Exp. Brain Res. 25, 279–290 (1976)

Experimental Brain Research

Maintained Activity of Cells in the Tree Shrew's Optic Tract

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Summary. The maintained activity of different types of ganglion cells in the tree shrew's retina has been investigated in darkness and different adaptation luminances, with particular reference to on-centre sustained and transient cells.

The firing rate of on-centre sustained cells rises with increasing luminance up to 5.10^{-2} W/m^2 (human photopic equivalent 5.10^4 cd/m^2) whereas, for on-centre transient cells no simple relationship between luminance and activity could be found.

The ratio of mean and standard deviation (regularity) of the interval length of sustained cells increases with light intensity, while in most transient cells a constant ratio is observed.

Various kinds of interval histograms are observed for sustained units: exponential, gamma, bimodal and other types. Transient cells tend to fire in bursts with correspondent bimodal interval histograms.

The first order serial correlation coefficient is positive for the majority of sustained cells and negative for most transient cells.

It is argued that the final statistical properties of the maintained activity of retinal ganglion cells are mainly determined by the retinal circuitry between photoreceptors and ganglion cells.

Key words: Retinal ganglion cells – Spontaneous activity – Adaptation.

Introduction

Retinal ganglion cells show a maintained discharge in light and dark-adapted conditions (cf. Granit, 1941; Kuffler et al., 1957). The sequence of action potentials in the cat's retina has a random character, and the statistical distribution of intervals has been compared to gamma-distributions or an exponential distribution both with an initial dead time (cf. Kuffler et al., 1957; Hertz et al.,

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1964; Fuster et al., 1965), although e.g. Rodieck (1967) did not find a reasonable correspondance to either of these distributions. The maintained discharge rate changes with light intensity (Kuffler et al., 1957; Hughes and Maffei, 1966; Straschill, 1966). Two types of on-centre cells have been shown to exist: cells which show a systematic change of discharge rate with adaptation level and those which show a decrease of activity at higher adapting intensities (Barlow and Levick, 1969; Sakmann and Creutzfeldt, 1969). Recently, the influence of general illumination on maintained activity of sustained and transient cells in cat retina has been briefly dealt with (Cleland et al., 1973; Stone and Fukuda, 1974). Since, in the cat (as well as in the tree shrew) even more cell types can be differentiated (Cleland and Levick, 1974; Stone and Fukuda, 1974; Dongen et al., 1975), it may be assumed that conflicting data on maintained activity are partly explained by recordings from different cell types.

We have investigated the mean interval length, its standard deviation, the shape of the interval histogram and the first-order serial correlation coefficient of sustained and transient on-centre cells as well as some other units of the tree shrew during darkness and illumination. It will be shown that with regard to the various statistical parameters of the maintained activity the on-centre sustained and transient cells form two discrete groups. From the characteristic features of the maintained activity conclusions will be drawn regarding the localization of the source of the stochastic properties of the maintained activity.

Methods

Twenty three adult tree shrews (Tupaia chinensis) were used in this study. Under halothane anaesthesia the animals received an intramuscular injection of 0.05 mg atropine sulphate and were intubated after tracheotomy. A small hole was made in the skull above the optic tract. All wounds and pressure points were locally anaesthetized by lidocaine or marcaine/adrenaline. The animals were then immobilized by an intramuscular injection of 14 mg/kg gallamine triethiodide (Flaxedil) and artificially respirated with an N_2O/O_2 (2:1) mixture. The respiration was stabilized to 5% CO_2 in the expired air (Laak, 1975) after which the halothane narcosis was stopped. If necessary, supplementary doses of gallamine triethiodide were given. The pupil was dilated and the lens muscles paralyzed by dripping atropine sulphate on to the eye. The eye-lids were retracted by phenylephrine. The eyes were anaesthetized by novesine drops and kept wet by plano contact lenses with an artificial pupil of 7 mm^2 area.

Recordings were made with tungsten microelectrodes (Hubel, 1957) from single optic tract fibres. The signal was amplified, fed into a window discriminator and converted into standard pulses. The time of occurrence of the action potentials was fed into a PDP-9 computer with an accuracy of 0.1 msec and analyzed. After changing the illumination the cell activity was allowed to reach a constant level for several minutes. By continuously displaying the firing rate in a histogram we checked whether this activity remained stationary. If not, the data were rejected. The destributions of the intervals (interval histogram), the parameters of these distributions and the first order serial correlation coefficient were computed.

