

COMPARATIVE STUDIES ON THE PERIPHERAL AND CENTRAL RETINA

III. SOME ASPECTS OF LOCAL ADAPTATION

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Received for publication June 27, 1930

The greater adaptability of the peripheral retina is one of the most obvious differences between central and peripheral vision. It was first noted by Troxler in 1804 that images falling on the peripheral portion of the retina quickly faded and finally disappeared, an observation that has been repeatedly confirmed since (Aubert, 7; Holth, 19; Dunlap, 11, and others). One factor at work in this process must be the local adaptation, but the final disappearance of a peripheral object during fixation, *fixation blindness* (translated from the Norwegian term "stirreblindhed" introduced by Holth, 19) seems also to involve another process, as indicated by Dunlap's (11) experiments, as well as by some observations of our own. The disappearance of the image is remarkably sudden. If this decrease in excitability be studied by following the gradual fading of flicker as fixation progresses one finds a coarse flicker preceding the final momentary abolishment of the seen effect of stimulation. This is strongly reminiscent of phenomena of binocular rivalry or reflex rebound and the analogy is further stressed by later reappearances and disappearances of the object.

Our problem was to follow the course of local adaptation. An attempt to solve the same question was made in 1877 by von Kries (21) who used concentric sectored discs and an equality of brightness method. He thus showed that the adaptive effect increased with the strength of the stimulus (see below, p. 234) and that within the first three seconds local adaptation seemed to be particularly rapid. The quantitative value of these experiments is greatly reduced by the fact that 1, the area stimulated was heterogeneous with regard to the distribution of receptor types (large object in central fixation); 2, the outer comparison ring fell on an especially adaptable area, and may also have interacted (Allen, 6; Granit, 15) with the fatiguing area; 3 the room was in nearly absolute darkness, which by creating dark adaptation not only exaggerated the effect of 1 and 2 but also introduced the problems characteristic of that state of adaptation.¹

¹ This was at a time (1877) when von Kries had not yet elaborated the conception of a functionally and structurally duplex retina. The work is not included among his collected papers on vision (22).

However, von Kries' experiments agree in a rough, qualitative way with those of Adrian and Matthews (1) who have found the frequency of discharge through the optic nerve of the Conger eel to decrease first rapidly and then more gradually during exposure to light. With this method Adrian and his successive collaborators (1-5) (8) in a series of important contributions to the general physiology of the special senses have also been able to describe similar reactions in other end organs.

The method employed in the present work was to measure the drop in fusion frequency of a flickering light during fixation and use this decrease as a criterion of the degree of adaptation. Because of the presence of fixation blindness in the periphery we were there restricted to short fixation periods and comparatively high intensities, it being known that under such conditions the decrease in excitability due to adaptation does not reach the low value necessary for the development of fixation blindness. The use of the flicker method also made it necessary to avoid even small movements of the eye and we soon found that it was difficult to obtain accurate results if the fixation time were extended beyond six seconds. However, within this time and with moderate or high intensities it seemed possible to follow the course of local adaptation with a considerable degree of accuracy. An advantage of the method is that no comparison light is needed and the relation between fusion frequency and intensity of stimulus can be determined experimentally. Furthermore, although the conclusions drawn from our experiments do not presuppose that the decrease in fusion frequency during continued stimulation actually follows the curve relating critical frequency to intensity, there is much evidence in favor of it (Granit and Harper, 16). Allen's (6) work on effects of "fatigue" is based essentially on the truth of this supposition. Our results are presented both in terms of computed intensities and in fusion frequencies as determined experimentally.

The experimental technique has been described in a previous communication (16) and the general conditions as regards state of adaptation, brightness of background, etc., are exactly the same as in that work. The time of exposure was measured by means of a stop watch, the shortest time being 1 second. Times shorter than 1 second need not be considered in connection with the questions to be discussed below, though experiments in progress have shown them to be of great interest from other points of view.

LOCAL ADAPTATION IN VARIOUS PARTS OF THE RETINA. The difference between the central and peripheral retina with regard to rate of local adaptation is shown by figure 1. With foveal fixation there is very little, if any, drop in critical frequency during the first six seconds. The diameter of the object in this case was 2° and it was therefore falling on a practically pure cone organ. The size of the peripheral objects was $2\frac{1}{2}^\circ$.

