CHANGES IN
THE MAINTAINED DISCHARGE WITH ADAPTATION LEVEL
IN THE CAT RETINA

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SUMMARY

1. The mean rate, impulse interval distribution, and pulse number
distribution of the maintained discharge of ganglion cells in the retina of
the cat have been studied after prolonged adaptation at different lumi-
nance levels.

2. From a state of complete dark adaptation up to a luminance of about
5 × 10⁻³ cd/m² (viewed through a 7 mm² pupil) the mean rate of on-centre
units increases. From darkness up to a somewhat higher luminance the
mean rate of some off-centre units decreases, but others show little change.

3. Above 10⁻² cd/m² the mean rate ceases to show a regular relation
with adaptation level. On units often decrease and then increase again at a
higher level. Rhythmical fluctuations are common near 10⁻² cd/m²,
especially if the retina is not in first class condition. Mean rates above
70/sec and below 1/sec are very rare at any adaptation level.

4. Over the range where mean rate increases monotonically with adapta-
tion level, it is shown that the surround of on-centre units does not inhibit
and off responses cannot be elicited. When the monotonic increase is
slowed or reversed it becomes possible to elicit responses from the sur-
round. We suspect that the surround exerts a sustained, tonic, inhibiting
effect at higher adaptation levels, thus holding down the maintained
discharge.

5. There are rare units, forming less than 1 % of those isolated, that show
a regularly increasing frequency with increase of adaptation level above
10⁻² cd/m². These units have concentric ‘on’ and ‘off’ zones in their
receptive fields, but the responses to rapidly changing stimuli are sluggish

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and they have an unusually regular maintained discharge. They have been tentatively called ‘luminance units’.

6. The impulse-interval and pulse-number distributions of on-centre units change predictably with adaptation level; the variance of the pulse number distribution is usually several times the mean at very low adaptation levels, but only a fraction of the mean at high levels. Off-centre units do not show predictable changes. Luminance units fire more regularly, and have narrower pulse-number and impulse interval distributions than other concentric units.

7. A simple model is proposed to account for the statistical characteristics of the maintained discharge of on-centre units.

**INTRODUCTION**

When single-unit recordings from the mammalian retina were first made the presence of a low frequency discharge of impulses, even in complete darkness, was one of the unexpected features (Granit, 1941; 1955; Kuffler, 1953). At first it seemed reasonable to attribute this maintained discharge to the unusual condition of the retina, or to factors like electrode pressure or anaesthesia, but it is now generally agreed that these are not responsible; maintained activity can be recorded from nerve fibres as well as ganglion cells (Bornschein, 1958), and is present in unanaesthetized preparations thought to be in the best possible condition (Kuffler, FitzHugh & Barlow, 1957). The constant presence of an irregular background of activity is important because classical psychophysical theories of threshold do not take it into account.

Recently we have been interested in describing the ‘threshold’ behaviour of single ganglion cells as signal/noise discriminations (Barlow & Levick, 1969). We showed that three factors are involved in determining whether a stimulus causes a response large enough to rise out of the noise level, namely the quantum/spike ratio, the duration of the response, and the irregularity of the maintained discharge. We know that the quantum/spike ratio changes a great deal at different background luminances, roughly parallelling the changes in incremental threshold, and there are also changes in the time course of the response that probably underlie the known changes in temporal integration and resolution: Our main purpose in this paper is to give the results of a more detailed study of the third factor, the statistical characteristics of the maintained discharge at different adaptation levels. These change relatively little, which is surprising in view of the enormous changes in the rate and irregularity of the quantal bombardment of the receptors. We have been led to conclude that the variable contribution of the surround plays an important part in keeping the maintained dis-
charge relatively constant at different luminances. We were also interested in how signals for the mean luminance of the retinal image are derived from the maintained discharge, which has previously been reported to change unpredictably with adaptation level. We have found small but consistent changes in the ordinary types of on- and off-centre units, and in addition there is a rare type of unit where the relation is more precise and reliable.