Interval histograms were made with 250 bins, the bin width being adjustable. In the histograms presented in this paper the frequency of occurrence of intervals exceeding the maximum bin will be represented by the content of the last bin. When the frequency within a bin exceeded the maximum value on the vertical axis, this will be indicated by a vertical arrow in the histogram. For the purpose of showing the distribution of the shortest intervals, sometimes only those shorter than 50 msec will be displayed. For easy inspection of interval histograms both linear and semilogarithmic plots have been drawn.

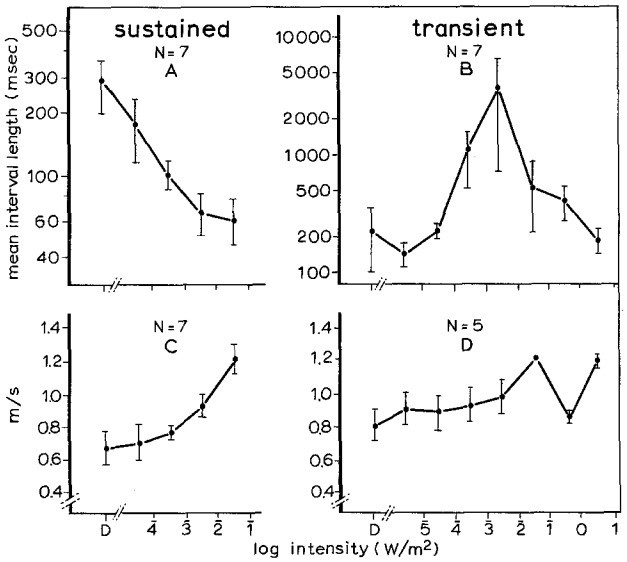

Fig. 1. (A, B) Relationship between light intensity and mean interval length with standard errors for on-centre sustained (A) and transient units (B). (C, D) Relationship between light intensity and ratio of mean and standard deviation (m/s) of interval length with standard errors for on-centre sustained (C) and transient units (D). Some on-centre transient units are not investigated at all levels of illumination

An optical stimulator was directed at the centre of the receptive field of a cell. This stimulator produced a uniformly illuminated field of 15° in Maxwellian view. The energy of the light produced by the stimulator was measured with an UDT-80X optometer. Light intensity will be given in W/m^2 at the cornea. For our light source 1 W/m^2 equals 10^6 cd/m^2 (human photopic light intensity). Further details of the experimental technique and cell classification have been described elsewhere (Laak, 1975; Laak et al., 1975; Dongen et al., 1975).

Results

Mean Interval Length and Light Intensity

Varying the illumination from darkness to 5.10^{-6} W/m^2 did not cause any change in the maintained activity nor in the sensitivity to standing stimuli (Laak, 1975). This seems to be due to the preponderance of cones in the tree shrew's retina. In the tree shrew the dependence of the maintained discharge rate of sustained cells on the luminance of an adapting light differs from that of transient cells.

In darkness, the mean interval length of on-centre *sustained cells* ranged from 40 to 2500 msec. Increasing the illumination from 5.10^{-6} to 5.10^{-2} W/m^2 resulted in a smaller mean interval length (Fig. 1A). This was a general characteristic of all nine sustained units investigated. In the range of 5.10^{-2} to

