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SPATIAL AND TEMPORAL SUMMATION IN IMPAIRED REGIONS OF THE VISUAL FIELD

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SUMMARY

1. Spatial and temporal summation have been measured in perimetrically impaired regions of the visual field. Two classes of impairment have been studied: that resulting from lesions in the pre-geniculate visual pathways, and that resulting from post-geniculate lesions (optic radiation and/or striate cortex).

2. Control measurements were made in the perimetrically normal visual fields of subjects without visual pathway damage.

3. Spatial summation was found altered in all impaired visual fields: the greater the threshold elevation produced by the lesion, the more nearly complete was spatial summation.

4. The above relation between threshold and spatial summation has also been given numerical form. This has been shown to be very nearly identical to the threshold–spatial summation relation which is seen as stimuli are increasingly peripherally presented in normal visual fields.

5. It has been shown that the alterations of spatial summation brought about by a lesion are found only in those parts of the visual field which are perimetrically impaired: spatial summation is always normal in perimetrically normal regions of a visual field, even if other parts of the same field show impairment.

6. Temporal summation has been found altered in visual fields impaired by post-geniculate lesions: the greater the threshold elevation produced by the lesion, the more nearly complete was temporal summation. These changes in temporal summation were found only in perimetrically impaired regions of the field.

7. Temporal summation was normal in visual fields impaired by pre-geniculate lesions.

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INTRODUCTION

It has been a longstanding clinical observation that a stimulus presented in a region of the visual field which is impaired by disease, appears to the observer much as it would if presented in a more peripheral, but normal, part of his visual field. Thus, Piéron (1916) noted that stimuli presented in a part of the visual field impaired by damage to the optic radiation appeared to the observer as if seen 'through a thick diffusing screen'. The stimuli appeared to have neither size, form nor colour, appearing to the observer as they might had they been presented in a more peripheral, but normal, part of the visual field. Klüver (1927), summarizing the clinical literature to that date, described the steps by which vision deteriorates as a visual field is progressively impaired; from the perception of discrete objects to amorphous form perception and then to size perception without definite form. This sequence of changes is similar to that observed when stimuli are presented increasingly peripherally in a normal visual field.

It was the purpose of the present investigation to determine whether the generalization that the function of a particular region of an impaired visual field resembles that of a more peripheral region of a normal visual field, is valid also for spatial and temporal summation. Spatial summation refers to the psychophysical observation that as the *area* of an incremental light stimulus is increased, the threshold luminance decreases. Temporal summation refers to the analogous relation between the *duration* of an incremental stimulus and its threshold luminance. Both temporal and spatial summation are readily quantifiable. It is possible, therefore, to make numerical comparisons between the changes in these functions accompanying increasing impairment of a visual field, and those changes seen as stimuli are presented in increasingly peripheral, but normal, parts of the field.

The subjects of this investigation were patients at the National Hospitals for Nervous Diseases, and all were inexperienced in sensory testing. Two main classes of subjects, those with impaired and those with normal visual fields, were established by routine clinical perimetry. Those with impaired visual fields were divided into two groups. The first group in which the lesion causing the field defect lay in the pre-geniculate visual pathways (retina, optic nerve, chiasma or tract), was designated group 'pre-G'. The second group in which the visual field defect was a result of damage to the post-geniculate visual pathways (optic radiation, with or without accompanying striate cortex damage) was group 'post-G'.

A number of subjects in group 'post-G' had neurological and psychological disabilities in addition to their visual field defects. A third group of subjects having intracerebral pathology but without perimetric visual field defects (group IC) was therefore established to control for the effect of these disabilities on visual thresholds. 'Normal' values for spatial and temporal summation were determined in a fourth group of hospital patients who had neither visual field defects nor intracranial pathology (group N).

METHODS

Apparatus. Stimuli were presented at the centre of a uniform white field of luminance 200 cd/m^2. This field was provided by the concave surface of a hemisphere 1 m in radius. The subject was seated facing into the hemisphere, the eye to be tested being located at the centre of its open side.

Stimuli were seen in Maxwellian view through a variable aperture in the centre of the hemisphere surface. Their diameter was limited by this aperture, while their duration was controlled by an electromechanical shutter. During spatial summation measurements a range of six stimuli, of diameter 5·7, 8·8, 14·1, 28·3, 46·8 and 80·8 min of arc, and of duration 1 sec, was employed. All stimuli presented during the temporal summation measurements were 80·8 min in diameter and of duration 5·1, 13·6, 46·5, 131, 317, or 950 msec. Stimulus luminance was varied in steps of 0·1 log. units, by means of neutral filters. The stimulus aperture was also lighted continuously in order that its brightness, between presentations of the stimulus, should match that of the surrounding hemisphere. This lighting was provided by a second Maxwellian view optical system. Only white light from incandescent tungsten sources was employed in these experiments.

The region of the retina on which stimuli fell was controlled by the position of a fixation mark on the (concave) hemisphere surface. The experimenter could readily detect eye movements which would alter the point fixated by more than 1°, by observing the subject's eye through a telescope which passed through the hemisphere surface. The fixation 'mark' actually consisted of a cluster of five small disks all lying within a circular area 42 min arc in diameter. Each disk was fixated in turn on successive stimulus presentations. This procedure minimized the effect on threshold of any local irregularities in sensitivity which may have existed in impaired visual fields.

Rigid head fixation was not necessary in these experiments. The images of the light sources for the two Maxwellian view optical systems exceeded 2·2 cm in diameter when focused at the subject's pupil. Eye movements large enough to place the pupil outside these images were readily seen through the telescope used to monitor fixation. Only the natural pupil was employed during these experiments.

Incremental thresholds determined in this manner with the natural pupil are dependent, in normal visual fields, on the function of cones. The same is probably true of thresholds determined in impaired parts of the field. The work of Aguilar & Stiles (1954) and of Fuortes, Gunkel & Rushton (1961), indicates that in the normal observer under these background conditions, the threshold value of log $\Delta I/I$ for rods is about $+3{\cdot}0$: a value greatly exceeding that for cones. At no time in the present experiments did threshold log $\Delta I/I$ reach this (normal) rod value, even in severely impaired visual fields. The highest value for log $\Delta I/I$ was $+2{\cdot}8$, and most threshold values were considerably smaller than this. It is therefore unlikely that any changes in summation observed in impaired visual fields are the result of a change from cone to rod-dominated function.

