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LIGHT ADAPTATION WITHIN THE RECEPTIVE FIELD CENTRE OF RAT RETINAL GANGLION CELLS

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SUMMARY

1. Responses from axons of single retinal ganglion cells in the rat's optic tract were used to measure the pooling of adaptive signals within the cell's receptive field. Computer-aided analyses of response measurements were used to evaluate sensitivity at a number of field locations.

2. A small adapting spot caused a localized decrease in sensitivity within the receptive field centre of ON- and OFF-centre ganglion cells.

3. The functions describing response versus test luminance were similar in shape for all test and adaptation configurations. This assured that, using a fixed criterion response, sensitivity determinations could be made just as well in any receptive field location and under any of the experimental conditions.

4. A concentric surround, antagonistic to the receptive field centre, was readily apparent only under conditions of light adaptation. Experiments on the local effects of small adapting spots, conducted with selective surround adaptation, showed that the non-uniform spread of adaptation within the receptive field centre was not linked to surround intrusion.

5. The possibility that the photopic mechanism intruded to contaminate these results was considered and rejected.

6. When a suprathreshold spot was alternated between two equally sensitive positions, the ganglion cell gave an approximately balanced response. An upset of this balance was produced by placing a small adapting spot at either position, thus demonstrating, in another way, the non-uniform spread of adaptation within the receptive field centre.

7. It is concluded that significant pooling of adaptation effects occurs prior to the combination of influences which contribute to the centre response of a ganglion cell.

INTRODUCTION

In the dark-adapted state stimuli falling anywhere within the receptive field of rat ganglion cells cause the same type of response. An ON cell produces a burst of impulses at the onset of the stimulus, and a reduction in firing at the termination of the stimulus and an OFF cell produces these responses at the opposite phases of the

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stimulus (Green, Tong & Cicerone, 1977; Tong & Green, 1977). A concentrically organized surround, antagonistic to the centre, is sometimes apparent under conditions of light adaptation (Partridge & Brown, 1970).

A dim, steady light falling on the receptive field reduces the response to an added test light as compared to the cell's response in the dark. What is it that becomes less sensitive? Intracellular records from rods have shown that they light-adapt in cold blooded retinas (Baylor & Hodgkin, 1974; Kleinschmidt & Dowling, 1975; Fain, 1976). This need not be what happens here. The observation that threshold can be elevated by additional light falling on a remote patch of retina has been used by Rushton (1965) to suggest that threshold does not depend directly on the size of the signals from rods directly stimulated but rather on the weighted combination of signals from many rods, within an adaptation pool. Cleland & Enroth-Cugell (1968) and Enroth-Cugell & Shapley (1973) have suggested that the receptive field centre of cat ganglion cells acts as a unit adding signals over a large number of receptors to produce responses and to control sensitivity. Other evidence both psychophysical (Barlow & Andrews, 1967) and electrophysiological (Green, *et al.* 1977; Enroth-Cugell, 1978) indicates that adaptation may occur before summation. We, for example, have reported that the desensitizing effect of illuminating a small part of a receptive field spreads non-uniformly over the receptive field centre. We measure a narrow spread of light adaptation with maximal desensitization near the adapting light. The distinction between physiological pooling and the effects of stray light is critical to any interpretation of the results. It was to gain information on this and the following technical points that the present experiments were conducted.

In previous experiments of ours, 'thresholds' for OFF cells were measured by listening to spike discharges or by gauging spike density on an oscilloscope dot-display. Using these methods it was difficult to study ON units, for small incremental responses to test spots could not easily be detected against the high maintained rate of response to steady adapting spots placed anywhere in the receptive field. The adaptive properties of only OFF retinal ganglion cells in the rat have been established. Since about half the units encountered are ON units it is important to ascertain whether the ON and OFF units adapt similarly. It should be noted that differences in the adapting properties of ON and OFF units would be inconsistent with a stray light effect, for any difference would imply that adaptation occurs after these response properties are determined.

Computer-aided, on-line analyses of spike discharges have now been used to evaluate sensitivities of both ON and OFF units. In addition, the analysis system allowed the responses of ON and OFF units to be quantified using spike counts to obtain stimulus–response functions for various test and adapting configurations. Determinations made near threshold cannot provide information on the magnitude and degree to which adaptation affects response amplitudes. In these experiments response measures provided a rapid assessment of the adaptive state of the ganglion cell.

METHODS

Animals

Long-Evans hooded rats were raised in dim illumination (about 0·1 lm/m²) to maximize the probability that the retinas were not light-damaged (Noell, Walker, Kang & Berman, 1966). The animals regularly experienced brief periods of brighter red illumination during feeding and cage cleaning.

Preparation

Rats were initially anaesthetized with urethane (1200 mg/kg) intraperitoneally with subsequent small doses as needed. All surgery was performed under dim, red illumination with the added precaution of an opaque contact lens placed over the rat's eye during surgery. A tracheal cannula was inserted. In some animals, blood pressure was monitored via a cannulation of the carotid artery. Drugs and dextrose were administered by continuous infusion through a cannula in the left femoral vein. The rat was placed in a Baltimore Instruments stereotaxic apparatus. A hole was made in the skull to the right of the mid line and included 0·5 cm to the side of bregma. The dura was reflected. We have found that urethane anaesthesia and mechanical stabilization of the eye are not sufficient to prevent eye movements reliably. In addition to mechanical stabilization neuromuscular blocking agents were therefore used to reduce eye movements to a minimum (Cicerone & Green, 1977). Slits were made near the temporal margins of the upper and lower eyelids of the left eye and the conjunctiva was severed just behind its attachment to the globe. A full eye ring anchored to the stereotaxic apparatus was sewn to the conjunctiva on the side attached to the globe using silk sutures. A solution of gallimine triethiodide (Flaxedil; 10 mg/kg per hr) tubocurarine chloride (0·67 mg/kg per hr), and urethane (30 mg/kg per hr) mixed with dextrose was infused after a loading dose of gallamine triethiodide (5 mg/kg) and tubocurarine chloride (0·3 mg/kg). The rate of urethane infusion was sufficient to maintain unparalysed animals anaesthetized. The animal was respirated with a gas mixture of 50 % air, 47·5 % O_2, and 2·5 % CO_2 at the rate of 200 ml./min, 50 strokes/min. We have previously checked that this combination of neuromuscular blocking agents, anaesthetic, gas composition and respiration rate does not adversely affect rat retinal ganglion cell responses (Cicerone & Green, 1977).

