Poppels Harvey 1973

Psychol. Forsch. 36, 145-161 (1973)
© by Springer-Verlag 1973

Light-Difference Threshold and Subjective Brightness in the Periphery of the Visual Field*

Ernst Pöppel** and Lewis O. Harvey, Jr.**

Department of Psychology, Massachusetts Institute of Technology, Cambridge, Massachusetts

> and Massachusetts College of Optometry, Boston, Massachusetts

> > Received December 30, 1972/April 2, 1973

Summary. Light-difference thresholds were measured in the center and periphery of the visual field at photopic and scotopic levels. Under *photopic* conditions the forea has the lowest light-difference threshold. From the forea to 10 degrees eccentricity threshold gradually increases. It remains constant up to approximately 35 degrees eccentricity in the temporal visual field (nasal retina). Beyond the edge of this plateau of constant light-difference threshold, it again increases to the limit of the visual field. Under *scotopic* conditions the extent of the plateau of constant light-difference threshold remains the same as under photopic conditions. The forea itself, however, and its immediate environment are less sensitive than the plateau area.

Subjective brightness of a supra-threshold target is not dependent on its position in the visual field. A target with a given luminance will elicit the same brightness sensation at all retinal positions. As a consequence of this brightness constancy throughout the visual field, peripheral targets at threshold appear brighter than foveal targets at threshold because a peripheral target at threshold has more luminance than a foveal target at threshold.

Zusammenfassung. Die Inkrementalschwelle wurde in der Fovea und in der Peripherie des Gesichtsfeldes bei photopischen und skotopischen Adaptationsbedingungen gemessen. Bei photopischen Bedingungen ist die Schwelle in der Fovea am geringsten (größte Sensitivität). Von der Fovea bis etwa 10 Grad in die Peripherie nimmt die Inkrementalschwelle allmählich zu. Die Schwelle bleibt dann konstant bis etwa 35 Grad im temporalen Gesichtsfeld (nasale Retina) und bis etwa 20 Grad im nasalen Gesichtsfeld (temporale Retina). Jenseits dieses Plateaus konstanter Sensitivität nimmt die Schwelle wieder zu, bis schließlich das Ende des Gesichtsfeldes erreicht wird. Bei skotopischen Adaptationsbedingungen wurde die-

* For Jürgen Aschoff's 60th Birthday.

** E.P. was supported by Deutsche Forschungsgemeinschaft, L. O. H. by the Sloan Foundation. L. O. H. is Assistant Professor of Physiology and Physiological Optics at the Massachusetts College of Optometry and Research Associate at the Department of Psychology, Massachusetts Institute of Technology.

This paper is based on presentations by both authors at the meeting of the Eastern Psychological Association in Boston, April 27-29, 1972.

10*

E. Pöppel and L. O. Harvey, Jr.:

selbe Ausdehnung des Plateaus konstanter Schwelle im temporalen und nasalen Gesichtsfeld beobachtet. Die Fovea und die unmittelbare Umgebung der Fovea haben bei skotopischen Bedingungen eine geringere Sensitivität.

Die subjektive Helligkeit überschwelliger Reize ist nicht abhängig von der Lage des Lichtreizes im Gesichtsfeld. Ein überschwelliger Reiz mit gegebener Intensität hat überall im Gesichtsfeld dieselbe subjektive Helligkeit. Als Konsequenz der Konstanz der Helligkeit im Gesichtsfeld erscheinen Schwellenreize in der Peripherie heller als Schwellenreize im Fovea-nahen Bereich, da die Lichtintensität für Schwellenreize in der Peripherie größer ist als im Fovea-nahen Bereich.

I. Introduction

In a recent review Aulhorn and Harms (1972) proposed that the special perimeter constructed by Harms should make it possible to determine various "functions in any part of the visual field and for any state of adaptation." One of the functions they mention is the "light-difference threshold". We have attempted to measure the light-difference threshold throughout the entire visual field. Previous measurements of the light-difference threshold in the visual field either were made exclusively along the horizontal meridian (e.g., Aulhorn, 1964), or were confined to an area close to the fovea (e.g., Kishto, 1970). There are various reasons, in addition to mere curiosity, for wishing to learn more about the light-difference threshold in the periphery of the visual field. In a great number of neurophysiological experiments, properties of receptive fields in the retina (e.g., Kuffler, 1953; Hubel and Wiesel, 1960), the lateral geniculate nucleus (e.g., Hubel and Wiesel, 1961), and the visual cortex (e.g., Hubel and Wiesel, 1968) have been described. One general observation has been that the diameter of receptive fields in all these structures increases with increasing distance from the visual axis. In order to relate this observation to the light-difference threshold in man, as Aulhorn and Harms (1972) have suggested, the light-difference threshold throughout the visual field needs to be defined. Visual information from the periphery of the visual field determines to a great extent orientation in space. If the light-difference threshold varies differentially along different meridians, there may be preferences in oculomotor reactions along the more sensitive meridians. Eye movements to targets appearing in more sensitive areas may be different than movements to targets in less sensitive areas. Thus, information is needed about the sensitivity of the peripheral visual field, if one wishes to study oculomotor performance (Frost and Pöppel, 1973). In addition, there are a number of practical reasons for measuring the sensitivity of the peripheral visual field. On any task involving surveillance of several control instruments, the observer — for instance

the pilot in a cockpit — has to rely on his peripheral vision. It seems therefore essential for the optimal construction of instrument panels that the receptive power of the visual field be taken into account (see for instance Senders et al., 1955).