Psychophysical procedure. Pilot studies indicated that sick and naive subjects frequently made a high percentage of false positive responses. The method of stimulus presentation therefore forced the subject to make repeated choices between a stimulus and a 'blank'. Two auditory tones were presented about 1 sec apart. During the sounding of one or other of such a pair of tones the visual stimulus was presented, no stimulus being presented during the sounding of the other tone. The observer was required, after hearing each pair of tones, to state whether he thought that the stimulus had coincided with the first or the second member of the tone pair. The sequence of presentation of stimuli of different luminance was determined by a new modification of Dixon & Massey's (1957) up and down method of limits, and the threshold level was that luminance at which 80 % of the choices made were correct. This procedure for stimulus presentation, and the procedure for the calculation of the thresholds from the subject's responses, were validated by separate experiments which are detailed elsewhere (Wilson, 1965). The standard deviations of the thresholds, so determined, in the control groups, are shown in Figs. 1–4.

Testing procedure. All subjects were first assigned on the basis of the clinical diagnosis of their illness, to one of the four test groups, pre-G, post-G, IC or N, and on a random basis to the spatial or the temporal summation measurements. The subsequent testing of each subject was carried out during five test sessions.

The first session was devoted to the perimetric mapping of the subject's visual fields and it had three purposes. First, to confirm the presence or absence of a defective region in the visual field. Secondly, to delimit precisely any defective region. Thirdly, to determine whether any defective regions present were suitable for summation measurements. (The criteria by which a region was judged to be 'suitable' are discussed under the headings 'Perimetry' and 'Light scattering within the eye'.)

In every subject a summation determination was made at each of three standard distances from the fixation point—at 5°, 15° and 30°—each determination occupying a whole test session. The loci tested lay, in all cases, on one or other of the four, 45°—diagonal meridia of the visual field. Within these limits the three loci tested were selected randomly in control group subjects, but in subjects with visual field defects they were also required to lie in suitably impaired regions of the visual field. These measurements provided the main body of experimental data.

Data for several subsidiary experiments were provided by a fourth summation determination at a locus which differed from one experimental group to another. In control group subjects, this point lay at 5° from the fixation point in the half of the visual field opposite to that in which a 5° locus had already been tested. In group post-G subjects, it lay at 5° or 15° from the fixation point in a perimetrically normal part of the visual field. In group pre-G subjects, the fourth locus lay at the fixation point. Control summation measurements at the fixation point were provided by a separate group of subjects, similar to group N, but who were participating in an experiment which is not reported in this paper. A small number of subjects failed to complete all four summation determinations, but the measurements which were made in these subjects have been included in the results.

In each group of subjects all the summation measurements made at one of the three standard distances from the fixation point were combined as will be described below. Three summation curves were thus produced for each group of subjects, one curve characterizing the performance of the group at 5°, one at 15° and one at 30° from the fixation point. The three loci were tested in a different order in each subject in a group so that training, cumulative from one session to the next, did not result in differences in the group summation curves characterizing different loci. Measurements made at the fourth locus were separately combined by group, and by distance from the fixation point.

Perimetry. Visual fields were mapped using white disks of various areas and constant luminance. These disks were moved slowly through the observer's (monocular) visual field, and the regions within which they were detectable by the observer were recorded. The smaller the stimulus detectable within a region, the more sensitive was it regarded as being. Regions of the visual field which showed a consistent decrease in sensitivity in comparison with other regions at the same distance from the fixation point, in the same visual field, were regarded as impaired. This was the commonest form of field defect. A small number of subjects, however, while having visual fields in which sensitivity was symmetrical about the fixation point showed a marked reduction in sensitivity in the foveal and parafoveal regions of their fields when compared with subjects in the control groups. When this finding was combined with normal or relatively normal sensitivity further into the periphery of the field, a foveal and parafoveal field defect was diagnosed.

It was important that all the stimuli presented at any one locus in the visual field should cover equally sensitive areas of the field. Points in defective visual fields were therefore regarded as suitable for summation measurements only if perimetry showed that the variations of sensitivity in the vicinity of the point to be tested, were small. The experimental validation of the criteria by which such a point was regarded as suitable for testing is described elsewhere (Wilson, 1965).

Summation measurements in individual subjects and their combination to form group data. All the spatial summation curves presented in Figs. 1–4 characterize the performance of a *group* of subjects rather than that of individual observers. These group curves were derived from threshold measurements made in different observers, as follows. Thresholds for four out of a range of six stimuli of different diameter were first determined in each subject. (The combination of four stimuli presented differed from one subject to another but, in a group of subjects taken together, thresholds for each of the six stimuli were determined on approximately the same number of occasions.) When the thresholds for the four stimuli had been determined in a subject his probable thresholds for the two remaining stimuli were estimated. (For details see Wilson, 1965.) The average of the threshold values from all the subjects in a group was then calculated for each of the six different stimuli in turn, and a group spatial summation curve drawn through the resulting points.

It was necessary to estimate the thresholds for the two stimuli which were not presented to an observer in order to ensure that the performance of every observer should be reflected in the group thresholds for every one of the six stimuli. This is particularly desirable when a group of subjects is small. If each observer were to contribute threshold values to the group threshold for only four of the six stimuli, then a very unusual performance by just one such observer would greatly influence the *group* threshold for only four of the six stimuli. The group thresholds for the other two stimuli would be uninfluenced. This would result in spurious irregularities in the group spatial summation curve.

The procedures outlined above for the calculation of the group spatial summation curves were also employed in the calculation of the group temporal summation curves shown in Fig. 6.

Light scattering within the eye. Precautions were taken to ensure that when a subject detected a stimulus he was detecting the retinal image of the stimulus itself, and not light scattered during its passage through the eye, diffusely illuminating wide areas of retina. In the normal subject such scattered light is still well below threshold when the retinal image of the stimulus is first seen by the observer. If, however, the stimulus image falls in a severely impaired region of the visual field which is surrounded by relatively normal field, the scattered light may become sufficiently intense to be detected by the subject while the retinal image of the stimulus itself remains below threshold. Thresholds measured under these conditions would therefore actually be those of a large area of normal visual field, and not those of the impaired region under investigation. This possibility was excluded by ensuring that stimuli were at no time sufficiently intense for the scattered light to come within 0·7 log. units of its threshold, and by testing severely impaired regions of the field only when the nearest normal field lay at least 5–10° away from the point tested. The necessary measurements of the thresholds for the detection of scattered light were made by projecting stimuli on to the physiological blind-spot, and into the totally blind half-field of several subjects with post-geniculate lesions. These experiments are detailed elsewhere (Wilson, 1965).