METHODS

The cats were prepared under ethyl chloride or methoxyfluorane (Metofane), ether and surital, then maintained on 70% N₂O, 27% O₂ and 3% CO₂ and a relaxant mixture of gallamine triethiodide (Flaxedil) at 5 mg/kg.hr and d-tubocurarine at 0·5 mg/kg.hr. An artificial pupil of area 7 mm² was always placed close to the cornea. Action potentials were picked up from retinal ganglion cells by usual methods, and recorded and analysed on an ND 180 multichannel scaler. Distributions of the numbers of impulses per unit time (number distributions), or distributions of the intervals between impulses (interval distributions) were compiled by suitable programmes; this was usually done after the experiment on samples of maintained discharge that had been recorded on magnetic tape. The memory of the multichannel scaler was read out on a teletype which yielded both a printed list of numbers and also a punched paper tape. These tapes were analysed by a small electronic computer (Mathatronics, Inc., Waltham, Massachusetts).

During the experiment the mean rate was continuously monitored on a slowly moving chart recorder, giving records such as those shown in Fig. 1. Luminances were measured with a visual photometer (SEI, Salford Instruments), converting to scotopic units by estimating the colour temperatures of the sources. All results are expressed in scotopic cd/m², since we are working mainly in the scotopic range (Barlow & Levick, 1968). Our methods and equipment have been more fully described previously (Barlow & Levick, 1969).

RESULTS

Mean rate and luminance

Figure 1 shows samples from the record of the mean rate of an on-centre unit obtained on a slowly moving chart recorder; these were taken over a period of 5½ hr while the adapting luminance was reduced in 1 log unit steps from 3·4 to 3·4 × 10⁻⁶ cd/m², then to complete darkness. Pupil area was 7 mm². The time of the luminance changes, and periods of stimulation, are shown below the trace; samples of the maintained discharge, each of duration 1/₃ sec, are shown above the mean rate trace. Transient changes of mean rate occur when the adapting luminance is changed, and during the periods of stimulation. Spontaneous fluctuations also occur at intermediate adaptation levels (3·4 × 10⁻² and 3·4 × 10⁻³ cd/m²). Below 3·4 × 10⁻³ cd/m² a more consistent relation is established and there is a monotonic decline in mean rate with reduction of adapting level. Notice also the greater irregularity of the maintained discharge at those low levels, as shown in the sample records.
Figure 2 shows the results on this unit plotted as a function of adapting luminance. The estimates for the decreasing series of luminances are shown as white lines in the records of Fig. 1 and are plotted as filled circles in Fig. 2. The adapting luminance was increased subsequently in 1 log unit steps and these values are shown as crosses in Fig. 2. It is clear that the monotonic relation with luminance is interrupted just above \(10^{-3}\) cd/m²,

and the mean rate declines, and then starts to increase again at the higher levels. This was the usual pattern for on-centre units, and the lower half of Fig. 2 shows the average results obtained on fourteen units. The luminance at which the low level relationship was interrupted lay in the range \(10^{-2}\) to \(10^{-3}\) cd/m², and the interruption was always present in on-centre units held long enough to study thoroughly.

Figure 3 shows the results for twelve off-centre units. Some of these show the approximate inverse of the relation for on-units, namely, an initial decrease of maintained discharge with increasing adapting intensity,
but little change above about $10^{-1}$ cd/m². Others, however, show little change with adapting luminance at any level. Figure 3 shows averages of all off-units, and also an attempt to separate the six units that changed, and the six units that did not change, with luminance; the conclusion is that some change more than others, but it is doubtful if a sharp division into two classes is justified.

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Fig. 2. The relation between mean rate of the maintained discharge and luminance of adapting field in a single on-centre unit (top), and the average of fourteen on-centre units (bottom); pupil area 7 mm². The single unit showed the same features for the declining (●) and the rising (×) sequences of adaptation levels; the firing rate was unstable at two levels, and the highest and lowest values maintained for a minute or more are indicated. In the lower figure the length of the line indicates the standard error of the mean of the fourteen units. There is much variation from unit to unit, but the mean shows the principal features of the single unit's behaviour.
Contribution of the surround to the maintained discharge

We show elsewhere (Barlow & Levick, 1969b) that 10^-3 cd/m^2 is about the lowest adaptation level at which it is possible to elicit responses from the off surround of on-centre units. It seemed possible that the interruption of the monotonic increase with luminance might be associated with this known change of receptive field organization (Barlow, Fitzhugh & Kuffler, 1957) and this was tested in the experiment of Fig. 4. The mean rate of an on-centre unit is plotted as a function of luminance, and is obviously similar to Fig. 2. In this unit we also tested the response to an annular stimulus, and compared this with the response to a small central stimulus at the same incremental luminance. At high adapting levels the

