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QUANTITATIVE ASPECTS OF GAIN AND LATENCY IN THE CAT RETINA

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SUMMARY

1. The gain of the central response mechanism and the latency of the pure central response of on-centre ganglion cells were studied by recording from single optic tract fibres the responses evoked by slow square-wave stimuli applied against some steady background.

2. The concept of effective flux was introduced and defined: if any portion of a stimulus extends beyond Ricco's area of complete summation, then that stimulus has an actual flux, equal to the product of its area and luminance, but it also has an effective flux which is that fraction of its actual flux which equals the actual flux of another stimulus which, when it falls entirely within Ricco's area, evokes an isobolic pure central response or has the same adaptive effect upon the central response mechanism as the first stimulus.

3. The most significant finding was that when the cell responded with a pure central response to the *incremental* flux (the square wave) applied against a steady effective background flux, then the gain and the latency were functions exclusively of the sum of the two fluxes (the total flux), not of the incremental or background flux as such. This shows that the level of field adaptation of the central mechanism is reset within the latent period of the response to an incremental flux.

4. Increment sensitivity curves based on isobolic suprathreshold responses all had the same slope of 0·9, when the log of the incremental flux was plotted against the log of the total flux. A plot of log latency against log total effective flux had a slope of $-0{\cdot}1$.

5. The stimulus–response relation derived from (3) and (4) was

$$R = (K_1 . \triangle F_e)/F_{et}^{0{\cdot}9}$$

and

$$L = K_2/F_{et}^{0{\cdot}1},$$

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where R is the response amplitude, F_{et} the total flux, $\triangle F_e$ the incremental flux and K_1 and K_2 are constants.

INTRODUCTION

When a light stimulus falls upon the receptive field of a retinal ganglion cell in the cat the response usually reflects the mutually antagonistic contributions of both the centre and the surround response mechanism. One approach to ultimately establishing the precise manner in which these two mechanisms interact to yield the mixed ganglion cell response is first to determine quantitatively the responses of each mechanism in isolation. In an earlier investigation (Cleland & Enroth-Cugell, 1968), sensitivity distribution and summation within the central response mechanism of on-centre cells were examined. The present paper, a continuation of the investigation of the central response mechanism alone, reports studies on latency and gain in on-centre cells, using the criteria for identification of purely central responses and for recognition of minimal surround antagonism which were established in the earlier work. From these results we have been able to obtain the stimulus–response relationship for the central response mechanism.

METHODS

Preparation and recording have been described in detail in an earlier paper (Cleland & Enroth-Cugell, 1968). In brief, single fibre activity was recorded in adult cats with tungsten electrodes (Hubel, 1957) stereotaxically placed in the optic tract. Light anaesthesia was maintained with urethane administered intravenously, eye movements were suppressed with gallamine triethiodide. Contact lenses with an artificial pupil (diameter ranging from 4·0 to 4·8 mm) focused the light stimulus on the retina.

It is well recognized that unfailing immobilization of the eye is absolutely necessary for reliable quantitative measurements of responses from single units in the visual system (Cleland & Enroth-Cugell, 1966; Rodieck, Pettigrew, Bishop & Nikara, 1967; Chow & Lindsley, 1968). During the present experiments it became evident that the general condition of the animal is an equally important requirement for obtaining meaningful and repeatable responses. In an effort to achieve optimal general conditions fluid balance was maintained with intravenous infusion of 5% glucose (w/v) in saline. Both the e.c.g. and the mean arterial pressure were monitored. The blood pressure was usually 135–145 mm Hg before infusion of gallamine triethiodide which caused a transient rise, often followed by a decline to 100–120 mm Hg over several hours. When the animal was in good condition, i.e. when the blood pressure remained at 100–120 mm Hg or above and the heart rate remained at 160–220/min, maintained activity of the retinal ganglion cells was high during low general illumination; thresholds were low and varied only over approximately 0·3 log units from cell to cell and cat to cat (measured against the same background with a 3·87° stimulus); suprathreshold response magnitudes were repeatable for hours within a few per cent. On the other hand, when the blood pressure fell below 100 mm Hg and the heart rate became slow ganglion cell thresholds rose by

1–3 log units, suprathreshold responses became erratic, maintained activity tended to be low and often showed various patterns of rhythmicity although the eye was exposed to constant illumination. In two cats, satisfactory blood pressure and heart rate were maintained with intravenous infusion of levarterenol bitartrate.