We shall first present data on light-difference thresholds in the periphery of the visual field obtained under low photopic conditions. We shall then give data on light-difference thresholds obtained at other levels of adaptation. Finally, we shall report observations on subjective brightness throughout the visual field. The data on the light-difference threshold have been published previously (Harvey and Pöppel, 1972).

II. Methods

All of the measurements for light-difference threshold and for subjective brightness were obtained using the Tübingen perimeter constructed by Harms. A detailed description of this device and of perimetric techniques has recently been given by Sloan (1971) and by Aulhorn and Harms (1972).

During an experimental session the subject views a fixation point located at a distance of 33 cm. The fixation point is projected onto the inner surface of an evenly illuminated hemisphere. A target can be projected at any position within the hemisphere. The luminance of the target, of the fixation point or of the background of the hemisphere can be varied independently. A telescope built into the perimeter can be used to monitor the eye position of the subject.

For all measurements, i.e., for the determination of the light-difference threshold and the subjective brightness in the periphery, the natural pupil was used. In studying the properties of the periphery of the visual filed, we were interested in the effect of natural viewing conditions. Under natural viewing conditions the visual system has to cope with refractive errors in the periphery (but see Ferree et al., 1933; Leibowitz et al., 1972), and with changes in the size of the effective pupillary area (Spring and Stiles, 1948; Sloan, 1950; Jay, 1961).

1. Light-Difference Threshold

The initial series of measurements was obtained with a background luminance of 0.85 millilambert, i.e., within the low photopic range. The fixation point was a 30 min arc circular red spot 0.5 millilambert above the background. The target was a 10 min arc circular spot of white light. The light sources were tungsten bulbs. Duration of target presentation was 200 msec.

The light-difference threshold was measured in the fovea and at 2° intervals from the fovea into the periphery. To measure the foveal threshold, the circular fixation point was replaced by four smaller spots forming a diamond pattern, and the subject fixated the center of this pattern. The ascending method of limits was employed. The subject was first shown at what position the target would be presented using a supra-threshold target. The experimenter then decreased the luminance of the target so that it was no longer visible to the subject. The experimenter then increased the luminance in 0.1 log unit steps until the subject indicated seeing the target by pressing a buzzer.

Target contrast as used here is defined as the luminance of the threshold target (Lt) subtracted from the luminance of the background (Lb) and then divided by Lb. The difference between L₁ and L_b (Δ L) is the amount of luminance which has to

be added to the luminance of the background in order to reach detection threshold The determination of the light-difference threshold along one meridian when

for the target. The measured values of ΔL are given as ordinate values in Figs. 1 and 3. measurements were taken at 2° intervals of visual angle took approximately 1 h. Because of the investment of time, most of the data were obtained from one of the authors (E.P.) as subject; the other author (L.O.H.) served as experimenter for this condition. Measurements in 13 other subjects were obtained and these observations confirmed the data reported here. All subjects who participated in these experiments had normal vision and did not need any corrections.

The light-difference threshold for E.P. was measured along 12 different meridians 15° apart. The sensitivity of each eye was tested separately; the eye which was not tested was covered by a translucent eye patch. In one experimental session usually only one meridian was tested; occasionally, data from two meridians were obtained. The measurements were always taken in the morning starting around 9 a.m.

An additional series of measurements along the horizontal meridian was obtained on subject E.P. using the following background luminances: 8.5×10^{-1} ; 8.5×10^{-2} ; 8.5×10^{-3} ; 8.5×10^{-4} ; 8.5×10^{-5} millilambert. This range covers photopic, mesopic and scotopic adaptation levels. Sufficient time was allowed before testing to allow the subject to become fully adapted to the background level used.

2. Subjective Brightness

During the experiments on light-difference thresholds, E.P. observed that the subjective brightness of targets at threshold was not the same for different eccentricities. This observation was subsequently confirmed by other subjects. All reported that the subjective brightness of the threshold targets increased with increasing distance from the fovea. Because of this intriguing observation we attempted to get some quantitative measurements of subjective brightness in the periphery of the visual field.