The pupil was dilated with atropine sulphate (1 %) and a clear plano contact lens (2·9 mm curvature) was placed over the left eye to protect the cornea. An opaque contact lens with a 1 mm artificial pupil was placed over the clear lens. We made no attempt to correct refractive errors, since Powers & Green (1978) have recently shown that even with a dilated pupil the small eye of the rat has a rather large depth of focus. Lenses in the range of $\pm$ 14 D do very little to alter retinal ganglion cell response.

Recording and stimulation

The results in this paper (from twenty-two animals) are based on twenty-nine ON units and twenty-five OFF units which were held long enough to be studied adequately. A Levick (1972) tungsten-wire-in-glass electrode was positioned stereotaxically in the optic tract. A half ping-pong ball was placed over the rat's eye and was illuminated with brief, dim flashes. Dark-adapted units encountered in the rat's optic tract fired in response to this diffuse illumination. After a single unit had been isolated, the ping-pong ball was removed and the geometric centre of the receptive field was carefully located on a tangent screen at a distance of 40 cm. A two-channel stimulator allowed two spots of light to be varied independently in size, location and luminance. One channel was provided by a 100 W solid tungsten lamp and other by a 150 W xenon arc lamp.

The photopic luminances of the lights from the two channel stimulator were measured with an SEI photometer. Measurements were made at various times throughout the course of the experiments but not on a daily basis. The mean values for the unattenuated tungsten beam and the xenon beam measured on our tangent screen were $1{\cdot}62 \pm 0{\cdot}20$ (S.D.) log cd/m² and $2{\cdot}51 \pm 0{\cdot}24$ (S.D.) log cd/m², respectively.

Data analysis

Histograms were created on-line using a computer and were displayed on the screen of a graphics terminal. Selected records were saved on a teletypewriter. Each spike was detected by the trigger circuitry of an oscilloscope which generated a pulse which was relayed to the computer. The computer divided the response into time intervals of 20 or 40 msec each. Time-locked with each stimulus presentation, the computer counted the spikes in each of seventy-five time intervals and displayed the resulting spike trains to the experimenters. After ten successive presentations of the stimulus the computer summed counts to form 160 msec time bins and added the counts from the corresponding bins in each presentation. The post-stimulus time histogram so formed was used to decide if a stimulus was at 'threshold.' The 160 msec bin width was a compromise between optimizing detection, by counting spikes over the duration of the response, and determining its structure, using shorter counting intervals. Typically, a response at the rate of 6 spikes/sec above base-line firing rate was chosen as the criterion for threshold. The just-perceptible response that we could discern by listening to the discharge on the audio monitor was always close to threshold. Audio criteria were used to adjust the stimulus intensity to be near 'threshold'. This method of data processing and evaluation allowed setting of 'thresholds' for ON as well as OFF units; they were easy to make regardless of changes in the base line rate of firing. Repeated determinations of threshold were usually within 0·1 or at most 0·2 log units of each other.

Ease of manipulation itself is not sufficient to justify using the above measure to estimate ganglion cell 'threshold.' Under differing conditions of light adaptation which cause changes in the maintained firing rate of the ganglion cell, threshold defined using criterion response above base line is not precisely the same as fixing the signal-to-noise ratios (Barlow & Levick, 1969). What is important to know is how far our criterion response measure of 'threshold' deviated from a constant signal-to-noise ratio which specifies a fixed amount of information about the presence or absence of a stimulus. Our first experiments deal with this question.

RESULTS

Signal-detection-based analyses of threshold responses

It seems reasonable to define 'threshold' on the basis of signal-to-noise ratios so that at threshold the ganglion cell discharge contains a fixed amount of information about the presence or absence of a stimulus. Frequency distributions of spike occurrences under our various stimulus conditions were generated. Test flashes were presented for 480 msec every 3 sec and the stimulus strength was adjusted to produce a criterion change of 6 spikes/sec over the base-line firing rate. This 'threshold' stimulus was then presented a large number of times. Frequency distributions of spike counts were determined from the responses to these multiple presentations immediately after the 0·48 sec period of stimulation (signal and noise) and during a 0·48 sec period 2 secs after stimulation (noise alone). These distributions are shown in Fig. 1*A* for a fully dark-adapted OFF unit and in Fig. 2*A* for an ON unit. A steady weak-adapting stimulus was superimposed on the test location and adjusted so as to elevate 'threshold' by tenfold. Multiple presentations were made of the ten times dark-adapted threshold light for 480 msec every 3 sec. Frequency distributions for spike counts in this light-adapted case are shown in Figs. 1*B* and 2*B*. Adaptation slightly reduced the average spontaneous firing rate of the OFF units. The signal-to-noise ratios have been assessed by plotting receiver operating characteristics (Green & Swets, 1966) using the pairs of spike frequency distributions (Cohn, Green & Tanner, 1975). These are shown in Fig. 1 for dark-adapted and light-adapted conditions. The curves are not

