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# REGIONAL VARIATIONS IN SENSITIVITY TO FLICKER.

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## INTRODUCTION.

IT is generally stated that intermittent images formed in peripheral parts of the retina require a higher rate of alternation to abolish flicker than those formed at the fovea. This view is unreservedly supported for white light by observations of Aubert [1865], Exner [1870], Bellarminow [1889], Sherrington [1904], Lohmann [1908], and Woog [1919], who employed various methods for the production of flickering images. In no case does very intense illumination appear to have been used, and the objects probably all subtended more than 2° at the observer's eye. Many of those who frequent cinemas are aware that flicker, under the conditions there obtaining, is more pronounced in indirect than in direct vision.

While Charpentier [1890] invariably obtained the same result with small objects, he could detect no difference between centre and periphery with objects whose images were much larger than the yellow spot. Moreover a second series of experiments by Exner [1886], using a much smaller object than in his earlier series, gave the same fusion frequency for centre and periphery with intense stimuli, although at lower frequencies of alternation flicker was coarser in indirect vision. With more feeble illumination, flicker was abolished for central vision at speeds insufficient to cause fusion in the periphery.

Rupp [1869], however, is reported by Exner [1870] (who contradicts him) to have found discs with alternate black and white sectors, seen by reflected light, to cease flickering in indirect vision at slower speeds of rotation than when viewed directly. Braunstein [1903] too has reported that the centre of the retina is more sensitive to flicker than the periphery. Dow [1910] was only able to confirm the usual finding with weak illumination; at high illuminations he states that fine flicker may persist at the fixation point when all trace of flicker is absent elsewhere in the field of vision[1].

Bellarminow [1889] found the rule to hold for coloured stimuli of moderate intensity. For red, yellow, and green, but not for violet, conditions were reversed at high intensities, *i.e.* the periphery became less sensitive to flicker than the fovea. Braunstein [1903] obtained similar results, except that the rule was also reversed for blue at high intensities. On a field subtending 4·5° Polimanti [1889] alternated spectral colours with white light. For short wave-lengths higher frequencies of alternation were always required to abolish flicker at 15° eccentricity than with central vision. For light of longer wave-length, however, the difference was much less marked, and beyond about 650 $\mu\mu$ conditions were sometimes reversed. Using monochromatic spectral colours, Allen [1909] found regions of the retina 10° and 20° from the fovea more sensitive than the centre to flickering lights of all wave-lengths. Dow [1910] reports the centre more sensitive to red flicker, and the periphery to green. Ives [1912] confirms this finding as regards red and blue of low intensities, but finds no difference between centre and periphery for very intense blue and red stimuli. According to Hardy [1920], who used a test object subtending 3·36°, the fovea is more sensitive than the periphery to red and yellow, while there is little to choose between different regions of the retina for blue-violet.

Conducted with improved technique and white light, recent experiments of Lythgoe and Tansley [1929] and of Granit and Harper [1930] provide further evidence. The former (pp. 29, 61) used a square object subtending 1° at the eye and determined the critical frequency for extinction of flicker both with central fixation and with seven peripheral fixation points ranging as far as 105° from the object. The luminosity of the object, at speeds sufficient to abolish flicker, was 93·6 metre-candles. With the dark-adapted eye and with the remainder of the field of vision in complete darkness, the critical frequency was highest for the fovea and progressively fell on passing out to the periphery. When the surrounding field was almost as bright as the object, the readings at 10° were higher than those at the fovea. Further out the values again fell, but the foveal figure was generally not reached until a fixation point about 70° from the object was used.

Granit and Harper [1930, Fig. 2] find that small objects (0·5–1·5°) give a lower fusion frequency in the periphery than in the centre, whereas large objects give a lower value in the centre than in the periphery. The brighter the object, the smaller must it be in order to give identical values in the two regions. At first sight these results seem in conflict with Charpentier's. Perhaps we may suppose that the latter's small objects

[1] Statements that have recently been made implying that Marbe [1896], Haycraft [1897], and (under certain intensities of illumination) Sherrington [1897] also observed higher fusion frequencies in centrally fixated objects than in the same objects when the images fell on peripheral regions of retina appear to be based on a misapprehension of the purpose and conduct of their experiments. They were concerned only with central vision.

subtended a visual angle of at least 2°, and that his large objects were very much larger than any used by Granit and Harper.

From the somewhat confusing literature, we are probably justified in concluding that flicker is more marked in the periphery than in the centre of the field of vision with moderate intensities of illumination and objects of moderate size, but that the contrary may often be found with small objects (subtending less than 1° or 2°) and with intense stimuli, and is especially apt to occur with coloured light of long wave-length.