Using a magnitude estimation procedure, the subject compared the subjective brightness of a peripheral target with that of a foveal target. Measurement conditions were essentially identical with those used to measure light-difference thresholds: 0.83 millilambert background and a 10 min arc peripheral target. A foveal target, 10 min arc in diameter and 19 millilambert above the background luminance, was continuously presented to the subject. The brightness of this target was arbitrarily designated as having a magnitude of "50". Peripheral targets were presented for 200 msec and the subject's task was to assign numbers to them which expressed subjectively their brightness relative to that of the foveal target.

Measurements were made in E.P.'s right eye. At each retinal locus (from 2° to 60° in the temporal visual field) 13 stimulus luminances covering the range from 3.2 to 57 millilamberts above the background luminance in 0.1 log unit steps, were each presented ten times in a random sequence. Under these conditions the 3.2 millilambert target is still above threshold at a retinal eccentricity of 60°. The geometric mean of the ten judgements elicited by each target luminance was calculated. These geometric means were then used to derive the target luminance at each retinal locus which would appear equal in brightness to the foveal target (see results).

It is important to emphasize that the subject's judgement is comparative. The foveal target was defined as having a magnitude of "50". Peripheral targets appearing dimmer than the fovea should yield numbers less than 50. Peripheral targets appearing brighter than the fovea should give numbers greater than 50. This method differs from that used by Marks (1966, 1968) which had no comparison stimulus and where judgements were absolute rather than relative.

III. Results

1. Light-Difference Threshold under Photopic Conditions

An example of the distribution of light-difference thresholds along the horizontal meridian of the right eye is shown in Fig. 1, where lightdifference threshold is plotted as a function of retinal eccentricity for subject H. L. The ordinate is logarithmic and inverted, i.e., higher values indicate lower light-difference thresholds (hence higher sensitivity). For the given adaptation level which falls into the low photopic range (0.85 millilambert background luminance), the fovea has the highest sensitivity as indicated by the peak at 0 degrees in Fig. 1. To either side of the fovea sensitivity decreases. This decrease is followed by an area between 6 and 16 degrees in the nasal visual field and between the blind spot and 34 degrees in the temporal visual field where sensitivity is constant. Beyond this "plateau", as this area of constant threshold might be called, a further increase in luminance is needed in order to render the 10 min arc stimulus visible. Finally, even targets with a contrast of 100 are no longer detectable.

Fig. 1 indicates that the visual field extends further to the temporal side (nasal retina) than to the nasal side (temporal retina). This result is not due to the fact that light coming from the nasal side cannot reach the temperal retina because of the nose. When the subject was asked to turn his head to the left but still fixate the central fixation point, the limits of the nasal visual field remained constant. Thus, the nasal visual



Fig. 1. Light-difference threshold $(\Delta L/L)$ as function of retinal locus. Measurements for one subject (H.L.) along the horizontal meridian of the right eye. The target subtended 10 min arc of visual angle and was presented for 200 msec. The background luminance was 0.85 millilambert (low photopic range). Note the constant light-difference threshold between 6° and 16° in the nasal visual field and between the blind spot and 34° in the temporal visual field

149



Fig. 2. Light-difference threshold ($\Delta L/L$) isopters for the right eye of E.P., determined with a 10 min arc target. The target was presented for 200 msec on a 0.85 millilambert background. The visual field is represented in polar coordinates with the fovea at the origin. Horizontal and vertical meridians are marked at 10° intervals. For the outmost isopter (heavy line) the contrast is 10.0; the contrast for the isopters is shown in the right lower quadrant. The contrast for foveal vision under these conditions (for the right eye of E.P.) is 0.1. The isopters are based on measurements along 12 meridians. The measurements along each meridian were obtained in steps of 2° visual angle from the fovea to the limits of the visual field. Note the plateau of constant lightdifference threshold surrounding the foveal and perifoveal region with its pronounced extension into the temporal visual field (nasal retina). (Data taken from Harvey and Pöppel, 1972)

field appears to be less extensive. The range of sensitivity between the maximum in the fovea and the minimum in the far periphery covers more than 2 logarithmic units.

Fig. 2 presents a polar coordinate plot of the sensitivity in the visual field of the right eye of one subject (E.P.). The contours represent the loci of equal light-difference thresholds and were derived from measurements made along 12 different meridians. These measurements are similar to those for subject H.L. along the horizontal meridian presented in Fig. 1. Each contour represents an interval of 0.2 log units of contrast $(\Delta L/L)$. The two heavy lines are separated by 1 log unit contrast. Thus, the threshold at the fovea has a contrast of 0.1; at the first heavy line, 1.0; and the second heavy line, 10.0.

Starting from the fovea in the center, light-difference threshold is increasing in all directions up to approximately 10 degrees eccentricity. This central cone of sensitivity — for photopic conditions — appears to "rest" on a large plateau of constant sensitivity which extends far into the temporal visual field (nasal retina). This plateau is less pronounced in the nasal visual field (temporal retina) as it extends only from approximately 10 to 20 degrees eccentricity. The blind spot is located within the plateau on the temporal side. Beyond this plateau, light-difference threshold is increasing until finally the limit of the visual field is reached. (During the measurements of light-difference thresholds along more vertically oriented meridians the subject raised his eyebrows in order to allow light to enter the pupil from above; with eyebrows and lids in normal resting position the normal visual field is considerably restricted in its superior positions.)