RESULTS

Spatial summation

Figures 1–3 show the spatial summation curves measured at each of the three standard distances from the fixation point. Each figure presents data from the four groups of subjects.

Two general points relating to these figures must be made before they are considered in detail. First, each of the group spatial summation curves illustrated in Figs. 1–3 combines summation measurements made in different quadrants of the visual field. This combination was carried out after it had been found that spatial summation measurements made at 5° from the fixation point in opposite halves of the same field did not significantly differ in control group subjects. Secondly, the summation curves for group post-G are based on measurements made in impaired regions of the visual fields of the subjects in this group. The measurements made in normal regions of the visual fields of these subjects are considered later.

The shape of the spatial summation curves. Figure 1 presents the results obtained at 5° from the fixation point. Its ordinates show the logarithm of the Weber fraction, or threshold log $\Delta I/I$. The abscissa shows the logarithm of the stimulus area relative to that of the smallest stimulus employed, together with the stimulus diameter in minutes of arc. The magnification of both log scales is the same. Thus, a slope of $-1{\cdot}0$ (the lowest interrupted line in the figure) represents complete spatial summation. Complete spatial summation, in which threshold depends only on the total stimulus flux, is normally seen only when stimuli of relatively small diameter are presented. As stimuli are made larger, the value of log $\Delta I/I$ falls and the slope of the spatial summation curve decreases. If sufficiently large stimuli were presented, log $\Delta I/I$ would eventually have a constant minimum value and the summation curve would be a horizontal line (a slope of zero).

Three conclusions may be drawn from features of Fig. 1. First, the group pre-G and post-G curves are higher on the log $\Delta I/I$ axis than those from the control groups IC and N. Thus, threshold is generally higher, and sensitivity lower, in impaired than in normal visual fields. The slopes of the group pre-G and post-G curves are also markedly greater than those of the control groups. Thus, when the sensitivity of a region of the visual field is impaired by either a pre- or a post-geniculate lesion, it also shows more nearly complete spatial summation than the same region in a normal visual field.

No significance should be attached to differences in the relative positions of the curves from groups pre-G and post-G. They are consequences of fortuitous differences in the mean severity of the field defects of the subjects making up the groups.

Secondly, the convergence of the four curves, as larger stimuli are presented, strongly suggests that if stimuli of even greater area had been presented then the thresholds found in impaired visual fields would have become equal to those found in normal visual fields. The results presented in Fig. 1 show that the threshold difference between impaired and normal visual fields was less than 1·0 log units when stimuli 80·8 min in diameter were presented, and the summation curves were still converging sharply.

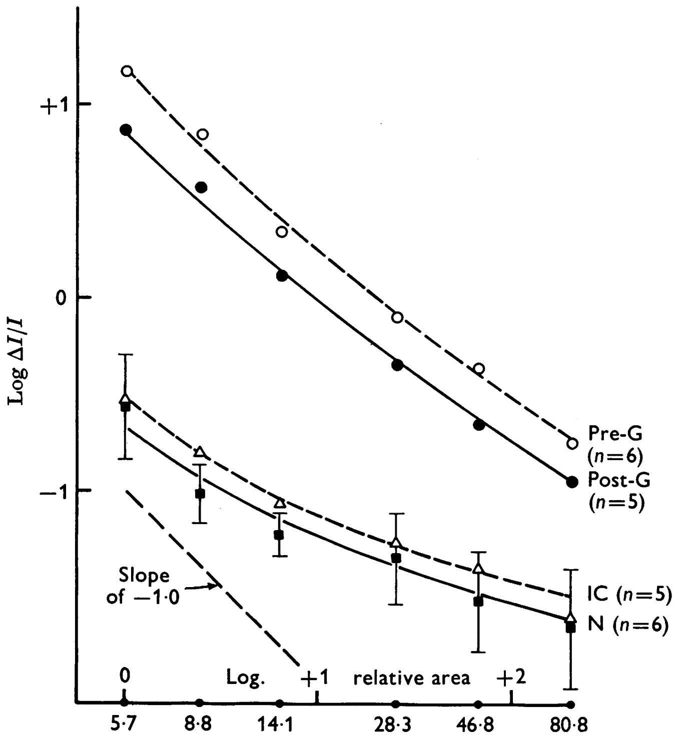

Fig. 1. Spatial summation curves measured at a locus 5° from the fovea. Each curve is based on the mean of the thresholds determined in '*n*' subjects. In groups pre-G and post-G, measurements were made in regions of the visual field defective as a consequence of lesions in, respectively, the pre- and post-geniculate visual pathways. Subjects in groups N and IC had normal visual fields, group N having extracranial pathology only while group IC observers had intracerebral lesions. The vertical line through each threshold point in group N indicates the value of $\pm$ 1 standard deviation for the individual thresholds about their mean value.

It is therefore probable that the threshold difference would be very small indeed by the time stimuli were large enough for all the curves to become horizontal lines. Thus, it appears to be possible to compensate fully for the reduced ability to detect luminance increments in stimuli presented in impaired fields, simply by making the stimuli larger.