In the hope of further elucidating the factors concerned in regional variations in the critical frequency for extinction of flicker, we decided to make series of measurements with a very small object at varying angular distances in a horizontal and vertical direction from the fixation point. Mixed white light at a range of intensities of moderate illumination has been used throughout. By the use of a small object, the complicating effects of areal summation, which is so marked a property of the peripheral regions of the retina [Kleitman and Piéron, 1929; Granit and Harper, 1930], are reduced to a minimum. The circular test patch actually employed subtended a visual angle of only 12′, thus giving a retinal image of diameter 54$\mu$ and area 2300 sq. $\mu$.

From observations on the limits of visual discrimination, Helmholtz [1896] calculated that there must be 13,466 separate visual units per sq. mm. in the fovea. By a similar method Wertheim [1887] had previously obtained the figure 14,000. Salzer [1880] actually enumerated about 135 cones per 0·01 sq. mm. in this region of the retina in three still-born infants. If this is so, the image of our test patch was formed on approximately 30 foveal cones. But although these figures appear to have been widely accepted by subsequent writers, they imply a much sparser distribution than might be expected of elements whose diameter is about 3 $\mu$. We have therefore examined microphotographs of tangential sections of the area centralis of the human retina. Andersen and Weymouth [1923, Fig. 12] reproduce one from Fritsch [1908], and another has been published by Fincham [1925, Fig. 7]. Both show between 120,000 and 130,000 cones per sq. mm. In the periphery of the retina Fincham's photograph (Fig. 4) shows about 90,000 rods and cones per sq. mm. A microphotograph by Heine [1900] shows more than 80,000 foveal cones per sq. mm. in a monkey. Some shrinkage may have occurred in the making of these preparations, but it is evident that Helmholtz' estimate was almost 10 times too small, and that in our experiments something approaching 300 receptor elements are involved.

Except in the centre of the retina, however, the number of afferent paths by which impulses are conducted to the brain is probably much smaller than the number of receptors stimulated. 3·2 mm. (11° 40′) from the fovea Chievitz [1889] found the ratio of rod and cone nuclei to ganglion cells 10·75 : 1, 4·6 mm. (16° 30′) from the fovea 42·00 : 1, and 6 mm. (21°) from the fovea 80·00 : 1. The figures of Mureddu [1930], expressed in a different and, for our purpose, less helpful way, are not obviously inconsistent with those of Chievitz.

## METHOD.

The apparatus employed is shown diagrammatically in Fig. 1. A vertical sheet of opal glass was illuminated from behind by an electric

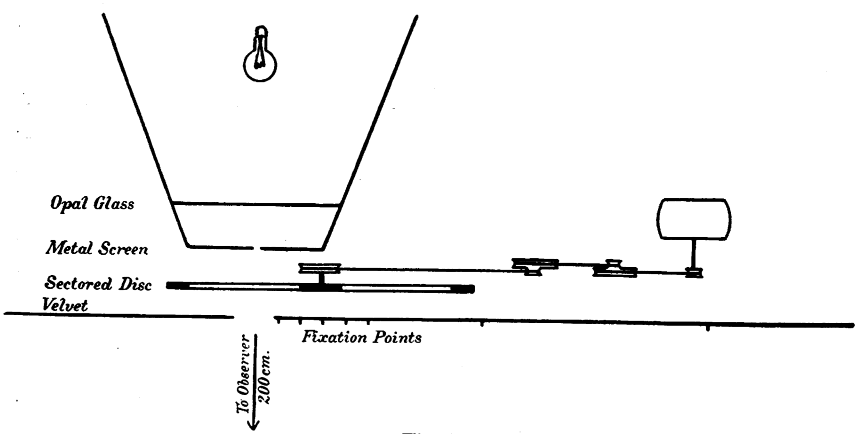


Fig. 1.

lamp. The intensity of the illumination was conveniently varied by employing lamps of different candle-power and by varying their distance from the glass. About 5 cm. in front of the glass was an opaque metal screen painted black and pierced by a hole 7 mm. in diameter. The small patch of white glass seen through this hole constituted the light stimulus to the observer's eyes. The hole was viewed from a distance of 2 m. and thus subtended only 12′ of arc. A large curtain of black velvet measuring 184 cm. horizontally by 90 cm. vertically was hung 13 cm. in front of the pierced metal screen. The bright object was observed through a round hole cut in this curtain 56 cm. from its left edge. Under the conditions obtaining during an experiment, the edge of the hole in the velvet was invisible. Uninterrupted blackness extended from the curtain to the test object.

A rotating black circular disc, with alternate equal sectors cut away, was placed between the metal screen and the curtain. It was driven through reduction gears by an electric motor. The speed was controlled by the observer by means of a sliding resistance in series with the motor. Two discs were used: one with 18 open sectors, and another with 10.

To furnish fixation points for observations with peripheral parts of the retina, squares of white paper, measuring 3 mm., were pinned on to the velvet curtain. One series of these, six in number, was placed to the right of the test patch at distances subtending between 1° and 20° to the observer. Another was arranged vertically above the test patch to give displacements of 1° to 10°. They were feebly illuminated by a 5 c.p. lamp 430 cm. distant from the hole in the curtain, and behind and to the right of the observer. The observer's head was shaded from the direct rays of this lamp.