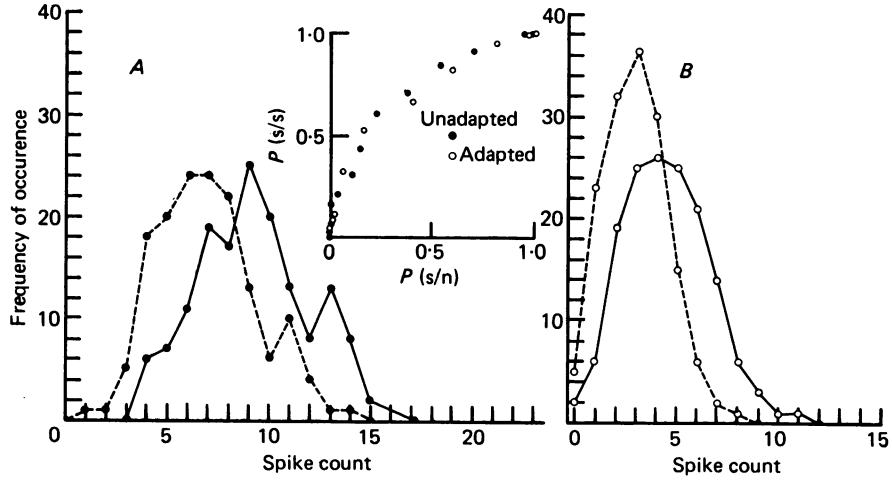

Fig. 1. Distribution of spike counts and receiver operating characteristics for an OFF unit under dark adapted (●) and light adapted (○) conditions are shown. The ordinate shows the number of times the count in a 480 msec interval was equal to the number on the abscissa. *A*. The signal distribution (—) of spike count was determined from 150 presentations of a 'threshold' stimulus, by counting for 480 msec starting 160 msec after the termination of each stimulation. The no-signal distribution (– – –) was obtained in a 480 msec interval starting 2 sec after termination of the stimulus. *B*, distributions of spike count obtained with a steady adapting stimulus and a 10X threshold flash are shown. The adapting stimulus was a 1° spot superimposed on the 1° test flash. The insert shows the receiver operating characteristics derived from the distributions in *A* and *B*. Plotted along the abscissa is the probability of incorrect identification of presence of stimulus; along the ordinate is plotted the probability of a correct identification.

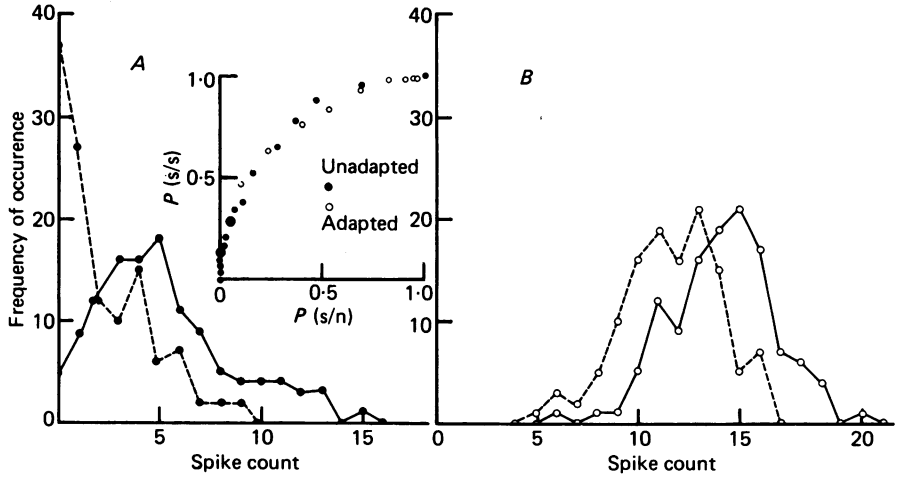

Fig. 2. Distributions of spike count for an ON unit are shown under dark-adapted (*A*) and light-adapted (*B*) conditions. The signal distribution (—) was determined by counting for 480 msec starting 160 msec after the onset of the stimulus (n = 120). The no-signal distribution (– – –) is for counts made in a 480 msec interval starting 2 sec after stimulation. For other details see Fig. 1*B*.

very different and correspond to a value of d' (signal-to-noise ratio measured along the negative diagonal) of 0·91 (dark-adapted) and 0·87 (light-adapted). Fig. 2*B* shows that adaptation greatly increased the average firing rate of the ON unit, but as the receiver operating characteristics for this unit and the d' values of 1·01 in the

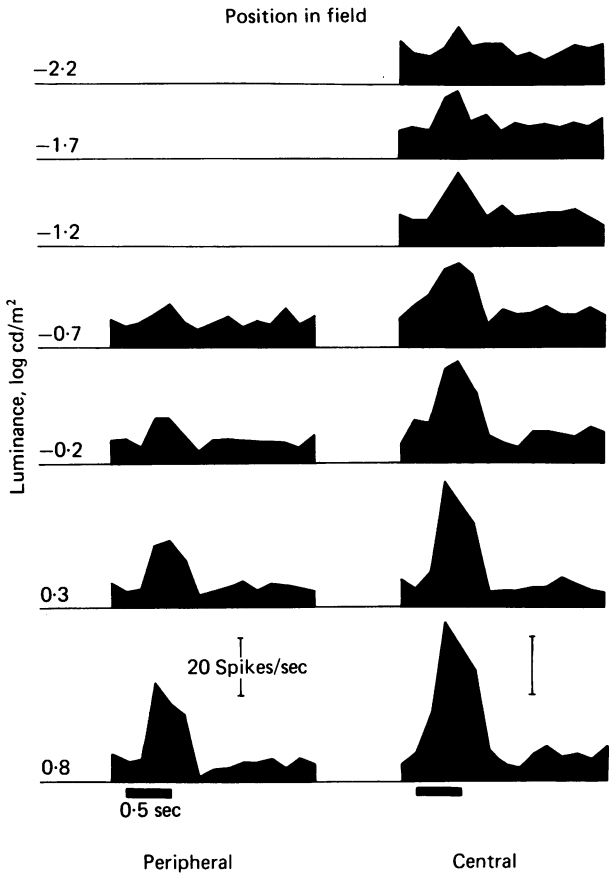

Fig. 3. Response as a function of luminance at two positions in the receptive field of an ON unit. The histograms to the left were determined with a 1° spot stimulus located 3° from the centre of the receptive field. The histograms to the right were obtained with the stimulus positioned slightly to the right of receptive field centre.

dark-adapted state and 1·05 in the light-adapted state attest, signal-to-noise ratios were stable under our experimental conditions. These kinds of measurements served to verify that the chosen definition of 'threshold' in fact reflected a more or less constant signal-to-noise ratio for ON and OFF units and for dark-adapted and light-adapted conditions of the experiments. Thus, threshold measures of sensitivity were used to quantify the effects of various experimental manipulations on the ganglion cell responses.

The restricted spread of adapting signals and its independence of suprathreshold response characteristics

Fig. 3 shows the responses of a typical ON unit to a 1° test spot, varying in luminance, presented at the centre and at the periphery of the receptive field. About 30 times less light was required in the centre to produce a response matched to that in the periphery. The two uppermost post-stimulus histograms respresent responses close to our definition of threshold.

