LOCAL ADAPTATION IN CAT LGN CELLS: EVIDENCE FOR A SURROUND ANTAGONISM

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PSYCHOPHYSICAL experiments indicate that the sensitivity of the visual system to a small flashing probe is related to the illumination of a larger region surrounding this test probe. Increasing the size of a circular, steady-adapting field immediately surrounding a test probe progressively decreases the sensitivity to the test probe. Further increases in the size of a steady-adapting field then increases the sensitivity to the test probe (WESTHEIMER, 1965). This phenomenon has been interpreted in terms of the center–surround receptive organization found for retinal ganglion cells (TELLER, ANDREWS and BARLOW, 1967; WESTHEIMER, 1965). According to this interpretation, increasing the size of an adapting field would progressively cover a cell's receptive field center and lead it to be more completely adapted. Further increases in size of an adapting field beyond the diameter of the receptive field center would cover the antagonistic surround and would then tend to make it again less adapted.

Curiously, attempts actually to perform such an experiment on retinal ganglion cells have shown that the surround has no influence on the adaptation level of the cell (SAKMAN, CREUTZFELDT and SCHEICH, 1969). Increasing the size of a steady-adapting field over the receptive field center leads to a decreased sensitivity, the result expected, since more of the center mechanism is being put under steady illumination. Further increases in the size of the adapting field over the surround, however, do not change the sensitivity of the cell. The surround mechanism of the ganglion cell does not exert the sensitizing effect expected from the interpretation of the psychophysical experiments. The central mechanism alone determines the adapting level of the ganglion cell.

Since retinal ganglion cells do not show the property of surround sensitization, antecedent elements, such as bipolar cells, are ruled out as determing links in accounting for the sensitization that is seen psychophysically. The only remaining cells with a center–surround organization are the cells of the dorsal LGN. Thus the present experiments were done to see if LGN cells have the properties of surround sensitization.

METHODS

Seven female cats were initially anesthetized with Metofane (Metahexafluorothane) followed by ether. For surgical procedures, Surital was administered intravenously. For recording, the animals were immobilized with a continuous infusion of Flaxedil (7·5 mg/kg/hr) and tubocurarine chloride (0·5 mg/kg/hr). Dextrose (6%) was also administered intravenously at the rate of 4·2 ml/hr. Anesthesia was maintained by a mixture of nitrous oxide, 70%; oxygen, 27%; and carbon dioxide, 3%.

Extracellular recordings were made from the dorsal LGN under stereotaxic guidance by means of tungsten microelectrodes, either coated with glass or insulated with Insul-X varnish. Spike amplitudes ranged from 300 μV–4 mV. LGN action potentials were clearly distinguishable from optic tract terminals

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by a number of reliable criteria, including the presence of grouped discharge, polyphasic action potentials and susceptibility to minute doses of barbiturate (HUBEL, 1960). Histological controls were performed successfully in two animals and the recording electrode lesion was confined to the dorsal LGN.

A contact lens was placed on the cornea to prevent drying. A white translucent screen was placed 57 cm in front of the cat's eye, and optical correction was provided by either placing spectacle lenses in front of the eye or by substituting appropriately powered contact lenses. Initial correction for each eye was determined ophthalmoscopically, and further correction was obtained after a cell had been isolated by choosing correction lenses which would enable the cell to resolve the smallest period grating (BARLOW and LEVICK, 1965). An artificial pupil (7 mm^2) was placed immediately in front of the cornea. Pupils were dilated by a 1% solution of atropine. Eye movements were controlled by combining the use of immobilizing agents (Flaxedil and Curare) with a bilateral sympathectomy. This method has been shown to reduce residual eye movements to less than 10 min arc/hr (RODIECK, PETTIGREW, BISHOP and NIKARA, 1967).

Optical stimulation came from three sources. A variable size-adapting field (I) was rear-projected by an overhead projector. The flashing test probe ΔI was rear-projected by a Leitz projector, whose beam was controlled by an electromagnetic motor which had a rise-and-fall time of less than 2 msec (Mechanics for Electronics, Cambridge, Mass.). Homogeneous illumination of the whole screen was provided by tungsten incandescent lamps placed overhead. Measurements of light intensity were made with an S.E.I. photometer. Spatial variations in ambient screen illumination were avoided and were kept to within 0·1 log unit. Intensity of the I and ΔI channel could be varied with neutral density filters in 0·1 log-unit steps.

