

COMPARATIVE STUDIES ON THE PERIPHERAL AND CENTRAL RETINA

I. ON INTERACTION BETWEEN DISTANT AREAS IN THE HUMAN EYE

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Adrian and Matthews (1) have recently demonstrated the interaction of retinal neurones by recording the impulses in the optic nerve of the Conger eel. The evidence for the occurrence of interaction has been summarized by them as follows: 1, "When the entire retina of the Conger eel is exposed to uniform illumination the action current discharge in the optic nerve may lose its usual irregular character and may consist of a series of regular waves caused by a rhythmical waxing and waning in the number of impulses in the nerve fibres. It follows that the ganglion cells of the retina must all be working in unison with alternating periods of rest and activity." 2, "when four points on the retina are illuminated simultaneously, the reaction time of the optic nerve discharge is shorter than when any one of the points is illuminated alone." This effect was similar to the one following an increase in the intensity of the stimulus. That it most probably is due to spatial summation of the type met with in reflex arcs was shown by the fact 3, that strychnine caused a marked increase in the range of area over which interaction occurred.

There is much evidence (see Parsons (2) pp. 103 and 130) which tends to show that also in the human eye spatial effects are easily obtained. For instance, it has been found that under certain conditions an increase of the area excited has an effect similar to that resulting from an increase in the intensity of the stimulus. An important link in the chain of evidence needed for allowing these experiments to be set in parallel with those of Adrian and Matthews (1) would seem to be within reach, if it were found that in the human eye distant areas affected one another in the way indicated by their experiment with the four test patches.

In order to apply this experiment to a visual test some method had to be used which would allow different degrees of brightness to be measured without the aid of a comparison light. This is possible with the flicker method, which also is accurate enough for the purpose in question. With this method an alteration of the physiological effect in the excited area

similar to the one following an increase in the intensity of the stimulus will raise the fusion frequency of an intermittent light. Such a relation, besides, was found by Adrian and Matthews (1) in some experiments with a flickering light to apply also to the excised eye of the Conger eel.

METHOD. A disc with two symmetrical opaque sectors of 90° each was rotated in a light beam projected on to a ground glass. This glass was covered on the back by a black paper, having a circular opening for the light. Two black metal discs having four circular holes of 1° of diameter, arranged as shown in figure 1, could be fitted to cover this opening. The distances between the holes in the two plates (*I, II*) are given in figure 1 in terms of visual angles. The fixation point, a thread cross, was either in the middle, *F*, or 10° out towards the periphery, *F*₁, and was viewed binocularly at a distance of 50 cm.

To the axle of the motor used for rotating the opaque sectors was joined a Weston electric tachometer, accurate to less than 1 per cent and cali-

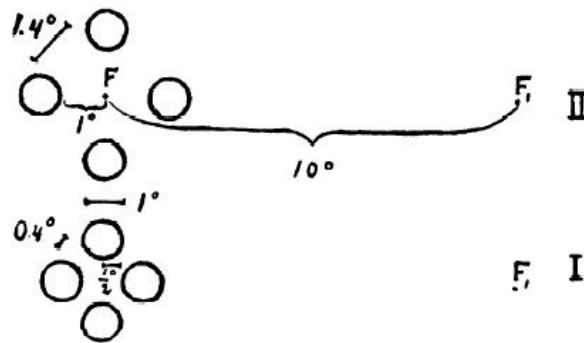


Fig. 1

brated by means of a revolution counter and an interposed speed reducing system. A Mazda lamp of the concentrated filament type was used as light source and the voltage supplied to it from the mains was kept at 110 v. The lamp was calibrated against a standard in a Lummer-Brodhun photometer and at the distance used projected 94.0 meter candles on to the ground glass. With a Tscherning neutral tint glass no. 2 the brightness of the test patches could be reduced 100 times. The background throughout the experiments was at a brightness of 0.0005 that of the stimulus (94.0 m.c.) but bright enough not to allow the light scattered by the diffusing ground glass to show around the test patches. The adaptation of the eye was at about 0.032 millilambert, as determined from the average size of the pupil of three observers and the standard values published by Reeves (3).

The experiments were always begun by taking two readings for each of the test patches viewed in turn, followed by three or four double readings for the four patches together. With arrangement I in the periphery,

simultaneous observation of all the patches showed but a small mean variation which for all observers averaged 0.08 revolution per second; for the single patches this value was larger, viz., 0.17, as is only natural in view of the different localization of the spots. Long fixation was avoided in the periphery because of its great adaptability. In two seconds the value may easily decrease as much as 1 revolution per second.