Lastly, it should be noted that the control summation curves, from groups IC and N, are very closely similar in shape and in position. Further, the standard deviations of the individual thresholds determined in group IC, about their mean, although not illustrated, were generally a little smaller than those shown for group N. These two facts indicate that in the absence of a perimetric visual field defect, the presence of intracerebral

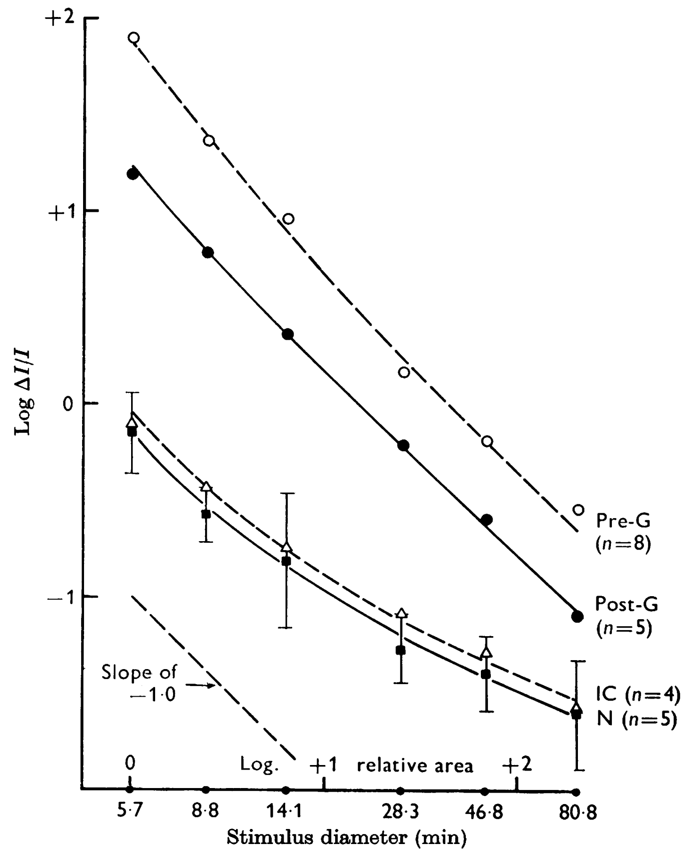

Fig. 2. Spatial summation curves measured at a locus 15° from the fovea. See also legend to Fig. 1.

damage (even if accompanied, as in some subjects in group IC, by severe dysphasia or motor disabilities) does not necessarily increase the value of the incremental luminance threshold, nor decrease the accuracy with which it may be determined.

The observations made about Fig. 1 apply equally to Figs. 2 and 3, which present analogous summation curves determined at, respectively, 15° and 30° from the fixation point.

Figure 4 presents spatial summation curves measured at the fovea in three subjects with pre-geniculate lesions, and in five group N subjects. The spatial summation curve measured at the impaired fovea is seen to be steeper than that measured at the normal fovea. These measurements are less complete than those made at loci 5°, 15° and 30° from the fixation point in impaired visual fields; only three subjects in one group were tested and,

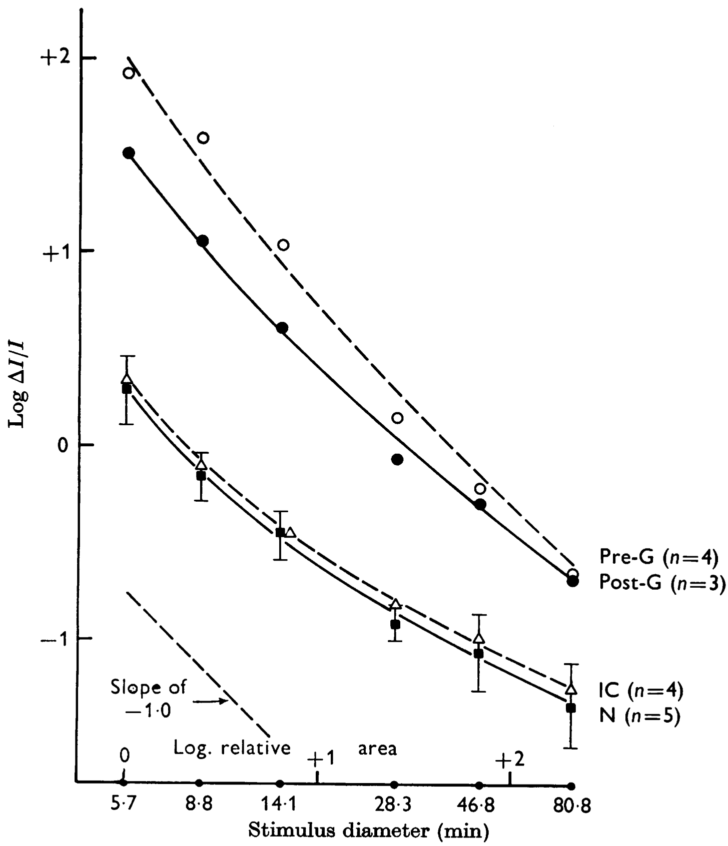

Fig. 3. Spatial summation curves measured at a locus 30° from the fovea. See also legend to Fig. 1.

because the field defect interfered with fixation, the impairment in these subjects was relatively mild. The results have been presented, nevertheless, because they do suggest that, even in foveal regions of the field, the effect of a lesion on spatial summation may be very similar to that already established for more peripheral regions of the field.

The spatial summation curves measured at increasingly peripheral loci in the normal visual fields of control group subjects may now be considered separately. A review of Fig. 4, followed by Figs. 1–3, shows that as stimuli are increasingly peripherally presented in normal fields, the thresholds for all stimuli are increased, and, as threshold increases, so spatial summation becomes more nearly complete.

The results shown in Figs. 1–4 provide, therefore, a preliminary answer to the question posed in the introduction. Impaired visual fields *do* resemble more peripheral regions of normal visual fields. In both cases an elevated threshold is accompanied by more nearly complete spatial summation.