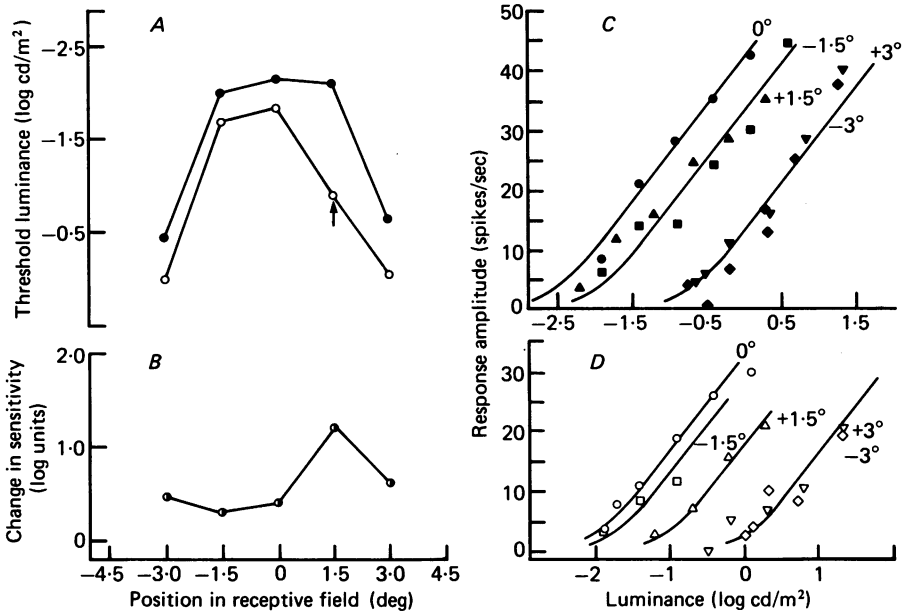

Fig. 4. *A*, the receptive field sensitivity profile (●) for the same unit as in Fig. 3; the profile was redetermined with a small steady adapting spot located at the position indicated with an arrow (○). *B*, the change in log sensitivity produced by the adapting spot. *C*, Response amplitude as a function of luminance at various positions in the receptive field are shown. Measurements were made at the centre of the field (●) and at positions symmetrically placed on either side of centre (■ at −1·5°, ▲ at 1·5°, ◆ at −3°, ▼ at 3°). *D*, response amplitude as a function of luminance measured with a steady adapting spot located at 1·5° are shown. Measurements were made at various positions (○ at 0°, □ at −1·5°, △ at 1·5°, ◇ at −3°, △ at 3°).

Each point in the sensitivity profile of Fig. 4*A* gives the luminance required for a threshold response at the indicated position in the receptive field. A steady, small adapting spot was presented in a fixed location near the centre of the field. The luminance of the adapting light had been adjusted so as to increase the threshold for a superimposed test by approximately one log unit. The unit's sensitivity profile was remeasured. The change in log sensitivity by the adapting spot is plotted in Fig. 4*B*. The maximum depression in sensitivity occurs at the location of the adapting spot. Using the above procedure, eleven other units, six ON and five OFF cells, were tested. In every case but one a small adapting spot more effectively depressed the sensitivity of neighbouring rather than remote locations.

In some instances, such as for the cell shown in Fig. 4*A*, there was evidence for a global as well as a local component to the pooling of adaptation. For the one exceptional cell out of eleven the adapting spot caused a 1 log-unit change in sensitivity at every position in the receptive field. It seems unlikely that an effect which spreads unattenuated over at least 3·5° is due to light scatter, particularly when other units in the same experiment show non-uniform spread of adaptation. This observation in

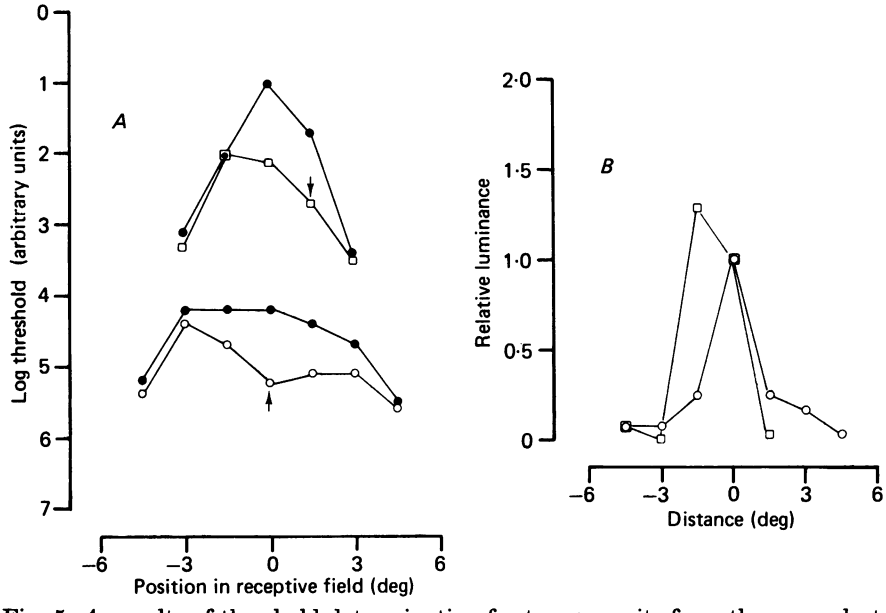

Fig. 5. *A*, results of threshold determination for two ON units from the same electrode penetration. The filled symbols mark the receptive field sensitivity profile measured with a 1° test spot. Open symbols mark the measurements of sensitivity made while a 1° adapting spot illuminated the location marked by an arrow. *B*, light distribution across the receptive field due to the 1° adapting spot as calculated using eqn. (3) and the data in Fig. 5*A*. Curves plot relative luminance as a function of distance from the adapting spot.

itself, however, does not exclude the possibility. If we assume for the moment that the remote effects are mediated solely by scattered light then the magnitude of scatter can be estimated from the fall-off of adaptation with distance.

Suppose that sensitivity is determined by small, independent subunits each influenced only by the light falling upon it and obeying Weber's Law:

$$\triangle I_t(x) = K(x)\,(I(x)+I_D), \tag{1}$$

where $\triangle I_t(x)$ is the threshold luminance of a small test flash positioned at x, $K(x)$ is a position-dependent weighting constant, $I(x)$ is the luminance of the scattered light at x due to the adapting spot, and I_D is a constant (the dark light). In the dark,

$$\Delta I_t^*(x) = K(x)\,I_D, \tag{2}$$

where ΔI_t^* denotes the dark-adapted threshold intensity. Dividing eqn. (1) by eqn. (2) yields

$$\frac{\Delta I_t(x)}{\Delta I_t^*(x)} = \frac{I(x)}{I_D} + 1. \tag{3}$$

In other words, the ratio of the light-adapted to the dark-adapted threshold should fall off with distance as the scattering function does. In this way, a scattering function can be estimated from the spread of adaptation.