The experiments were performed in a room with black walls and ceiling. The only illumination was the lamp just described and some scattered light from the 6·6 c.p. or 46 c.p. source behind the curtain. Before each day's observations were begun, 20–30 min. were spent in becoming adapted to the low illumination. The observer was seated comfortably with his chin resting on a support. While gazing steadily with both eyes at one of the fixation points, he accelerated the motor until the flickering quality of the bright object gave way to a continuous sensation. When the speed at which flicker was just abolished had thus been found, the experimenter timed with a stop-watch 25 revolutions of the 18-sector disc or 50 revolutions of the 10-sector disc to the nearest tenth of a second. For this purpose the black posterior surface of each disc carried a patch of white paint on a short segment of its edge. Two stop-watch readings were taken, and a third in case of serious disagreement. The difference, however, did not as a rule exceed 0·2 sec. The same procedure was followed for other fixation points until the series was complete. Observer and experimenter then changed places.

All observations were made without knowledge of results, and the order in which they were made was varied from day to day. At least one of the earlier observations was repeated at the end of each series to check the reliability of the values obtained. The experimenter frequently also asked for repetitions of several determinations when irregularities appeared to be present. The first determination of a series was found in particular to be often unreliable. It has therefore been omitted in some of the records published below. With that exception, no readings have been concealed.

Evidence of the suitability of our method for the purpose in view is afforded by the regularity of curves plotted from the results. At the same time, we do not wish to minimize its difficulty, nor do we claim a high degree of accuracy for any single figure. It is impossible to obtain a sharp end-point with so small an object. The long period of regard necessary makes fatigue inevitable, while with eccentric fixation, especially in the vertical meridian, spontaneous disappearances and reappearances of the object introduced a distracting element. Both obstacles were in some degree overcome by shifting the gaze or closing the eyes at intervals during the observations.

In some control experiments the fusion frequency with the 18-sector disc was compared with that with the 10-sector disc under otherwise identical conditions. The former, to our surprise, gave slightly, but definitely, higher rates than the latter. The finding, however, is in accordance with observations of Grünbaum [1897] and others, since the ratios of sector breadth to diameter of object in the two cases were approximately 2·5 : 1 and 4·5 : 1 respectively. For no single series was more than one of the discs employed.

The illumination of the object is expressed in arbitrary units based on the candle-power of the source and the distance of the source from the opal glass. If the glass could be assumed neither to reflect nor to absorb any of the light incident upon it, this unit would be equivalent to 26·3 metre-candles. It was found by measurement, however, that less than one-sixth of the incident light was transmitted, so that our unit is not in effect more than 4·4 metre-candles or 0·44 millilambert. When flicker is abolished, the apparent intensity is, of course, half that of the bright phase alone. Some of the higher illuminations may seem unduly intense, but it must be remembered that the subjective brightness is very greatly reduced by the smallness of the object.

## Results.

### 1. *Object surrounded by black.*

Of 40 series obtained in the way described above, with intensities of illumination varying from 2·8 to 552 arbitrary units, all have shown a higher critical frequency for extinction of flicker in central than in peripheral vision.

When frequencies are plotted as ordinates on a graph relating fusion frequency with degree of eccentricity of the fixation point, the curve falls steeply from the value for foveal vision to that representing images 2° or 3° out towards the periphery. The changes occurring still further out are

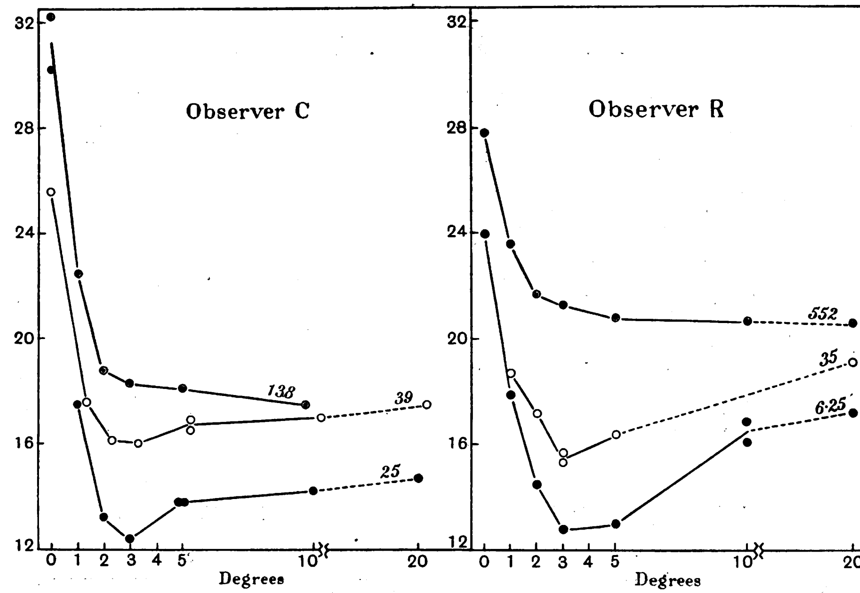


Fig. 2. Three series with each observer. All the results are plotted which were obtained in the single experiments for which each curve is drawn. Ordinates: fusion frequencies in flashes per second. Abscissæ: angular distances of fixation points from the object. The numbers above each curve express the brightness of the object (during its bright phase) in arbitrary units.