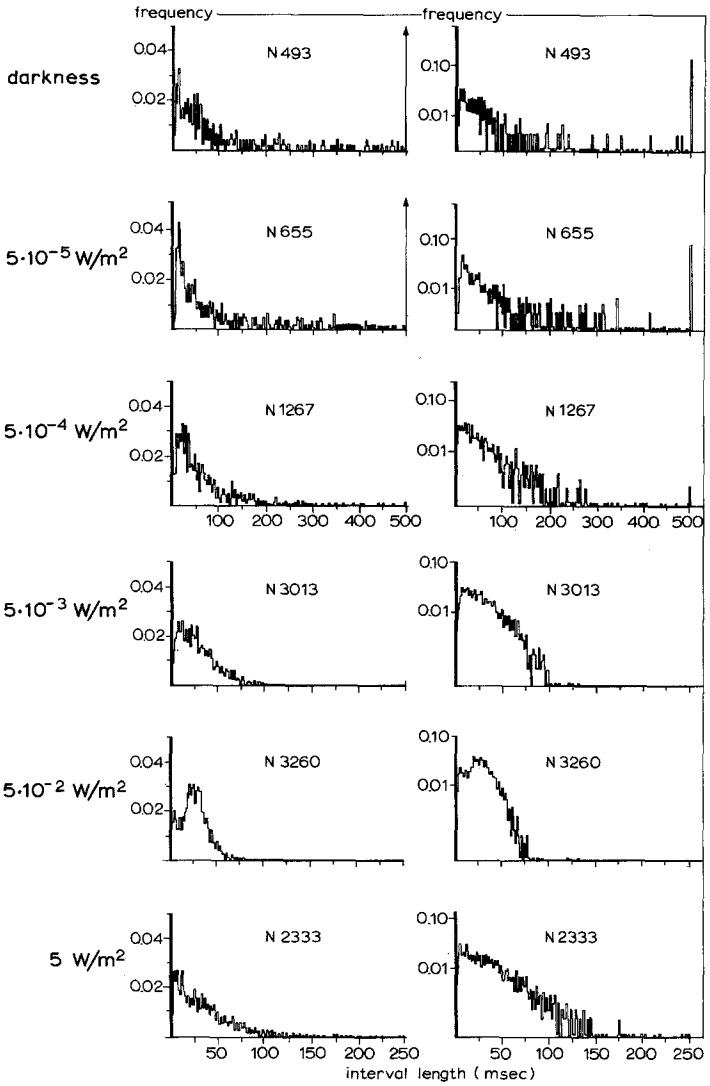

Fig. 2. Interval histograms of an on-centre sustained unit on linear and semi-logaritmic coordinates at different intensities of general illumination (same unit as in Fig. 2)

5 W/m^2 a slight increase of the mean interval length was observed in the single ganglion cell tested.

The mean interval length of on-centre *transient units* ranged in darkness from 70 to 1000 msec. From darkness to 5.10^{-2} W/m^2 some on-centre transient cells tended to show increasing interval lengths, at higher levels of light intensity a decrease of the mean interval length was occasionally observed (Fig. 1B).

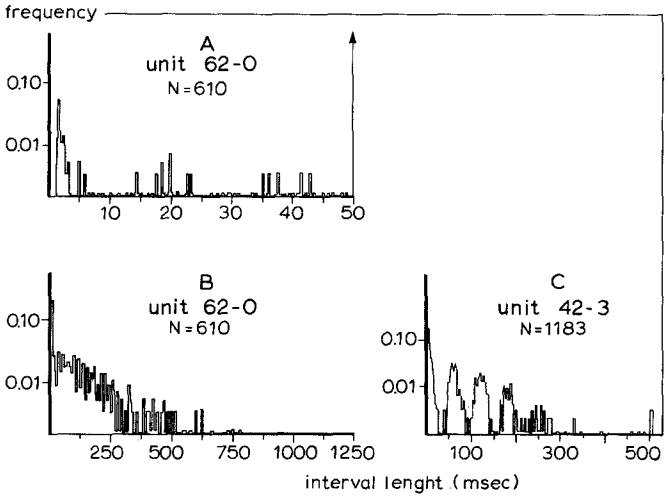

Fig. 3. Interval histograms of on-centre transient units in the dark-adapted situation. (A) Unit 62–0, intervals shorter than 50 msec only. (B) Unit 62–0, all intervals. (C) Multimodal interval histogram

Regularity of the Maintained Discharge

The ratio of the mean to the standard deviation of the interval length (m/s) was taken as a measure of regularity of the maintained activity. In 6 out of 7 *sustained units* the ratio m/s rises with increasing illumination to values above 1.0 (Fig. 1C). In one cell the ratio remained constant. At higher intensities ($> 5.10^{-2}$ W/m^2) a decrease of m/s was observed for the one ganglion cell tested in this range.

In 3 out of 5 *transient units* the ratio was relatively stable at a value of 1.0 for different intensities of general illumination. In two transient units the ratios increased with increasing light intensities in the same way as in on-centre sustained units. On the average a slight increase of the m/s ratio at higher light intensities was observed (Fig. 1D) These findings for the parameters of interval distributions are in agreement with Laak's for pulse-number distributions (1975).

Interval Histograms

The interval histograms of 18 on-centre *sustained cells* showed various forms which changed with luminance. A typical example is displayed in Fig. 3 and the parametric descriptions of the histograms are listed in Table 1. The modal values of the histograms ranged from 3–47 msec. Only one cell which was very insensitive had a smaller modal value and furthermore showed an interval histogram like transient cells (see below).