RESULTS. In table 1 the results with five subjects are summarized. The average fusion frequencies in revolution per second for the single test patches and for all of them together as well as the corresponding mean variations (within brackets) are given on the right of each column; on the left will be found the maximum and minimum values obtained. The figures I and II indicate the grouping of the patches as shown by figure 1. The terms "singles" and "fours" will be used as convenient abbreviations in referring to the columns headed "single patches" and "all together" respectively.

With the higher intensity and arrangement I there is evidently a great deal of interaction taking place in the periphery. The fusion frequencies are regularly from 1.6 to 3.1 (average for all subjects 2.5) revolutions per second higher than those of the singles. With central fixation and the spots falling on the edge of the fovea and on the paracentral area there is much less summation under otherwise similar conditions. Observer D. G. shows no signs of interaction in the centre; she had little practice with flicker. The regular observers have an average increase of 0.24 for the fours over the singles. This value is greater than the mean variation, but, on the other hand, the maximal value for the singles may reach the average value for the fours. Evidence derived from experiments to be published shortly tends to show that this slight increase in value for the central fours, as compared with the singles, actually is caused by slight interaction between the stimuli.

With the 100 times lower intensity there still remains some interaction in the periphery, though the increment in fusion frequency, when all four patches are taken together, is much less, only about 0.6 revolution per second, as compared with 2.5 for the same subjects with the brighter stimulus. In the centre there seems to be no summation at all.

Turning to arrangement II, where the patches are further apart, we find an average increase for the fours over the singles amounting to about 1.6 revolutions per second with the higher intensity. This means that doubling the radius of the circle on the circumference of which the patches lie and more than trebling the shortest distance between them does not diminish the interaction between them by more than about 46 per cent. In two out of three cases there is a definite although slight interaction with the weaker intensity.

From these observations it will be seen that there is a very striking

TABLE 1

SUBJECT	METER CANDLE	ARRANGEMENT I				ARRANGEMENT II			
		Peripheral fixation		Central fixation		Peripheral fixation		All together	
		Single patches	All together	Single patches	All together	Single patches	All together	Single patches	All together
R. G.	94.0	23.12	24.25	25.10	24.96	22.56	24.25	22.56	23.41
		(0.28)	(-)	(0.17)	(0.06)	(0.25)	(0.06)	(0.25)	(0.08)
		22.48	24.25	24.53	24.82	21.71	23.27	23.27	23.27
	0.94	14.95	15.51	15.79	15.79	14.95	15.09	14.95	15.09
		14.58	15.28	15.54	15.71	14.69	15.00	14.69	15.00
		(0.20)	(0.23)	(0.11)	(0.17)	(0.11)	(0.06)	(0.11)	(0.06)
14.10	14.10	14.95	15.36	15.36	14.52	14.95	14.52	14.95	
	20.02	22.84	23.12	23.12	20.30	21.57	20.30	21.57	
	19.88	22.76	22.84	23.07	19.88	21.52	19.88	21.52	
19.74	19.74	22.56	22.56	22.98	19.46	21.43	19.46	21.43	
	(0.14)	(0.11)	(0.14)	(0.06)	(0.23)	(0.06)	(0.23)	(0.06)	
	12.41	12.69	13.40	13.40	13.40	13.31	13.40	13.31	
11.84	11.84	12.69	13.25	13.25	13.25	13.25	13.25	13.25	
	(0.17)	(-)	(0.06)	(0.06)	(0.06)	(0.06)	(0.06)	(0.06)	
	26.23	29.32	25.66	25.94	26.09	27.35	26.09	27.35	
25.80	25.80	28.75	25.24	25.80	25.94	27.07	25.94	27.07	
	(0.17)	(0.06)	(0.17)	(0.06)	(0.06)	(0.08)	(0.06)	(0.08)	
	19.18	20.87	19.18	19.74	19.18	19.74	19.18	19.74	
18.92	18.92	20.73	18.75	20.58	18.92	19.66	18.92	19.66	
	(0.11)	(0.08)	(0.11)	(0.11)	(0.11)	(0.11)	(0.11)	(0.11)	
	18.75	20.58	20.58	20.58	18.75	19.46	18.75	19.46	

F. H.	94.0	18.89	18.64	21.15	22.56	22.27	22.70	18.61	20.02
			(0.11)	20.95	(0.23)	22.62	18.25	19.82	(0.11)
		18.47	20.87	21.71	22.56	17.77	19.74		
		11.56	12.97			11.84	12.13		
		11.42	12.83			11.70	11.93		
		(0.14)	(0.06)			(0.14)	(0.14)		
D. G.	94.0	20.30	20.05	22.56	21.86	21.74	21.86	11.56	11.70
			(0.25)	22.48	(0.06)	21.74	21.74	11.70	11.93
		19.74		22.48	21.71	(0.06)	21.71	11.70	(0.14)

difference between the fusion frequencies for the singles and fours especially with the higher intensities. At a frequency just about adequate to produce complete fusion of the single spot with the higher intensity, the group of four will still show a coarse flicker. (It is indeed surprising that so clear cut an effect has not been described but that it remained for Adrian and Matthews to indicate the possibility on the excised eye of the eel.)