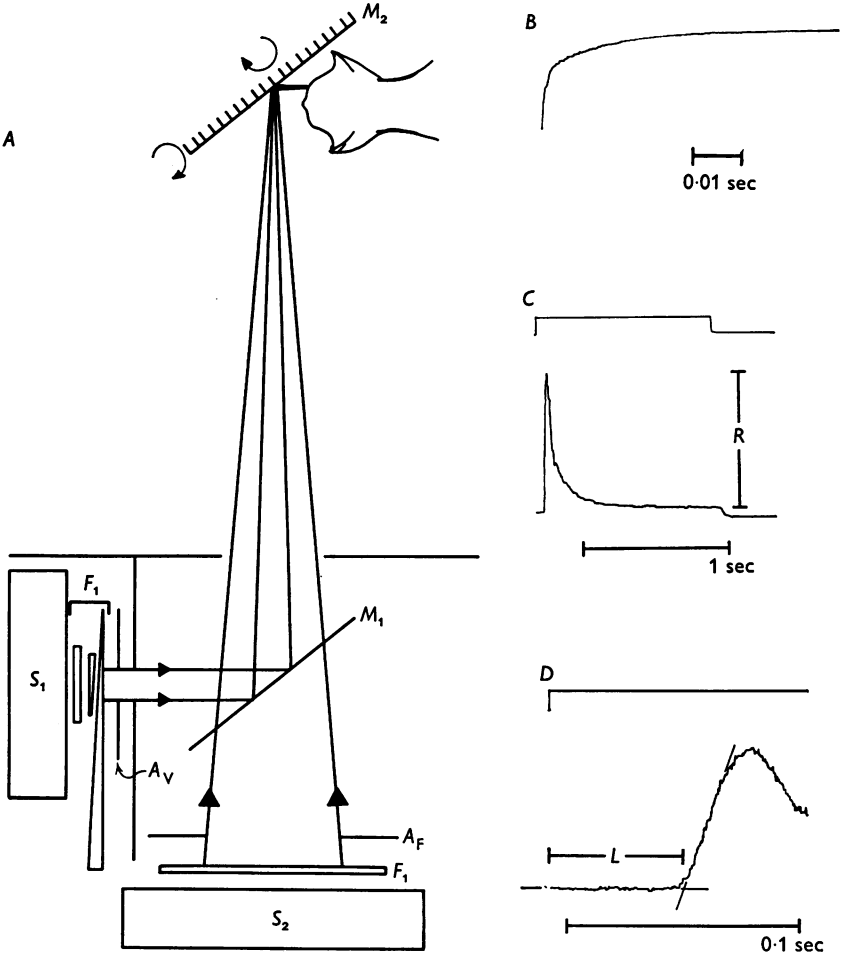

Fig. 1. *A*, Diagram showing the two light sources, S_1 and S_2, and the optics of the system. The variable apertures of S_1 are contained in a disk A_V. The fixed aperture of S_2 is located in A_F. F_1 and F_2 are filter holders. S_1 is superimposed on S_2 with the half silvered mirror M_1. The two stimuli were moved in the visual field of the cat by adjusting the position of the mirror M_2. *B*, Time course of the onset of a 0·4 c/s square-wave stimulus (S_1) recorded with a 1P42 photocell (time to 60 % is 1 msec, to 90 % is 15 msec). *C*, Sixty responses to a square-wave stimulus (0·4 c/s) averaged on the Enhancetron and displayed on an *x–y* recorder. Response amplitude (*R*) was measured between the two horizontal lines passing through the response peak and the final steady level. *D*, Same response as in *C* on a faster time scale to indicate manner in which latencies have been measured.

Results are presented from seven cats on a total of fourteen on-centre cells with receptive fields widely distributed over the visual field. Only if the general condition of the animal was good, as judged by the criteria given above, and the action potential was held long enough to complete an experiment, have the results been presented.

The stimulator (Cleland & Enroth-Cugell, 1968) was modified so that source S_1 (Fig. 1*A*) delivered only a square-wave stimulus modulated at 100%; two frequencies, 4 or 0·4 c/s, were used. Source S_2 provided an unmodulated circular (13° diam.) background. Coarse luminance changes of S_1 and S_2 were provided by Wratten neutral-density filters whose densities were determined with a MacBeth Densitometer (Model EP-1000). Fine, continuous luminance attenuation was provided for S_1 by a calibrated neutral density wedge and for S_2 by changing the current through the fluorescent tubes. S_1 was superimposed upon the centre of S_2 with a mylar thin film mirror, coated with stainless-steel for approximately 50% transmission. The maximum luminance, as presented to the cat, was 200 cd/m^2 for S_1 and 400 cd/m^2 for S_2, measured with a Salford Instrument Photometer. The optic path was 88 cm and the diameter of the S_1 apertures varied from 1·7 to 60 mm (0·11–3·87°). The rise time of the square-wave stimulus was determined with a 1 P42 phototube and is shown in Fig. 1*B*.

With the aid of a smoothing network and a digital memory oscilloscope (Enhancetron 1024) retinal ganglion cell spikes were converted into a plot of instantaneous pulse density (Cleland & Enroth-Cugell, 1966) and averaged over sixty individual responses to the square-wave stimulus (0·4 c/s). Two properties of such averaged responses were measured: (1) amplitude and (2) latency. Amplitudes were measured on an oscilloscope during the experiment and as all data were recorded on magnetic tape both amplitude and latency of averaged responses could also be measured at a later time on an oscilloscope or on a x–y plot (for details see Fig. 1*C* and *D*).

Throughout every experiment the mean spike frequency was continuously graphed on a heavily damped servo recorder (time constant 5 sec; Heath-Kit EUW-20A). This constituted a valuable check on the stability of the preparation in two respects: (1) even small eye motions showed up as fluctuations in the mean rate of discharge, (2) at each background level a constant stimulus which produced some small response resulted in a mean spike frequency pattern that did not vary much from cell to cell. A mean firing rate which at a certain background illumination was substantially lower than usual, or rhythmic, signified poor general condition of the animal.

