PROPAGATING INHIBITION

A study on the spatiotemporal properties of inhibition in the human visual system

P.C. Vrolijk

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A study on the spatiotemporal properties of inhibition in the human visual system

LOPENDE INHIBITIE
Een onderzoek naar de dynamische eigenschappen van inhibitie in het visuele systeem van de mens

PROEFSCHRIFT

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aan de Erasmus Universiteit Rotterdam
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Sinamus igitur & has nouas hypotheſes, inter ueteres, nihilo ueriſimiliores inno teſcere, præſertim cum admirabiles ſimul, & faciles ſint. ingen temq; theſaurum, doctiſsimarum obſeruationum ſecum ad- uehant. Neq; quiſquam, quod ad hypotheſes attinet, quicquā certi ab Aſtronomia expectet, cum ipſa nihil tale præſtare que at, ne ſi in alium uſum conficta pro ueris arripiat, ſtultior ab- hac diſciplina diſcedat, quàm acceſſerit. Vale.

"... Zo gunne men ook deze nieuwe hypothesen een plaats te midden van haar even onzekere voorgangsters, en dat te meer, omdat zij daardoor uitmunten, dat zij zeer bevattelijk zijn en een schat van geleerde waarnemingen eraan verbonden is. Wat de hypothesen zelf aangaat, verwachte men hier geen zekerheid, die de sterrenkunde niet in staat is te bieden. Wie dat zou doen en het verdichte zou aanzien voor waarheid, zou zich blootstellen aan het gevaar, dat hij minder wijs uit de school zou terugkomen dan hij er ingegaan is. Vaarwel."

Voorbericht in "De Revolutionibus Orbium Coelestium" (Over de omwentelingen der hemellichamen) door N. Copernicus (1543).

Voorwoord

Gewoonlijk wordt op deze plaats een groot aantal mensen genoemd die op de een of andere manier meegewerkt hebben aan de totstandkoming van het proefschrift. Als de dank van de promovendus voor die activiteiten aan de desbetreffende personen nog niet bekend was, lijkt het mij weinig zin hebben het op deze plaats alsnog mede te delen. Ik hoop dat ik erin geslaagd ben om door mijn gedrag duidelijk te maken welke mensen ik, binnen en buiten de werkkring, dankbaar ben voor het bereikte resultaat.

Contents

1.

INTRODUCTION

Chapter 1 INTRODUCTION

The response of the human visual system to spatially and/or temporally modulated luminance distributions has been the subject of considerable interest for a long time. Many researchers have been especially puzzled by the relations between the percept (i.e. the subjective sensation) and the stimulus (the physical presence). The large amount of interaction between the components of the system offers the opportunity for a wide range of investigations, most of which provide the answer to one question while at the same time raising many new ones.

Studying the visual system is an elegant way of studying the functioning of the brain, since some 40 % of the brain's input signals come from the eyes.

In this thesis attention is paid to the interactions between small flashes of short duration in order to throw some light on the combined spatiotemporal point spread function, with especial respect to the inhibitory effects. When the point spread function of a system is known and the system fulfils certain conditions, it is possible to predict the response of that system to any stimulus.

One of the first people to study the visual system by referring to physical procedures was Ernst Mach (who lived from 1838 to 1916). He looked at the subjective impressions of stimuli with several known luminance distributions. While experimenting with rotating discs he found bright and dark bands appearing where, according to physical calculations, none were to be expected. The percept of a gradual transience between two luminance levels seem to exhibit an overshoot at the borders of the gradients. These effects are now known as Mach bands (Ratliff, 1965). Formerly, such phenomena had generally been attributed to "unconsious inferences" or "errors of judgement" unworthy of study. But Mach sought an explanation for this phenomena in the mutual dependence of neighbouring retinal points on one another, a dependence which he believed could be accounted for in terms of the function of the neural network which was known to exist in the retina.