Action potentials were amplified by a Grass P-9 preamplifier and monitored on a Tektronix 502 oscilloscope and Grass audio monitor. Schmitt trigger- and pulse-forming circuits converted each action potential into a standardized pulse which was then either fed into a gated digital counter, displayed on the face of a Tektronix 564 storage oscilloscope as a dot display (WALL, 1959), or fed into a magnetic tape recorder for later analysis. Reliability of the Schmitt trigger circuit in picking out only one action potential was ensured by feeding the Schmitt pulse into the Z-axis of the monitor oscilloscope so that a small brightening occurred superimposed on the waveform of the action potential (PETTIGREW, NIKARA and BISHOP, 1969).

RESULTS

The procedure began by roughly locating the receptive field of the cell, plotting its exact location and extent with a 0·25 deg spot, occluding the unresponsive eye, and then proceeding with the experiment. The visual stimuli were designed to parallel the WEST-HEIMER (1965) psychophysical procedure as closely as possible. A small brief stimulus ΔI was placed on the center of the receptive field center. Usually it was a 0·25-deg spot. A variable-size adapting disk (I) was formed concentric to this center by the overhead projector system. The main experiment consisted of varying the diameter of the adapting field
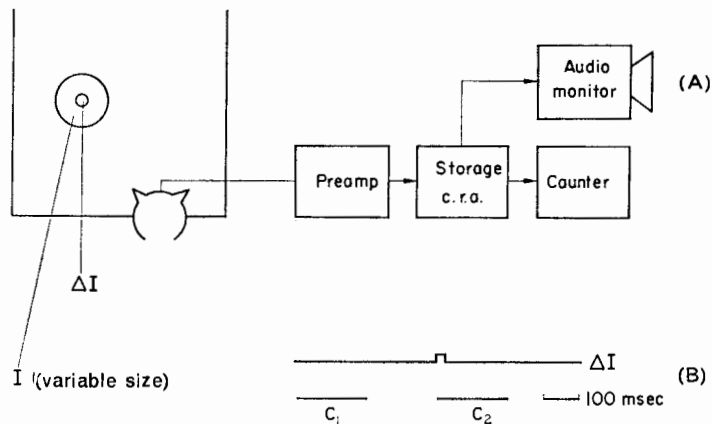

FIG. 1. Summary of the stimulation and recording situation. (A) Cat was placed 57 cm in front of a white translucent screen which was homogeneously illuminated. I and ΔI disks were rear-projected. (B) Summary of impulse counting: Spikes were counted for a 200 msec period before the stimulus and for a 200 msec period after the onset of the stimulus. Response defined as the difference in number of impulses in C_1 and C_2.

and observing changes in the responsiveness of the cell. The ΔI stimulus was always smaller than the smallest adapting disk (I). The exact choice of parameters was dictated by the size of the receptive field and its sensitivity to small spots. In general, large-size receptive fields were tested with larger test flashes and adapting fields. Luminances of I and ΔI were deliberately selected so as to see the phenomenon of surround sensitization (see WEST-HEIMER, 1965). The luminance for the screen varied for different units and ranged between 1 and 10 cd/m². The luminance of the I background ranged from 0·7 to 1·3 log units greater than the screen. The luminance of the ΔI stimulus was never more than 0·2 log units greater than the adapting field.

LGN cells have extremely variable discharge rates in the absence of changing visual stimulation, and it is extremely difficult to determine small changes in thresholds by noting fluctuations of the discharge rate correlated with dim flashes. Therefore, counting of impulses and the tabulation of many individual trials were essential to obtain reliable results. For all experiments, impulses were counted for a fixed 200 msec counting period before the stimulus, and then for an identical-duration counting period beginning at the onset of the stimulus. The difference between the pre- and post-impulse count was taken as the test probe response. Stimuli were never delivered more than 0·5/sec. Figure 1 summarizes the stimulation and recording situation.

For ON center cells, the stimulus was a brief flash (25 msec) to the receptive field center. For OFF center cells, an analogous experiment was performed on which the ΔI spot was left on continuously and then switched off briefly—for 25 msec. This switch-off constituted the stimulus for the OFF cells.