RESULTS

The concept of effective flux

Before describing the present results the concept of effective flux, which rests upon the results of an earlier paper (Cleland & Enroth-Cugell, 1968), must be introduced. In that study a circular stimulus (modulated at 4 c/s) was centred on the receptive field and then for each of a series of stimulus diameters the luminance was determined which rendered a pre-existing response from the ganglion cell just inaudible. The log of the sensitivity (reciprocal of this threshold luminance) was then plotted against the log of the diameter to yield the *area–sensitivity* curve. This curve consists of two linear segments joined by a near-discontinuity, or knee

(genu). For stimuli of subgenual diameters, the curve rises with a slope of 2, in accordance with Ricco's law, i.e. *equal* fluxes (area × luminance) evoke the same threshold response, but for stimuli of supragenual diameters the curve is horizontal, revealing that *increasing* fluxes (increasing area but constant luminance) are required to evoke a threshold response from the central response mechanism. It is clear therefore that for *supragenual* stimuli only a portion of the *actual* flux is effective, the portion of the flux which does not fall on receptors belonging to the central response mechanism being without effect upon the purely central response. Thus for any *supragenual* stimulus we may define an *effective* flux, F_e, as being equal to the *actual* flux of a subgenual stimulus yielding a purely central threshold response. A convenient feature of the area-sensitivity curve for the central response mechanism is that the curve can be constructed from only two points. One from a subgenual stimulus that establishes the linear segment with a slope of two, and the other from a *supra*genual stimulus that establishes the horizontal segment. These two linear segments intersect at an *intra*genual point which corresponds to a diameter d_t, and area A_t', of the receptive field within which Ricco's law applies (except for the narrow genual curvature). For any one ganglion cell, d_t was found to be unaffected by background luminance.

A light falling upon the retina diminishes the sensitivity to a subsequent increment in light, a phenomenon known as field adaptation; this very fast adaptation occurs at retinal illuminations too low and too brief to induce bleaching adaptation (Rushton, 1965; Blakemore & Rushton, 1965*b*). The behaviour of field adaptation was explored at the ganglion cell level by Cleland & Enroth-Cugell (1968); a circular test *stimulus* of constant diameter (0·14°), modulated at a constant depth, at a constant frequency, about a constant mean luminance, was first centred on the receptive field. Then an unmodulated *adapting* field was similarly centred; for each of a series of diameters of the *adapting* field, its luminance was adjusted until a pre-existing response to the fixed *test stimulus* just disappeared. The log of the reciprocal of this adapting luminance (actually the filter density at threshold) was then plotted against the diameter to yield an *area–adaptation* curve. Precisely as in the preceding case, this curve exhibited a rising segment of slope two for subgenual diameters and a horizontal segment for supragenual diameters of the adapting field. The point of intersection of these two linear segments again defined a diameter D_t, and area A_t, for that portion of the receptive field of the ganglion cell within which (excepting the genu) Ricco's law applies to field adaptation. When both area–sensitivity and area–adaptation curves were obtained for the same cell, the values of d_t and D_t were identical. Thus the retinal area over which the central response mechanism summates visual signals and the retinal

area from which it collects adaptive information are co-extensive, and the concept of effective flux can be extended to field adaptation.

The above definition of effective flux was based on threshold experiments but is of course also valid at higher flux levels; any *supra*genual stimulus yielding a *supra*threshold response, generated by the central mechanism alone, has an *effective* flux which is equal to the actual flux of a *sub*genual stimulus yielding an isobolic purely central response.

In experiments employing background fields which cover the entire receptive field it is important to know the adaptive effect of each background luminance used. In the following experiments A_t was therefore determined for every cell so that the effective background flux could be calculated as the product of A_t and background luminance I. A_t was obtained using either threshold or suprathreshold responses elicited against a background of 4×10^{-3} cd/m^2 (stimulus centred on the most sensitive region of the receptive field). For *threshold* responses the stimulus was modulated at 4 c/s and the threshold luminance determined at one *sub*genual stimulus diameter of 1·7 mm (0·11°) and at one *supra*genual diameter of 60 mm (3·87°). The average of three determinations for each size was obtained. For *supra*threshold responses the stimulus was modulated at 0·4 c/s and 60 responses averaged on the Enhancetron; at diameter 0·11° the stimulus luminance was adjusted to evoke a small, purely central, suprathreshold response. The diameter was then changed to 3·87° and the luminance which yielded an isobolic central response found. Whether the isobolic responses were threshold or suprathreshold, A_t was calculated from the following formula (equivalent to the graphic construction):

$$A_t = (\tfrac{1}{4}\pi . 0{\cdot}11^2 . I_{0{\cdot}11})/I_{3{\cdot}87}.$$

The area–sensitivity experiments together with the results on isobolic *supra*threshold responses elicited by subgenual stimuli (Cleland & Enroth-Cugell, 1968) mean, of course, that the *magnitude* of the purely central response is a function of (effective) flux rather than luminance. It is only reasonable to expect that the same is true for the *latency* of purely central responses and this has already been experimentally demonstrated for stimuli of *sub*genual diameters (Cleland & Enroth-Cugell, 1968); isobolic suprathreshold responses could be superimposed without lateral translation (i.e. had the same latency) as the stimulus luminance was varied but the flux kept constant. In this paper we show that responses to *sub*genual and *supra*genual stimuli have the same latency as long as the two effective fluxes are the same (although the luminances are unequal). These experiments, on five cells, were performed as follows: the background, S_2, was 4×10^{-3} cd/m^2 and the stimulus, S_1, diameter set to 0·11°, was positioned

in the centre of the most sensitive portion of the receptive field. At a modulation frequency of 0·4 c/s a stimulus luminance which produced a small suprathreshold response was chosen. The stimulus diameter was than changed to 3·87° and the luminance adjusted to yield an isobolic response, i.e. the effective fluxes of the two stimuli were equalized. (By measuring the magnitude of averaged responses on the oscilloscope it was always possible to determine the required luminance to within 0·05 log. units.) The response latency for the 0·11° and 3·78° diameter stimuli for the five cells were 57–56, 59–58, 57–56, 59–60 and 60–61 msec; that is, the latency remained constant within experimental error. It is thus true in general that the latency of purely central responses is not a function of luminance (or area) but must be a function of effective flux.