At 2° toward the periphery, i.e., within the macula, there is a definite effect of local adaptation, (more marked with observer R. G. (on the right)) although the typically peripheral curve is not reached until at 4° . The approximate curve at 10° for observer R. G. is also given in terms of intensities (= intensity necessary for eliciting corresponding original fusion frequency, other conditions similar). Below similar curves are plotted on a greater number of data.

Interpreted in terms of the results of Adrian and his co-workers our curves indicate that the centre is of the slowly adapting type to which belongs for instance the muscle spindle, whereas the periphery is a rapidly adapting organ, though by no means so rapid as the receptors at the hair

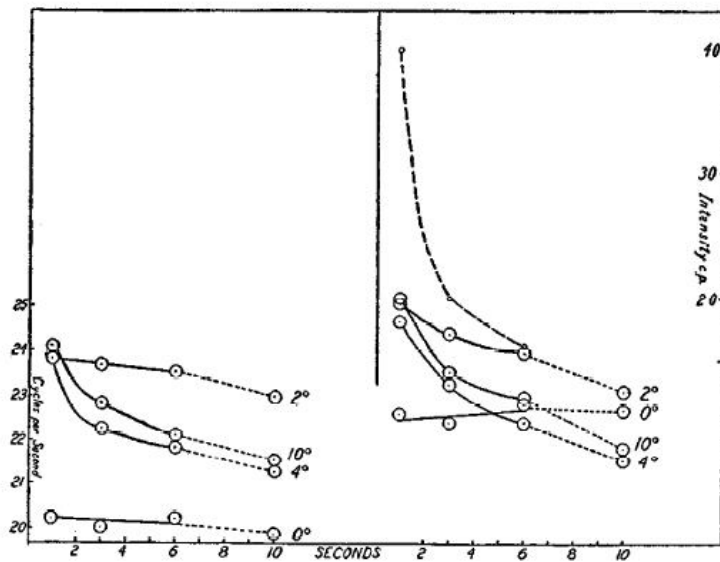


Fig. 1. Observers: v.A. (left), R.G. (right). The numerals against the curves refer to distance from fovea (= 0°) in degrees of visual angle. The dotted curve is the 10° curve of R.G. plotted against ordinates showing intensities computed from the critical frequencies.

roots which on Adrian's scale represent the other extreme. The validity of this interpretation rests upon the assumption that the main differences found refer to processes in the receptors. Since Adrian and Matthews (2), (3) obtained similar results in the excised eel's eye which greatly resembles the human periphery (15), we may safely infer that the phenomenon is essentially retinal. However, the peripheral and central retina differ not only as regards the relative distribution of rods and cones. An equally important difference between them is the amount of summative power (16) or, from the structural point of view, the amount of convergence of lateral and frontal (= receptor) paths upon the sensory neurones in the retina. It is, of course, possible that the many receptors converging upon the ganglion cells in the periphery (Chiewitz, 10; Cajal, 9) exert a

greater fatiguing effect upon those cells than does the single frontal path which in the fovea corresponds to each ganglion cell. However, in our opinion such an effect would not be so rapid as the one encountered. These questions will be considered experimentally in the next section.

ADAPTATION A RECEPTOR EFFECT. It was shown in parts I and II of this series (15), (16) that the convergence of lateral and frontal paths upon the sensory neurones leads to synaptic reactions such as occlusion and summation. The latter was described previously by Adrian and Matthews

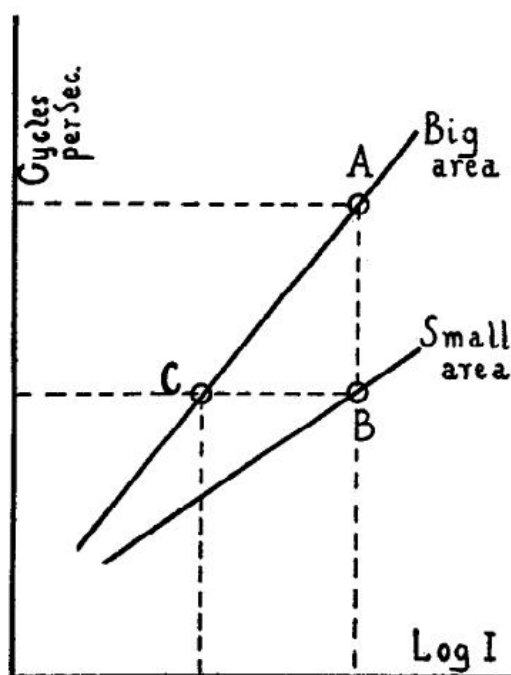


Fig. 2. Schematic. *A*, *B* and *C* are points selected to show equal fusion frequencies (*B*, *C*) for different area, and equal intensities (*A*, *B*) for different fusion frequencies on two curves relating log intensity to fusion frequency for two objects of different size. Data from the paper of Granit and Harper (16, fig. 7).