A very similar polar coordinate plot has been obtained for the left eye of E. P. (Harvey and Pöppel, 1972) also showing the central cone of ·low light-difference threshold surrounded by a plateau extending pre-

Table 1. Extent of the plateau of constant light-difference thresholds on the temporal and nasal side of the visual field in degrees of visual angle. Stimulus diameter: 10 min arc. Stimulus duration: 200 msec. Luminance of background: 0.85 millilambert. All measurements were obtained along the horizontal meridian. The right eye (R) of E.P. was tested on two different days; the left eye (L) was tested only in three subjects

Subject	Eye	Temporal Side	Nasal Side	
E.P.	R (1)	38	22	
E.P.	R(2)	36	20	
H.L.	RÚ	34	16	
J.D.	R	34	20	
S.Ch.	\mathbf{R}	34	20	
R.H.	\mathbf{R}	36	20	
S.T.	\mathbf{R}	32	22	
R.D.	\mathbf{R}	38	14 ·	•
P.T.	R	38	14	
W.B.	R	36	20	
R.W.	\mathbf{R}	34	20	
D.H.	\mathbf{R}	32	16	
S.C.	\mathbf{R}	36	24	
E.P.	L	36	24	
S.T.	\mathbf{L}	32	20	
A.M.	\mathbf{L}	28	20	
	$\bar{x} = 34.6$		19.4	

dominantly into the temporal visual field. Although the measurements given in Fig. 2 are based on only one subject, additional measurements along the horizontal meridians of 13 other subjects (e.g., Fig. 1) confirm the existence of a temporal and nasal plateau lateral to the foveal region. The extent of the plateau toward the nasal and temporal side is given in Table 1. The plateau on the temporal side extends much farther into the periphery than on the nasal side (approximately 35 vs. 20 degrees eccentricity.)

2. Light-Difference Threshold under Scotopic Conditions

The question arises of whether the plateau of constant light-difference threshold depends on photopic conditions of adaptation or whether it can be observed also under dark adaptation. Crozier and Holway (1939) and Riopelle and Bevan (1953) made similar measurements on scotopic sensitivity as we did on photopic sensitivity and they also observed, under their conditions, an area of constant light-difference threshold. Our own measurements on light-difference threshold under scotopic conditions are therefore not as extensive as for photopic conditions and only serve to verify the previous observations.

In Fig. 3 light-difference thresholds along the horizontal meridian for one subject are shown for five different levels of adaptation. As in Fig. 1, the ordinate scale is logarithmic and inverted, so that values higher up the scale indicate higher sensitivity, i.e., lower light-difference threshold. On the abscissa distance from the fovea is indicated in degrees. The five different levels of adaptation were: 8.5×10^{-1} ; 8.5×10^{-2} ; 8.5×10^{-3} ; 8.5×10^{-4} ; and 8.5×10^{-5} millilambert. The other experimental parameters were the same as for the measurements under photopic conditions.

As the adaptation level decreases from 8.5×10^{-1} to 8.5×10^{-5} millilambert (a to e in Fig. 3), light-difference threshold in general increases. This increase is not the same for all retinal positions along the horizontal meridian. The fovea and environment of the fovea (perifoveal area) looses relatively more sensitivity than more peripheral areas, if the adaptation level is decreased from the photopic over the mesopic to the scotopic range. Under the lowest level of adaptation (Fig. 3, curve e), fovea and perifovea are considerably less sensitive than the adjoining peripheral areas.

Although the change in light-difference threshold is different for various retinal areas, if one goes from a photopic to a scotopic adaptation level, one feature appears to be preserved, namely the region of constant light-difference threshold for all levels of adaptation. Not only is this plateau preserved, but also the lateral extent of the plateau appears to



Fig. 3. Light-difference thresholds $(\Delta L/L)$ as a function of retinal locus and adaptation level. Measurements obtained from the right eye of E.P. along the horizontal meridian under five different adaptation levels: $a: 8.5 \times 10^{-1}$; b: 8.5×10^{-2} ; c: 8.5×10^{-3} ; d: 8.5×10^{-4} ; e: 8.5×10^{-5} millilambert. Target size: 10 min arc of visual angle. Duration of target presentation: 200 msec. Note the decrease of foveal sensitivity compared to the periphery under dark adaptation (e) and the remaining constancy of light-difference threshold in the "plateau" area irrespective of the level of adaptation. (Data taken from Harvey and Pöppel, 1972)

remain fairly constant both on the temporal and on the nasal side. In the mesopic region (Fig. 3, curve d, 8.5×10^{-4} millilambert) the lightdifference thresholds for fovea, perifovea and plateau are the same.

