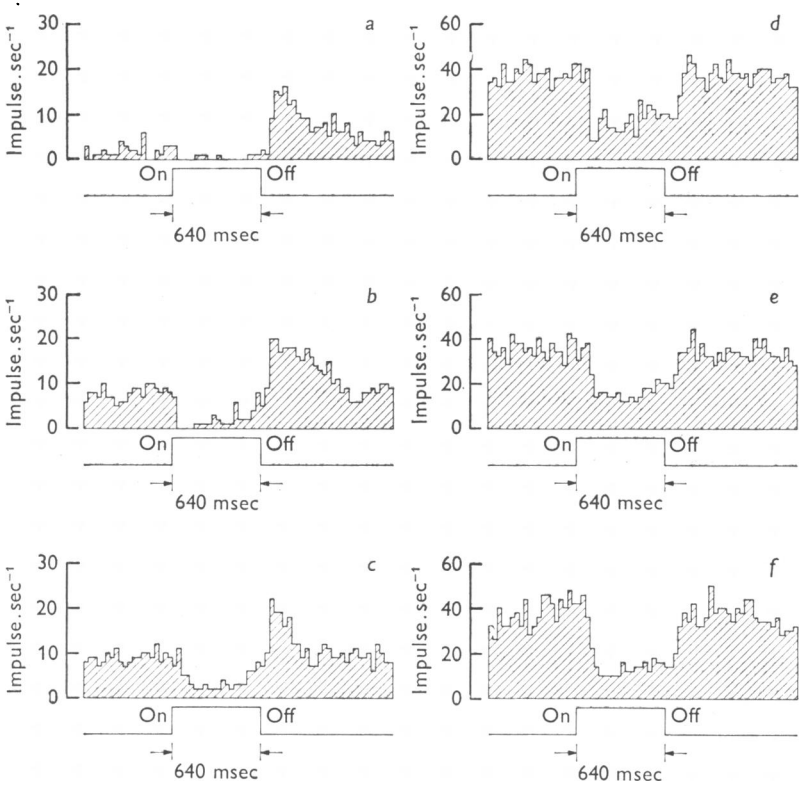

Fig. 3. Post-stimulus time histograms obtained from the centre of an off-centre unit (YY:1) at the following values of background illumination: *a*, 2×10^6; *b*, 2×10^5; *c*, $1{\cdot}8 \times 10^4$; *d*, $1{\cdot}4 \times 10^3$; *e*, $1{\cdot}4 \times 10^2$ photons (523 nm).sec^{-1}.deg^{-2} (via 5·7 mm^2 pupil); *f*, in darkness. The size of the test spot was 0·48° in diameter and its duration was 640 msec.

light which was scattered from the surround on to the much more sensitive centre of the receptive field. A similar change of the response pattern was also observed by stimulating the whole receptive field at the mesopic background level (Fig. 2*c*) and in complete darkness (Fig. 2*f*).

At what value of background illumination does the change of response pattern occur? Fig. 3 shows profiles of responses elicited by stimulating the centre of an off-centre unit (YY:1) with a small light spot (0·48° in

diameter) at various background illumination levels between zero and 2×10^6 photons (523 nm).sec^{-1}.deg^{-2} (via 5·7 mm^2 pupil). The luminance of the test stimulus was adjusted to or near 0·2 $\log_{10}$ unit above the threshold value at each background level. In the range of background illumination between 2×10^6 and $1{\cdot}8 \times 10^4$ photons.sec^{-1}.deg^{-2}, the centre of the off-centre unit gave a compound response showing inhibition at 'on' and excitation at 'off' (Fig. 3*a*, *b*, *c*). When the background level was reduced to or below $1{\cdot}4 \times 10^3$ photons.sec^{-1}.deg^{-2}, the compound response changed into a simple sustained response showing inhibition during 'on' and cessation of the inhibition at 'off'. Therefore the transition of response pattern occurred at a background illumination between $1{\cdot}8 \times 10^4$ and $1{\cdot}4 \times 10^3$ photons (523 nm).sec^{-1}.deg^{-2} (via 5·7 mm^2 pupil) in the scotopic range.