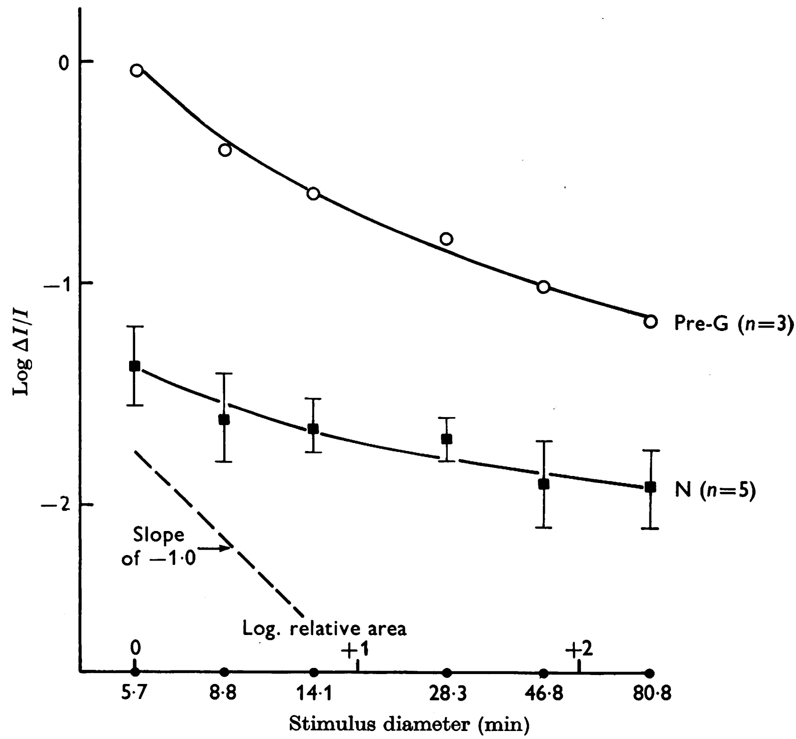

Fig. 4. Spatial summation curves measured at the fovea. See also legend to Fig. 1.

A closer comparison of increasing impairment and increasingly peripheral stimulus presentation requires the establishment of the precise *numerical* relationship between mean threshold and spatial summation as it is seen under these two different conditions. The derivation of this relationship will be described in the following section.

The numerical relationship between threshold and spatial summation. The calculation of the relationship between threshold and spatial summation requires pairs of corresponding values for these parameters. One such pair of values may be derived from any spatial summation curve. The value of log $\Delta I/I$ corresponding to the mid-point of the curve is a measure of mean threshold for the locus tested. The mean slope of the curve is a measure of the mean spatial summation at the same point.

Mean threshold–slope values were calculated directly from the original spatial summation measurements made in the individual subjects whose averaged results appeared in Figs. 1–4. These individual measurements provided a wide range of threshold and slope values, making possible a good estimate of the relationship between threshold and slope.

Threshold values for the six stimulus diameters were available from each individual subject. However, such values showed considerably more scatter than is seen in the averaged threshold values through which the summation curves of Figs. 1–4 are drawn. Therefore, rather than draw a somewhat arbitrary spatial summation curve through each individual's thresholds, the least-squares line was plotted through them. The value of log $\Delta I/I$ corresponding to the mid-point of the least-squares line was then taken as the mean threshold for that subject, and the slope of the line as an index of spatial summation.

Thirty-four pairs of mean threshold–slope values, based on measurements made in individual normal visual fields at loci between the fovea and 30° into the periphery, are represented by the symbol × in Fig. 5. Line *A* is the least-squares line through these values and is therefore the best estimate of the way in which mean threshold and spatial summation are related together in normal visual fields. Mean threshold–slope values based on thirty-four summation determinations made in impaired visual fields are represented by the symbol o in Fig. 5. Line *B* is the least-squares line through these points, and is therefore the best estimate of the relationship between mean threshold and spatial summation in impaired visual fields.

The results shown in Fig. 5 indicate that the numerical relationship between mean threshold and spatial summation is very closely similar in all visual fields, whether normal or impaired. Thus, if a particular value of mean threshold is observed, the same value for spatial summation may always be anticipated whether measurements are being made in impaired or normal visual fields. This conclusion is based on the fact that lines *A* and *B* in Fig. 5 are close to being parts of the same straight line. Their slopes are certainly very similar, being $-1{\cdot}79$ and $-1{\cdot}93$ respectively. Their position on the log. mean threshold axis does differ by about 0·35 log. units, but this difference is so small that it may well be a consequence of the fact that the measurements in impaired and normal visual fields were made in different subjects.

A further conclusion may be drawn from the similarity of lines *A* and *B*. The various loci tested in normal visual fields differed only in their distance from the fixation point. Line *A* reflects, therefore, the changes in mean threshold and spatial summation resulting only from increasingly peripheral stimulus presentation. In impaired visual fields, however, the loci tested differed not only in their distance from the fixation point, but also in the severity of their impairment. Line *B* therefore reflects the combined effect of both increasingly peripheral stimulus presentation and increasingly severe impairment on threshold and spatial summation. Despite this difference, lines *A* and *B* are almost identical. It follows that the changes in threshold and spatial summation brought about by in-