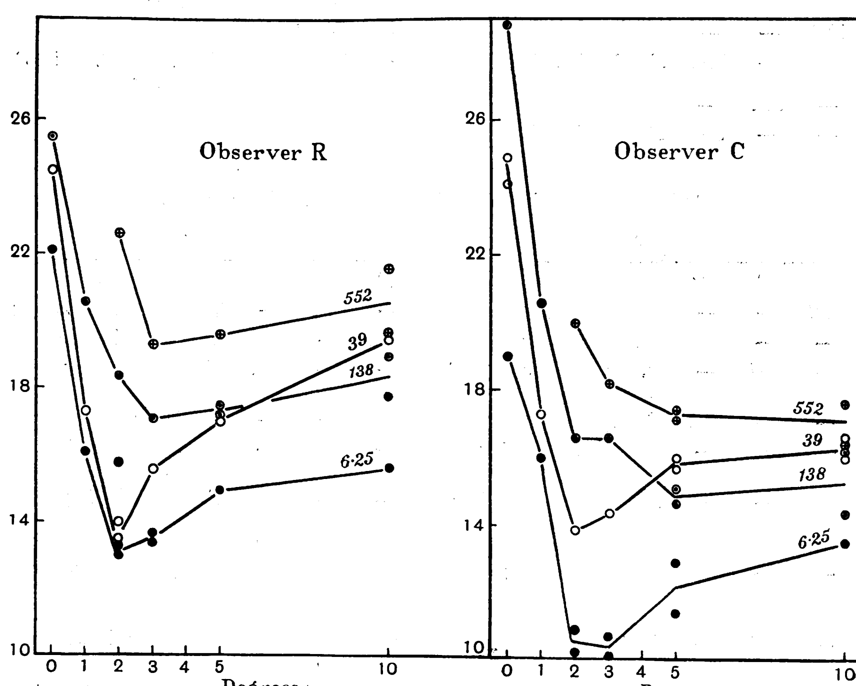


Fig. 3. As Fig. 2, except that the fixation points are vertically above, instead of horizontally to the right of, the object.

much less striking, but almost always there has been some increase in frequency on passing to more peripheral regions. Fig. 2 summarizes the results of several experiments in which horizontal displacements have been studied, while in Fig. 3 are shown similar curves obtained with the vertical series of fixation points. (No systematic comparison has been attempted of the vertical and the horizontal meridian. So far as our observations go, sometimes points on one and sometimes corresponding points on the other have given the higher readings.)

In such long experiments as these no doubt local adaptation and fatigue are liable to influence the results. The main features of the curve have therefore been checked and confirmed in experiments designed to

**Fusion frequency in flashes per second for horizontal fixation points to right of object.**

| Observer *R* | | | | Observer *C* | | | |
|---|---|---|---|---|---|---|---|
| 1° | 3° | 20° | Notes | 1° | 3° | 20° | Notes |
| — | 16·0 | — | | — | 11·5 | — | |
| — | — | 17·2 | 3° not flickering | — | — | 14·1 | 1° and 2° only flickering |
| — | 15.4 | — | 5°, 10°, and 20° flickering | — | 11·2 | — | |
| | | | | 17·5 | — | — | No flicker elsewhere |
| 19·9 | — | — | | — | — | 14·0 | |
| — | — | 19·2 | 1° only flickering | — | 11·5 | — | 1°, 2°, 5°, 10°, and 20° flickering |
| — | 15·7 | — | | | | | |
| — | — | 17·8 | 1° only flickering | | | | |