other factors being equal, the effect of adaptation increases with the intensity of stimulation as would be reasonable to expect. Accordingly, if the rate of adaptation were determined by total amount of energy, spreading over the synaptic layer, *A* should give a much larger effect than *B*, and *C* should also give an effect approaching that of *B*.

Table 1 shows the relations between stimuli *A*, *B* and *C* of figure 2. The intensities are calculated in relation to *A* ($= B$) which was at an intensity of 94 m.c. They are taken from smoothed curves relating log intensity to fusion frequency. However, as the differences between *A*, *B*

(3) as being present in the excised eye of the Conger eel. This being the case the total energy, as determined by the processes in the synaptic layers will be somewhat greater than the energy liberated in the neurone by each receptor. The total energy in the synaptic layers was shown to increase with the number of neurones activated owing to the increasing number of junctions. As a result of this the curve relating log intensity to fusion frequency has a steeper slope with larger areas. This is shown by figure 2, which is based on the results of the previous communication (16). Considering the points *A* and *B* it is evident that the intensity or energy per unit is the same. Because of spatial summation *C* reaches the fusion frequency of *A* in spite of its much lower energy value per receptor. It has been shown by von Kries (21) and his result will be confirmed below (p. 234) that,

TABLE 1

TIME	R. G.			W. v. A.		
	Fusion frequency cycles per second	Calculated intensity	Per cent decrease	Fusion frequency cycles per second	Calculated intensity	Per cent decrease
A = 4° diameter, high intensity						
<i>seconds</i>						
1	10.8 (0)	94.0	0	10.3 (0)	94.0	0
2	10.0 (0)	37.5	60.0	9.96 (0.053)	64.8	31.1
3	9.74 (0.046)	28.4	69.8	9.83 (0.056)	56.7	39.7
4	9.45 (0.03)	20.8	77.9	9.71 (0.05)	49.9	46.9
6	9.08 (0.056)	13.9	85.2	9.66 (0.05)	47.2	49.8
B = 1° diameter, high intensity						
1	8.33 (0.04)	94.0	0	7.7 (0.03)	94.0	0
2	7.53 (0.11)	33.2	64.7	7.03 (0.09)	33.8	64.1
3	7.07 (0.09)	18.0	80.85	6.75 (0.10)	21.8	76.8
4	6.7 (0.067)	11.0	88.3	6.53 (0.056)	15.5	83.5
6	6.53 (0.04)	8.9	90.54	6.4 (0)	12.4	86.8
C = 4° diameter, low intensity						
1	8.37 (0.04)	6.28	0	7.77 (0.03)	6.0	0
2	7.87 (0.04)	3.84	38.86	7.45 (0.03)	4.55	24.
3	7.52 (0.02)	2.59	58.76	7.33 (0.02)	4.02	33.0
4	7.3 (0.067)	2.08	66.9	7.22 (0.02)	3.57	40.5
6	7.12 (0.03)	1.71	72.8	7.12 (0.02)	3.23	46.17

and *C* with respect to area and intensity were considerable the main findings were not interfered with by casual variations. As mentioned above a direct comparison of the fusion frequencies (table 1) will show the important points brought out by this experiment. Since in our opinion it is safe enough to compute the effective intensity from the critical frequencies, we prefer to discuss the results as they appear in terms of percentage decrease of brightness during continued fixation (fig. 3 and table 1). A comparison of stimuli *A* and *C* which only differ in intensity confirms von