The scattering function is an optical property, hence it should not vary greatly from cell to cell in the same region of the retina. Fig. 5*A* shows two sensitivity profiles from ON units successively encountered in the same electrode penetration. Thresholds were obtained in darkness and with a 1° adapting spot placed at a fixed position. Eqn. (3) was used to compute the scattering functions shown in Fig. 5*B*. Two aspects of these functions are inconsistent with an effect mediated by scattered light: (1) the two functions do not have the same shape, (2) one of the functions violates the principle that scatter should be greatest at the scatter source.

The preceding would be less satisfying if the shape of the functions describing response vs. test luminance varied with the receptive field location of the test spot or was affected by the presence of an adapting spot. Any variation in the form of the function under differing experimental conditions would mean that the shapes of the sensitivity profiles would have differed depending on response criteria. Therefore response amplitudes were derived from the post-stimulus histograms (generated from ten presentations of the stimulus) for our various experimental conditions. Response amplitudes were computed as the difference between the stimulated rate of firing (estimated by counting spikes starting 160 msec after the onset of the test and for 480 msec thereafter) and the base-line rate (estimated from the spike count in the 320 msec period just prior to stimulation).

Fig. 4*C* shows the response as a function of test luminance for measurements made near the centre and at 1·5° and 3° in the periphery of the receptive field on either side. In addition, measurements were made at each of these positions when an adapting spot was placed near the centre of the field (Fig. 4*D*). The same smooth curve appropriately displaced along the abscissa has been drawn through each set of data points. As can readily be seen, the shapes of these response vs. test luminance functions vary little. This experiment was conducted on three other units with similar results.

The possible intrusion of the surround

As is shown in Fig. 3, post-stimulus histograms for centrally and peripherally placed test stimuli can be matched when sensitivity differences are taken into account. Figs. 3 and 4 show an unchanging polarity of the responses and an invariance in the shape of the functions describing response *vs.* test luminance, regardless of location in the receptive field. This suggests that purely central responses (Enroth-Cugell & Pinto, 1972) are elicited everywhere in the receptive field, even for suprathreshold stimulation, under dark-adapted conditions.

In other units such as the one depicted in Figs. 6 and 7, suprathreshold stimulation produced hints of surround effects which subsequently were clearly demonstrated by light-adapting the centre. Fig. 6. shows the receptive field profile for such an OFF unit. At threshold, the histograms (not shown) derived from different locations were indistinguishable. The suprathreshold responses shown in Fig. 6 are similar in time course and amplitude, yet responses recorded near the periphery are very slightly smaller than those recorded in the centre, even though stimulation was increased uniformly 10X above threshold. This might reflect a small consistent error in setting

thresholds, but we think it more likely that peripheral locations are affected by the surround mechanism.

Further evidence for the presence of a surround comes from experiments in which the receptive field centre was adapted with a small steady adapting spot. This is shown in Fig. 7. A 1° test stimulus of 480 msec duration was located in the periphery at −4·0° and a 1° steady adapting spot was located near the centre at −1·5°. The test luminance was fixed at one log unit above dark-adapted threshold. The adapting spot

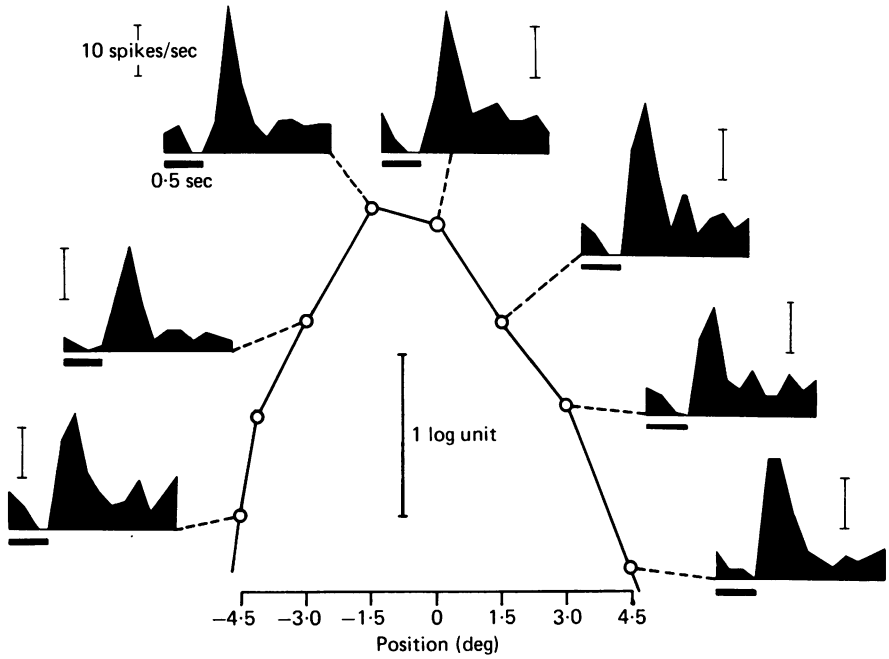

Fig. 6. The receptive field sensitivity profile and 10X threshold responses at different receptive field locations for an OFF unit are shown. The histograms show the average spike frequency obtained by counting over 160 msec bins for ten presentations of a 480 msec flash.

had been adjusted to elevate the threshold of a superimposed test spot by one log unit. The four records in Fig. 7 show the change in response to this test flash in the presence of a steady adapting light. The histogram in Fig. 7*A* shows an increase in firing rate at cessation of stimulation that is the basis for our classification of this as an OFF unit. As the luminance of the steady adapting stimulus was increased in steps of 0·3 log units, the response to the test decreased (Fig. 7*B*, *C* and *D*) and for higher adapting luminances the peak of the response occurred during stimulation rather than at offset of stimulation (Fig. 7*C* and *D*).