**Fusion frequency for vertical fixation points above object.**

| Observer *R* | | | | Observer *C* | | | |
|---|---|---|---|---|---|---|---|
| 1° | 3° | 10° | Notes | 1° | 3° | 10° | Notes |
| 17·7 | — | — | | — | 13·1 | — | 1°, 5°, and 10° flickering |
| — | — | 16·6 | 1° flickering; 3° not | 19·2 | — | — | No flicker elsewhere |
| — | 14·4 | — | 1°, 2°, 5°, and 10° flickering | — | — | 15·7 | 1° only flickering |
| — | — | 17·8 | 1° only flickering | 18·8 | — | — | No flicker elsewhere |
| — | 15·3 | — | All others flickering | — | 13·3 | — | All others flickering except 2° |
| 17·6 | — | — | ? 10° still flickering; others not | — | — | 15·6 | 1° only flickering |
| | | | | — | 12·8 | — | |
| — | — | 17·0 | 1° only flickering | — | — | 15·6 | 1° only flickering. (More peripheral points also flicker) |
| — | 14·5 | — | All others flickering | 17·0 | — | — | No flicker elsewhere |
| | | | | | 2° 12·0 | | All others flickering |

avoid these factors. Thus, with the object at brightness 17·4 units, the speed of revolution of the 18-sector disc was increased until flicker was abolished everywhere except at 0° and 1°. After prolonged rest, no trace of flicker was detectable elsewhere even on momentary observation in the extreme periphery of the field of vision. In four other experiments the brightness of the object has been 25 units and we have confined our attention to three only of the fixation points. In the above tables, which give the results of these experiments, the temporal sequence of the observations is indicated. The notes refer to momentary transfer of gaze to other points while the experimenter was timing the revolutions of the disc. Central fixation, for which higher rates than any of those quoted would have been necessary, is disregarded in the notes.

The general features of the curves in Figs. 1 and 2 may now be regarded as established. The region of minimum sensitivity to flicker has nearly always lain between 2° and 3° from the fovea, but occasionally the lowest values have been obtained at 5°, especially with the more intense stimuli. Indeed, when the illumination has exceeded 130 units, the peripheral rise in the curve has sometimes been absent altogether. With weaker stimuli we have never failed to find it.

### 2. *Object surrounded by white.*

In this section will be reported a few observations made under somewhat different conditions from those which have hitherto been described. Immediately in front of the velvet curtain was placed an evenly diffusing white screen, 64 cm. × 51 cm., carrying black fixation marks at appropriate distances from the centre of a circular hole, 1·5 cm. in diameter, through which the test object could be viewed. The screen was illuminated by two powerful electric lamps placed behind, and to each side of, the observer's head. This illumination was kept constant throughout the experiments (including those in which the white screen was removed at intervals in order that the effect of the black velvet surround might be compared with that of the white screen). The illumination of the object was varied as before. When its intensity was about 16 of our arbitrary units and the disc was rotated rapidly enough to abolish flicker, screen and object appeared to the observer of approximately equal luminosity. The brightness of the screen was therefore about 8 units. (Unfortunately no exact determination of this figure was made.) The object thus appeared separated from the screen by a black ring about half the diameter of the object in width.

Determinations of fusion frequency were found more difficult under these conditions than when the surroundings were dark. The test patch was often difficult to see at all in indirect vision, and especially so at eccentricities exceeding 5° when the object was much less luminous than the screen. Even with central fixation it was sometimes difficult to state confidently the exact point at which flicker ceased. Nevertheless, certain quite definite conclusions can be drawn.

It was found by Schenck [1896] that a higher frequency of intermission is required to abolish flicker when the surroundings are white than when they are black. The matter has been very fully investigated by Lythgoe and Tansley [1929], who, for objects brighter than their background, obtained increasingly high frequencies with increasingly bright surroundings in all regions of the retina provided the illumination of the test patch (which subtended 1°) exceeded about 10 metre-candles. When the background was made brighter than the object, the frequency began to fall again. We shall consider their interpretation of the phenomenon later. Our findings with the very small object are in general agreement with these results.

In the experiments tabulated below, alternate observations were made with and without the white screen. Central fixation and a fixation point 5° to the right of the object were used. The luminosity of the white screen was about 8 units in all experiments, while that of the object when fused was half the value given for the physical intensity of its bright phase. The readings are given in flashes per second.

Bright phase intensity 2·8.
Observer *C*.

| Fixation central | | Fixation 5° peripheral | |
|---|---|---|---|
| White screen | Black velvet | White screen | Black velvet |
| 25·5 | — | 13·8 | — |
| — | 20·6 | — | 11·8 |
| 21·8 | — | — | — |
| — | 19·3 | — | — |
| 22·9 | — | — | — |
| — | 18·9 | — | — |

Bright phase intensity 6·25.
Observer *C*.

| Fixation central | | Fixation 5° peripheral | |
|---|---|---|---|
| White screen | Black velvet | White screen | Black velvet |
| 28·8 | — | 17·6 | — |
| — | 23·0 | — | 13·8 |
| 27·7 | — | 17·0 | — |
| — | 23·7 | — | 13·4 |
| 25·5 | — | — | — |
| — | 22·1 | — | — |

Bright phase intensity 35.
Observer *R*.

| Fixation central | | Fixation 5° peripheral | |
|---|---|---|---|
| White screen | Black velvet | White screen | Black velvet |
| 31·8 | — | 25·0 | — |
| — | 28·5 | — | 19·4 |
| 28·9 | — | 26·2 | — |
| — | 26·9 | — | 19·4 |
| 28·9 | — | 27·7 | — |
| — | 27·1 | — | 21·2 |