Fig. 3. Maintained discharge of 12 off-centre units. Six show a marked decline with increase of adaptation level (A), but 6 show little change (B). The average of all 12 shows a distinct decline (C).
MAINTAINED DISCHARGE AND ADAPTATION

annulus gives an off response, as expected, and at low adaptation levels it gives an on response, possibly as a result of scattered light falling on the receptive field centre. It will be seen that the off response and on inhibition appear at the adapting luminance at which the monotonic increase of maintained discharge is being interrupted. One is led to conclude that the

Fig. 4. Maintained discharge and surround effectiveness. Post-stimulus time-histograms at the top show responses to a central spot and an annulus at three different adapting luminances. At each adapting level the spot and annular stimuli were of equal luminance: at the lowest level the annulus gives a weak ‘on’ response, possibly as a result of scattered light, at the middle adapting level it gives no response, and at the upper level it gives inhibition at ‘on’. The monotonic increase of maintained discharge with adapting luminance is slowed at the intermediate level and reversed at the upper level.
maintained discharge represents the difference between tonic excitatory influences from the centre and tonic inhibitory influences from the surround.

The variable behaviour of the off-centre units may also fit this explanation, for we know (H. B. Barlow & W. R. Levick, in preparation) that the surround does not always become ineffective at low luminances in off-centre units.

Rhythmic fluctuation of mean rate. On a number of occasions the mean firing rate of a unit was found to undergo a series of slow oscillations. A wide variety of patterns appeared at different times. Similar behaviour has frequently been observed by others (Granit, 1941; Kuffler et al. 1957; Levick & Williams, 1964; Rodieck, 1967). In many cases these rhythmic fluctuations appeared when the condition of the eye or the preparation as a whole was in doubt because of traumatic eye puncture, clouding of the cornea, retinal oedema, excessive dosage with anaesthetics or tubocurarine, respiratory obstruction, or towards the end of a very long experiment. However, fluctuations in rate also appeared when we could find no fault with the preparation; these were relatively minor and infrequent and appeared only in some units and over only a limited range of adaptation levels (see Fig. 1). The unstable range was usually just above $10^{-3}$ cd/m$^2$, where we know the surround is becoming effective, and in the same preparation firing rates were usually stable at higher and lower levels. At the critical backgrounds, cycles of fluctuation were often provoked by stimuli of large spatial extent, or by movement of large targets in the peripheral visual field (‘periphery effect’, McIlwain, 1964; Levick, Oyster & Davis, 1965). It is possible that the factors controlling the mean firing rate are normally rather critically balanced, especially in the region where the surround is beginning to exert a subtractive effect. Instability might occur normally under special luminance conditions but abnormally from a wide variety of non-specific noxious influences.

Statistical parameters

Even when there are no rhythmical fluctuations the maintained discharge is highly irregular, and we were interested in seeing if there were any changes in the statistical characteristics with adaptation level. This is important not only in determining how many extra impulses are required for reliable detection, but also in considering the mechanism of production of the maintained discharge and in comparing the retina with other photodetecting systems.

The change in the discharge of impulses that results from a stimulus is due to a change in the number of quantal absorptions in the receptors, and it is natural to suppose that the maintained discharge itself also results from quantal absorptions from the adapting light. This view is strengthened
by the fact that, for weak stimuli, the number of added impulses is proportional to the number of added quanta (Barlow & Levick, 1969). Furthermore, experiments (unpublished) in which the intensity of the adapting field was locally either decreased or increased showed that there was no discontinuity in the relation between quantal absorptions and

numbers of spikes in the range around the maintained discharge, though saturating type non-linearity was evident as the impulse frequency became high, and obviously a threshold-type non-linearity was present at zero-frequency of discharge.

Fig. 5. Pulse-number and impulse-interval distributions for three examples of maintained discharge. A, B, C are from an on-centre unit at a background of 3.4 cd/m²; D, E, F from the same unit dark-adapted. Notice the pronounced change in the shape of the impulse interval distribution, though a gamma distribution (continuous lines) can be selected to fit both of them. The change in shape is not shown up as clearly in the pulse-number distributions, to which symmetrical Gaussian curves have been fitted. G, H, I are from an off-centre unit at a background of 3.4 cd/m². Gaussians fit the pulse-number distributions, but the gamma distribution matched to the mean and variance is not a good fit to the impulse-interval distribution of this off-centre unit.
If the maintained discharge is caused by quantal absorptions, then the fluctuations of the maintained discharge should be related to the fluctuations in quantal absorptions. We have therefore measured various statistical parameters of the maintained discharge as a function of adaptation level. The changes in these parameters should reflect the fact that the absolute amplitude of the quantum fluctuations increases as $\sqrt{I}$, while their relative amplitude decreases as $1/\sqrt{I}$ ($I = $ adapting field luminance).

