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LOCAL ADAPTATION IN STABILIZED VISION

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WHEN one views a sharp border separating two regions of unequal luminance, the well-known phenomenon of simultaneous contrast occurs; the region of higher luminance makes the dim region appear darker, and vice versa. The physiological basis for this is probably lateral inhibition in the retina and higher in the visual pathway. Light falling in the inhibitory surround of the receptive field of a retinal ganglion cell reduces the response elicited by light falling in the central zone (BARLOW, 1953; KUFFLER, 1953). It is easy to show this effect in single unit preparations, but it has proved surprisingly difficult to investigate it in psychophysical experiments on humans. Many researchers report a small elevation of threshold near a border in the visual field (TELLER, 1965), but a method of producing changes large enough to study at different adaptation levels and in various retinal regions has only recently been devised (WESTHEIMER, 1965).

The principal reason for this difficulty is that one deals with many parallel pathways in psychophysical experiments instead of with a single, well-isolated unit. For instance, on such an isolated unit lateral inhibition may be shown by measuring threshold as a function of the area of a stimulus spot; as the spot spreads into the inhibitory zone the threshold intensity required to excite the ganglion cell rises. However, in a human experiment, as the spot is increased in size it covers the receptive fields of more units, thus introducing the possibility of summation of sub-threshold influences. Furthermore, the newly covered units lying near the edge of the spot will be less strongly inhibited than those at the center of the spot, since part of their inhibitory surround will be uncovered, and there is also the possibility that large spots may preferentially excite ganglion cells with large receptive fields. For these reasons, it is not surprising that threshold always decreases monotonically with area in these psychophysical experiments.

Westheimer overcame these difficulties by measuring the threshold for a small test light of constant size as a function of the area of the adaptation field upon which it was superimposed. The small test flash ensured that only a few units were favorably placed to respond to the light, and the effect of the adapting field could be studied upon these few units alone. The conditions of the experiment, in the form in which we have repeated it, are shown in Fig. 1. The scotopic, rod system was isolated 6° peripheral to the fovea by employing deep red adapting fields and a green test flash (AGUILAR and STILES, 1954).

The result on one subject is shown in Fig. 2 (circles and dotted line). Increment threshold rises as the adapting field diameter is increased to approximately 40 min (0·2 mm on the retina). This rise is presumably due to the increased flux of adapting light falling in the

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central summatory areas of the receptive fields of ganglion cells underlying the test spot. However, as the adapting field spreads onto larger areas, presumably invading the inhibitory surrounds of the receptive fields centered under the test spot, the threshold for the test spot decreases again. Adapting light on the test area itself makes the retina less sensitive, as shown in many earlier psychophysical experiments; but adapting light a short distance away from the test area makes it more sensitive.

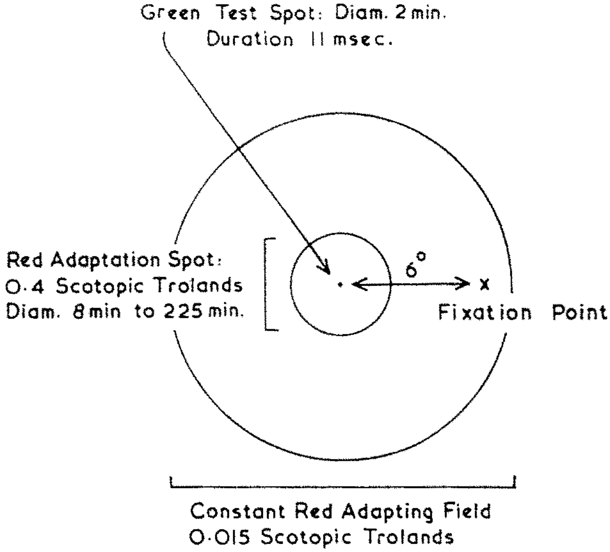

FIG. 1. Field of view as seen by subject. The adaptation spot of variable diameter is superimposed upon a dimmer adapting field of about 15° diameter. The test spot is added to the center of the adapting spot.

If this is the correct interpretation, the threshold-elevating influence of adapting light falling in the different subdivisions of the receptive field exactly parallels the excitatory influences revealed in area-threshold curves on single units. We were not, however, satisfied that this interpretation of Westheimer's experiment is correct, for the following reason. It is known that increment thresholds are elevated near the times of changes of adapting field intensity (BAKER, 1963). The eye is constantly executing small saccadic movements, drifts, and tremors (BARLOW, 1952; RIGGS, ARMINGTON and RATLIFF, 1956), all of which move the adapting field over the retina. It is arguable that the threshold of the test spot depends upon how recently the test region has undergone the great excursions of illumination that occur when the image of the edge traverses it, and that the time that has elapsed since such edge stimulation increases, on the average, with the area of the adapting field. The falling limb of Westheimer's curve could, in fact, result from these threshold changes combined with eye movements, rather than from spatial interactions. In order to investigate this we have repeated his experiment using a stabilized retinal image (Fig. 2, continuous lines).