Table 1. Classification of interval histograms at different levels of light intensity for on-centre sustained cell 46–0

darkness	bimodal, long intervals very frequent
5.10^{-5} W/m^2	short intervals exponentially distributed, long intervals more frequent than for exponential distribution
5.10^{-4} W/m^2	exponential (m/s = 0.99)
5.10^{-3} W/m^2	gamma (m/s = 1.41)
5.10^{-2} W/m^2	bimodal, long intervals infrequent
5.10^{-1} W/m^2	bimodal, long intervals infrequent (not shown)
5 W/m^2	exponential (m/s = 1.12)

On-centre sustained cells could have bimodal (16 out of a total of 51) but never multimodal interval histograms. There was some trend towards exponential and gamma-like distributions at low and at higher intensities, respectively. Bimodal histograms could become unimodal and vice verse. Since in darkness and at low light intensities the values of m/s were considerably below 1.0, the gamma distributions were undefined. For such m/s values 11 histograms out of a total of 25 were found to have a larger number of short intervals than was expected from an exponential distribution. Also other types of distribution were found. At values of m/s ranging from 0.9 to 1.1, the distribution in 5 out of 10 cases was close to exponential. 10 interval histograms displayed a gamma-like form for m/s values greater than 1.0. The m/s value never exceeded 1.75, hence the maximum order of the gamma distributions was 3 (cf. Barlow and Levick, 1969).

Interval histograms of on-centre *transient cells* were in general bimodal. The modal values in darkness ranged from 0.9 to 3.0 msec. This type of interval histogram is best demonstrated by separately displaying the distribution of intervals with a duration shorter than 50 msec (Fig. 3A, B). Intervals ranging from 1 to 5 msec were very frequent, those from about 5 to 15 msec rare. Intervals longer than 15 msec followed exponential, gamma and other distributions. These interval histograms reflect the bursty firing pattern of on-centre transient cells. 13 out of 14 on-centre transient cells showed a similar bimodal distribution in darkness. One transient cell presented a multimodal distribution with a fixed distance between the modes (Fig. 3C).

At different luminance levels the interval histogram of some on-centre transient cells showed unsystematic changes. In two cases the bimodal histogram became multimodal with fixed distances between the modes. Only at light intensities where the firing rate was very low, the cells sometimes stopped firing bursty: the sharp initial peak in the histogram then disappeared. This property was observed in two on-centre transient cells.

Other cell types: As has been mentioned elsewhere (Dongen et al., 1975) in the retina of the tree shrew many types of ganglion cells can be differentiated. Interval histograms were measured for one *on-centre-orientation-selective,* three *on-off,* one *opponent-colour* and one *suppressed-by-contrast* cell in the dark-adapted situation. In the case of on-off units the on- and the off-burst

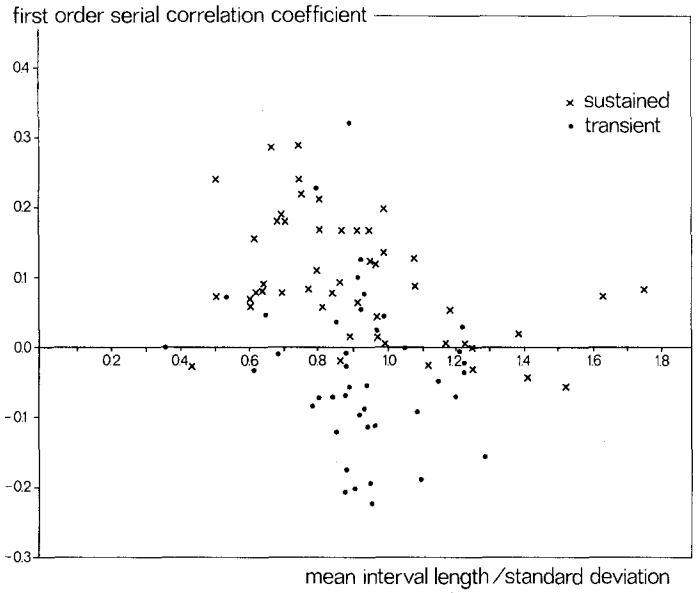

Fig. 4. Diagram of ratio of mean and standard deviation of interval length v. value of first order serial correlation coefficient for on-centre sustained and transient units

in the response to periodic light-on light-off stimulation could be equally strong (symmetrical response) or not (Dongen et al., 1975). Interval histograms were also made of the maintained activity of two on-off units with symmetrical response and of one on-off unit with an asymmetrical response. The on-off units with a symmetrical response and the opponent-colour cell showed interval histograms resembling those of sustained cells. The interval histograms of the other cells resembled those of the on-centre transient cells.