Gain-setting and latency

The ultimate goal is to establish the stimulus–response relationship for the central mechanism alone. For this purpose we can accept only pure central responses and only stimuli (or those portions of them) that fall in the receptive field of the central mechanism. A key characteristic of any stimulus–response relationship is the *gain*, defined in general terms as the ratio of response magnitude to stimulus magnitude. In particular, a change in field adaptation can be described as a light-induced change in gain. It is clear that the gain for the central response mechanism of the retinal ganglion cell does not stay constant and it will be shown below that the setting of the gain is accomplished quite rapidly, which would be in accord with the observations on field adaptation in psychophysical experiments (Rushton, 1963; Blakemore & Rushton 1965*b*).

Before going further it is necessary to identify the particular aspects of the light and the characteristics of the response which are appropriate for the central response mechanism. In the cat the retinal summation area for visual signals and for adaptive effects within the central response mechanism are coextensive and here the spatial distribution of stimulus and adaptive lights is irrelevant (see above). Thus, the appropriate aspect of the light is flux, rather than luminance, and, specifically, *effective* flux since whatever falls outside the receptive field centre was shown neither to influence the response magnitude nor to affect the field adaptation level of the central response mechanism (Cleland & Enroth-Cugell, 1968).

In the present experiments background flux is continually present, and an incremental flux is superimposed in the form of a square wave. The *total effective flux*, F_{et}, can then be partitioned into its two components (*a*) the *background flux*, F_{eb}, calculated as the product of luminance and A_t, since it is supragenual, and (*b*) the *incremental* flux, ΔF_e which, being subgenual, is entirely effective.

In such a procedure, it is clear that the *stimulus* flux, whose response is observed at the ganglion cell, is the *incremental* flux. But what is the appropriate *adaptive* flux that sets the gain of the central response mechanism? Traditionally the incremental stimulus required for a threshold response in psychophysical experiments (e.g. Barlow, 1957) or for isobolic neurophysiological responses (e.g. Weinstein, Hobson & Dowling, 1967) have been plotted as though the gain were set by the background. There is no obvious way in which the central response mechanism of the retinal ganglion cell can differentiate between background and incremental fluxes when both are present. Hence it seems reasonable to suggest that it is the total flux, F_{et}, which sets the gain and quite possibly within the latent period.

This postulate has consequences which can be tested experimentally. It dictates that if background and incremental fluxes are varied in a complementary fashion so that the *sum* of their effective fluxes remains constant, then the gain should remain constant. This would yield a direct proportion between the response magnitude and *either* background flux, F_{eb}, or incremental flux ΔF_e, with only a sign difference. Moreover, latency too is a function of effective flux (p. 79), and if indeed it is a function of the total effective flux (F_{et}), rather than of the background (F_{eb}) or the incremental flux (ΔF_e), then, as the two latter fluxes are varied in a complementary fashion to yield a constant total effective flux, the latency should stay constant.

Before presenting the results of experiments where the total flux F_{et} remained constant, the reasons why we chose our particular measure of response magnitude must be stated. A slow square-wave stimulus amounts to a step increase ('on') followed by a step decrease ('off') in stimulus luminance. For on-centre cells, to which we have restricted our experiments, the purely central response is characterized by its latency period, L, easily measured in milliseconds, terminated by an abrupt increase in spike frequency to a peak followed by a slower decline to a steady-state level, all of this transpiring within the on-period of the square-wave stimulus (Cleland & Enroth-Cugell, 1968). At 'off' the spike frequency falls abruptly to near zero or zero level, then rises slowly to a new steady value which as a rule is nearly the same as the steady level of the on-periods. In this situation it is reasonable to consider the transient of the on-response as the physiologically significant signal. Further, if the gain changes *during* the on-latency then the firing level just prior to the 'on' and the peak firing frequency are generated during *different* gain-settings, whereas the peak and the steady level of the on-period are generated during one constant gain-setting. Therefore we measured the transient response between the peak and the steady level during the on-period. We have

called this the response amplitude and symbolized it by R (see Fig. 1*C*).

Experiments where incremental and background fluxes varied in a complimentary manner to yield a constant total flux were carried out with five ganglion cells. Having measured A_t for the cell in question so that the effective background flux could be calculated, a subgenual diameter was chosen for the stimulus which was centred on the receptive field. Then for each complementary combination of unmodulated background flux and incremental flux modulated at 0·4 c/s, the ganglion cell response was recorded for measurement of response amplitude and latency. When it was possible to maintain a cell for sufficient time, the entire set of complenentary flux combinations was repeated in reverse order; otherwise the repeatability of the response was checked only at one or two of the first combinations.