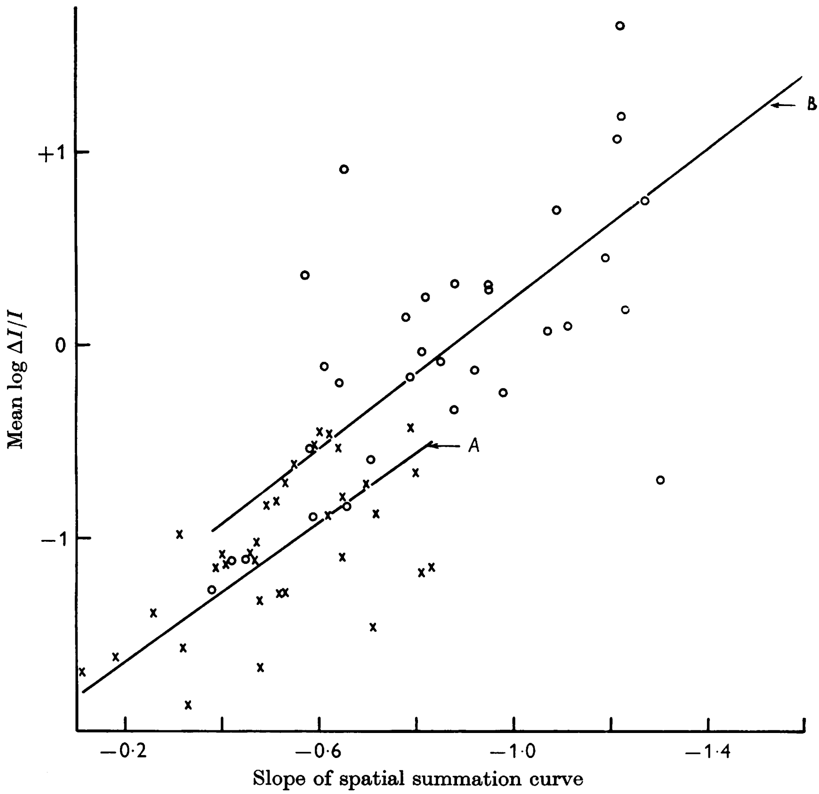

Fig. 5. The relationship between the mean of the thresholds for six stimuli of different area, and the slope of the spatial summation curve drawn through these six thresholds. Each mean threshold–slope value in this figure is based on a spatial summation determination in one of the individual subjects whose measurements were combined in making up Figs. 1–4. Mean threshold–slope values derived from summation measurements made in control group subjects are shown by the symbol ×. Mean threshold and slope are significantly correlated in these subjects. *A* is the least-squares through the results, and it shows how mean threshold and slope are related in normal visual fields. Mean threshold–slope values from subjects with impaired visual fields are shown by the symbol o. Mean threshold and slope are significantly correlated in these subjects also, and *B* is the least-squares line through the results. Line *B* therefore shows how mean threshold and slope are related in impaired visual fields.

creasingly severe impairment and by increasingly severe stimulus presentation, must also be almost identical.

Two subsidiary conclusions may also be drawn from the results presented in Fig. 5. First, line B is an estimate of the *mean* threshold–slope relationship found when all the subjects with visual field defects are considered together. It is of importance, however, to know whether threshold and slope are similarly related in each individual subject with a visual field defect, or whether line B is simply a mean value through data obtained from subjects in whom impairment had widely different effects on threshold and slope. A measure is therefore required of the scatter about line B, of the thirty-four mean threshold–values from impaired visual fields; a measure provided by the coefficient of correlation of mean threshold and slope, calculated from these values. The value of this coefficient is $-0{\cdot}58$. This is identical to the coefficient of correlation calculated from the thirty-four mean threshold–slope values determined in the normal visual fields of subjects in the control groups. It may therefore be concluded that individual subjects with impaired visual fields conform as closely to a common mean threshold–slope relationship, as do subjects with normal visual fields.

Secondly, the scatter of the points represented by $\times$ and $\circ$, about, respectively, lines A and B is also influenced by the reliability of the threshold determinations on which the points are based. Since the scatter is the same for both sets of data, it follows that the reliability of the threshold determinations made in impaired visual fields was about the same as that of thresholds determined in normal visual fields.

Spatial summation and retinal oedema in perimetrically normal regions of the visual field. It has been suggested (Dubois-Poulsen & Magis, 1957), that spatial summation is disturbed only when the pre-geniculate visual pathways are damaged. These authors therefore suggested that changes in spatial summation are found in areas of the visual field impaired by post-geniculate lesions only if these same lesions result also in retinal oedema and consequently in retinal damage. Now, the oedema associated with a post-geniculate lesion is not confined to those regions of the retina corresponding to the field defect. Thus, if sufficient retinal oedema has accompanied a post-geniculate lesion to result in altered spatial summation in an impaired part of the field, spatial summation changes should also be shown by perimetrically normal parts of the field. Spatial summation was therefore measured at 5° and 15° from the fixation point in perimetrically normal parts of the visual field in subjects in group post-G. The resulting spatial summation curves are not illustrated, but they coincided closely with the curves measured at the same loci in control group IC and shown in Figs. 1 and 2. Since changes in spatial summation are confined to perimetrically impaired regions of the visual field they cannot be a consequence of generalized retinal damage.

Temporal summation

Remarks analogous to the two general points prefacing the spatial summation results, apply also to the temporal summation results presented in Fig. 6. The units of the axes of Fig. 6, and the significance of the slopes of the curves shown in the figure, are also analogous to those described in detail for Figs. 1–3.

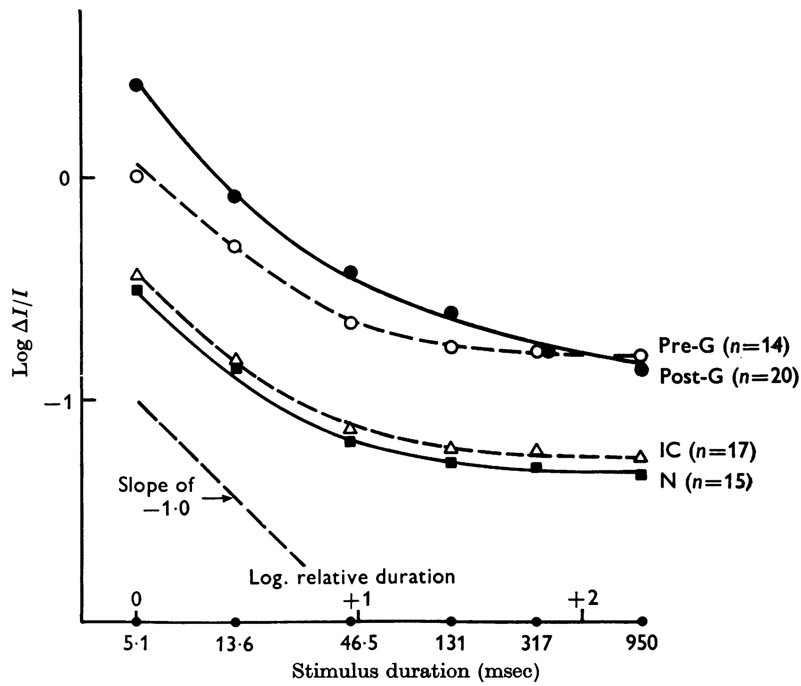

Fig. 6. Combined temporal summation curves from loci 5°, 15° and 30° from the fovea. See also legend to Fig. 1.

The shape of the temporal summation curves. Figure 6 presents temporal summation curves from the four groups of subjects. Curves measured at 5°, 15° and 30° have been combined to produce this figure.

Curves measured at different loci were combined for the following reason. When data from each of the three loci were plotted separately, the three resulting figures were each almost identical with Fig. 6. The curves differed from figure to figure only in that they lay higher on the log $\Delta I/I$ axis the more peripheral the locus tested. The curves measured at 15° and 30° were therefore displaced downwards on the log $\Delta I/I$ axis, and arithmetically averaged with the curve determined in the same group at 5° from the fovea. No information about the relative shapes of the curves in the four groups of subjects was lost by this combination.