Serial Dependence

Correlation between adjacent intervals has been investigated by calculating the first order serial correlation coefficient, ϱ. Table 2 shows the ϱ-values relative to zero in the two groups of ganglion cells.

Table 2. Number and percentage of cases in which the value of ϱ significantly differs from zero

Total	sustained 53 (100%)	transient 36 (100%)
Significantly positive ($p < 0.05$)	34 (64%)	4 (11%)
Not significantly different from zero	16 (30%)	19 (53%)
Significantly negative ($p < 0.05$)	3 (6%)	13 (36%)

For on-centre *sustained units* the value of ϱ was mostly significantly positive and only in three cases negative (see Fig. 4). At high levels of general illumination the value of ϱ approached zero for the on-centre sustained units. If ϱ is plotted against m/s (see Discussion), it can be seen that at values of m/s between 0.9 to 1.1 ϱ is systematically positive.

In most on-centre *transient units* ϱ is negative, although sometimes positive values were found. We did not find a generally valid relationship between illumination and the value of ϱ for on-centre transient cells.

Discussion

The findings for the tree shrew will now be compared with data measured in the cat other authors. Any difference observed between these animals may be due to the rod-dominance in the cat and the cone-dominance in the tree shrew.

Mean Firing Rate and Illumination

At scotopic luminance levels the maintained activity of cat on-centre retinal ganglion cells, sustained as well as transient ones, will increase regularly with light intensity (Barlow and Levick, 1969; Sakmann and Creutzfeldt, 1969; Cleland et al., 1973; Stone and Fukuda, 1974).

At mesopic and photopic ranges the activity of some on-centre cells remained rather constant and in others a decrease was observed at the highest light intensities (Barlow and Levick, 1969; Sakmann and Creutzfeldt, 1969). The first group of ganglion cells had a weak, the second group a strong inhibiting surround (Sakmann and Creutzfeldt, 1969). However, Cleland et al. (1973) and Stone and Fukuda (1974) found no clear differences between the luminance dependence of the maintained activity of on-centre sustained and transient cells in these ranges of light intensity.

The findings in the tree shrew's retinal ganglion cells indicate a clear distinction between sustained and transient on-centre units at light intensities comparable with mesopic and photopic ranges for the cat. *Sustained cells* displayed a monotonously decreasing mean interval length with increasing illumination up to 5.10^{-2} W/m^2, whereas on-centre *transient cells* presented a rather irregular behaviour. This is in agreement with Laak's (1975) data on pulse-number distributions. The present results are much more consistent than those known of the cat's retina. Possibly, the great preponderance of cones in the tree shrew's retina may result in a simpler behaviour of the different cell types.

Interval Histograms

Interval histograms of the cat's retinal ganglion cells were described as *exponential* with initial dead time (Herz et al., 1964; Fuster et al., 1965), *gamma* (Kuffler et al., 1957; Barlow and Levick, 1969), *bimodal* (Heiss and

Bornschein, 1966; Rodieck, 1967), and other (Fuster et al., 1965; Rodieck, 1967; Sanderson et al., 1973). This situation is comparable to that in the tree shrew. Furthermore, it could be shown in the tree shrew that for the *sustained cells* the parameters and the shape of the interval histograms could vary with adaptation luminance. In the dark and at low intensity levels a few exponential-like histograms were found and a tendency towards gamma distribution was present at higher levels. Similar observations were described for cat retinal ganglion cells (Barlow and Levick, 1969; Sanderson et al., 1973). The first order serial correlation coefficient is significantly positive for the tree shrew's sustained cells as opposed to a zero (Herz et al., 1964; Barlow and Levick, 1969) or even a negative value (Kuffler et al., 1957; Gestri et al., 1966; Rodieck, 1967) found for the cat. It may be interesting to note, that in 4 out of 5 cells with exponential histograms and with values of m/s ranging from 0.9 to 1.1, the correlation coefficient significantly differed from zero ($P < 0.005$). This indicates, that a Poisson process for the generation of spikes is clearly no adequate proposition.