These observations suggest that the plateau of constant light-difference threshold can also be found under mesopic and scotopic adaptation conditions. The extent of this peculiar area appears to be rather unaffected by the level of adaptation. What is affected is the sensitivity of the foveal region relative to the rest of the visual field.

3. Subjective Brightness in the Periphery of the Visual Field

Fig. 4 presents the geometric mean of magnitude estimates for subjective brightness as a function of target luminance for two retinal locations (5 and 30 degrees, temporal visual field). Each point is the mean of ten judgments. It can be seen in Fig. 4 that there is a monotonic relationship between stimulus luminance (abscissa) and magnitude estimates (ordinate). The next step was to describe these data mathematically. To this end, a modified power function (Marks, 1966) was

E. Pöppel and L. O. Harvey, Jr.:



Fig. 4. Subjective brightness of different supra-threshold targets presented at two positions in the periphery of the visual field at 5° and 30°. Target 10 min arc, presented for 200 msec. Background: 0.83 millilambert. Measurements for the right eye of E.P. along the horizontal meridian. Each point or circle is the geometric mean of 10 individual magnitude estimates. Note the increase of magnitude estimates with increasing luminance. For further details see text

fitted to the data for each retinal location using the least-squares criterion. This function has the form:

$$\psi = \mathrm{K}(\phi - \phi_0)^{\beta}$$

where $\psi =$ subjective magnitude; $\phi =$ stimulus luminance; $\phi_0 =$ threshold correction factor; $\beta =$ slope of curve in log-log coordinates; K = constant. We attach no theoretical significance to our use of the power function. It serves to describe the data well by accounting for over 95% of the variance in each set of data.

The solid lines in Fig. 4 represent the best-fitting curves for the two sets of data. These two were selected to show the range of slopes found. The best-fitting function had the steepest slope at 5 degrees eccentricity $(\beta = 0.62)$ and the shallowest slope at 30 degrees ($\beta = 0.42$). This small range of slopes suggests that the subject is capable of discriminating among luminances equally well at all peripheral positions. There was no systematic relationship between slope of the best-fitting function and retinal position.

Since the data represented in Fig. 4 are magnitude judgments made relative to a foveal comparison target whose brightness was assigned a value of 50, the data can be used to derive the luminance at each retinal locus which would equal the brightness of the foveal target. To this end, the least-squares power function for each retinal eccentricity was used to calculate the luminance value of the target which would have elicited



Fig. 5. Subjective brightness as a function of retinal eccentricity. Those luminances of the targets at various eccentricities are shown (black dots) which correspond to the apparent brightness of the foveally presented stimulus (cf. Fig. 4). The curve connecting the open circles would be obtained, if apparent brightness of threshold targets were the same for all peripheral positions; more luminance would be needed in the periphery to obtain a sensation of equal brightness because of the higher threshold, or a target with constant luminance would appear dimmer in more peripheral areas. The actual measurements (black dots), instead, suggest that apparent brightness is related to light intensity irrespective of the stimulated position in the visual field. Targets with the same luminance appear to have approximately the same subjective brightness when they are presented in different areas of the visual field, as long as both are supra-threshold

a judged magnitude of 50. In Fig. 4, the dashed lines represent this process. It can be seen that the criterion luminance for the target at 5° is 21 millilambert above background and the criterion luminance for retinal eccentricity of 30° is 23 millilambert.

The criterion luminance (that luminance which would be judged The upper curve in Fig. 5 represents the result to be expected if, in

equal in brightness to the foveal stimulus) as a function of retinal locus is presented in Fig. 5. The dashed line in Fig. 5 represents the luminance of the foveal comparison target (19 millilambert). It can be seen that in order to appear equally bright a peripheral target must have a luminance which is approximately equal to 19 millilambert. Fig. 5 shows that the luminance for equal brightness does not change as a function of retinal locus. order to appear equally bright, peripheral stimuli had to have luminances equally elevated at any given location above the local threshold. Put in another way, under test conditions given, a 19 millilambert target has about 210 times its threshold luminance at 2 degrees eccentricity but only 9 times its threshold luminance at 60 degrees. Yet the results shown



E. Pöppel and L. O. Harvey, Jr.:

in Fig. 5 indicate that these two stimuli are equally bright. These data suggest that stimuli of equal luminance appear equally bright at different retinal loci.

The present data do not agree with those of Marks (1968). This conflict is probably due to the following factors: 1) We were interested in relative brightness judgments which simultaneously compared the periphery with the fovea whereas Marks was interested in absolute brightness judgments made for different retinal locations 2) Our range of target luminances was only 1.3 log units, varying around the luminance of the foveal comparison target since the purpose was to derive luminances of equal brightness. Marks used a range of luminances of 4 log units, a very wide range which falls outside the operating range of the adapted retina; 3) Our data were collected with the entire retina maintained at a constant level of light adaptation. Marks extinguished the adaptation field one second before the presentation of the test target which remained on for one second. The judged magnitudes were undoubtedly influenced by the rapidly changing state of the darkened retina.