Mach was probably the first to attempt to express the integrative action of the nervous system in precise mathe-

matical terms. The basic neural process postulated in Mach's mathematical formulation was a reciprocal inhibitory interaction between neighbouring elements of the retina. The integration of opposed excitatory (i.e. positive, stimulating) and inhibitory (i.e. negative, suppressive) influences is the basic process utilized in practically all the quantitative models of neural networks that have since been proposed to explain the Mach bands and similar contrast effects.

Mach's formulation, which was based almost entirely on psychophysical evidence, anticipated the much later discovery, by modern electrophysiological techniques, of inhibitory interaction in the retina and in other parts of the nervous system. The importance of this discovery was acknowledged when Hartline and Ratliff were awarded the Nobel prize for their research in this field. Mach's mathematical approach to the study of the nervous system was so far ahead of the times that his papers attracted little attention when they first appeared (5 of Mach's articles were published between 1865 and 1868 by the 'Kaiserlichen Akademie der Wissenschaften, Wien'. An English translation of them was made by Ratliff in 1965, a century later).

Von Bekesy (1928) considered that some form of neural interaction similar to that which supposedly caused the Mach bands in vision might be the neural basis for the remarkable sharpness of the frequency discrimination of the auditory system. In his paper he used a visual analogy to illustrate how the sharpening mechanism might work. The bands in the photograph that he published were quite distinct even so that it was insinuated that the photograph might have been retouched. Anyhow, the Mach bands were again in the picture, and they still are (see e.g. Ratliff, 1984).

Later on, a number of possible neural networks were suggested to account for the interaction between neighbouring elements in the retina. These networks were based on a variety of experiments: e.g. perception threshold measurements of two points on the surface of the skin (Von Bekesy, 1960, 1967); direct electrophysiological measurements on the retina of vertebrates (Fry, 1948) or on the eye of Limulus (Hartline and Ratliff, 1954). The models are slightly different in their mathematical forms but they all refer to the same basic neural processes: central excitatory influences are opposed

by surrounding inhibitory effects.

The excitatory centre of the proposed mechanism leads to a form of integration which results in a restriction of the resolving power of the system. As a result of this, fine details are not distinguishable from each other. On the other hand, inhibition between neighbouring elements in the retina may serve to enhance the appearance of borders and contours and, in so doing, to compensate for blurring of the retinal image by imperfections in the lens and other optical components of the eye.

The study of the integrative properties of the human visual system has received much attention. It was found that the effect of a small stimulus on the receptors only depends on the total amount of energy presented within a certain time and area. This is true for both the temporal domain (Bunsen and Roscoe, 1856; Bloch, 1885; Aiba and Stevens, 1964) and the spatial domain (Ricco, 1877). Using separate simultaneously presented small test spots, i.e. the double flash technique, Hartline (1940) demonstrated that when small spots are presented within the so-called "receptive field", summation occurred.

This double flash technique has been widely used for the psychophysically study of interaction between stimuli. With spatial twin flashes (two simultaneously presented small flashes of light at a certain distance) it was found that for separations between the stimuli smaller then a few minutes of arc, complete summation occurred while for large separations probability summation was detected. For intermediate separations there is a gradual transition between these two effects (Bouman and van den Brink, 1952; Van den Brink, 1957; for a review see Hallett, 1963). It was found that spatial summation depends on the configuration of the stimuli (Sakitt, 1971; Thomas, 1978) and on the eccentricity (Hines, 1976; Scholtens and Bouman, 1977) while Martinez et al. (1979) concluded that the temporal course of the stimuli also has a great influence on the summation behaviour.

Temporal twin flashes (two identical flashes presented to the same retinal area, separated in time by a certain interval) yield similar results: complete summation for short interval times and probability summation for longer interval times

(Van den Brink and Bouman, 1954; Van den Brink, 1957; for a review see Boynton, 1972). The fact that temporal summation is also found when the stimuli are presented binocularly (van der Heide, 1980) indicates that temporal summation is not a purely retinal phenomenon, but is also influenced by more proximal processes, in which phenomena such as attention play a role.