The interval histograms of *transient cells* display a characteristic peak of intervals shorter than 5 msec, which is followed by a deep trough (cf. Fig. 3A). The resulting bimodal interval histograms have a composite distribution function (cf. Bishop et al., 1964; Hoopen, 1966; Heiss and Bornschein, 1966), that may be explained by two stochastic processes acting at the spike generating mechanism (cf. Heiss and Bornschein, 1966). A transient cell fires in bursts during maintained activity, so the part of the interval histogram at short durations (< 5 msec) displays the distribution of intervals within a burst and at longer durations (> 15 msec) of the intervals between bursts and solitary spikes (Fig. 3B). Similar interval histograms were observed for cat retinal ganglion cells (Gestri et al., 1966; Heiss et al., 1966, 1968; Schmidt and Creutzfeldt, 1968; Sanderson et al., 1973). These histograms can change into multimodal types due to anaesthesia or other unphysiological conditions (Heiss et al., 1968; Schmidt and Creutzfeldt, 1968), but also when the animal is believed to be in optimum condition (Sanderson et al., 1973 and this study). Subsequent increase of the illumination produced in two cases again a normal bimodal histogram. Moreover, multimodal histograms were never observed for on-centre sustained cells. So we conclude that multimodal interval histograms can occur in on-centre transient cells depending on the illumination.

The trough in the interval histogram between 5 to 15 msec may be functionally related to the transient character of the response of transient cells at light-on. The reason for this may be that a phasic inhibitory influence is activated following excitation, or that the gain for excitation becomes transiently smaller (cf. Heiss and Bornschein, 1966; Cleland et al., 1971; Laak, 1975).

The frequently found negative value of the first order serial correlation coefficient in transient cells may be related to the type of firing in short bursts. Further study of this aspect is presently undertaken.

Other cell types: The on-off cells with a symmetrical type of light-on/light--off response as well as the one opponent colour cell (cf. Dongen et al., 1975) had interval histograms like those of on-centre sustained cells. All the other types of cells found in the tree shrew displayed interval histograms closely re-

sembling those of the on-centre transient cells. Hence, the remarks made above also apply to these cell types.

Theoretical Implications

The model of neural information processing of Gestri (1966, 1970) that extends the original work of Fitzhugh (1958) implies that the stochastic properties of the spike generating mechanism remain invariant while changing adaptation level and stimulation light intensities. In this case, the type of interval histogram should be independent of luminance. This appeared not to hold for the tree shrew. Similar observations for the cat were given by Fuster et al. (1965), Barlow and Levick (1969), Rodieck (1967) and Sanderson et al. (1973). Therefore the above described model of Fitzhugh, Siebert and Gestri should be considered to be valid only for restricted stimulus conditions.

Origin of Stochastic Characteristics

Psychophysical studies of luminance perception and the differential luminance sensitivity revealed a variability in the responses given by human subjects. Some characteristics of this so-called physiological noise could be specified (cf. Thijssen, 1969; Thijssen and Vendrik, 1971) but the localization in the neural chain of information processing was not completely known. Laak (1975) and Cohn et al. (1975) could correlate the signal to noise properties of spike trains and the response variability to the psychophysical data. The variability observed at the ganglion cell level can be caused by the quantal nature of the light stimulation, or by a mechanism within the ganglion cell itself. A third possibility could be the signal processing stages between photoreceptor cells and ganglion cells.

When quantal fluctuations were the most important source of variability, the intervals should have an exponential or gamma distribution, the regularity of the interval distribution should equal the square root of the quantum to spike ratio (if Q.R.S. ≥ 1) for short light flashes (cf. Barlow and Levick, 1969; Levick and Zacks, 1970; Barlow et al., 1971) and the first order serial correlation coefficient should equal zero. Since these conditions were not fullfilled in the tree shrew (cf. also Laak, 1975) quantum fluctuations cannot greatly determine the stochastic nature of maintained discharge. If the ganglion cell itself caused the fluctuations in maintained discharge rate, the interval distribution should be independent of light or adaptation level. Schellart and Spekreyse (1973) concluded for the goldfish that retinal ganglion cells are the most likely site of the statistical characteristics of the maintained discharge. The invariance of the interval histogram found by these authors could not be confirmed in the tree shrew or the cat (see above "Theoretical implications"). Therefore our conclusion is that the statistical parameters of maintained discharge are greatly determined by retinal signal processing between the receptor and the ganglion cells, although primarily driven by an essentially random process in the photoreceptor cells.

Acknowledgements. The authors like to thank Professor Dr. A.J.H. Vendrik for the hospitality at the Department of Medical Physics and Biophysics and for his supervision of a part of this investigation, and W. Braakhuis, J. Bakker and G. Meulman for their technical assistance.

This work has been supported by the Netherlands Organization for the Advancement of Pure Research (Z.W.O.) via its Biophysics Foundation.

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Received October 20, 1975