In the majority of cells studied, there was a clear effect indicating that illumination of the surround indeed sensitized the cell's response to the ΔI test probe. Figure 2A indicates the results for an ON center cell. The solid line represents the test probe response as a function of adapting spot diameter. Note that the first segment of the curve shows decreasing responsiveness with increasing diameter, and with further increase in size of the adapting field the curve reverses, and increasing the adapting disk over the receptive field surround leads to increased responsiveness. A similar finding (Fig. 2B) can be seen for OFF center cells. The turnover point, where a progressive decrease in the response is followed by a progressive increase, is consistent with the turnover point seen when determining the size of a receptive field center by using flashes of variable size. For example, the bottom two graphs in Fig. 2 show the response of the same pair of cells to a flashing spot of variable size and constant intensity flashed against a homogeneous background (i.e. background field I absent). The response progressively increases and then decreases. Note the similarity of the turnover point within cells to both procedures. For the ON center cell, it is a 2-deg. dia., and, for the OFF center cell, it occurs at 1-deg. dia.

Evidence for a sensitization by the surround was seen in a majority of LGN cells using this method (9 out of 14). The remaining cells did not show this effect, although two of these cells do show a sensitization effect if one considers the cells' capacity to detect flashes from a statistical viewpoint (see later in this section).

The foregoing results show that the adaptation pool of an LGN cell can be divided into two antagonistic regions and that these regions roughly correspond to the center–surround antagonism seen for the receptive field of the same cells; this result also parallels the psychophysics (WESTHEIMER, 1965). In order to make a better comparison with psycho-physical experiments, however, the threshold of the cell should be determined rather than its responsiveness since psychophysical results are stated in terms of thresholds. I have
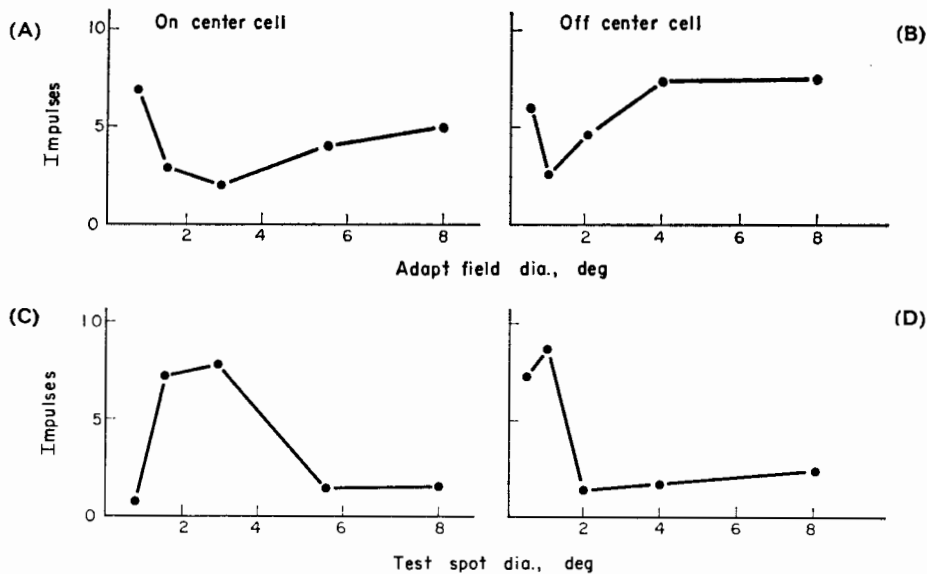
FIG. 2. (A) Response of an ON center cell to a 0·25 deg flash placed on the receptive field center. Adapting disk varied in diameter. Response is measured as the difference between pre- and post-stimulus impulse counts. Screen luminance was 5·5 cd/m². Adapting disk luminance was 38·4 cd/m². (B) Response of an OFF center cell to an "off" pulse of a ΔI spot placed on the receptive field center. Adapting disk varied in diameter. Screen background is 6·8 cd/m². Adapting disk luminance is 34·3 cd/m². (C) Response of the cell in (A) to a variable-size flash placed concentric to the r.f. center. Adapting disk absent. (D) Response of the cell in (B) to a brief "switch-off" of a variable-size spot placed concentric to the receptive field center. Adapting disk absent. All data points in (A), (B), (C) and (D) represent the average of 20 trials.

mentioned earlier that it is extremely difficult to determine thresholds reliably in LGN cells by merely listening to the discharge rate. BARLOW and LEVICK (1969) have developed an objective method of determining thresholds in retinal ganglion cells by applying notions of signal detection theory. Thresholds are determined by measuring the minimum quantity of light which will yield a reliable detection with a given false positive rate. They found that the major determinant in retinal thresholds was the gain of the retina (response/quanta). Changes in the variability of the maintained discharge had a smaller but noticeable effect. Therefore, the variability of the maintained discharge in addition to the response of the cell must be considered in determining a cell's change in threshold. In the present experiments, I have endeavored only to show indirectly that surround illumination does decrease the cell's threshold and not to give a quantitative account of the fall in threshold.