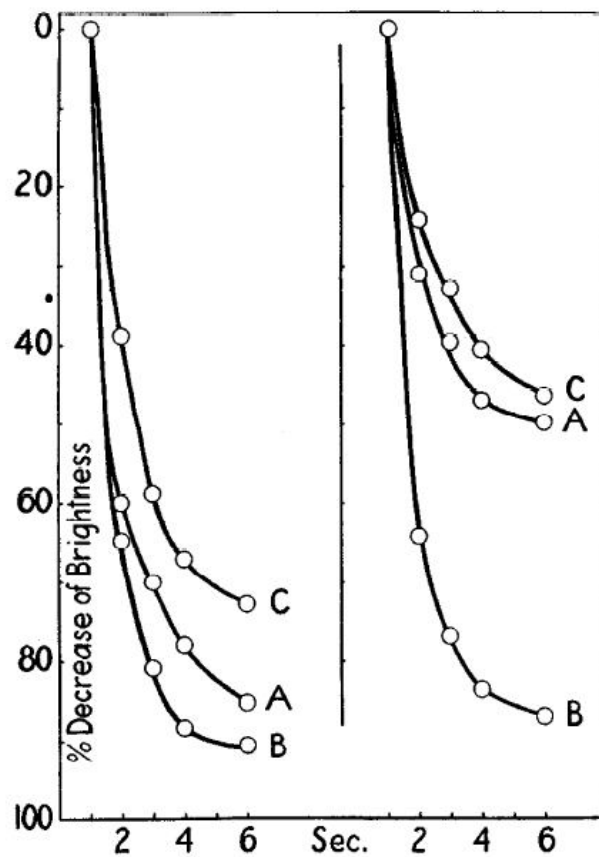


Fig. 3. Observers: R.G. (left) and v.A. (right). Region of stimulation 10° toward periphery. The letters *A*, *B* and *C* against the curves refer to conditions of area and intensity as indicated by the same letters in figure 2 and table 1.

Kries' observation that, other factors being equal, the stronger stimulus gives the greater effect. As to the main issue, figure 3 and table 1 clearly show that an increase in the total amount of energy does not in the least accelerate the rate of adaptation, since the decrease of *A* actually is smaller than that of *B*. Likewise *C* gives a much smaller drop in intensity during fixation than *B*. Thus there is no spatial compensation for lack of intensity in *C* as far as adaptation is concerned. As the process of adaptation is not accelerated by an increase in total energy propagated along lateral

paths of interaction later in the synaptic layers it must be "presynaptic," evidently determined by the nature of the receptors. This outcome of the experiments was to be expected on account of the results of Adrian and his co-workers. They found adaptation to be a general property of the sense organs, not confined to receptors which like the eel's eye have a central structure interposed between the actual end-organ and the afferent nerve.

The fact that *A* did not give a greater drop in excitability during fixation than *B* thus justifies the conclusion that total energy, as defined by the particular properties of synaptic structures, does not primarily determine the rate of adaptation. But it is nevertheless probable that the neurones may be capable of modifying the final response. The fusion frequency in the end is influenced by synaptic processes as well. Inasmuch as the central structure is more efficiently charged the larger the area stimulated, the "central excitatory state" (Eccles and Sherrington, 12) in this case drops less rapidly to subliminal values (Sherrington, 26) and may thereby retard the appearance of the maximal adaptive effect. In other words, the excitatory state in the neurones of the small area is more dependent upon the frontal (receptor) input. In the large area the greater lateral input compensates for loss in frontal input through adaptation. Thus we may understand why the drop with a large area, *A*, is even smaller than the drop with a small area, *B*. Although other interpretations of this phenomenon may be suggested this one seems best to fit the experimental facts at present.

Finally it is worth noting that these experiments are of some general interest as a type of approach which makes it possible partially to localize processes in the eye by using the effect of the size of area stimulated as an indicator. In this particular case the local adaptation has been found to take place in the end organs and further experiments have been planned in which objects of *constant* size will be compared as to other variables with the aim of obtaining data enabling a closer understanding of the processes in the photoreceptors.

INFLUENCE OF RED AND BLUE LIGHTS ON LOCAL ADAPTATION. The conclusion that the rate of local adaptation is determined by the nature of the end organ will be subjected to another test in this section. At the same time we will try to gain some information regarding an important—and hitherto much neglected—question referring to the concept of a functionally and structurally duplex retina, developed by Schultze (1868), Parinaud (1881) and in particular by von Kries (1894 (22)).