Three conclusions may be drawn from the shapes of the curves in Fig. 6. First, it is apparent that pre- and post-geniculate lesions differ in their effect on temporal summation. Thus, while the group pre-G curve lies higher on the log $\Delta I/I$ axis than the control group curves, its shape is very similar to that of the control curves. This means that temporal summation remains undisturbed when the sensitivity of a region of the visual field is reduced by a pre-geniculate lesion. In contrast, the group post-G curve is both above, and steeper than the control curves. Thus, temporal summation is more nearly complete in a region of the visual field whose sensitivity has been reduced by a post-geniculate lesion, than it is in the same region of the normal visual field.

Secondly, in visual fields impaired by pre-geniculate lesions, as in normal visual fields, no further temporal summation is seen when stimuli exceed 317 msec in duration. In contrast, in visual fields impaired by post-geniculate lesions, temporal summation is seen with stimuli up to at least 950 msec in duration.

Thirdly, the temporal summation curves from the two control groups are closely similar in shape. Further, the standard deviations of the individual thresholds determined in group IC, about their mean, while not illustrated, were very closely similar to those shown for group N. Thus, the presence of an intracerebral lesion which does not result in a perimetric visual field defect, does not necessarily disturb temporal summation, nor does it reduce the reliability with which it may be determined.

It may be noted here that the changes in temporal summation seen in group post-G subjects are confined to the impaired regions of their visual fields. Temporal summation was measured in perimetrically normal parts of the visual fields of six of these subjects. The resulting summation curves are not illustrated, but their shape was almost identical with that of the control group curves shown in Fig. 6. The temporal summation changes seen in visual fields impaired by post-geniculate lesions are not, therefore, consequent upon any generalized damage to the visual system.

The numerical relationship between threshold and temporal summation. The results presented in Fig. 6 show that when the temporal summation measurements made in a number of different subjects in group pre-G are combined, the resulting temporal summation curve is similar to that determined in normal visual fields. On the other hand, the temporal summation curve resulting from the averaging together of measurements made in a number of subjects in group post-G is unlike the control curve. It is now important to know whether the curves of Fig. 6 are the result of averaging together data from subjects having widely different temporal summation curves, or whether all the subjects in a group have similar temporal summation curves.

To answer the above question, pairs of mean threshold–slope values were calculated from all the individual temporal summation measurements which had been combined to produce Fig. 6. These values were calculated

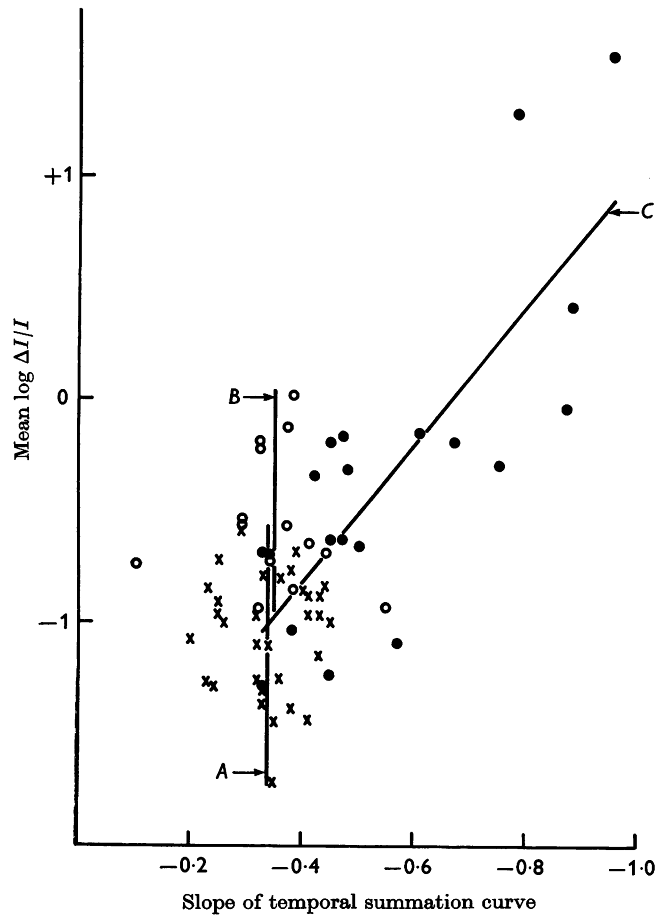

Fig. 7. The relationship between the mean of the thresholds for six stimuli of different duration, and the slope of the temporal summation curve drawn through these six thresholds. Each mean threshold–slope value in this figure is based on a temporal summation determination in one of the individual subjects whose measurements were combined in making up Fig. 6. Mean threshold–slope values from control group subjects are shown by the symbol ×. In these subjects mean threshold and slope are uncorrelated, mean threshold changing along line *A* as stimuli are increasingly peripherally presented. Similarly, mean threshold and slope are uncorrelated in group pre-G, whose results are represented by the symbol o. In this group mean threshold changes along line *B* as increasingly impaired visual fields are studied. Mean threshold–slope values from group post-G are shown by the symbol ●. Mean threshold and slope are significantly correlated in these subjects, and *C* is the least-squares line through the results.

using the procedure which has been described already in connexion with the spatial summation results.

Thirty-two pairs of mean threshold–slope values, based on temporal summation measurements made in the control groups, are shown by the symbol × in Fig. 7. The coefficient of correlation of mean threshold and slope calculated from these values is $-0{\cdot}034$. This coefficient does not differ from zero at the 5% level of confidence. The vertical line A has therefore been drawn through the mean slope value for the group ($-0{\cdot}34$) to emphasize the fact that, in these control subjects, slope is constant despite variations in threshold. Fourteen mean threshold–slope values from group pre-G subjects are shown by the symbol ○ in Fig. 7. Mean threshold and slope are similarly uncorrelated in this group, the coefficient of correlation being $+0{\cdot}13$; a value which does not differ from 0 at the 5% level of confidence. The vertical line B has been drawn through the mean slope value for this group ($-0{\cdot}35$), again to emphasize the independence of slope from threshold in these subjects. These results confirm the similarity already noted between visual fields impaired by pre-geniculate lesions and normal visual fields. Although both pre-geniculate lesions and variations in locus of presentation in normal visual fields are able to alter mean threshold, neither alters temporal summation.