The optical apparatus followed the design of DITCHBURN (1963). In this design, light from a projection system is reflected from a mirror attached to a contact lens worn by the subject. The subject then views the reflected light through a telescope with an angular magnification of 1/2. In stabilized image experiments of this type, slip of the contact lens, scattered light, and poor optical resolution are serious problems (BARLOW, 1964). In order to minimize lens slip, contact lenses were made to fit the eye at the limbus, and were held in place by reduced pressure applied through rubber suction cups. To minimize scattered light on the retina the contact lenses were painted black on the inside, leaving a 2 mm diameter artificial pupil. To avoid smearing by blinking, the mirror was mounted on a side arm; and to reduce the tendency of the lens to rotate, this side arm and the rubber suckers were mounted low down on the front of the lens, about at the positions of the hands of a clock at 23 min to 5 o'clock. This had the further advantage of allowing the upper lid to clean the optical path through the contact lens by blinking right across it. Tests of the apparatus when wearing the contact lens showed that a grating of bar width 75 sec was easily resolvable; the resolution of the peripheral retina used in these experiments was, of course, much lower than this. Calibrations indicated that the image movements would be reduced to less than 2 per cent of their normal magnitude if the lenses did not slip: movements of the eye outside the field within which the target could be seen, and residual slip, are probably more important causes of loss of stability.

The procedure in these experiments was as follows. Two subjects were used, both of whom had 20/20 vision in the eye concerned. Both were experienced in psychophysical experiments. Each did four experimental sessions in a series. In the middle two sessions, the subject wore the contact lens with the mirror attached, and the image was stabilized on the retina. In the first and last sessions the subject still wore the contact lens, but the mirror was attached to a fixed mount instead of to the side arm of the lens; thus the optical conditions were exactly the same as in the stabilized runs, but the image was unstabilized. The test spot was flashed for 11 msec once every second. Thresholds were determined by the subject adjusting a wedge until he could just see the flash on the majority of trials. After taking the wedge reading the experimenter haphazardly upset the wedge setting and changed the size of the adaptation spot to the next in the session. All sessions were done from small area to large, then back to small.

The results for one subject are shown in Fig. 2. Each plotted point is the average of four settings, a pair from each of two experimental sessions. The standard deviation of repeat settings calculated from these paired readings, is 0·11 $\log_{10}$ units, but it is less for stabilized and more for unstabilized conditions.

It will be seen that there is a definite diminution of threshold when the adapting spot is enlarged above 50 min diameter. The reduction is more pronounced under stabilized conditions, and occurs at a somewhat smaller diameter of adapting spot. All these features of Fig. 2 were present in the results obtained from the other subject. It is therefore certain that Westheimer's phenomenon cannot be explained by successive contrast combined with eye movements—indeed, Fig. 2 shows that eye movements tend to obscure the effect. Lateral inhibition in the retina, or higher in the visual pathway, must be the cause.

It is of interest to compare the results of this experiment with the results of area-threshold experiments on single units in the frog or cat retina. In them, as the area of a spot of light is increased, threshold first falls, and then rises again as the stimulating spot invades the inhibitory surround of the cell (BARLOW, 1953; BARLOW *et al.*, 1957). In the present psychophysical experiment, the increment threshold at the center of an adapting field first rises and then falls again as the diameter of the field increases. It is clear that the total

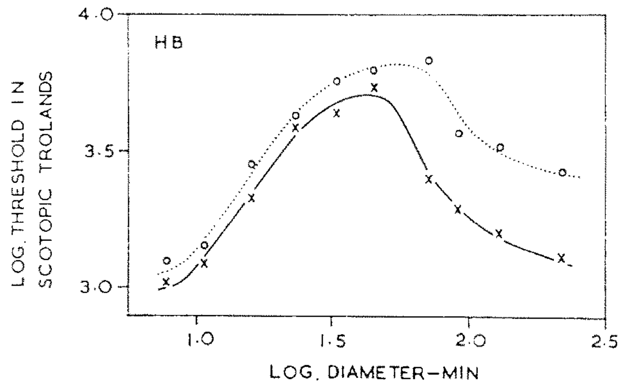

FIG. 2. Threshold for the test spot (diameter 2 min, duration 11 msec) as a function of diameter of adapting spot for unstabilized (circles) and stabilized (crosses) viewing.

excitatory effect of the stimulating spot in the first case and its adaptational effect in the second case run parallel courses.