The discriminative capacity of a cell to detect flashes can be appreciated by plotting pulse number distributions of spike counts for epochs when a stimulus has not occurred and when it has occurred. The upper pair of histograms in Fig. 3A gives the distribution of spike counts for the pre-stimulus discharge with a small adapting field (1 deg.), which just covers the receptive field center (left histogram) and for the post-stimulus discharge following a ΔI spot superimposed on this same adapting field (right histogram). The bottom pair of histograms plots the pulse number distributions of the same cell for an 8-deg. adapting field with and without the ΔI spot. In this situation, the 8-deg. adapting field covers both center and surround of the receptive field. Note that the separation of the two distributions
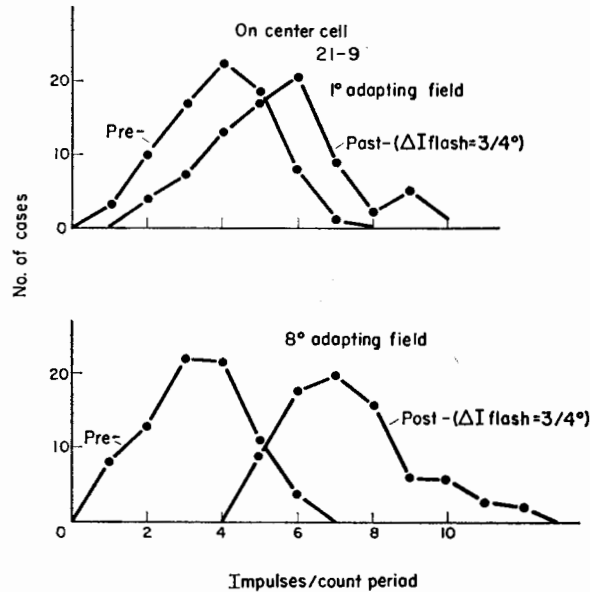
FIG. 3. Pulse number histograms of an ON center cell with two different-size adapting fields. Histograms show the number of occurrences of a particular spike count during the pre-stimulus and post-stimulus count period. ΔI flash is 0·75 deg. Each pair of distributions represents the result of 80 stimulus presentations.

is greater for the large adapting disk than it is for the small adapting disk. Therefore, from a simple statistical consideration, the cell can better discriminate flash from no-flash when there is a large background than for a small one.

More specifically, let us assume that the nervous system can adopt a criterion which, if exceeded, means that a flash has occurred. If we assume differing criterion for detection, we can generate an operating characteristic curve from the data in the pulse number histograms which relates the percentage of correct detections to the percentage of false positives. Figure 4 presents such a plot from the data in Fig. 3. Note that, for any assumed false positive rate, there are more hypothetical correct detections of the ΔI spot against the larger 8-deg. background than the smaller 1-deg. background. Since the LGN discharge is monotonically increasing with flash intensity (BAKER et al., 1969), it will take more ΔI against a small background to yield a defined threshold response (for example, a 50 per cent seeing with a 0·2 per cent false positive rate). Put in the language of thresholds, the threshold will fall with an increase in size of a steady-adapting field which covers the receptive field surround. This finding parallels the findings of Westheimer.