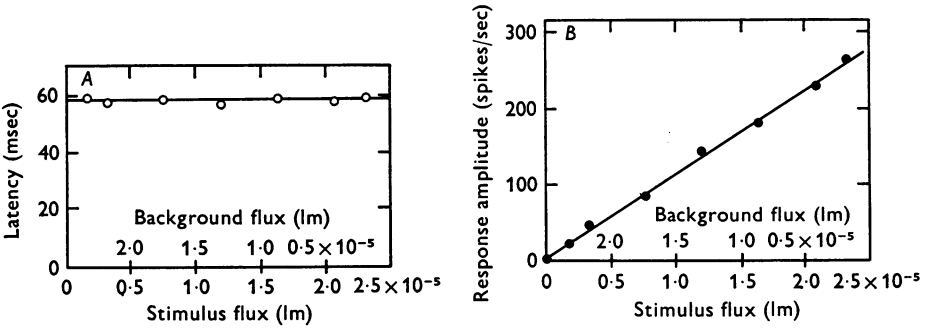

Fig. 2. Latency (L) and response amplitude (R) for one cell (D_t = 3·1°) measured under conditions of constant total effective flux (F_{et}). Note that horizontal axis gives both stimulus flux (ΔF_e) and background flux (F_{eb}) and that the sum of these two fluxes remains constant. Stim. freq. 0·4 c/s, stim. diam. 0·65°, pupil diam. 4·8 mm.

The latent period was found to be remarkably constant in the face of complementary changes in background and incremental fluxes, as plotted for one cell in Fig. 2*A*. In none of the five cells could a significant slope be determined by regression analysis (Table 1). The response amplitude was found to be directly proportional to the incremental flux (negatively for background flux) as illustrated for the same cell in Fig. 2*B*. For each of the five cells, regression analysis yielded a significant slope, but an insignificant intercept, as displayed in Table 1. The slope of the relationship, is, of course, the gain, which remained quite constant in the face of complementary changes in background and incremental fluxes. This is a convincing demonstration that neither background nor incremental fluxes

TABLE 1. Responses to complementary changes in background and incremental effective fluxes

		Latency			Response amplitude			
Cell no.	Total flux F_{et} (mlm)	n	Mean ± S.E. (msec)	Slope ± S.E. (msec/mlm)	n	Mean (spikes/sec)	Intercept ± S.E. (spikes/sec)	Slope ± S.E. (10^3 spikes/sec mlm)
21/2	$1{\cdot}2 \times 10^{-2}$	7	64·0 ± 0·5†	− 205 ± 133*	8	115	3 ± 12*	20 ± 2†
22/2	$0{\cdot}3 \times 10^{-2}$	5	78·3 ± 0·4	− 166 ± 544	7	186	− 4 ± 9	126 ± 4
22/3	$2{\cdot}5 \times 10^{-2}$	7	58·3 ± 0·3	9 ± 43	8	161	6 ± 6	15 ± 1
22/5	$0{\cdot}1 \times 10^{-2}$	6	55·7 ± 0·7	− 1620 ± 1900	7	175	5 ± 4	269 ± 4
22/7	$1{\cdot}3 \times 10^{-2}$	5	57·8 ± 0·8	590 ± 245	7	94	4 ± 5	15 ± 1
Mean	—	5	—	− 278 ± 364*	5	—	3 ± 2*	—

* Not significantly different from zero at 10 % level. † Significantly different from zero at 0·1 % level.

n For small responses amplitude could be measured but not latency, hence difference in the two n columns.

alone set the gain and latency for the central mechanism; the only alternative is that the total effective flux sets the gain and the latency and does so within the latent period.

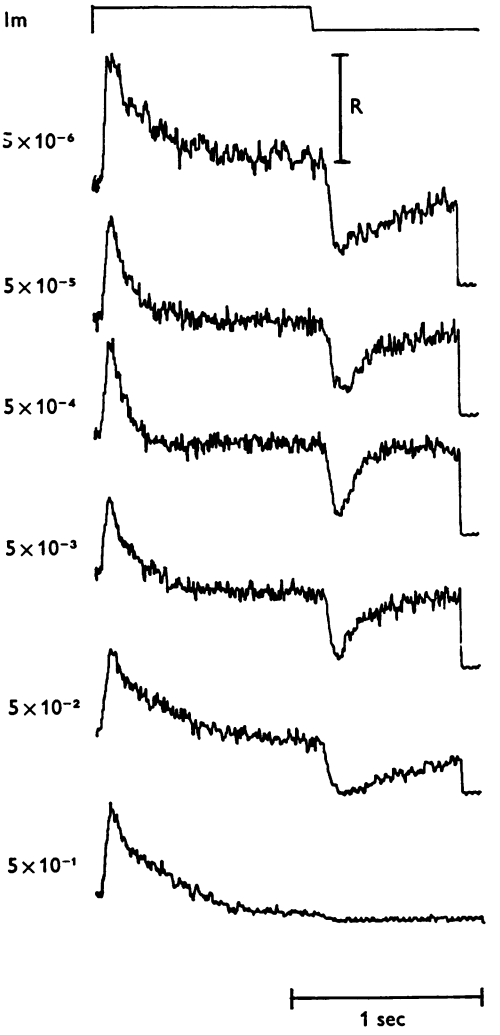

Fig. 3. Average responses upon which the latency and increment sensitivity curves of Fig. 4 are based (D_t = 1·5°). Deflexion upwards of top trace indicates stimulus onset. Horizontal portion at end of each response trace indicates zero spikes/sec. Background flux (F_{eb}) is indicated to the left of the responses. Stim. freq. 0·4 c/s, stimulus diam. 0·65°. Pupil diam. 4·8 mm. R = 70 spikes/sec, indicated in uppermost response.