There seems to be no doubt about the general validity of this concept in so far as it presupposes a close correspondence between rods on the one hand and scotopic vision on the other and more and more cones becoming active as the photopic state of adaptation is approached. But as yet it is

an open question as to how the rods function in daylight vision (cf. Parsons, 23, p. 177). Some writers (cf. e.g., Piéron, 24) assume that red light to which the dark adapted eye undoubtedly is less sensitive (e.g., Purkinje effect) does not stimulate the rods under any conditions. Grindley (18) furthermore has recently gone so far as to apply a crucial test to a hypothesis concerning interaction between rods and cones (Granit, 13, 14) on the basis of this rather hypothetical assumption. It should be remembered, that experiments in scotopic vision do not give any information as to the function of the rods in photopic vision, that there is no reason to believe that rods saturated with visual purple react like ones that have

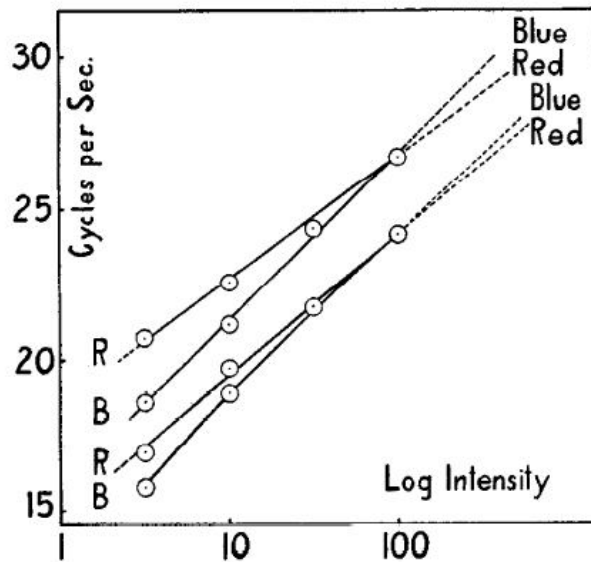


Fig. 4. Observers: R.G., upper pair of curves, v.A., lower pair. Region of stimulation 10° toward periphery. Diameter of object 3° of visual angle. Fusion frequency—log intensity (arbitrary units) curves for red and blue light.

had their visual purple bleached, and that, furthermore, phenomena at the absolute threshold showing selective sensitivity to the one or the other wave length hold only for the receptors of lowest threshold. It is also questionable whether absolutely valid conclusions as to general differences between rods and cones can be based upon differences pertaining to central and peripheral daylight vision. The fovea is a highly specialized organ, differing somewhat from the periphery as to types of cones² but especially with regard to synaptic arrangements (Greeff, 17) which in parts I and II

² To prevent misunderstanding it should be mentioned that with this remark we do not intend to confess adherence to a line of reasoning which hypothecates functional similarity between certain types of rods and cones because of certain superficial structural resemblances between them. According to Greeff ((17) p. 123) it is always possible to distinguish a cone from a rod, the basal ends and the nuclei of the cones being characteristically similar all over the retina.

of this series (15), (16) were shown to cause specific functional reactions varying in amount with the distance from the fovea. The fact that in some respects the general concept of a functionally and structurally duplex retina is sufficiently well founded to be accepted should not be allowed to hide some of the questionable issues of the duplicity *theory* and its need of further elaboration.

Before describing the effects on local adaptation that were obtained with red (Wratten filter no. 27) and blue (no. 47) light let us consider the curves relating critical frequency to the logarithm of the intensity. Figure 4 shows them for two observers over the range in which we are interested. It will be seen that the slope of the curves referring to red and blue light respectively differ in a similar way for both observers. This is in agreement with Ives' (20) results. Two pairs of points on these curves were chosen for each observer and their intensity so adjusted that the red and the blue gave approximately equal fusion frequencies both for the upper high intensity pair of points and for the lower intensity pair. Table 3 shows that when the intensity of the upper pair is taken arbitrarily as 100, the red and the blue are of equal brightness (= equal fusion frequency) if the ratio of intensity for blue and red of the lower pair is 19.1:11.6 for R. G., 15.48:12.31 for v.A. Although the absolute energy values were not determined it is questionable whether they would aid materially in our reasoning, since the physiological effectiveness must depend upon the thresholds of the receptors and not merely upon the energy. A determination of the latter therefore need not give any information about the former, except in the particular case when physiological threshold values are compared with the amount of radiant energy needed for eliciting liminal effects. The important factor is the variation in the relative energies of blue and red at the two intensities that give equal brightness. This is shown by the slope of the curves and also by the following values (table 2) calculated from the known transmission of the coloured filters, interposed neutral filters (Wratten) and the intensity of the lamps. Therefore in