The change of response patterns due to variations of adaptational level occurred not only in the case of common on-centre or off-centre units but also in the case of an extraordinary unit (Yoon, 1970): When the unit was adapted to a background level in the mesopic range, its response showed transient inhibitions at both 'on' and 'off', whereas the response pattern changed into a contrasting form showing transient excitations at both 'on' and 'off' when the background illumination level was reduced to or below $1{\cdot}4 \times 10^3$ photons (523 nm).sec^{-1}.deg^{-2} (via 5·7 mm^2 pupil). The transitions of response patterns were reversible with the change of adaptational level in all cases. In general a response pattern depends also on the luminance of test stimulus (Granit, 1944; Donner & Willmer, 1950) as well as on its size and location in the receptive field (Kuffler, 1953). The above mentioned trend held if the test stimulus luminance did not exceed about 1 $\log_{10}$ unit above the threshold value at each background level.

Change in the spatial distributions of response types and of their sensitivities with adaptational level

Receptive fields were mapped with a small test spot (0·09° in diameter) at two different adaptational levels, one in a mesopic level and the other in darkness. Fig. 4*a* shows spatial distributions of dominant response types and of their threshold values along the nasotemporal axis passing through the centre of the receptive field of an on-centre unit (YAA: 1). At the mesopic adaptational level, the predominant component of the compound 'on-excitatory and off-inhibitory' response of the centre was of 'on-excitatory' type (○) whereas the predominant component of the compound 'on-inhibitory and off-excitatory' response of the surround was of 'on-inhibitory' type (▲). As the test spot moved from the central zone into the surrounding zone, the experimenter had to change the type of response used as a criterion in his subjective judgment of threshold response from

'on-excitatory' to 'on-inhibitory' response. When the same unit was dark-adapted, however, only one type of sustained 'on-excitatory' response (●) was evokable throughout a circular area about 4° in diameter, which would have enclosed the antagonistic surround (▲). This agrees with Barlow *et al.* (1957) who showed that the antagonistic effect from the annular surround of the receptive field disappears during dark adaptation.

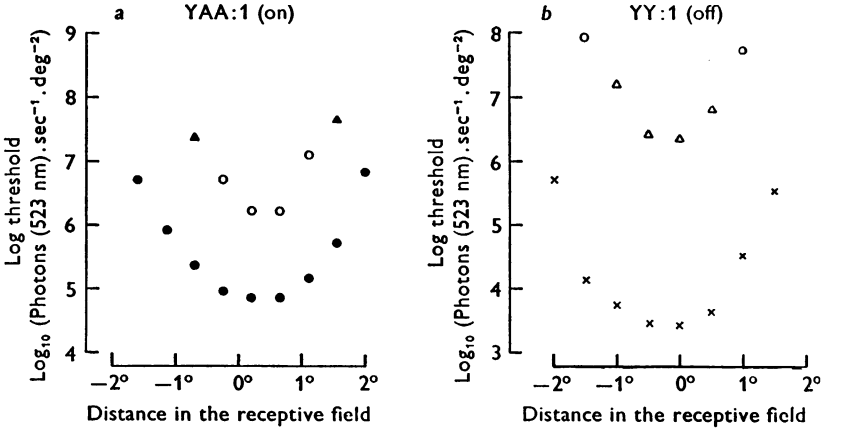

Fig. 4. Spatial distributions of dominant response types and of their visual thresholds along the diameter of receptive field at two different adaptational levels. *a*, on-centre unit (YAA: 1). In darkness, thresholds were determined on the basis of 'on-excitatory' response type (●) throughout its receptive field. At high background illumination, about 2×10^5 photons (523 nm).sec^{-1}.deg^{-2} (via 5·7 mm^2 pupil), however, thresholds were determined on the basis of 'on-excitatory' response type (○) in the central zone and of 'on-inhibitory' response type (▲) in the peripheral zone of the receptive field. The size of test stimulus was 0·09° in diameter and its duration was 640 msec. (*b*) Off-centre unit (YY: 1). In darkness, thresholds were determined on the basis of 'on-inhibitory' response type (×) throughout its receptive field. At high background level, 2×10^6 photone.sec^{-1}.deg^{-2}, thresholds were based on 'off-excitatory' response type (△) in the central zone, and on 'on-excitatory' response type (○) in the peripheral zone. The size of test stimulus was 0·23° in diameter and its duration was 640 msec.

Note that both profiles of threshold distributions along the nasotemporal axis of the receptive field were hyperbolic at the two adaptational levels. It implies that the visual sensitivity of the ganglion cell decreases very rapidly from the centre towards the periphery of its receptive field more or less in symmetry along its diameter (Kuffler, 1953; Rodieck & Stone, 1965; Cleland & Enroth-Cugell, 1968). These hyperbolic profiles of threshold distributions are compatible with the dome-shaped distribution of response

amplitudes along the diameter of a receptive field described by Rodieck & Stone (1965).