Bright phase intensity 216.
Observer *C*.

| Fixation central | | Fixation 5° peripheral | |
|---|---|---|---|
| White screen | Black velvet | White screen | Black velvet |
| 35·4 | — | 22·5 | — |
| — | 32·5 | — | 18·5 |
| 33·2 | — | 21·9 | — |
| — | 30·8 | — | 17·3 |
| 33·5 | — | 19·9 | — |
| — | 29·8 | — | 14·5 |

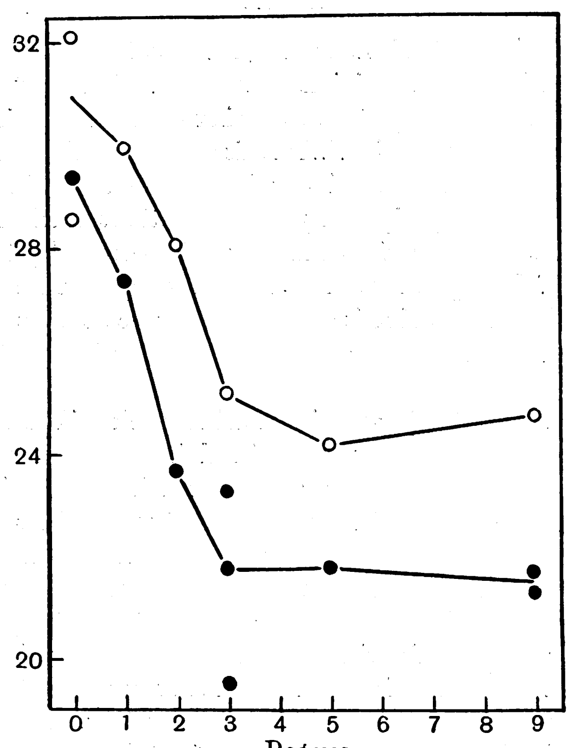


Fig. 4. Upper curve: observer *R*; brightness of object 6·25. Lower curve: observer *C*; brightness of object 22. Horizontal fixation points. As Fig. 2, except that object has white surroundings of luminosity 8.

The steady downward creep in each of these series is doubtless a phenomenon of adaptation—a factor difficult to control when the eyes are alternately exposed to light and to dark fields. In every case, when the disc was rotating just fast enough to abolish flicker with the black background, flicker at once appeared on replacing the white screen, and *vice versa.*

Curves relating fusion-frequency with region of retina stimulated (Fig. 4) resemble those obtained with black surroundings. Both show a rapid fall on passing outwards from the fovea, but, for a given luminosity of the test object, the former show higher readings at all points than the latter. The occurrence of a secondary rise beyond 3° is, however, very doubtful in these experiments. It has already been stated that determinations in the periphery are not easy. Our general impression is that the values for 3°, 5°, and 9° are identical.

## Discussion.

As was explained in the introduction, the experiments which have been described were intended to minimize such areal effects as "spatial summation," which may be expected to vary in the extent of their occurrence in different regions of the retina. With this end in view the test object was made extremely small. We shall therefore ascribe the differences found between the foveal and peripheral parts of the retina to intrinsic properties of the receptors of those regions and their retino-cerebral pathways. For convenience of description we shall frequently neglect the afferent path and speak only in terms of rods and cones. But we do not thereby mean to imply that the receptors alone form the physical basis of flicker phenomena.

Both when the test object was isolated in a black void and when it was surrounded by a white screen, the critical frequency for extinction of flicker fell rapidly as the gaze was transferred from the object itself to points 2° or 3° away from it. Cones are believed to be the dominant receptor elements in this region (see Creed and Granit, 1928). We therefore conclude that the foveal cones require a higher frequency for fusion than do the peripheral, or alternatively that the increasing proportion of rods to cones accounts for the drop. Beyond 3° the fusion frequency changes little. In conformity with this, the structure of the retina becomes here more uniform, with rods preponderating. Chievitz [1889] found the ratio of cones to rods to be 1 to 15–18 all over the periphery of the retina, although their absolute numbers decreased considerably as one approached the ora serrata. Other authorities are less definite and give the impression that the ratio becomes progressively smaller on passing outwards.