Since slope does not vary with threshold in either group pre-G or in the control groups, a simple measure is available of the variation of temporal summation from one subject to another. It is provided by the standard deviation of the slopes of the temporal summation curves determined in the individual subjects in these groups, about the mean value of slope for the group. The standard deviation of individual slopes in group pre-G is $\pm 0{\cdot}09$, about a mean slope of $-0{\cdot}35$. The corresponding values from the control groups are closely similar, being respectively $\pm 0{\cdot}07$ and $-0{\cdot}34$. It may therefore be concluded that the temporal summation curves measured in visual fields impaired by pre-geniculate lesions show little more variation in slope than do similar curves measured in normal visual fields. This finding implies that all the pre-geniculate lesions encountered in these experiments were similar in leaving temporal summation undisturbed.

The standard deviation of the individual temporal summation curves is influenced by the accuracy with which thresholds were determined. The results, therefore, also indicate that the accuracy of the threshold determinations made in impaired visual fields was comparable with that in normal visual fields.

Twenty mean threshold–slope values from group post-G subjects are represented by the symbol ● in Fig. 7, and C is the least-squares line through them. The coefficient of correlation between threshold and slope has a value of $-0{\cdot}77$ which differs from 0 at better than the $0{\cdot}05$% level of confidence. This result confirms the observation that in visual fields impaired by post-geniculate lesions, an increase in threshold is accompanied by an increase in temporal summation.

The above coefficient of correlation of mean threshold and slope in group post-G subjects, is a measure of the scatter, about line C, of the mean threshold–slope values from these subjects. It is therefore also a measure of the extent to which the relationship between mean threshold and temporal summation differs from one group post-G subject to another. This coefficient cannot be compared with the coefficient of correlation from the temporal summation control groups, since threshold and temporal summation were uncorrelated in these latter groups. It may, however, be compared with the coefficient of correlation observed in the control groups for the spatial summation experiments in which threshold and summation *were* correlated. Both coefficients are found to differ from zero at about the same level of confidence. Thus, the relationship between mean threshold and *temporal* summation is about as consistent from one group post-G subject to another, as was the relationship between mean threshold and *spatial* summation in normal observers. It may therefore be concluded that the temporal summation curve observed in group post-G subjects is not the result of the averaging together of data from subjects in whom the relationship between threshold and temporal summation differed widely.

The scatter of mean threshold–slope values around line C is also dependent on the accuracy with which thresholds were determined in group post-G. It may therefore be concluded further, that the accuracy with which thresholds were determined in group post-G was comparable to that in the control groups in which spatial summation was measured.

DISCUSSION

It has been shown that the changes of threshold and of spatial summation, which occur as a visual field is increasingly impaired, are very nearly identical to those which accompany the increasingly peripheral presentation of stimuli in normal visual fields. This functional similarity requires explanation. Within the normal visual field, changes in spatial summation with increasingly peripheral stimulus presentation are generally regarded as consequences of structural differences between the visual pathways subserving increasingly peripheral parts of the field. Therefore, the changes in spatial summation seen in increasingly impaired visual fields may well be consequences of structural changes occurring in damaged visual pathways. If it could be further shown that there is a structural similarity between a damaged visual pathway and a pathway subserving a more peripheral region of the normal field, then the functional similarities described above would be explained.

In normal visual fields, the great overlap in the receptive fields of retinal ganglion cells makes it probable that a threshold stimulus alters the activity in more than one optic nerve fibre (Adrian & Matthews, 1927; Hartline, 1940), and probably also in more than one optic radiation fibre. Several authors (Baumgardt, 1953; Gregory & Cane, 1955; Barlow, Fitzhugh & Kuffler, 1957; Barlow, 1958) have used this structural feature as the basis for explanations of spatial summation. They have proposed that the perception of a threshold stimulus may depend on the combined activity in several such fibres, the combination of activity resulting in a lower threshold luminance than would be possible if only one fibre were active. Spatial summation is thus explained in principle, since the greater the area of a stimulus, the larger is the number of nerve fibres which it will activate, and the lower will be its threshold luminance. It is also necessary, however, to provide a structural explanation of the fact that spatial summation becomes progressively more complete as smaller stimuli are presented. It has therefore been proposed (Gregory & Cane, 1955) that spatial summation is most nearly complete when the number of fibres activated by a stimulus is small.

It follows from the above 'structural' explanation of spatial summation that any factor which reduces the number of nerve fibres which can be activated by a given stimulus will necessarily increase the incremental luminance threshold for that stimulus, and also make spatial summation more nearly complete. There is good reason to expect that just such a reduction in the number of nerve fibres available for activation may be brought about both by increasingly peripheral stimulus presentation and by damage to the visual pathways. In the first place, the number of optic nerve (and consequently optic radiation) fibres activated by a stimulus depends on, among other things, the number of retinal ganglion cells per unit area of retina. This latter number is known to decrease as more peripheral regions of the retina are studied (Weymouth, 1958). In the second place, it is known that one of the effects of damage to a sensory nerve is to block conduction in many of its constituent neurones. If, therefore, either the optic nerve or optic radiation are damaged, they will contain fewer functional fibres than usual, the number of fibres remaining intact decreasing as the damage is increasingly severe. Increasingly impaired regions of the visual field are, therefore, probably subserved by visual pathways containing fewer and fewer functional fibres. Thus, a similar increase in threshold and spatial summation would be expected both in increasingly impaired and in increasingly peripheral visual fields. This expectation is confirmed by the findings of the present investigation.

An alternative structural explanation of spatial summation is the 'two-quantum' hypothesis developed by Van der Velden, Bouman and others

(Van der Velden, 1946; Bouman, 1950; Bouman, 1961). This regards the integration of the excitation originating in different retinal receptors as taking place only within the receptive fields of single retinal ganglion cells. This hypothesis could account for the findings of the present investigation only if a lesion were to increase the area of such receptive fields in proportion to its severity. There is, however, no evidence to suggest that this occurs, nor are any mechanisms known by which a lesion could bring about such a change.

No mechanism is known by which damage to the visual pathways could bring about more nearly complete temporal summation, nor is it clear why pre- and post-geniculate lesions should be so different in their effect on temporal summation.

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