The data displayed in Fig. 7 point to centre–surround antagonisms which could cause an underestimation of sensitivity in the periphery when an adapting spot is placed centrally. For example, the centrally placed adapting stimulus used in Fig. 7*B* was found to reduce the sensitivity of a superimposed test stimulus by one log unit. With this adaptation the response to a 10 times threshold stimulus at −4·0° in the

periphery shows an increase in firing rate both during and after stimulation (ON–OFF response). For this reason, surround antagonism would seem to be an unlikely contributor to the localized adapting effect of a centrally placed spot but could, on the contrary, lead to the inference that adaptation spreads more uniformly over the receptive field centre than it actually does. None the less, in order to assess the extent to which the surround contributes to the basic results on local adaptation, a set of experiments were conducted using an annulus to adapt the surround selectively.

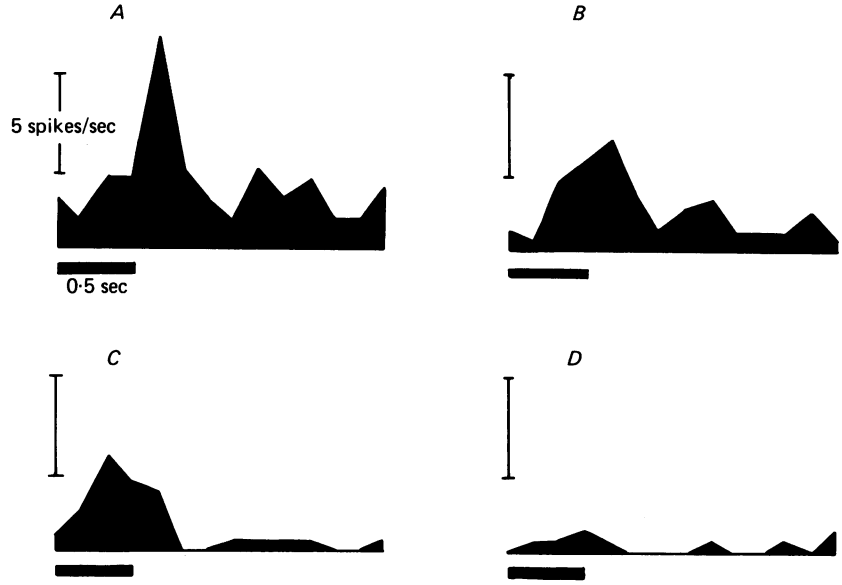

Fig. 7. Shown are responses of an OFF unit (same as in Fig. 6) to peripheral, 10X threshold stimulation in the presence of a small steady central adapting spot. The test stimulus was at $-4°$ with adapting spot at $-1·5°$. The adapting spot luminance was increased progressively in 0·3 log unit steps in *A–D*. The response changed from an OFF (*A*) to an ON–OFF (*B*) to an ON (*C* and *D*) as the luminance of the adapting spot was increased.

The receptive field sensitivity profile of a unit was determined under four adapting conditions (Fig. 8). First, in the usual way, a roving small test spot was used to determine the luminance which yielded the same criterion response at a number of different locations in the receptive field. A second determination with the roving test was made while a small adapting light steadily illuminated a spot near the centre of the field. Fig. 8 shows the usual depression in the sensitivity profile near the location of the adapting spot.

Then, the sensitivity profile was redetermined with a steady adapting annulus (inner diameter, 9·75°; outer diameter, 21°) centered on the receptive field. There was no systematic change in the shape of the profile and the same smooth curve, displaced uniformly, can be drawn through these data and those generated without the annulus. Next, a small adapting spot was placed near the centre of the field. The sensitivity profile now showed a localized decrease in sensitivity at the location of the adapting spot. The dotted curve which was drawn through the data generated without

the adapting annulus fits the set generated with the annulus when smooth and dashed curves are equally displaced. The differential changes across the receptive field due to the small adapting spot were independent of the adaptive state of the surround, and so the surround mechanism is not likely to be markedly influencing the results.

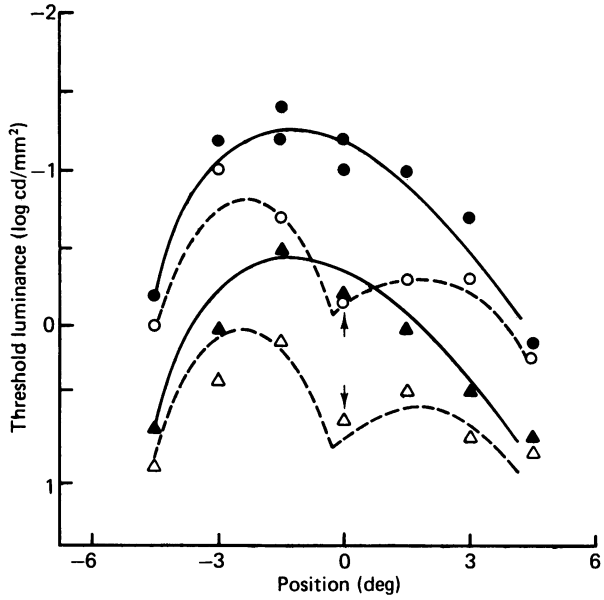

Fig. 8. The effects of annular adaptation on an ON unit are described. Four receptive field sensitivity profiles measured under different adapting conditions are shown. The (●) mark the thresholds measured at a number of receptive field locations in the usual way with a small, roving test spot. Another determination (○) was made while a small adapting light steadily illuminated the location marked by an arrow. The receptive field sensitivity profile was also measured with a steady adapting annulus of light ± i.d. 9·74°; ± o.d. 21°) centred on the receptive field (▲). There was no systematic difference in the shape of the profile measured in this way as compared to the measurements without the annulus (●). Finally, the open triangles plot the results when both an annulus and a small adapting spot were applied. The annulus uniformly reduced the sensitivity across the field, and local adaptation was demonstrated with or without the annulus.

The possible intrusion of the photopic mechanism

It has been shown that in the rat there is both a scotopic and a photopic system (Dodt & Echte, 1961; Green, 1971; Cicerone, 1976). The two systems might adapt to light differently. Do the differential effects of the adapting spot on near and far locations represent purely adaptational effects on the scotopic system without contamination by the photopic mechanism? The location of the photopic threshold relative to the dark-adapted threshold was determined by measuring increment thresholds for three monochromatic test lights (500, 600 and 625 nm) on backgrounds of increasing luminance. Representative results for one unit are shown in Fig. 9. The lights have been equated for the dark-adapted retina so that the separation of the curves for higher luminances of approximately 0·5 log units increase in sensitivity to

the long wave length stimuli, reflects the change from scotopic to photopic mechanisms. The photopic threshold for a 600 nm light in this cell lies 2·4 log units above the dark-adapted threshold for a 500 nm stimulus. For the nine units we have tested in this way, there was a mean separation of 2·07 ($\pm$ 0·11 S.E. of mean) log units. Since the white-adapting spot depresses sensitivity by one log unit in these experiments it can be safely assumed that the scotopic mechanism is still over one log unit more sensitive than the photopic and thus the only one involved in these measurements.