In order to obtain a measure of the irregularity of the discharge we looked first at the impulse interval distribution, about which quite a lot has already been written (Kuffler et al. 1957; Gerstein & Kiang, 1960; Levick & Williams, 1964; Herz, Creutzfeld & Fuster, 1964; Rodieck, 1967). Our work on the detection of threshold signals (Barlow & Levick, 1969) leads us to believe that the distribution of the number of pulses in samples of a fixed duration is more important than time between successive impulses. Therefore we have also looked at two members of the family of impulse number distributions, namely for 100 msec and 1 sec sampling durations. These three distributions are not, of course, independent of each other. The interval distribution is more easily related to the mechanism of production of the maintained discharge, but the number distributions are more important in discussing the effect of ‘noise’ on discrimination and threshold.

Figure 5 shows samples of each type of distribution. The histograms in the same row are from the same unit under the same adaptation conditions, the same tape record of maintained discharge being used to generate the three distributions. The tapes were selected to demonstrate a considerable range of different types of discharge. A gamma distribution has been fitted to the interval distributions, a Gaussian to the number distributions. In every case the first and second moments of the distribution were calculated to fit those of the experimental histograms. The Gaussians fit quite well, except for truncation errors. Although the gamma distributions fit the very differently shaped distributions $C$ and $F$, the fit is not satisfactory for the off-centre unit shown in $I$ (Fig. 5).

*Change of parameters with adaptation.* In Fig. 6 certain parameters of the experimental histograms have been plotted as functions of adapting luminance for an on-centre and an off-centre unit. Consider first the upper left set, which refer to the 1 sec number distributions of an on-centre unit. The points for the mean (circles) show a monotonic rise as the rate rose over the whole range. The points for the variance (squares) drop, as the discharge became more regular at the higher adaptation levels. Note that these two lines cross between $10^{-3}$ and $10^{-2}$ cd/m$^2$; at lower luminances the variance is greater than the mean, at higher luminances it is less. Before considering the third set of points (triangles) turn to the lower left set of
MAINTAINED DISCHARGE AND ADAPTATION

These are the parameters of the interval distributions for the same unit. The mean interval (filled circles) declines as the impulses are packed more tightly at higher luminances, and the standard deviation (filled squares) declines rather more rapidly.

The third sets of points (triangles) in both top and bottom parts of the figure represent measures of the regularity of the discharge, and in both cases they show an increase. The reasons for the choice of \( \mu(m)/V(m) \) and

\[ \mu^2(t)/V(t) \]

arise from a possible model of the generating mechanism, and will be explained in the Discussion. For this on-centre unit the results can be summarized by saying that the mean rate increases with luminance, and it also becomes more regular. Four other on-centre units showed similar trends, though there was a good deal of variability.
The results in the right half of Fig. 6 are characteristic of the three off-centre units we have examined, and we cannot make satisfactory generalizations. A decline in mean rate was visible, though, as shown in Fig. 3, this is less prominent than the rise with on-centre units (Fig. 2). The regularity, as indicated by $\mu(m)/V(m)$ for the number distribution and by $\mu^2(t)/V(t)$ for the interval distribution, did not seem to show any reliable trends, but the mean was always greater than the variance.

Serial correlation coefficients. These will affect the relation between impulse-interval and pulse-number distributions, but their influence on threshold is the same as their influence on the pulse-number distribution. Therefore for estimating sensitivity even large serial correlations would be immaterial, but they would of course be interesting from the point of view of retinal mechanisms. Rodieck (1967) has made a thorough study of serial correlations, but so far as we know he did not investigate the very irregular, slow, maintained activity that occurs in on-centre units after thorough adaptation to low luminances. We therefore analysed some records of such maintained activity, but in spite of the bunched appearance of the records we have not found evidence of large serial correlation coefficients.