IV. Discussion

1. Distribution of Sensitivity in the Visual Field

The data on light-difference thresholds obtained from 14 subjects afford a generalized picture regarding the distribution of sensitivity in center and periphery of the human visual field. This picture is schematically represented in Fig. 6. Under photopic conditions, the fovea has the highest sensitivity (Fig. 6, A). The perifoveal area (B) has a decreasing sensitivity beginning at the fovea and ending where the plateau starts. The radius of the perifoveal area is approximately 10 degrees. If the data on sensitivity from both eyes are superimposed, the plateau of constant sensitivity (C) extends from the perifoveal area to approximately 35 degrees along the horizontal meridian and to approximately 20 degrees along the vertical meridian. The stippled circle outlines the limits of the plateau from the nasal sides of both eyes. The plateau areas peripheral to the stippled circle are provided by the larger extent of the temporal plateaus for both eyes. Beyond the peripheral edge of the plateau, sensitivity again decreases until the end of the visual field is reached. This peripheral area of decreasing sensitivity is over its larger part binocular (D). The areas marked E in Fig. 6 indicate the monocular crescents, i.e., those peripheral parts of the temporal visual fields that fall beyond the edge of the nasal visual fields in both eyes.

The data obtained under scotopic conditions (Fig. 3) and the measurements reported by Crozier and Holway (1939) suggest that the plateau is rather stable and presumably uninfluenced in its extent when the

156



Fig. 6. Schematic representation of the human visual field obtained from measurements of the light-difference threshold throughout the visual field of the right and left eye. A: Foveal region with highest sensitivity (lowest lightdifference threshold) under photopic conditions. B: Perifoveal area with a radius approximately 10° with increasing light-difference threshold under photopic conditions. C: Plateau with constant light-difference threshold extending from approximately 10° to 20° both below and above the fixation point and from approximately 10° to 35° along the horizontal meridian. The stippled circle on the left (right) side indicates the limits of the plateau for the right (left) eye; the nasal limits do not extend as far as the plateau in the temporal visual field. The dark dot on the right (left) represents the blind spot of the right (left) eye. D: Peripheral area of increasing light-difference threshold extending from the lateral edge of the temporal plateau of each eye to the border of the binocular visual field. E: Monocular crescents, i.e., E on the right (left) signifies the area which is only seen by the right (left) eye

adaptation level is changed. Since under scotopic conditions fovea and perifoveal area are less sensitive than the "periphery", the plateau is the most sensitive part of the visual field in night vision. It is interesting to note that early measurements of acuity by Aubert and Foerster (1857) and Dobrowolsky and Gaine (1867) already showed such a horizontally extended plateau.

The plateau is not concentric with the fovea but with a point approximately seven degrees lateral of the fovea in the temporal visual field. The optical axis of the eye does not coincide with the visual axis (fovea) either but with a point between fovea and blind spot; both axes are roughly in the same horizontal plane but the optical axis lies approximately five degrees more towards the temporal side (Le Grand, 1957). The geometric center of the plateau and the optical axis of the eye thus roughly coincide.

We are not aware of any statement which in a satisfactory way explains why visual and optical are displaced from one another. The aft north and and presumably uninfluenced in its extent when the

157

proximity between geometric center of the plateau and optical axis suggests, however, a speculation why there is such a displacement. The reason may be historic. Eyes with a fovea have developed rather late in evolution; many mammals still lack a fovea. Perhaps the plateau corresponds to an "early" fovea, similar to the visual streak in rabbits, and the fovea itself has developed later. For some reason the fovea did not develop in the geometric center of the plateau which also coincided with the optical axis, but slightly shifted to the temporal side of the retina.

2. Relationship between Behavioral and Anatomical Data

The distribution of receptors in the human retina (Østerberg, 1935) shows a peak for the cones in the fovea and a peak for the rods at approximately 20 degrees eccentricity. A plateau in the distribution of receptors is not found even if one takes the sum of rods and cones for each retinal position. If one looks, however, at the distribution of the ganglion cells in the retina, one finds a pattern which corresponds closely to the sensitivity distribution in the visual field.

Van Buren (1963) has determined the distribution of ganglion cells throughout the retina. He observed that the ganglion cells are arranged in layers with one to five ganglion cells in thickness. In the most central part of the retina one finds a ganglion cell layer of five cells in thickness; this layer is surrounded by a layer of four cells in thickness, which in turn is surrounded by a layer of three cells in thickness, and so on. There are two different kinds of layers with only one ganglion cell in thickness, a more central one with no intercellular gaps, and a more peripheral one with intercellular gaps.