It has been generally assumed that there is less interaction between adjoining retinal elements in the centre than in the periphery due to the rich supply of horizontal cells in the latter. It is, however, surprising to find the summative power of the periphery so great that areas separated by unstimulated regions of 1.4° of visual angle in diameter (as in arrangement II) should show such marked interaction. Yet, the summation is not complete. If an area as the one covered by the patches in I or II is filled out completely by the same stimulus the fusion frequency will be higher than for the fours. This is shown for two observers in table 2. For one of them (P. H.) the summation is not very far from being complete with arrangement I, for the other one (R. G.) the difference is higher.

TABLE 2
Fixation 10° toward periphery. Intensity 94.0 m.c.

SUBJECT	ARRANGEMENT I	SAME AREA, FILLED OUT COMPLETELY	ARRANGEMENT II
R. G.	24.25	27.35	23.27
P. H.	29.19	30.03	27.21

These questions will be discussed at some length in a later report of work on quantitative aspects of summation, now in progress.

It is well known that contours are normally blurred in peripheral vision. This is at least partly due to defects of the refractory system at oblique angles of incidence, the irradiation being less marked in the centre. As the amount of irradiation is proportional to the size of the blur-circle and the effect in its essential details can be deduced from well established physical principles Helmholtz (4) was led to suppose that the phenomenon is purely physical. The present experiments, however, show that with the higher intensity and if the stimuli are close to one another (arrangement I), the peripheral flicker spreads over almost all of the interjacent area, even though care be taken to choose a brightness of background against which no scattered light can be distinguished. Coarse peripheral flicker always surpasses the edge of the objects. By giving some information as to what is taking place in the area between the light patches these experiments therefore seem to show that at least in the periphery blurred contours are in part due to a physiological spread of excitation. This is in accord-

ance with the view originally advocated by Plateau (5) which was overthrown on the authority of Helmholtz.

If the stimuli are further apart (arrangement II) four bright flickering centres are seen, the edges of which diffusively infringe upon a steady interjacent area of less brightness. The bright patches seem to be able to influence each other's rate of flicker without causing definite flicker in the area between them. This was still more evident in some experiments with a 100 times brighter background than the one generally used. Thus the spread of the powerful rhythmically waxing and waning excitatory process must be mediated either by ganglion cells in the interjacent area discharging at a lower frequency because of their lower state of excitation (1), (6), or else by direct interconnective fibres joining the four stimulated areas. In view of the little effect visible on the adjacent area compared with the considerable influence on the fusion frequency which remained in spite of trebling the shortest distance between patches, it seems more probable that the spatial summation between distant areas is conveyed along uninterrupted paths between the areas stimulated.

Cajal (9, p. 123) mentions that he has observed in the mammalian eye horizontal branches exceeding 0.8 mm. (over 3° of visual angle), a fact which would seem to presuppose effects of the kind described and also to be in favour of the explanation given to account for them. He also finds the lateral junctions more developed in the higher species of vertebrates.

DISCUSSION. It is interesting to notice that the peripheral retina of the human eye closely resembles the primitive retina of the Conger eel as regards its structure, whereas the human fovea is differently composed. Even the proportion between rods and cones (15-18:1) as given by Chiewitz (7) for various peripheral parts of the human eye is approximately the same as found by Adrian and Matthews (8) in the eye of the Conger vulgaris. The eel's retina also has a complicated structure of interconnected cells, and the receptors outnumber the ganglion cells as in the periphery of the human eye. The similarity of structure between the eel's eye and the periphery of the human retina is not surprising. According to Cajal (9) the histology of the retina shows but small variations between different classes of vertebrates.

Anatomically then the periphery of the human eye seems to be the nearest approach to that prototype of nervous pattern which on evidence derived from work on motoneurones by Sherrington and his co-workers must be expected to display summation *par preference*. The possibility that this interaction should be of the nature of a spread of a photochemical process in the rod and cone layer seems to be definitely ruled out by the work of Adrian and Matthews (1). This view is also strengthened by the striking similarity of the behaviour of motor and sensory neurones more recently pointed out by Adrian and Bronk (10) and by Sherrington (11).