TABLE 2

	R.G.	BLUE/RED	W. v. A.	BLUE/RED
Blue—low intensity.....	15.6	} 1.43	7.64	} 0.70
Red—low intensity.....	10.92		10.92	
Blue—high intensity.....	81.1	} 0.86	49.3	} 0.56
Red—high intensity.....	94.1		88.7	

order to produce equal apparent brightness (Porter, 25; Ives, 20) at high intensities the red light requires relatively more energy than the blue as

compared with the ratio at the low intensities. Or on the other hand at a high intensity, there is relatively less energy of a short wave-length needed for giving an effect equalling that of a long wave-length than at a low intensity, provided that the range of the Purkinje effect with concomitant specific low intensity effects is not included.

Proceeding now to a comparison of the effects of adaptation with the red and blue lights used in the experiments of figure 5 the question evidently is whether the relative fall in intensity is determined by the factors

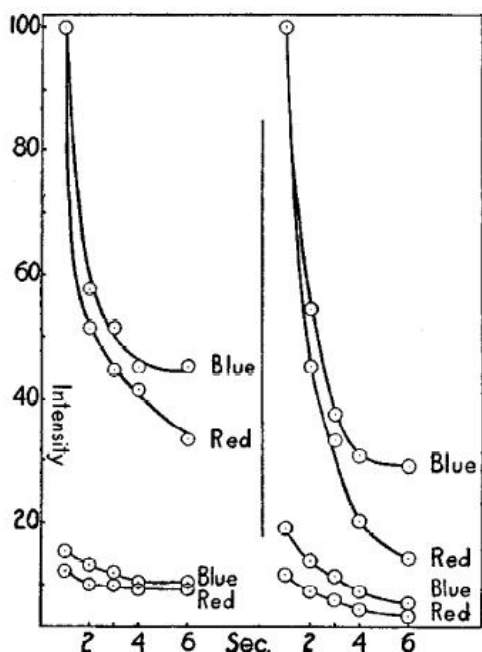


Fig. 5. Observers: v.A (left), R.G. (right). Course of local adaptation for red and blue light at two intensities (see table 3). Ordinates computed from the data of figure 4 (see text).

that are equal, i.e., brightness, or by those that alter, i.e., energy values. The curves in figure 5 are plotted to show decrease in intensity directly instead of percentage decrease, although the latter values may be found in table 3. It can be seen in this table that the relative effectiveness of red and blue at the two intensities chosen alters just as the energy values. Taking for instance the percentage decrease in six seconds for observer R. G. the relation blue:red is 71.1:85.8 at the high intensity, and 64.26:60.35 at the low intensity to be compared with corresponding variations in energy of 81.1:94.1 and 15.6:10.92 respectively. This means that the red light gives a relatively greater adaptive effect than the blue at the higher intensity compared with the effects at the lower intensity. The energy variation shows, accordingly, that the light which requires relatively more energy

for an equal increase in brightness has a greater effect on adaptation, which in this case was equal to lower final value in 6 seconds. This result wholly confirms our conclusion that the rate of adaptation is determined by energy per unit receptor. Thus von Kries' finding that higher intensities give more rapid adaptation is again confirmed. Although this confirmation follows from a consideration of the percentage decrease in brightness it is especially striking if the actual drops in intensity are compared.

Figure 5 also shows that if the difference in intensity between the two blue lights or between the two red lights is large enough, the high intensity

curves tend to flatten out before the lowest value of the low intensity curves is reached. This may be accounted for by a compensation for loss in frontal input through lateral channels (as above with regard to area, p. 235) or by differences in threshold.