Off-centre units showed the same trend of simplification in their receptive field organization in darkness as shown by Fig. 4*b* for an off-centre unit (YY:1). At the mesopic adaptational level, the receptive field of the off-centre unit was organized in two concentric zones, where the predominant component of the compound 'on-inhibitory and off-excitatory' response of the central zone was of 'off-excitatory' type (△) whereas that of the surround was of 'on-excitatory' type (○). In darkness, however, only one type of sustained 'on-inhibitory' response (×) was evokable wherever in the receptive field. In order to obtain lower values of incremental threshold for the centre of an off-centre unit, it was necessary to shift the type of response component used in threshold judgment from 'on-inhibitory' response into 'off-excitatory' response as the adaptational level exceeded a certain critical value.

Correlation between the change in response pattern and the change in sensitivity with adaptational level

Adaptational level affects not only the discharge patterns but also the sensitivities of ganglion cells in the retina. The sensitivity or gain of a ganglion cell may be measured as the inverse of 'quantum/spike ratio', that is, the number of extra photons required to elicit an average of one extra impulse (Barlow & Levick, 1969*a*). Fig. 5 shows a logarithmic plot of quantum/spike ratio versus background illumination for the off-centre unit (YY:1) whose response profiles are shown in Fig. 3. In darkness, the unit required about 13 photons (523 nm) at the cornea to eliminate an average of one impulse from its maintained spontaneous discharges, and the value of its quantum/spike ratio did not change significantly up to a background illumination of $1{\cdot}4 \times 10^3$ photons (523 nm).$\sec^{-1}$.$\deg^{-2}$ (via 5·7 mm^2 pupil). When the background level was increased from $1{\cdot}4 \times 10^3$ to $1{\cdot}8 \times 10^4$ photons (523 nm).$\sec^{-1}$.$\deg^{-2}$, the quantum/spike ratio increased from about 16 to $5{\cdot}6 \times 10^2$ photons (523 nm) at the cornea per one impulse, and it continued to increase as the background level increased, approximately obeying Weber's law. The mean rate of maintained discharges from the off-centre unit showed a significant decrease when the background level was increased from $1{\cdot}4 \times 10^3$ to $1{\cdot}8 \times 10^4$ photons (523 nm).$\sec^{-1}$.$\deg^{-2}$ as shown in Fig. 5. It is interesting to note that the same unit showed also the change in its response pattern between these two levels of background illumination (see Fig. 3).

The same trend held also for the majority of on-centre units as shown by Barlow & Levick (1969*a*): The quantum/spike ratio of their on-centre unit

(EE:1) did not change significantly as the background luminance increased from zero up to about $3{\cdot}4 \times 10^{-4}$ cd/m^2, which is equivalent to background illumination of about 10^3 photons (507 nm).sec^{-1}.deg^{-2} (via 7 mm^2 pupil) (see Fig. 7 of Barlow & Levick, 1969*a*), and the response pattern at the latter background level showed sustained excitation during 'on' and cessation of the excitation at 'off' (see Fig. 8 of Barlow & Levick,

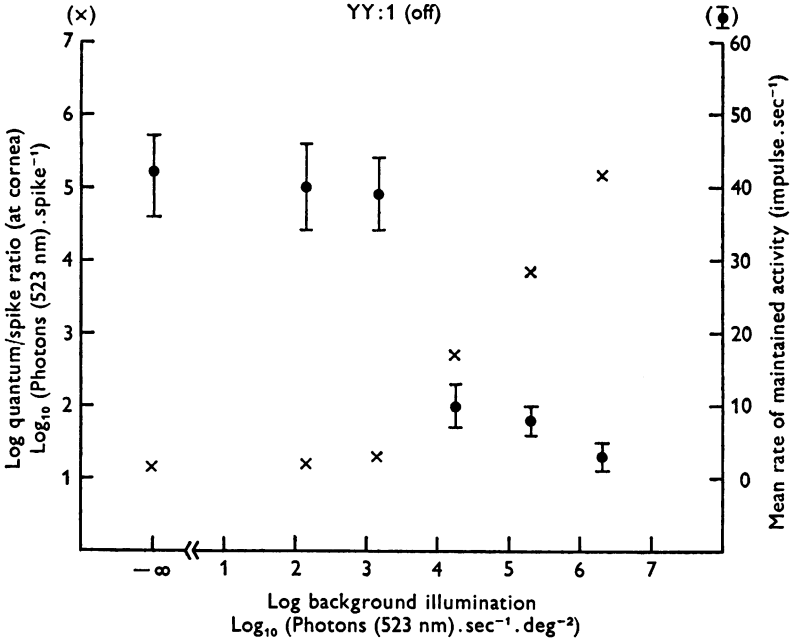

Fig. 5. Changes in quantum/spike ratio and in the mean rate of maintained discharges with background illumination for an off-centre unit (YY: 1). × represents the number of extra photons at the cornea, which were required to eliminate an average of one impulse from the maintained discharges. ⊕ represents the mean rate and the range of S.D. of the maintained discharges.