But if the peripheral parts of the retina are intrinsically less sensitive to flicker than the fovea, why is it that so many workers have found higher values for the fusion frequency of intermittent lights in indirect than in direct vision? The apparent discrepancy can hardly be because our tiny object only throws a sharp intense image on the fovea whereas optical imperfections make the image less sharp and dimmer in eccentric vision; for the fall is most marked quite close to the fovea. It is not a matter of the intensity of illumination, for in Sherrington's experiments [1904] the brightness of the object (subtending 2° 17′) must have been well within our range (probably 250–300 of our arbitrary units). Yet "an image would fail to flicker when received on the fovea that would distinctly flicker when its image fell just outside the fovea." Nor is it a matter of the method employed for producing the intermissions, for with a slightly modified technique we too have found flicker more marked in indirect vision with objects subtending 2°–8° visual angle at intensities between 0·01 and 17 units. In these experiments, when flicker has been abolished for fixation of the centre of the object, it has still been obvious when points from ½° to 10° from the centre have been tested. The object has sometimes appeared to flicker more at eccentricities between 4° and 7° than at points more central or more peripheral (cf. Lythgoe and Tansley, 1929, p. 61). We have not, however, investigated the last point carefully.

We know from personal observations as well as from the published work of others that increase in the size of a flickering object resembles increase in luminosity in that it causes marked increase in the fusion frequency [Bellarminow, 1889; Baader, 1891; Ives, 1912; Granit and Harper, 1930]. But Granit and Harper have also shown that this effect is much greater for images in the periphery than for images in the centre of the retina (as is to be expected from anatomical and other physiological considerations). The correct answer to the question propounded in the last paragraph appears then to be that with these larger objects interaction between neighbouring areas of retina becomes of importance. The excitation caused by one part of the image is added to that caused by other parts. This areal summation is so much more marked a property of the peripheral than of the central retina [Heinz and Lippay, 1928; Kleitman and Piéron, 1929; Granit and Harper, 1930] that its effects more than compensate for the intrinsically lower fusion frequency of the former as compared with the latter[1].

The peripheral rise seen in many of our curves may well indicate that the same factor has been at work even with our minute object. At 20° the excitation caused by its image is probably converging on only about one-eighth as many ganglion cells as at 10° (perhaps on 6 instead of on 45). It may also be tentatively suggested that the absence of peripheral rise at high intensities and in the experiments with the white screen is due to summation having, under these conditions, already attained its limit.

Lythgoe and Tansley [1929] put forward a very different explanation of fusion frequencies higher in the periphery than in the centre. From their very thorough and careful experiments they were led to the conclusion that all "responses at high illuminations are due not to the rods but to the cones" and that "the critical frequency of the peripheral cones is higher than [that of] those of the fovea" (pp. 40–2). We agree with them in believing that the phenomenon cannot be ascribed to the peripheral rods (which may or may not be responding), but it seems clear from our experiments that over a wide range of "high" illuminations the foveal cones exhibit a higher fusion frequency than do any structures, whether rods or cones, in the periphery.

One other subject which merits brief discussion is the influence of bright surroundings on fusion frequency. Graham and Granit, in a recent paper [1931], have described the alterations which occur in the fusion frequency of a semicircular object, the radius of which subtends 1°, when an adjacent similar object is illuminated simultaneously. When the two were of equal brightness, the fusion frequency of the first was always raised by the presence of the second. With the brightnesses unequal, the fusion frequency of the darker was unaltered or lowered by the presence of the brighter. This they ascribe to retinal inhibition. It is interesting that no such effect was manifest in our experiments where, instead of a small adjacent object, a large area completely surrounding the test object was used. Indeed, the results recorded in the table above show, if anything, the reverse effect. With central fixation, the percentage increase in fusion frequency caused by the white screen was greater (viz. about 20 p.c.) with objects darker than with objects brighter than the screen (about

[1] The possibility of variation in the size of the pupil according to the region of retina stimulated, with consequent alteration of fusion frequency, should also be borne in mind. It seems highly improbable, however, that this factor should come into play with stimuli of large, but not with those of small, area.

9 p.c.). It is possible, however, that percentage increase is not a justifiable basis of calculation.

The simplest explanation of the effect of the white screen in raising fusion frequency would seem to be in terms of interaction between the structures excited by its image and those excited by the image of the object. Possible types of interaction are an increase in the effective intensity of the bright phases by spatial facilitation (summation) or an increased blackness of the dark phases by simultaneous contrast. The effect is more marked in the periphery (5°), where at three different intensities the fusion frequency was raised by 25–30 p.c., than at the fovea. The same is true of the striking examples of interaction studied by Granit and Harper [1930] and by Roaf [1931].

An alternative explanation is offered by Lythgoe and Tansley [1929], viz. that it is a phenomenon of adaptation and not one of simultaneous contrast or spatial induction (p. 37). They find the critical frequency for cones to fall during the course of dark adaptation, and suggest that the effect of luminosity of surroundings is to determine the general level of adaptation. This view seems hardly compatible with their finding that the critical frequency falls, not only on lowering the field brightness below, but also on raising the field brightness above, the illumination of the test patch (p. 34). Moreover, to account for the fusion frequencies tabulated in Part II of our results, changes in the level of adaptation would have to occur with surprising rapidity in both directions. It therefore seems preferable to postulate nervous interaction as part, at least, of the mechanism by which white surroundings raise sensitivity to flicker.