Luminance units

These are distinguishable from the commoner on- or off-centre concentric units by a number of criteria. First, and probably most important functionally, is the fact that the mean rate shows a regular, monotonic, relation to the adapting luminance in the range above $10^{-2}$ cd/m². Secondary characteristics are important in identifying these units when they are isolated: one usually notices first that the maintained discharge is much more regular than usual, and when they are tested with moving stimuli the responses are found to be sluggish, lacking the high frequencies that give the ordinary concentric units their crisp discharge.

Unfortunately these units are very rare; we positively identified a total of only three units, all on-centre, out of many hundreds of units held long enough to identify. Only one was held long enough to yield results such as those shown in Figs. 7 and 8. The numbers of impulses in successive 1 sec periods were stored in the analyser, and Fig. 7 shows the graphical read-out for three 512 sec periods while the adapting luminance was lowered in steps and then raised again. The final values at each luminance are plotted on double logarithmic co-ordinates in Fig. 8. Figure 9 shows interval and number distributions for another luminance unit compared with an ordinary on-centre unit.

These units would appear to be capable of giving fairly reliable information about luminance for values over $10^{-2}$ cd/m², that is over the range where the monotonic relation of the ordinary units is interrupted. Because
these units are rare we cannot feel certain that they represent a separate class: they may represent the extremes of a normal distribution. However, they certainly seem qualitatively dissimilar when first isolated, and this impression is confirmed when one again records from an ordinary unit after losing a suspected ‘luminance unit’.

![Diagram of maintained discharge of a luminance unit at different adaptation levels.](image)

**Fig. 7.** Maintained discharge of a luminance unit at different adaptation levels. Impulses were counted for 1 sec periods in successive channels of the analyser; there are gaps in the record while the memory contents were printed out. Notice the regular decline with decreasing luminance, and the return to nearly the same values when the luminance was increased.

**DISCUSSION**

The most interesting physiological question is the origin of the maintained discharge and the reason for the changes in its mean rate and regularity with adaptation level. The real problem here is to explain why these do not change more when the mean rate and regularity of the quantal absorptions in the receptors are changed by many orders of magnitude, but two aspects will be considered before describing mechanisms to account for the relative constancy of the maintained activity. These are the meaning of the mean rate as a luminance signal and of its irregularity as a limit to sensitivity, and the relation of our findings to previous work on the maintained discharge and on psychophysical limits to visual performance.
Mean rate and luminance signals

Previous reports have tended to emphasize that the maintained discharge changes irregularly with luminance (Kuffler et al. 1957; Rodieck, 1967) and thus could not provide a reliable signal for luminance or for the control of pupil area. We think there are two important reasons why the changes we report here have not previously been found. First, is the fact that the regular behaviour only occurs at very low levels, below $10^{-2}$ cd/m$^2$ with our 7 mm$^2$ pupil. At higher levels the mean rate of on-centre units often shows a small decrease with increased luminance, and such results have given rise to misleading generalizations. Of course the effect of completely extinguishing the light has often been tested, but one cannot expect a unit to settle down to equilibrium activity for many minutes after a large step-down of background. If there is a small proportion of bleached rhodopsin one may expect spurious light signals to continue until it is resynthesized (Barlow & Sparrock, 1964), and this appears to be an unusually slow process in the cat.

Straschill (1966) examined the firing rate during the presentation of a large uniform light stimulus kept on for not longer than 10 min, and he
observed that the ongoing discharge settled down to a steady level monotonically and linearly related to the logarithm of light intensity. The retinal illuminations produced were mostly above the strongest applied in our experiments and since his preparation was returned to darkness for 8 min between presentations there is some doubt as to whether an equilibrium was ever reached despite his statistical controls on the discharges.

In a few cases he avoided the periods of darkness and a more detailed evaluation of this form of his experiment would have been of considerable interest in extending upward the range of our own investigations.

It is not easy to explain the increase in maintained activity in darkness that Arduini & Pinneo (1962) found in most of their records from the optic chiasma. They used focal illumination, and it is hard to assess the illumination of the receptive fields of the fibres near their recording electrode; also in some preparations they found the opposite results. We would expect an over-all decrease in the massed activity of the optic nerve in darkness, for on-centre units decrease more than off-centre units increase (Figs. 2
and 3), but this would not necessarily be the case if on-centre and off-centre ganglion cells do not have the same mean axon diameters, nor at luminances above \(10^{-2} \text{cd/m}^2\) (7 mm\(^2\) pupil).