It is very interesting to note that the ganglion cell layer with one cell in thickness and no intercellular gaps has the same asymmetric distribution and also approximately the same extent as the plateau of sensitivity. The layer of one cell in thickness and with no intercellular gaps extends from 12.14 to 32.45 degrees in the nasal retina (temporal visual field) and from 12.23 to 19.05 degrees in the temporal retina (average data for 14 human retinae). These numbers coincide fairly well with those obtained from the threshold measurements (Table 1).

One would like to know whether the distribution of receptive fields in the retina shows a pattern which would agree with the distribution of sensitivity. In particular, one would expect that the size of receptive fields in the retina remains constant throughout the plateau. Such data on the human retina are of course not available, but even for the monkey retina there is a lack of information. The only measurements available indicate that the receptive field size increases with increasing distance from the fovea (Hubel and Wiesel, 1960), but in order to make the in-

tended correlation one needs to know the exact position of the receptive fields in the retina. Such correlation appears to be feasible for the monkey retina, as a similar asymmetric distribution of the ganglion cell layer with one cell in thickness and no intercellular gaps can be found in the monkey retina (Van Buren, 1963).

3. Constancy of Brightness in the Visual Field

We noted that the subjective brightness of threshold stimuli increases when the stimulus position is changed from the center to the peripheral visual field. This chance observation led us to measure subjective brightness for supra-threshold stimuli at various retinal locations. We found that supra-threshold stimuli with a given luminance do not change in subjective brightness when their position within the visual field is varied. This result fits our initial observation that more eccentric threshold stimuli appear subjectively brighter than more central ones. If a suprathreshold stimulus is moved toward the periphery, it will keep its subjective brightness, but will at one point in the periphery become a threshold stimulus beyond which it is no longer visible. Because the sensitivity decreases toward the periphery, a suprathreshold target with less luminance and therefore less subjective brightness will reach threshold at a smaller distance from the fovea, if it is moved toward the periphery. Thus, contours of constant brightness throughout the visual field for supra-threshold stimuli and the fact that light-difference threshold increases toward the periphery, would explain that peripheral threshold stimuli are subjectively brighter than central ones. As light-difference threshold does not change in the region of the plateau, subjective brightness of threshold stimuli is constant throughout the plateau.

Although this explanation may appear rather simple, it gains in complexity if one considers the neuronal properties which are necessary to account for the reported observations. One might begin by looking for the mechanism underlying this brightness constancy in the retina, with more central projection areas presumably involved in other tasks, like spatial and temporal contrast enhancement (Singer and Creutzfeldt, 1971; Singer et al., 1972) and feature analysis (Creutzfeldt et al., 1971; Hubel and Wiesel, 1959, 1965, 1968). We lack information about those properties of the vertebrate retina which could account for our observations, but recently Braitenberg and Hauser-Holschuh (1972) have discussed a possible compensating mechanism for the visual system of the fly. Somewhat similar conjectures have been advanced by one of us regarding the possible mode of action of ganglion cells in the vertebrate retina (Pöppel, 1973). If confirmed, these conjectures would help in understanding the phenomenon of brightness constancy in the visual

159

field. The central assumption that has to be made is that the firing frequency of a ganglion cell is positively correlated with apparent brightness. Specific predictions based on these conjectures are repeated here: a) More eccentric receptive fields which on the average are larger than more central ones should have the same spontaneous firing frequency as more central ones — because there is constancy of brightness throughout the visual field if the eye is exposed to the homogeneous background in the perimeter. b) Stimulated by a stimulus of constant size, more eccentric receptive fields should need higher luminances to get excited --because the contrast threshold is increasing toward the periphery. c) The firing frequency at threshold should be higher in more eccentric receptive fields — because the apparent brightness of threshold stimuli is greater for more eccentric positions. d) The slopes for the intensity summation curves should be parallel irrespective of position of receptive fields — because there is equality of apparent brightness for suprathreshold stimuli for different retinal positions. These predictions apply only for a homogeneous population of ganglion cells, differing only with respect to the diameter of their receptive fields.

The authors would like to thank Drs. E. Bizzi, H. Leibowitz and H.-L. Teuber for their critical reading of the manuscript.

References

Aubert, Foerster: Beiträge zur Kenntnis des indirekten Sehens. Arch. Ophthal 3, 1 - 67 (1857).