It is worth noting that the appearance of these synaptic reactions in the human eye at least serves the obvious purpose (cf. Adrian and Matthews (1, p. 295)) of being exactly fitted to make the best usage of the contourless, fuzzy light patches thrown upon peripheral parts of the retina. The defects of the refractory system restrict the activity of the photopic periphery to perceiving light. For discrimination of contours there is another organ, the fovea, where each ganglion cell is known to be connected to a single cone and the interconnections between them are less developed.

The basic assumption in this work has been that recording fusion frequencies with the sensory apparatus of vision in simple cases may be closely analogous to the registration of discharges in the optic nerve by means of a galvanometer. The results so far have justified this assumption, though, on the other hand, it is probable that conditions can be found that would alter the fusion frequency as an outcome of processes taking place in higher centres. Thus Sherrington (12) working on binocular flicker in patches joined stereoscopically found even alternating rates of flicker in the two eyes not to influence the fusion point markedly, whereas with very different rates of flicker the fusion frequency altered, probably owing to processes analogous to retinal rivalry. He concluded that under most circumstances the fusion point was determined before the conscious level was reached. Now, the experiments on flicker of Adrian and Matthews (1) show conclusively that the fusion point caused by asynchronism in the discharge as regards intensity and size of the stimulus behaves exactly as the *seen* fusion point in experiments on intermittent vision. At present the best explanation that can be given to account for the occurrence of fusion at certain rates of flicker therefore is that fusion is perceived when the discharging volleys are asynchronous, as they also were found by Adrian and Matthews (8) to be, if steady illumination was employed. Rhythmic waxing and waning with steady illumination, as mentioned above, was found only if the entire retina was illuminated or after application of strychnine.

It has been tacitly assumed that the interaction met with in these experiments is of the nature of a summation. This, of course, has not been directly proved; the inference is mainly based on the fact, pointed out above, that an increase in the intensity of the stimulus is known to raise the fusion frequency. But there remains the possibility that interaction between retinal neurones has an effect upon the fusion frequency *similar* to the one following an increased intensity of the stimulus without necessarily being identical with it. If this interpretation be true, then it certainly would be a rare case of coincidence that would make the reaction time of the discharge of the optic nerve, recorded by Adrian and Matthews, also behave similarly both as regards intensity of stimulus and interaction. This criterion was used by the latter authors, evidently because they

believed a shortening of the reaction time to indicate a physiological effect equivalent to the one following an increased intensity of the stimulus. When the same effect occurred owing to interaction, their natural—though tacit—inference was that the interaction was of the nature of a summation. In a following communication it will be shown that there is an effect of area which cannot be explained on this basis, but apparently conclusive evidence will, however, be added in support of the stated view as to the nature of the interaction described in this paper.

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SUMMARY

In order to obtain information as to whether there is any interaction between distant areas in the human eye, the fusion frequency of four circular test patches, separated by an unstimulated area, has been measured for each of the patches in turn and for all of them together. The four stimuli (see fig. 1), each of a diameter of 1° of visual angle, have been placed symmetrically with their outer edges on an imaginary circle, the diameter of which has been either 3° (arrangement I) or 4° (arrangement II) of visual angle. The test patches have been illuminated at two different intensities, the one 100 times lower than the other. The fixation point has been either in the centre between the stimuli or 10° out towards the periphery.

With central fixation and the higher intensity there is very slight interaction between the stimuli in arrangement I, as shown by the fact that the fusion frequency of all the patches illuminated together is only about $\frac{1}{4}$ of a revolution per second higher than the corresponding value for each of them viewed in turn. With the weaker intensity there is no interaction at all.

With peripheral fixation under similar conditions there is an increase in the fusion frequency of about 2.5 revolutions per second for all the patches together over the value obtained with the single stimuli. The interaction is definite still with arrangement II where the patches are further apart, the fusion frequency for all of them together being about 1.6 revolutions per second higher than the average for the singles. Even if the intensity of the stimuli is diminished 100 times there are still definite signs of interaction left.

The results prove the existence of physiological irradiation in the human eye and thereby give a definite solution of an old problem of vision.

The difference between central and peripheral vision with regard to interaction is correlated with corresponding structural differences in the two parts of the retina.

The general agreement between the outcome of the experiments recorded

above and recent work on interaction in motor and sensory neurones is pointed out.

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