By taking account of both the variability and the responses (spikes added per flash) in all cells, two cells which did not show clear surround sensitization in terms of spikes added per flash did show a surround sensitization if an index of discriminability, d', was computed. $[d' = (\bar{X}_s - \bar{X}_n/S_n)]$: $\bar{X}_s$ = mean counts associated with the flash, $\bar{X}_n$ = mean counts associated with pre-flash count, S_n = measured standard deviation of the pre-flash count (maintained discharge). Figure 5 shows the influence of increasing the size of an adapting disk on the maintained discharge ($\bar{X}_n$), stimulus-induced discharge ($\bar{X}_s$), and on the standard deviation of the maintained discharge (S_n). Note that increasing the size of an adapting disk decreases
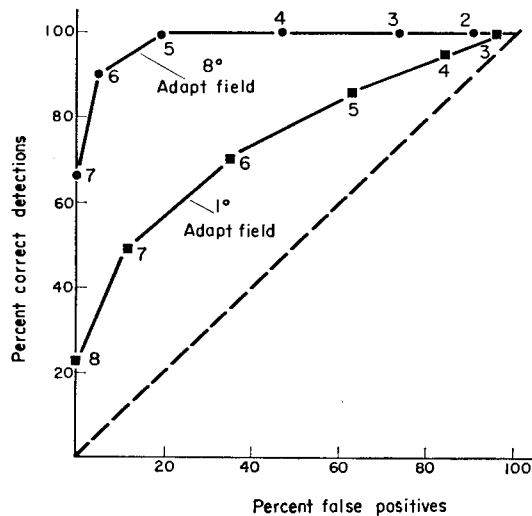
FIG. 4. Receiver operating characteristic curves obtained from the data in histograms in Fig. 3. Different detection criteria are selected (No. of impulses), and the resulting percentage of correct detections is plotted versus the percentage of false positives. Each curve represents a particular background diameter. Small numbers next to plotted points on graph represent criteria selected (impulse/count period) which determines the relation of correct detections versus false positives.

the absolute level of the maintained discharge and also the evoked discharge in a parallel fashion. Therefore, in terms of spikes added per flash, there is only a small difference between large and small adapting disks. The standard deviation of the maintained discharge, however, shows a twofold decrease with increasing adapting disk size, and hence the discriminative capacity of the cell in terms of $(\bar{X}_s - \bar{X}_n)/S_n$ clearly increases with increasing surround size. In this cell, I was unable to see the effect of increasing the size of the adapting disk over the center of the receptive field due to the choice of a relatively large ΔI flash (0·75-deg.).

The failure to see any clear effect of surround sensitization in the remaining three cells (two ON center, one OFF center) does not necessarily mean that a true surround sensitization was absent. The data from these cells was taken close to the end of the experiment when the optics had clearly deteriorated. Under these circumstances, increasing the surround size may have appreciably increased the light scatter to the center of the receptive field. This condition would have masked any genuine neural sensitization mediated by the surround.

DISCUSSION

The foregoing results show that the LGN cell's response to a small, centrally placed flash is greater in terms of spikes added per flash if the center and the surround are under steady illumination rather than if the center alone is illuminated. Steady illumination of the surround has a sensitizing effect on the cell whose response has been depressed by steady illumination of the center mechanism. This result indicates that, for LGN cells, there is a parallel between receptive field organization and the spatial arrangement of the effects of steady adaptation. In both instances, the surround mechanism can be considered to be antagonistic to the center.
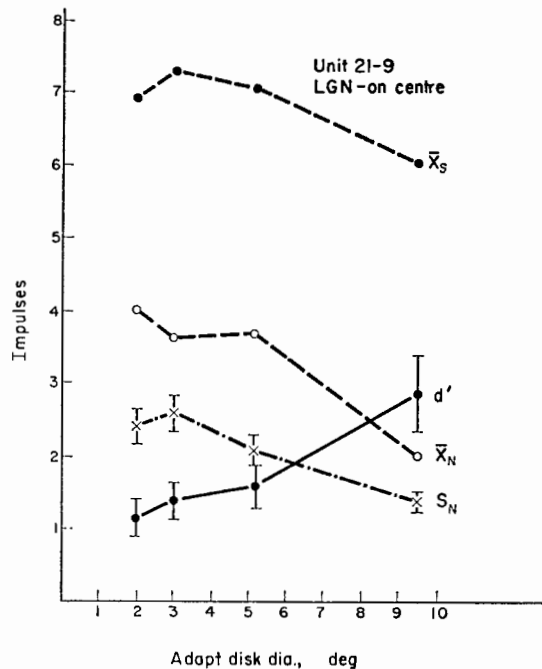
FIG. 5. Parameters of the impulse discharge as a function of adapting disk diameter. Top dotted curve ($\bullet$ - - - $\bullet$), mean counts in the post-stimulus period ($\bar{X}_s$). Middle dotted curve ($\bigcirc$ - - - $\bigcirc$), mean counts in the pre-stimulus period ($\bar{X}_n$). Bottom dotted curve ($\times$-·-·-$\times$), standard deviation of the pre-stimulus count (S_n). Bottom solid curve $[d' = \dfrac{(\bar{X}_s - \bar{X}_n)}{S_n}$, a measure of statistical discriminability. Markers represent one standard error. Screen luminance—6·8 cd/m², adapting disk luminance—105 cd/m².