Aulhorn, E.: Über die Beziehung zwischen Lichtsinn und Sehschärfe. Albrecht v. Graefes Arch. Ophthal. 167, 4-74 (1964). Aulhorn, E., Harms, H.: Visual perimetry. Jameson, D., Hurvich, L. M. (Eds.) Handbook of sensory physiology, Vol. VII/4: Visual psychophysics, p. 102-145. Berlin-Heidelberg-New York: Springer 1972. Braitenberg, V., Hauser-Holschuh, H.: Patterns of projection in the visual system of the fly. II. Quantitative aspects of second order neurons in relation to models of movement perception. Exp. Brain Res. 16, 184-209 (1972). Creutzfeldt, O., Pöppel, E., Singer, W.: Quantitativer Ansatz zur Analyse der funktionellen Organisation des visuellen Cortex (Untersuchungen an Primaten). Grüsser, O.-J., Klinke, R. (Eds.): Zeichenerkennung durch biologische und technische Systeme, p. 81-96. Berlin-Heidelberg-New York: Springer 1971. Crozier, W. J., Holway, A. H.: Theory and measurement of visual mechanisms. I. A visual discriminometer. II. Threshold stimulus intensity and retinal position. J. gen. Physiol. 22, 341-364 (1939). Dobrowolsky, W., Gaine, A.: Über die Sehschärfe (Formsinn) an der Peripherie der Netzhaut. Arch. ges. Physiol. 12, 411-432 (1876). Ferree, E. E., Rand, G., Hardy, C.: An important factor in space perception in the peripheral field of vision. Amer. J. Psychol. 45, 228-247 (1933). Frost, D., Pöppel, E.: Programming of saccadic eye movements as a function of stimulus eccentricity. Meeting of the Society for Neuroscience, San Diego 1973. Harvey, L. O., Jr., Pöppel, E.: Contrast sensitivity of the human retina. Amer. J. Optom. 49, 748-753 (1972).

¹¹ Psychol. Forsch., Bd. 36

- Hubel, D. H., Wiesel, T. N.: Receptive fields of single neurones in the cat's striate cortex. J. Physiol. (Lond.) 148, 574-591 (1959).
- Hubel, D. H., Wiesel, T. N.: Receptive fields of optic nerve fibers in the spider monkey. J. Physiol. (Lond.) 154, 572-580 (1960).
- Hubel, D. H., Wiesel, T. N.: Integrative action in the cat's lateral geniculate body. J. Physiol. (Lond.) 155, 385-398 (1961).
- Hubel, D. H., Wiesel, T. N.: Receptive fields and functional architecture in two-non-striate visual areas (18 and 19) of the cat. J. Neurophysiol. 28, 229-289 (1965)⁻
 Hubel, D. H., Wiesel, T. N.: Receptive fields and functional architecture of monkey striate cortex. J. Physiol. (Lond.) 195, 215-243 (1968).
- Jay, B. S.: The effective pupillary area at varying perimetric angles. Vision Res. 1, 418-424 (1961).
- Kishto, B. N.: Variation of the visual threshold with retinal location. Pt. 1. The central 20 degrees of visual field. Vision Res. 10, 745-767 (1970).
- Kuffler, S. W.: Discharge patterns and functional organization of mammalian retina. J. Neurophysiol. 16, 37-68 (1953).

Le Grand, Y.: Light. color and vision. London: Chapman & Hall 1957.

Leibowitz, H. W., Johnson, C. A., Isabelle, E.: Peripheral motion detection and

- refractive error. Science 177, 1207-1208 (1972).
- Marks, L. E.: Brightness as a function of retinal locus. Perception and Psychophysics 1, 335-341 (1966).
- Marks, L. E.: Brightness as a function of retinal locus in the light-adapted eye. Vision Res. 8, 525-535 (1968).
- Østerberg, G.: Topography of the layer of rods and cones in the human retina. Acta ophthal. (Kbh.) Suppl. 6-10, p. 11-96 (1935).
- Pöppel, E.: Apparent brightness in the peripheral visual field. Naturwissenschaften 60, 110 (1973).
- Riopelle, A. J., Bevan, W., Jr.: The distribution of scotopic sensitivity in human vision. Amer. J. Psychol. 66, 73-80 (1953).
- Senders, J. W., Webb, I. B., Baker, C. A.: The peripheral viewing of dials. J. appl. Psychol. 39, 433-436 (1955).
- Singer, W., Creutzfeldt, O. D.: Reciprocal lateral inhibition of on- and off-center neurons in the lateral geniculate body of the cat. Exp. Brain Res. 10, 311-330 (1970).
- Singer, W., Pöppel, E., Creutzfeldt, O.: Inhibitory interactions in the cat's lateral geniculate nucleus. Exp. Brain Res. 14, 210-226 (1972).
- Sloan, L. L.: The threshold gradients of the rods and cones in the dark-adapted and in the partially light-adapted eye. Amer. J. Ophthal. 33, 1077-1089 (1950). Sloan, L. L.: The Tübinger perimeter of Harms and Aulhorn. Arch. Ophthal. 86, 612-622 (1971).

Spring, K. H., Stiles, W. S.: Apparent shape and size of the pupil viewed obliquely. Brit. J. Ophthal. 32, 347-354 (1948).

Zigler, M. J., Wolf, E.: Uniocular and binocular scotopic parafoveal sensitivity. Amer. J. Psychol. 71, 186-198 (1958).

11*

Dr. Ernst Pöppel Dr. Lewis O. Harvey, Jr. Department of Psychology Massachusetts Institute of Technology Cambridge, Massachusetts 02139 USA