Threshold measurements with temporal twin flashes showed that the increment threshold energy is constant for interval times shorter than about 10 ms and also constant (at a higher level) for interval times longer than about 100 ms. For intermediate interval times, however, a peak in threshold energy is found (Ikeda, 1965; Herrick, 1972 and 1974). Ikeda suggested an explanation in terms of a function which is generated by each flash. This function would exhibit a positive and a negative stage. For the twin flash experiments, the algebraic sum of two shifted functions would determine the threshold. Roufs (1972 and 1973) further explored this view and improved it by taking the temporal pulse response, as calculated by means of inverse Fourier transformation from the temporal modulation transfer function (the "de Lange" curve), as the function generated.

The system-analytic approach to vision was introduced in 1954 by De Lange for temporal aspects of vision and in 1956 by Schade for the study of the spatial aspects of vision. Campbell and his co-workers extensively studied the spatial aspects (see e.g. Campbell and Green, 1965, or Campbell and Robson, 1968). In the spatial case too, the pulse response can be calculated from the spatial modulation function (the so-called contrast sensitivity curve), see e.g. Van Meeteren (1973).

The application of the systems approach to vision proved to be fruitful. It is, for example, possible to describe the response of the human visual system to spatial gratings in terms of line spread functions (Wilson and Bergen, 1979) or point spread functions (Kretz et al., 1979). This was done for stimuli of long duration. Evidence for inhibition is found in the results of the grating measurements as well as in those of the point spread function. The same applies to the temporal domain: Roufs (1972) showed a relationship between flicker and flash thresholds for stimuli of 1 degree diameter,

both of which involved inhibition.

Thus, in order to describe the results for extended or prolonged stimuli it is necessary to assume the presence of inhibition. However, measurements of the point spread function for stimuli with diameters in the order of a few min arc and durations of a few ms, do not show any evidence at all for the presence of inhibition. The problem remains that it is not clear when inhibition effects are to be expected and when not. Comparing the experimental conditions used by different authors for the study of temporal twin flashes, Meijer et al. (1978) found that investigators who used stimuli with a diameter greater than about 0.5 degree all reported inhibition while no inhibition was detected when small stimuli were used (diameter a few min arc). Therefore, Meijer performed the experiments with a number of flash diameters. It was found that the response was only subject to an inhibition effect beyond a certain flash diameter and a certain interval time. He suggested that the spatiotemporal point spread function of the visual system consists of an area of summation surrounded by an interaction-free zone, which in its turn is encircled by an inhibition region. This would account for the fact that inhibition occurs with large stimuli while it is absent when small stimuli are used.

The results found with spatial twin flashes of short duration also fail to show any inhibition effects (the duration of spatial twin flashes is analogous to the diameter of temporal twin flashes). To the best of our knowledge vision has not been studied using small spatial twin flashes of long duration. This is in contrast to the study of periodic stimuli (spatial grating and temporal flicker) for which there is an extensive body of literature.

When a grating pattern is used as a stimulus and the presentation time exceeds 50 ms, the spatial modulation transfer function has the form of a bandpass filter characteristic (Rohler and Hilz, 1966; Campbell and Robson, 1968). The pulse response obtained from this transfer function by inverse Fourier transformation shows a negative part, indicating the presence of inhibition. When the grating is only presented for a short time (less than 30 ms) Rohler and Hilz (1966) and Kelly (1971) reported low-pass filter characteristics. The inverse Fourier transform of these results show no inhibition.

Similarly, Fiorentini and Maffei (1970) found that measurements of the "de Lange" curves with stimuli of restricted dimensions resulted in low-pass filter characteristics, whereas the use of larger stimuli resulted in band-pass filter characteristics. Thus, in order to detect inhibition with flickering stimuli, the diameter has to exceed a certain value.

All these findings indicate that inhibition cannot be detected with stimuli of short duration and small dimensions, but that it is to be expected provided that the stimuli are large enough and last long enough.

This does not necessarily mean however that inhibition is not generated by small stimuli of short duration. It is possible that the inhibition is generated but that it is not detected since the "probes" are presented to other areas and at other times then those where inhibition is active.