## SUMMARY.

1. The critical frequency for extinction of flicker in a white object subtending 12′ visual angle has been determined at various positions in the field of vision, viz. up to 20° from the fixation point in the horizontal meridian, and up to 10° in the vertical meridian.

2. Over a considerable range of brightness, so small an object flickers much more when its image falls on the fovea than when it is viewed eccentrically. The lowest fusion frequency occurs at about 2–3° from the fovea.

3. When the surroundings of the object are black, the fusion frequency rises somewhat on passing to regions more peripheral than this. This statement probably does not apply either at the more intense luminosities investigated or when the object is surrounded by a white screen.

4. It is argued that the foveal receptors and their central connections have a higher intrinsic fusion frequency than the peripheral, and that the apparently contrary results obtained with larger objects are due to spatial summation in the periphery.

5. The fusion frequency in all positions is raised by surrounding an object with a bright background. This is ascribed to interaction between the structures excited by the image of the test object and those excited by that of the background.

6. The generally accepted figure for the density of foveal cones, viz. 13,500 per sq. mm., is inaccurate. There are actually about 120,000 cones per sq. mm. in the human fovea.

REFERENCES.

Allen, F. (1909). *Phys. Rev.* **28**, 45.
Andersen, E. E. and Weymouth, F. W. (1923). *Amer. J. Physiol.* **64**, 561.
Aubert, H. (1865). *Physiologie der Netzhaut*, p. 379. Breslau.
Baader, E. G. (1891). *Über die Empfindlichkeit des Auges für Lichtwechsel.* Inaug.-Dissert. Freiburg im Br.
Bellarminow, L. (1889). *Graefes Arch.* **35**, 25.
Braunstein, E. P. (1903). *Z. Psychol. Physiol. Sinnesorg.* **33**, 171.
Charpentier, A. (1890). *Arch. Ophtal.* **10**, 406–409.
Chievitz, J. H. (1889). *Arch. Anat. (Physiol.) Leipzig.* Suppl. Bd. 139.
Creed, R. S. and Granit, R. (1928). *J. Physiol.* **66**, 287.
Dow, J. S. (1910). *Phil. Mag.* **19**, 58.
Exner, S. (1870). *Pfluegers Arch.* **3**, 214.
Exner, S. (1886). *Graefes Arch.* **32**, Abt. 1, 233.
Fincham, E. F. (1925). *Trans. Opt. Soc. Lond.* **26**, 198.
Fritsch, G. (1908). *Ueber Bau und Bedeutung der Area Centralis des Menschen.* Berlin.
Graham, C. H. and Granit, R. (1931). *Amer. J. Physiol.* **98**, 664.
Granit, R. and Harper, P. (1930). *Amer. J. Physiol.* **95**, 211.
Grünbaum, O. F. F. (1897). *J. Physiol.* **21**, 396; **22**, 433.
Hardy, A. C. (1920). *Proc. Nat. Acad. Sci. Wash.* **6**, 221.
Haycraft, J. B. (1897). *J. Physiol.* **21**, 126.
Heine, L. (1900). *Graefes Arch.* **51**, 146.
Heinz, M. and Lippay, F. (1928). *Pfluegers Arch.* **219**, 462.
von Helmholtz, H. (1896). *Handbuch der physiologischen Optik.* 2te Aufl. Hamburg and Leipzig, p. 260.
Ives, H. E. (1912). *Phil. Mag.* **24**, 352.
Kleitman, N. and Piéron, H. (1929). *C. R. Soc. Biol. Paris*, **100**, 1174.
Lohmann, W. (1908). *Graefes Arch.* **68**, 395.
Lythgoe, R. J. and Tansley, K. (1929). *Med. Res. Council. Spec. Rep. Ser.* No. 134.
Marbe, K. (1896). *Philos. Studien (Wundt)*, **12**, 279.
Mureddu, G. (1930). *Ann. Ottalm.* **58**, 142 and 247.
Polimanti, O. (1899). *Z. Psychol. Physiol. Sinnesorg.* **19**, 263.

Roaf, H. E. (1931). *J. Physiol.* **71**, 13*P*.
Rupp, O. J. (1869). *Ueber die Dauer der Nachempfindung auf den seitlichen Theilen der Netzhaut.* Inaug.-Dissert. Königsberg.
Salzer, F. (1880). *SitzBer. Akad. Wiss. Wien,* Math.-nat. Cl. Abt. 3. **81**, 7.
Schenck, F. (1896). *Pfluegers Arch.* **64**, 165.
Sherrington, C. S. (1897). *J. Physiol.* **21**, 33.
Sherrington, C. S. (1904). *Brit. J. Psychol.* **1**, 26.
Wertheim, T. (1887). *Graefes Arch.* **33**, Abt. 2, 137.
Woog, P. (1919). *C. R. Acad. Sci. Paris,* **168**, 1222; and **169**, 93.