This finding in LGN cells stands in contrast to the results of parallel work in retinal ganglion cells (SAKMAN *et al.*, 1969). Retinal ganglion cells show no increase in responsiveness when a circular adapting disk is enlarged to include the surround of a receptive field. This result suggests that the surround mechanism has no influence on the adaptive state of the ganglion cell. The receptive field antagonisms seen for retinal ganglion cells do not correspond with the "receptive field of adaptation". This phenomenon stands in contrast to the present experiments in LGN cells where such a correspondence has been shown to exist.

The experiments of MAFFEI (1968) and MAFFEI, CERVETTO and FLORENTINI (1970) blur the picture somewhat. Using a different procedure, consisting of a sinusoidally modulated spot on the receptive field center and a satellite spot in the surround, they found that steady illumination of a spot in the surround increased the amplitude of a sinusoidally modulated response of the center mechanism. Several factors distinguish this experimental approach, however. First, the optical arrangement is clearly different from those of SAKMAN *et al.* (1969), and this condition might have some bearing on the discrepancy. A second difference lies in the fact that Maffei mainly utilized axonal recording from fibers of the optic tract, whereas Sakman and coworkers recorded from the soma of ganglion cells. Two populations of ganglion cells may have been sampled using the two recording methods.

Furthermore, it is possible that an analysis of a cell's discriminative capacity, i.e. a computation of d', would show the retina also to parallel the psychophysics. The results of SAKMAN *et al.* (1969) indicate no change in the number of spikes added per flash with larger as opposed to small background, but the statistical properties of the maintained discharge were not considered. Figure 5 in this paper indicates that it is possible for an LGN cell to show little change in response (spikes added per flash) but yet show a clear increase in statistical discriminability with large adapting fields. This result is due to a decrease in the variability of the maintained discharge with larger adapting fields. Retinal ganglion cells may show similar properties.

In summary, LGN cells show a surround sensitization which parallels the psychophysics. It remains to be seen whether this property is attributable to earlier stages in the visual pathway.

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Résumé—Westheimer a montré que le seuil psychophysique de détection d'un faible éclair sur un grand fond est plus petit que pour détecter le même éclair sur un fond moins grand. Ce phénomène (sensibilisation par le fond) n'est pas constaté sur les expériences analogues dans les ganglionnaires de la rétine. On décrit des expériences sur le corps genouillé du chat qui indiquent qu'à ce niveau existe un effet parallèle à celui de Westheimer. Quand on augmente la dimension d'un disque d'adaptation de fond autour du champ récepteur, on accroît la capacité de la cellule à détecter un petit éclair produit au centre.

Zusammenfassung—Es wurde von Westheimer psychophysikalisch gezeigt, dass die Entdeckungsschwelle für einen kleinen, auf einem grossen Hintergrund abgebildeten Blitz kleiner ist, als wenn derselbe Blitz auf einem kleinen Hintergrund abgebildet wird. Dieses, als Umrahmungssensitierung bezeichnete Phänomen ist nicht in analogen Versuchen mit Netzhautganglionenzellen zu beobachten. Aber die gegenwärtigen mit Katzenkniehöckerzellen ausgeführten Versuche zeigen, dass es an diesem Niveau ein dem Westheimerschen pyschophysikalisch parallel laufendes Ergebnis gibt. Wenn eine scheibe, welche den Hintergrund umstimmt, als Umrahmung des Rezeptivfeldes vergrössert wird, so erhöht sich die Zellenfähigheit einen kleinen, auf die Mitte bestimmten Blitz zu entdecken.

Резюме — Westheimer показал психофизическим методом, что порог обнаружения малой по площади вспышки света, проецируемый на большой фон, ниже, чем порог обнаружения той же самой вспышки на меньшем фоне. Этот феномен, названный сенсибилизацией от окружения (surround sensitization), не был обнаружен в аналогичных экспериментах в ганглиозных клетках сетчатки. Настоящие эксперименты на клетках наружного коленчатого тела, однако, показывают, что явления параллельные обнаруженным Westheimer психофизическим методом существуют на этом уровне. Увеличение фонового адаптирующего диска ь окружении рецептивного поля увеличивает способность клетки обнаруживать малые вспышки света подаваемого на центр рецептивного поля.