Gain and latency as functions of total effective flux, F_{et}

Since the preceding experiments demonstrated that the gain ($R/\Delta F_e$) and latency of the central mechanism remain unaffected by changes in either background or incremental fluxes alone they must be functions of the total flux:

$$R/\Delta F_e = f(F_{et}), \tag{1}$$

$$L = g(F_{et}). \tag{2}$$

The simplest means of evaluating these two functions is the method in which one measures the incremental flux required to yield an isobolic response amplitude for successive values of background flux. Symbolizing a *constant* response by R_i, eqn. (1) becomes

$$\Delta F_e = R_i/f(F_{et}). \tag{3}$$

To evaluate the functions f and g, ΔF_e and L must be plotted as functions of total flux, F_{et}, rather than as functions of background flux, F_{eb}.

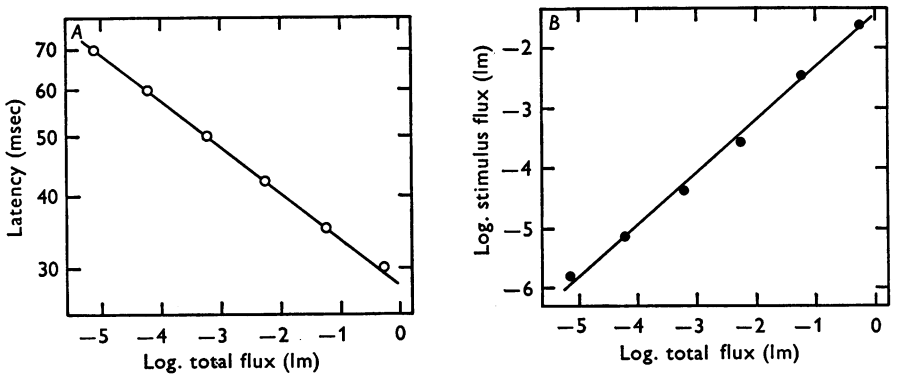

Fig. 4. Latency and increment sensitivity for the cell in Fig. 3. To calculate the total effective flux ($F_{et} = F_{eb} + \Delta F_e$), stimulus diam. 0·65° and D_t 1·5° were used.

Incremental experiments were conducted on seven cells in the following way. The supragenual, non-modulated background was initially set at a luminance of 4×10^{-3} cd/m^2, and A_t having been measured, F_{et} could be calculated. A subgenual stimulus ($< \frac{1}{2}A_t$), centred on the receptive field, was modulated at 0·4 c/s. Its luminance was adjusted to yield a small suprathreshold response, R, which served throughout as the isobolic response (R varied from cell to cell but was always between 50 and 70 impulses/sec). The background luminance was then increased in one log unit steps, allowing time after each step for the spike frequency to settle to a steady-state value; for each of these background levels the stimulus

TABLE 2. Latency and gain for changes in the total flux

Cell no.	A_t (cm²)	n	Latency: Slope ± S.E. (log sec/log. lm)	Latency: Mean* (msec)	Incremental gain: Slope ± S.E. (log. lm/log. lm)	Incremental gain: Mean total flux* F_{et} (mlm)
14/7	4·2	6	−0·077 ± 0·001†	46	0·878 ± 0·027†‡	1·75
16/1	8·6	5	−0·085 ± 0·005	43	0·875 ± 0·022	10·06
17/7	1·8	5	−0·099 ± 0·001	47	0·910 ± 0·001	0·33
18/1	10·2	5	−0·136 ± 0·009	40	0·895 ± 0·006	1·72
18/2	10·2	6	−0·105 ± 0·001	36	0·881 ± 0·022	4·55
18/3	3·1	6	−0·110 ± 0·004	36	0·893 ± 0·023	1·41
18/5	1·8	6	−0·093 ± 0·004	40	0·908 ± 0·019	0·87
Mean	—	7	−0·101 ± 0·007†	—	0·891 ± 0·017†‡	—

* Geometric mean. † Significantly different from zero at 0·1 % level.
‡ Significantly different from one at 1·0 % level. Total flux range in log units equals $n-1$.

luminance was adjusted until the isobolic response was again elicited. If it appeared possible, on the basis of spike amplitude, to record for a sufficient length of time, the series was repeated for the same steps in background in *de*creasing order; otherwise the initial background level only was repeated. The range of background luminance covered 5 log. units in four cells, 4 log. units in two cells and 3 log. units in one cell.