Previous reports failed to show how the signals from the retina could convey any information about the average luminance of the retinal image. Our results show that there are small but consistent changes in the discharge of most on- and off-centre units. In addition there are special units where the relationship with luminance is more precise and reproducible; their rarity is a sufficient explanation why they have been missed. On the basis of the three units we have found, it is obviously risky to conclude that there is a functional set of units making appropriate central connexions to enable them to represent luminance specifically. If there is, one may hope to study them further by finding a site where they can be regularly recorded. DeValois (1960) has reported well sustained responses from neurones in the pregeniculate nucleus of the monkey, and the pupilloconstrictor pathway mapped out in the cat by Magoun & Ranson (1935) would be worth exploring.

**Maintained discharge as ‘noise’**

In our treatment of retinal responses as signal/noise discriminations (Barlow & Levick, 1969) we showed that the stimulus strength required for reliable detection varies directly with the standard deviation of the pulse number distribution for an analysis period chosen to match the expected duration of the response. The important question here is, ‘How much does this standard deviation change with adaptation level?’ Using the figures for variance plotted in Fig. 6 (1 sec analysis period), the standard deviation of this on-centre unit changes from a maximum of 6·6 at low luminance to 2·8 at the highest level tested, 6 log units above the low level. Four other on-centre units (excluding the luminance units) showed a total range of 8 down to 1·5. The off unit of Fig. 6 varied irregularly between 3·2 and 5·6, three other off-centre units extending the range down to 2 and up to 6·3. Considering the fact that the measured thresholds increase with illumination by a factor of at least 1000 over this range of luminances, it will be seen that the changes in the standard deviation of the pulse-number distributions are relatively unimportant. This small change in the ‘noisiness’ of the maintained discharge is more remarkable when one considers that the mean rate may change by a much bigger factor; this means that increases of mean rate are usually accompanied by increased regularity, and the records in Fig. 1 show this clearly.

The remarkably small changes in the irregularity of the maintained discharge suggest that there may be a homoeostatic mechanism tending to hold it constant, and the result of a deliberate attempt we made to increase the
noise of the retinal output is worth recalling (Barlow & Levick, 1969). By substituting an irregularly moving pattern of dots for a uniform field of the same mean luminance we succeeded in increasing the standard deviation of the pulse-number distribution 3 times, but it would have increased very much more if the quantum/spike ratio had been linked only to the mean luminance and thus had remained unchanged. The quantum/spike ratio in fact increased 7 times, thus greatly reducing the change in the irregularity of the background discharge.

**Dark light and the maintained discharge.** In psychophysical studies the natural way of expressing the 'noisiness' of the visual system is as a certain intensity of 'dark light' (Barlow, 1957). The principle is similar to expressing the dark current of a photocell by the light intensity that produces the same value of photocurrent, and a measure of this kind seems necessary to make sense of a wide range of psychophysical findings (Barlow, 1964). The question will be asked whether it is meaningful to specify visual noise as an adapting field intensity when the results of this paper indicate that changes of this intensity cause only small changes in the noise at the ganglion cell output. Doubts on this point would be justified if the performance of the retina did not change, but the number of quanta required to elicit an additional impulse changes greatly with adapting luminance, and it also changes during dark adaptation. These changes in quantum/spike ratio must obviously be taken into account in relating a noise level specified at the input (i.e. the dark light) to a noise level at the output (i.e. standard deviation of pulse number). This problem arises especially in interpreting the work of Hughes & Maffei (1965), who followed the maintained activity during dark adaptation and found that it changed much more rapidly and over a smaller range than the threshold. They concluded that the maintained discharge did not arise from spontaneous firing of receptors, but this is not justified without considering changes in quantum spike ratio, and it has been criticized on other grounds by Rodieck (1967). There is thus no evidence against the view that maintained activity arises in the receptors. The question whether it arises from thermal isomerization of rhodopsin will be considered elsewhere.

**Retinal mechanisms**

The input to the retina is the fluctuating spatio-temporal sequence of quantal absorptions in the receptors, and its output is the train of impulses in each of the optic nerve fibres. The question to be discussed here is whether we can account for the statistical parameters of the maintained discharge by known properties of the ganglion cells and their receptive fields. For some, at least, of the on-centre, units we think a simple model may explain our results satisfactorily, but it is likely to be necessary to
postulate special mechanisms generating the maintained discharge of off-centre units.