1969*a*). When the background luminance exceeded the above critical value, the quantum/spike ratio increased and its response pattern became compound with transitory excitation at 'on' and inhibition at 'off' when the background luminance was raised to 3·4 cd/m^2.

DISCUSSION

The present experiments show that response patterns of cat retinal ganglion cells change reversibly with adaptational level: if background illumination did not exceed a critical value, about 10^3 photons

(523 nm).sec^{-1}.deg^{-2} (via 5·7 mm^2 pupil), stimulation of the centre of a receptive field resulted in either sustained excitation (i.e. increase in the rate of impulse discharge) during on-phase of a stationary light stimulus and cessation of the excitation when the light was turned off (on-centre unit) or sustained inhibition (i.e. decrease in the discharge rate) during 'on' and cessation of the inhibition at 'off' (off-centre unit). When the background level exceeded the critical value up to 2×10^6 photons (523 nm).sec^{-1}.deg^{-2} (via 5·7 mm^2 pupil), the sustained responses changed into compound responses with two transient components, either excitation at 'on' and inhibition at 'off' (on-centre unit), or inhibition at 'on' and excitation at 'off' (off-centre unit). These results suggest that response patterns become more complex as the background illumination increases from darkness up to an adaptational level in the mesopic range. At higher background illumination within the photopic range, however, an opposite trend was observed in the cat's retina by Kuffler (1953): a decrease in the background illumination from 19 to 4 metre candles resulted in a change in discharge pattern of the centre of an on-centre unit from 'on' response (i.e. excitation at 'on') into more complex 'on-off' response (i.e. excitations at both 'on' and 'off'). The variability of response patterns under different stimulation conditions makes it necessary to describe a response pattern more explicitly than has been done by just saying 'on', 'off' or 'on-off' response. In the case of the centre of an off-centre unit, for example, its 'off' response would imply the predominant 'off-excitatory' component of the compound 'on-inhibitory and off-excitatory' response at a high background level, whereas the same term would imply the sustained inhibition during 'on' at a low background level. This change of predominance in the response components makes one necessary to shift the type of response component used in threshold judgment in order to obtain lower values of incremental threshold.

It is interesting to note that the effect of background illumination on response pattern may be correlated with its effect on the visual sensitivity of a ganglion cell in the cat's retina. In the majority of both on-centre and off-centre units the relation between background illumination and quantum/spike ratio shows two separate phases as shown in Fig. 5 for an off-centre unit; when the background illumination does not exceed a critical value, about 10^3 photons (523 nm).sec^{-1}.deg^{-2} (via 5·7 mm^2 pupil) a static phase prevails, that is, the quantum/spike ratio does not depend on the level of background illumination. This implies that a ganglion cell maintains its maximum gain (or minimum quantum/spike ratio) regardless of whether the weak light is present or not. The values of quantum/spike ratio in the static phase are extremely low as shown by Barlow *et al.* (1972) that only two or three photons (507 nm) at the cornea are enough

to elicit an average of one extra impulse under optimal conditions. A dynamic phase emerges in the gain control mechanism of a ganglion cell when the background illumination exceeds the critical value: the quantum/spike ratio begins to increase as background level increases, approximately obeying Weber's law (see Fig. 5). The antagonistic interaction between the centre and the surround (Kuffler, 1953; Barlow *et al.* 1957; Rodieck & Stone, 1965). 'Automatic gain control' (Fuortes & Hodgkin, 1964; Rushton, 1965), 'self-inhibition' (Purple & Dodge, 1965) and other mechanisms of gain control should operate only in the dynamic phase, not in the static phase. The present results suggest that a ganglion cell gives simple, sustained response when its gain control mechanism remains inactive at a low background illumination below a critical level, whereas it gives compound response with two transient components of opposite polarities when its gain control mechanism becomes active as background illumination exceeds the critical level.

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