Figure 3 presents the Enhancetron-averaged isobolic responses obtained from one cell. When latencies and incremental fluxes were plotted as functions of total flux, F_{et}, the resulting curves were nicely rectified by double log transforms, as illustrated for the same cell in Fig. 4. Regression lines were fitted to these log-transformed data from each of the seven cells, with results presented in Table 2. The value of the intercept constants depends upon the size of A_t and the magnitude chosen for the isobolic response, the significance lying in the slope constants. For the seven cells these average $0{\cdot}891 \pm 0{\cdot}017$ S.E. for the ΔF_e function and $-0{\cdot}101 \pm 0{\cdot}007$ S.E. for the latency function. We may consider these values as approximately $+0{\cdot}9$ and $-0{\cdot}1$; they are exponents in the untransformed relationships, which when expressed in the form of eqns. (1) and (2), become

$$R/\Delta F_e = K_1/F_{et}^{0{\cdot}9} \tag{4}$$

$$L = K_2/F_{et}^{0{\cdot}1} \tag{5}$$

Thus, both gain and latency are negative power functions of total effective flux. Equation (5) is, of course, the stimulus–response relationship for latency.

Stimulus–response relationship

Rearranging eqn. (4) yields a *general* form of the stimulus–response relationship

$$R = (K_1.\Delta F_e)/F_{et}^{0{\cdot}9} \tag{6}$$

or expressed in an alternate form by substituting $(F_{eb} + \Delta F_e)$ for F_{et}

$$R = (K_1.\Delta F_e)/(F_{eb} + \Delta F_e)^{0{\cdot}9}, \tag{6a}$$

in which ΔF_e is the *visual stimulus* flux and the *total* flux, F_{et} or $(F_{eb} + \Delta F_e)$, is the *adaptive* or *gain setting* flux. Thus, the background flux (F_{eb}) *as such* is not one of the factors that determine the response amplitude of the central mechanism. Nor does the background *as such* set the gain; *only* in its capacity of one of the two components that together constitute the *total* flux will the background flux affect gain and response amplitude.

Under special conditions these equations reduce to more convenient relationships. For example, when background and incremental fluxes are varied in complementary fashion so that the total flux F_{et}, remains constant, eqn. (6) clearly becomes a family of direct proportions with one

member for each constant value of $F_{e'}$, this was previously established by experiment (p. 81). As another example, when background flux, F_{eb}, is held constant, eqn. (6*a*) becomes a family of curves with one member for each constant value of F_{eb}; if the latter is zero, we have the limiting member of this family:

$$R = K_1.\Delta F_e^{0.1} \quad \text{for} \quad F_{eb} = 0. \tag{7}$$

Figure 5 is presented as an aid in visualizing some of these relationships.

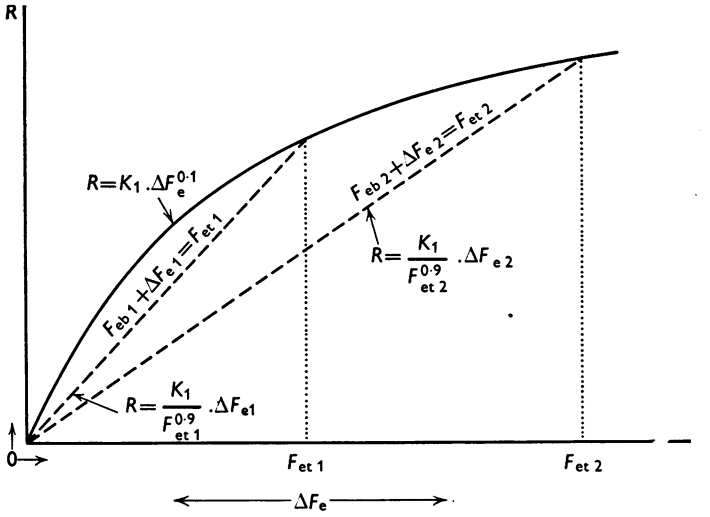

Fig. 5. Schematic representation of stimulus–response relationships. F_{et1} and F_{et2} represent two different total effective fluxes.

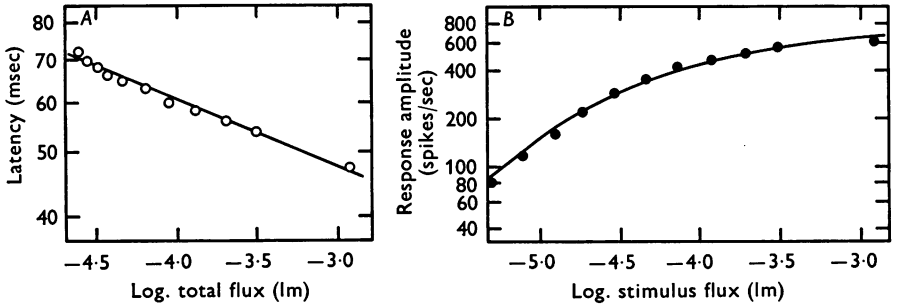

Fig. 6. Experiment in which the background (F_{eb}) remained constant while the stimulus (ΔF_e) was successively increased (D_t = 2·58°). Stim. freq. 0·4 c/s, stim. diam. 1·42°. *A*, Latencies plotted against total effective flux ($\Delta F_e + F_{eb}$). *B*, Response amplitude plotted against stimulus flux. The line is the stimulus–response curve calculated from eqn. (6*a*). Its vertical position was chosen to provide a suitable fit over the central region.