Mean rate. From the results shown in Figs. 2, 3 and 4, it is clear that the mean rate increases monotonically with adapting luminance up to the level at which the surround enters. Above this point, centre and surround weigh against each other, and mean rate may either increase or decrease with increasing luminance. It is as if the ganglion cells at adapting levels above about $10^{-2}$ cd/m² (with 7 mm² pupil area) acquired a differential input. Thus it now appears that centre and surround, taken separately, each have maintained outputs in response to maintained inputs, possibly behaving similarly to *Limulus* (Hartline & Graham, 1932). This is independent confirmation of the picture we develop elsewhere from different evidence (H. B. Barlow & W. R. Levick, in preparation).

Irregularity. We have considered various mechanisms that might account for the statistical irregularity of the discharge. The first model gives exact predictions about the distributions, but the parameters are seriously wrong. The second gives less exact predictions on the form of the distributions, but correctly predicts the order of magnitude of the irregularity of the maintained discharge.

We know that it usually requires many additional quantal absorptions to elicit an extra impulse. Call this number $s$, and let us suppose that for given adaptation and stimulus conditions there is no variation around this average figure: when $s$ quanta have been absorbed, an impulse is generated, when $2s$ have been absorbed, the second impulse is generated, and so on. If such a scaler is driven by an input that follows the Poisson distribution expected for quantal absorptions, the interval distribution for the output pulses is a gamma distribution,

$$P(t) = \frac{\lambda a^{-1} e^{-\lambda t}}{\Gamma(a)}.$$

With an ideal scaler, the parameter ‘$a$’ of this distribution is equal to the scaling factor $s$, and it can be shown that $a = [\mu(t)/\sigma(t)]^2$ (Marriott, 1958).

Similarly, one can estimate the hypothetical scaling factor from the pulse-number distribution. The number of quantal absorptions in a fixed time interval will follow a Poisson distribution, and its variance will be equal to the mean number of absorptions within this interval: $V(n) = \mu(n)$. After scaling, the mean number of output pulses is $\mu(m) = \mu(n)/s$, and if one neglects quantization errors, $V(m) = \mu(n)/s^2$. Rearranging these to eliminate $\mu(n)$, $s = \mu(m)/V(m)$. These estimates of $s$ from the impulse-interval and pulse-number distributions are the figures plotted as triangles in the lower and upper part of Fig. 6, where they were previously described simply as measures of regularity.

Note that the apparent scaling factors calculated from interval and
number distributions are roughly, but not exactly, equal, and that both rise at higher adaptation levels. However, the actual values pose a serious problem. According to the model, the rate of the postulated driving process is the rate of the output pulses times the scaling factor, that is $\mu^2(m)/V(m)$ for the number distribution and, $\mu(t)/V(t)$ for the interval distribution. These should be proportional to the mean rate of quantal absorptions, and hence to the adaptation level, but this is very far from being the case, and the calculated figures are too low by several orders of magnitude at high luminances. There is also another curious feature. A gamma distribution is predicted, and the experimental distributions fit rather well; however, this fit extends to the cases where the variance is greater than the mean and the gamma parameter $\alpha$ has fractional values. This is not explicable by scaling.

There are two simple ways of modifying the model. In the first the notion is retained that the rate of quantal absorption divided by the scaling factor gives the mean rate of the maintained discharge, but we suppose that the scaling is imperfect so that the irregularity of the maintained discharge is largely caused by added noise, and is not attributable to quantum fluctuations, at least at high luminances. In the second, we introduce a property we already know about, namely the inhibiting influence of the surround which holds down the mean rate of the maintained discharge. With this modification we expect the standard deviation of the quantal absorption rate divided by the scaling factor to equal the standard deviation of the pulse-number distribution of the maintained discharge, and we do not make exact predictions about the mean rate of the output. The two modifications can be distinguished by direct measurements of the scaling factor, that is by determining the quantum/spike ratio. The results so far favour the second modification; the quantum/spike ratio for the receptive field centre is very low in the dark-adapted state, and in many units it rises approximately as the square root of the adapting luminance, thus explaining why the standard deviation of the pulse-number distribution changes so little. It seems likely that the fluctuations of the maintained discharge are mainly caused by the quantum fluctuations over the centre of the receptive field, but the mean rate depends upon the balance between tonic influences from centre and surround.

There appears to be hope of giving a complete picture of how the irregular maintained discharge is generated, but our optimism applies only to the on-centre units; we have not yet made sense of the on-going discharge of off-centre units.
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