In addition to this definite conclusion, it is worth making comments upon two aspects of the subjective experience while performing these experiments. Without stabilization one is very much aware of the disturbing effects of eye movements. A small change of fixation position causes an intense subjective effect as the adaptation field moves, and one is disturbed by this flashing of the adapting field since it is subjectively similar to the appearance of a suprathreshold test flash. This makes the threshold settings under unstabilized conditions unsatisfactory from a subjective point of view. We think that this difficulty was the cause of the thresholds being higher for unstabilized than for stabilized conditions, and it is probably also the cause of the variance of settings being nearly twice higher under unstabilized conditions. Certainly, under stabilized conditions the threshold settings are noticeably easier to make; one is not disturbed by the blurring, misting and fading of the stabilized adapting spot, for the appearance of the test flash is always a clearly defined, separate experience, in contrast with the situation without stabilization.

The second point concerns the subjective appearance of the test stimulus at threshold, which changes when it is superimposed upon fields of different sizes. On a large field it is seen, as one would expect, as a small central spot. When the adapting field is less than about 30 min diameter, however, the threshold experience is of a diffuse flash in the region surrounding the adapting spot. Either scattered light from the test spot is being detected, or the stimulus is exciting the receptive fields of ganglion cells whose centers lie outside the adapting spot. Different units may well determine the threshold when the adapting field is small instead of large, but this does not upset the conclusions reached, because these follow from the fall in threshold at large adapting spot diameters. We have clearly substantiated Westheimer's finding that adapting light at a distance can make an area of retina more sensitive to an incremental flash; and we have shown that he is correct in attributing this to spatial interactions.

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Abstract—The increment threshold for a small stimulus superimposed upon adapting spots of various diameters was measured under scotopic conditions in the peripheral retina. Confirming WESTHEIMER (1965), it was found that adapting spots of about 1° diameter raise the threshold more than either larger or smaller spots. This experiment was repeated using a stabilized-image technique to avoid movements of the adapting field over the retina. The reduction of threshold with increase of the adapting spot diameter above 1° was found to be more pronounced with stabilization than without. Hence, Westheimer's phenomenon cannot be explained by eye movements and temporal excitability changes, and must be attributed to physiological interactions within the visual system.

Résumé—On mesure dans des conditions scotopiques dans la rétine périphérique le seuil différentiel pour un petit stimulus superposé sur des fonds d'adaptation de divers diamètres. On trouve en accord avec WESTHEIMER (1965) que des fonds d'adaptation de 1° de diamètre environ augmentent le seuil plus que des fonds plus petits ou plus grands. On a répété cette expérience avec la technique d'image stabilisée pour éviter les mouvements du champ d'adaptation sur la rétine. La réduction du seuil quand le diamètre du fond d'adaptation dépasse 1° est plus prononcée avec stabilisation que sans. Par conséquent le phénomène de Westheimer ne peut pas s'expliquer par des mouvements des yeux et des changements temporels d'excitabilité, et doit être attribué aux interactions physiologiques dans le système visuel.

Zusammenfassung—Unter skotopischen Bedingungen wurde peripher die Unterschiedsschwelle für einen kleinen Testreiz bestimmt, der Adaptationsfeldern mit verschiedenen Durchmessern überlagert wurde. In Übereinstimmung mit WESTHEIMER (1965) ergab sich, dass Adaptationsfelder von etwa 1° Durchmesser die Schwelle mehr erhöhen als grössere oder kleinere Felder. Dieser Versuch wurde mit stabilisiertem Netzhautbild wiederholt, um Bewegungen des Adaptationsfeldes über die Netzhaut zu vermeiden. Die Abnahme der Schwelle bei einer Zunahme der Grösse des Adaptationsfeldes über 1° war mit stabilisiertem Netzhautbild ausgeprägter als ohne. Westheimers Phänomen kann also nicht mit Augenbewegungen oder zeitlichen Empfindlichkeitsschwankungen erklärt werden, sondern ist auf physiologische Wechselwirkungen innerhalb des visuellen Systems zurückzuführen.

Резюме—Инкрементный порг для малого стимула, налагаемого на адаптирующее пятно различных диаметров, был измерен при скотопических условиях на периферии сетчатки. В подтверждение данных Вестгаймера (WESTHEIMER, 1965) было найдено, что адаптирующее пятно около 1° в диаметре повышает порг в большей мере, чем пятна больших или меньших угловых размеров. Эти опыты были повторены с применением техники стабилизированного изображения, для того чтобы исключить движения адаптирующего поля по сетчатке. Было найдено, что понижение порога при увеличении диаметра адаптирующего пятна свыше 1° более выражено при стабилизаци, чем без нее. Таким образом феномен Вестгаймера не может быть объяснен движениями глаз и изменениями возбудимости во времени, а должен быть приписан физиологическим взаимодействиям в зрительной системе.