Although eqn. (4), from which all others are derived, was established experimentally one additional experimental check on these derivations was made for the special case when F_{eb} in eqn. (6*a*) is constant. The steady background was 4×10^{-3} cd/m^2, the stimulus (0·4 c/s) was of subgenual diameter. Average responses were obtained for a series of incremental fluxes starting with one which just barely elicited a suprathreshold response. Then successively larger increments, ranging over 2·5 log. units, were applied and the logarithm of the response amplitude was plotted against the logarithm of the incremental flux. Equation (6*a*) was then converted to log. form and plotted on the same graph; a value for the constant, K_1, was chosen so that the curve passed through the experimental points in their mid-range. The results are presented in Fig. 6*B*. The fit is excellent, even the extreme values falling well within the experimental error of the predicted curve. Also, a plot of the log of the latency against the log of the total flux (Fig. 6*A*) yielded a straight line with a slope of $-0{\cdot}105$, in accordance with the previously established stimulus–latency equation (5).

DISCUSSION

The most significant finding of the present study is that the stimulus–response relationship for pure central on-responses of cat retinal ganglion cells (with centre-surround organization) is one in which the total effective flux sets the gain for the response to an incremental flux, which lasts longer than the critical duration. For the special case in which background and incremental fluxes are varied in complementary fashion so that the total flux, and hence the gain, remain constant there will be a simple proportionality between the stimulus and the response. These relationships have in the past been obscured by the use of mixed responses showing interaction between the antagonistic centre and surround mechanisms as well as by the practice of expressing stimulus–response relationships in terms of luminance rather than in terms of *effective* flux.

For example, with flashes of one or a few seconds duration no consistent relatonship to stimulus luminance could be established for the mixed responses elicited with diffuse retinal illumination in early studies on the cat (Granit, 1947). Stone & Fabian (1968) accepted only pure central responses, evoked by 1 sec flashes, and their results are therefore those that can best be compared to ours. However, they pooled results from several cells and plotted magnitude of response against stimulus *luminance* (their fig. 3*a*). Now, gain is determined by the *sum* of effective stimulus and background fluxes which, for any individual cell, necessarily increases as successively more luminous stimuli of constant area are applied against some constant background luminance. Hence, for any one cell, in Stone's

& Fabian's experiments, the gain decreased as stimulus luminance increased. Assuming for simplicity that the stimulus area was not only subgenual but also equal for all the cells, then any point on their luminance axis represents *both* the same stimulus *luminance* and the same effective stimulus *flux* for all the cells. But only if A_t had been determined and the background luminance adjusted accordingly could the effective background flux have been kept identical for all the different cells. And then, and only then, would each individual point on the luminance axis (fig. 3*a*, Stone & Fabian, 1968) have represented the same *total* effective flux, and hence gain, for all the cells pooled. Since the effective background flux was not rendered equal for all the cells it would not seem permissible to plot response magnitudes against stimulus luminance and to pool the results from different cells. This probably explains why the stimulus–response relationship obtained by Stone & Fabian differed from ours.

It was also shown in this investigation that the *latency* of the pure central response, just as the gain, depends upon the *total* flux alone. Consequently, when background and incremental fluxes were varied in a complementary fashion the amplitude of the responses varied while their latency stayed constant (Fig. 2). On the other hand, when at different background fluxes the flux increment was adjusted to yield isobolic responses, the total flux varied and this yielded a series of responses of constant amplitude but with different latencies (Figs. 3, 4*B*). The findings under these two stimulus conditions are different from those which have been generally reported (as well as from those in our Fig. 6*A*, *B*). Stimuli of increasing 'strength' (constant area) have in the past commonly been flashed against a steady background as for example in fig. 4 of Ogawa, Bishop & Levick (1966). Such increases in stimulus luminance, keeping stimulus area and background luminance constant, yield a successively larger *total* effective flux and hence a decreased gain and latency. However, the increasing *stimulus* flux offsets the effect of this lower gain with the result that the response gets larger as the latency gets shorter. Clearly the response magnitude (peak firing rate) and latency in the experiment by Ogawa *et al.* qualitatively behave as predicted by our eqns. (5) and (6*a*). Quantitative comparison of their results with ours is prohibited by the differences in the two sets of experiments. Stone & Fabian (1968) did not publish any latency data for their purely central responses.

Traditionally psychophysical increment sensitivity curves are plots of threshold *luminance* against background *luminance* and the slopes of such curves are known to vary with duration and size of the stimulus (e.g. Barlow, 1957; Blakemore & Rushton, 1965*a*). Our increment sensitivity determinations were all carried out with the same stimulus duration (1·25 sec) but with varying areas (always smaller than $\frac{1}{2}A_t$) and the results

were plotted in terms of the incremental *flux* required for an isobolic suprathreshold response, against *total effective flux*. The probably most noticeable difference between the psychophysical and our increment sensitivity curves is that all our curves rose with the same slope of 0·9 even though the stimulus size varied. However, for the pure central response of ganglion cells one cannot expect stimulus area to affect the slope of the increment sensitivity curve. This follows from the previous finding (Cleland & Enroth-Cugell, 1968) that the magnitude of the purely central response is a function of *flux* alone and that A_t, for any one cell, is the same at all backgrounds. Consideration of Fig. 8 of that paper shows that the vertical distance (= difference in log. threshold luminance) between any two area-sensitivity curves is a constant, i.e. it is the same at both very small and very large diameters, and this is only true because A_t is a constant. Thus for a given change in background the change in stimulus luminance required to elicit the isobolic response would be the same for any given stimulus size, leading to a constant slope of the increment sensitivity curves whatever the stimulus diameter. This would not be true if A_t was a function of background conditions.

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