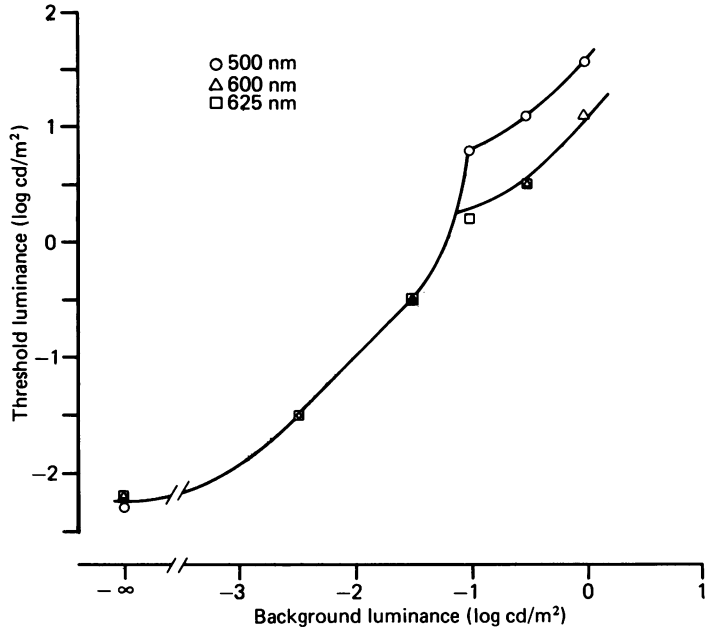

Fig. 9. Shown are increment threshold functions measured for three test wave-lengths (500, 600, 625 nm) on increasing luminances of a background light. The test lights have been scotopically equated so that the separation of the curves at higher intensities reflects a change in spectral sensitivity. This change of approximately 0·5 log unit increase in sensitivity to the longer wave-length stimuli has been interpreted as a change from scotopic to photopic mechanism. The photopic threshold in this example lies 2·4 log units above the scotopic.

The balanced response experiments

The design for the balance experiments is illustrated in Fig. 10. The experiment went as follows. The centre of the receptive field of an OFF unit was located on a tangent screen. The receptive field sensitivity profile (Fig. 10*A*) was determined as before, and two equally sensitive positions on either side of centre were chosen. At one of the two positions, two 1° spatially superimposed test spots were presented in temporal alternation. The luminance of one of the spots was set to be 10 times threshold and the luminance of the other was adjusted until there was no residual response to the alternating test stimuli. It was always possible to make this kind of silent substitution. The stimuli were then separated so that each fell on one of the two equally sensitive positions. Fig. 10*B* shows a histogram generated by averaging 10

cycles of response to this alternating stimulation. The first half of the histogram was obtained during stimulation of position 1 and the second half stimulation of position 2. As the histogram shows, there are residual responses to every interchange of the stimuli. These could be equalized but could not be eliminated by adjusting the luminance (or position) of the spots. The effects of placing a steady adapting spot either at position 1 (Fig. 10*C*) or at position 2 (Fig. 10*D*) was to cause an imbalance in the response.

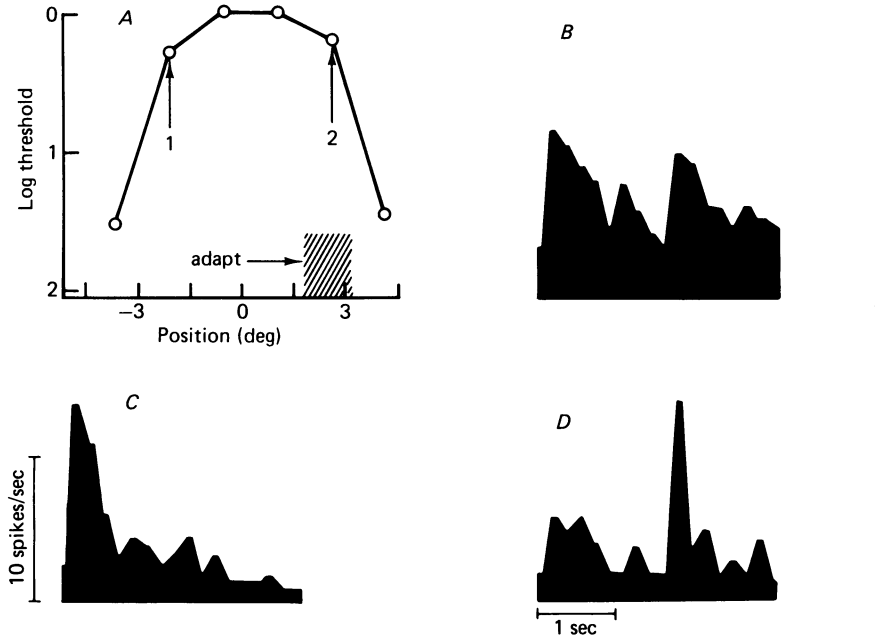

Fig. 10. The design for the balance experiments. *A*, a typical receptive field sensitivity profile measured along a horizontal line passing through the receptive field centre of an OFF unit is shown. Two nearby equally sensitive and symmetrically placed positions were chosen as marked by the arrows. Two equal intensity suprathreshold test spots of light (1° diam.) were alternated between position 1 and position 2. *B*, balanced response to alternating the stimulus between the two positions. Small adjustments of luminance or position sufficed to equate (balance) the ganglion cell's response to interchanging the spots of light. *C*, a small spot (1°) adapting light at position 1 upset the balance. The histogram shows that the unit responds to termination of the spot in position 2. *D*, histogram recorded when the small adapting spot is moved to position 3.

Fig. 11 shows two other examples of balance experiments. The results for an OFF unit are shown at the top and those for an ON unit at the bottom. In each case, with adapting spot focused selectively on one position, there is an imbalance in the responses. Disruption of the balance indicates a localized adaptation effect, for if adaptive signals were pooled uniformly over the receptive field centre the steady adapting spot should equally affect positions 1 and 2. This might cause a generalized decrease in responsivity, but the balance should hold. Of twenty-two ON units and twenty OFF units studied in this way only two units, one ON-centre and the other

OFF-centre, showed a maintenance of the balanced state after selective adaptation of a subarea of the field.