TABLE 3

SEC- ONDS	RED						BLUE					
	R.G.			W. v. A.			R.G.			W. v. A.		
	Fusion frequ- ency	Calcu- lated inten- sity	Per cent de- crease	Fusion frequ- ency	Calcu- lated inten- sity	Per cent de- crease	Fusion frequ- ency	Calcu- lated inten- sity	Per cent de- crease	Fusion frequ- ency	Calcu- lated inten- sity	Per cent de- crease
High intensity												
1	26.77 (0.13)	100	0	24.12 (0.13)	100	0	26.74 (0.09)	100	0	24.15 (0.06)	100	0
2	25.37 (0.13)	45.2	54.8	22.82 (0.18)	51.29	48.71	25.37 (0.13)	54.5	45.5	22.96 (0.09)	57.6	42.4
3	24.53 (0.15)	33.2	66.8	22.54 (0.18)	44.67	55.33	24.44 (0.11)	37.6	62.4	22.74 (0.16)	51.29	48.71
4	23.94 (0.09)	20.2	79.8	22.40 (0.18)	41.69	58.31	24.00 (0.28)	30.6	69.4	22.40 (0.28)	45.19	54.81
6	23.30 (0.40)	14.2	85.8	22.12 (0.37)	36.31	63.69	23.86 (0.28)	28.9	71.1	22.40 (0.28)	45.19	54.81
Low intensity												
1	22.96 (0)	11.6	0	19.94 (0.06)	12.31	0	22.82 (0.18)	19.1	0	19.94 (0.06)	15.48	0
2	22.48 (0.12)	8.8	24.06	19.49 (0.13)	10.00	18.77	22.12 (0.18)	13.9	27.2	19.52 (0.12)	13.18	14.86
3	22.12 (0.09)	7.25	37.5	19.46 (0.09)	9.89	19.65	21.36 (0.26)	11.3	40.84	19.32 (0.18)	12.03	22.29
4	21.70 (0.28)	5.76	50.35	19.32 (0)	9.12	25.92	21.06 (0.11)	8.8	53.93	18.98 (0.06)	10.48	32.30
6	21.31 (0.23)	4.6	60.35	19.32 (0.09)	9.12	25.92	20.44 (0.28)	6.83	64.26	19.98 (0.21)	10.48	32.30

None of the facts revealed by a detailed analysis of the relation between adaptive effects and energy values are so striking as the general similarity of the reactions to red and blue light. This is shown particularly in figure 5.

The type of behaviour is the same in the two cases, and is in marked contrast with the adaptation in the rod free fovea. We must conclude that the peripheral rods and cones are either functionally very similar or that both wave-lengths stimulate both types of receptors, since we know that the first rapid drop in effective intensity—or fusion frequency—is caused by a decrease in excitability in the *end organ*. It seems to us that if the former suggestion be accepted then there is little left of the duplicity theory except the obvious difference between the fovea and the rest of the retina. The fundamentally different general adaptability of the two types of receptors (dark adaptation) is one of the main facts underlying the concept of a functional duplicity related to rods and cones. Why then should they behave so similarly with regard to local adaptation?

On the other hand the assumption that above a certain intensity both red and blue lights stimulate both types of receptors is more in accordance with the duplicity concept. The first rapid drop which is so typical a characteristic of both the human peripheral retina and the eel's retina must then be a rod phenomenon. This is stressed by the fact that the rapid decrease in excitability is not very marked until the edge of the macula has been reached (see above, p. 231). Finally, on the basis of the evidence of Adrian and his collaborators, there is every reason to correlate the marked differences in rate of adaptation with structural differences; the more so as in this case we have been able to show that the difference found between the fovea and the periphery is not dependent upon synaptic reactions. Thus the duplicity theory, if not too dogmatically interpreted, instead of being invalidated is actually supported by our observations and receives further development.

SUMMARY

The rate of local adaptation has been determined by following the drop in fusion frequency of an intermittent light during 6 seconds.

With central fixation there is little or no local adaptation demonstrable within the period in question. Passing towards the periphery the effect becomes more marked, and from 4° outwards there is a comparatively large drop in critical frequency during the first three seconds of fixation. The effect gradually diminishes in amount as the time of stimulation is lengthened.

The rate of local adaptation is greater with stimuli of higher intensity.

It has been found that the rate of local adaptation is determined primarily by the energy per receptor unit rather than by total energy increased by processes of summation in the synaptic layers of the retina. This was likewise shown to be the case in experiments with red and blue light.

A greater total amount of energy, however, seemed capable of causing a retardation of the rate of adaptation assumed to be due to more effective charging of the central structures in the retina.

In general the effect of red and blue light upon the rate of adaptation was essentially similar. This indicates that with intensities above the range of the Purkinje effect red and blue light must either stimulate both rods and cones or that there is practically no functional difference between peripheral rods and cones with regard to local adaptation. Neither assumption is in keeping with the concept of a complete functional-structural duplicity of rods and cones.

It is shown that the former assumption is preferable to the latter particularly on account of its greater conformity to the main facts underlying the duplicity theory. The first rapid decrease in fusion frequency with peripheral fixation is assumed to be a rod effect.

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