The differential effect of the adaptation on these responses from the two positions confirms previous findings and demonstrates in another way for ON and OFF units that in the pooling of adaptive signals the receptive field centre does not function as a single adaptive mechanism.

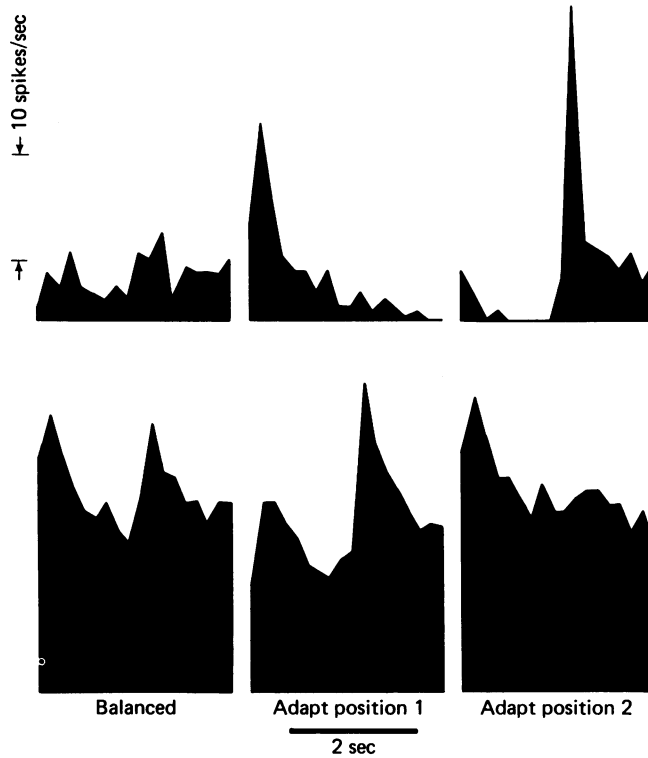

Fig. 11. Two other examples of the results of experiments in which the responses at two equally sensitive positions in the receptive field were used to test the differential effects of small spot adaptation applied at only one of the positions. The results for an OFF unit (top) and ON unit (bottom) are shown. The first record in each set shows the balance between the responses when a 10 × threshold light was flashed alternately at position 1 alone (first half of record) and at position 2 alone (second half of record). The second record shows the results when a small adapting spot was focused on position 1. Then the adapting spot was focused instead on position 2, and those results are shown in the third record. With the adapting spot focused selectively on either position 1 or position 2 there was an upset of balance, thus demonstrating local spread of adaptation.

DISCUSSION

The computer allowed us to study local adaptation in ON and OFF cells. As already had been established for OFF cells (Green *et al.* 1977), we showed the receptive field centres of ON cells do not uniformly pool adaptive signals. Small adapting spots placed in the receptive field caused a restricted depression of sensitivity. In some cells, regions only 1·5° from the adapting spot did not show any measurable change in

threshold. For others there was a global as well as a local component of light adaptation. That is, there was a significant threshold change at the edges of the receptive field, 3·5° or more from the adapting stimulus. These observations suggest the possibility that pooling occurs at several levels.

Light scatter is a possible contributor to both the local and global components. The cat, for instance, has an optical spread function with a narrow central component which rides on a broad base of scattered light (Robson & Enroth-Cugell, 1978). In our experiments, if any difference in local adaptive properties had been found to be correlated with physiological properties (e.g. ON or OFF centre, large or small receptive field), this would have been an argument against scattered light effects. Although we were unable to demonstrate local adaptation in a few units (three of fifty-four) there was nothing to distinguish these cells from the large number showing non-uniform spread of adaptation. Light scatter cannot, however, explain all of our results pointing to pooling. First, in accord with the earlier psychophysical result of Rushton (1965) we have shown that only a small fraction of rods need absorb a quantum of light for ganglion cell sensitivity to be changed (Green *et al.* 1977). Secondly, in the present experiments, there were a number of units which showed the greatest decrease in sensitivity, not at the location of a centrally placed adapting spot but at adjacent locations. Fig. 5 shows an example of such a unit with a displaced maximal adaptation effect. Thirdly, if these results are totally due to scattered light, the scattering function should be invariant for a given area in a particular animal. Fig. 5 suggests that this is not so. Of course any analysis of this sort is flawed because any local variation affecting scattered light, such as blood vessels overlying part of the receptive field, may play a major role.

Evidence for physiological spread of adaptation has been used to argue that the site of adaptation lies proximal to the photoreceptors (Rushton, 1965). This conclusion requires the receptors to function independently, an assumption which may not be justified since Leure-Dupree (1974) describes filament-like processes in the albino rat retina which arise from the bases of cone-type terminals and extend laterally to contact several surrounding rod-type ones. Apparently, there are no similar inter-receptor contacts between rods or between cones. Local adaptation occurs when thresholds are within one log unit of dark-adapted values, and as the results of Fig. 8 show, cone thresholds lie at least two log units above dark-adapted threshold. Consequently our findings suggest the existence of an adaptive mechanism which acts on the cells or synapses located between the rods and the ganglion cells.

A number of possible contaminants of these results were confronted by these experiments. The experiments of Figs. 3 and 4 show that the functions describing response vs. test luminance measured near the centre of the field (with or without the adapting spot) did not markedly differ from those measured near the periphery. This assures that sensitivity determinations could be made just as well in any receptive field location and under any of our experimental conditions. The anatomical observations noted above hint that the photopic and scotopic mechanisms might adapt differently. The high luminance portions of the stimulus–response curves, such as those illustrated in Fig. 4*B*, were obtained with stimuli which could excite cones; there is nothing in the behaviour of this portion of the curve which indicates a change in adaptation properties. If the photopic receptive field had been smaller

than the scotopic we might have been able to use the photopic sensitivity profile to give an upper limit to the stray light. A surround-adapting annulus was used to test whether the surround was playing a part in these results. The effect of the annulus was to depress sensitivity uniformly within the receptive field centre. With or without the surround adaptation a localized adaptive effect of a small spot could be exhibited within the centre (see Fig. 7). It is concluded that the surround did not influence these measurements.

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