This view is explored in the present study. If the point spread function of the human visual system resembles the one suggested by Meijer et al. (1978) it should be possible to detect inhibition effects using small flashes of short duration when the flashes are given not only a certain spatial separation but also a temporal separation. With this stimulus, which is called a jumping flash, the spatiotemporal aspects of inhibition can be determined with high resolution, both spatially and temporally. This kind of experiment (which apparently has not previously been described in the literature) and the results are described in the present thesis.

The methods and the experimental set-up are described in Chapter 2. In Chapter 3 measurements for elementary point flashes are given and discussed and relations are sought between aspects of inhibition and the summation areas. Some further aspects of the inhibition are discussed in Chapter 4. In Chapter 5 and 6 the relationships which have been identified are tested using stimuli of longer duration and/or larger diameter. The influence of the background luminance is studied in Chapter 7. In Chapter 8 results are given for suprathreshold stimuli and these results are compared with those for metacontrast in Chapter 9. Results found with spatial and temporal twin flashes are given in Chapter 10. Finally, Chapter 11 gives

a general discussion of the results.

Chapters 3, 5, 7, and 8 (combined with 9) are adapted from articles published in Vision Research (Van der Wildt and Vrolijk, 1981; Vrolijk and van der Wildt, 1982a, 1985c and 1985b). Abstracts of the material have been published (Vrolijk and van der Wildt 1981, 1983a, 1983b, 1982b, 1985a).

2.

METHODS

Chapter 2 METHODS

2.1 MEASURING PROCEDURE.

The aim of the experiments was to determine the spatio-temporal course of inhibition with high resolution. This was done by using two small flashes with a diameter of about 1 min arc and a duration of about 10 ms as stimuli. The flashes, which were presented with a time interval and a certain distance between them, are referred to as "jumping flashes". A schematic representation of the stimuli used is given in Fig. 2.1 in a distance versus time plot.

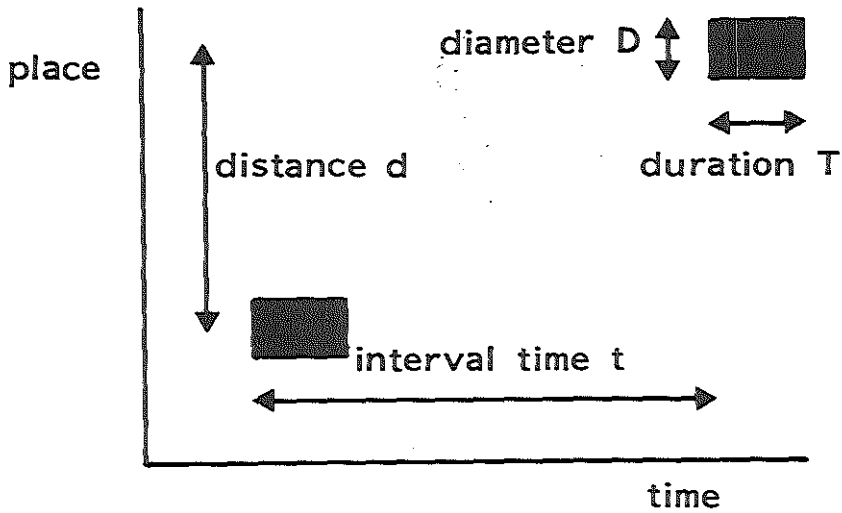

Fig. 2.1 Parameters of the jumping flash stimulus used: two flashes separated in time and space.

In this thesis, two measuring procedures were employed; firstly the method of constant stimuli using stimuli presented at the increment threshold luminance. Secondly, the method of adjustment which is based on suprathreshold stimuli (for reviews see Graham, 1966; and Sidowski, 1966).

2.1.1 THE METHOD OF CONSTANT STIMULI. Because of the statistical character of light and that of the visual system, there is no sharply defined threshold energy for the perception of light. The relative frequency of positive response shows a gradual increase with the stimulus energy. In Fig. 2.2 an

example of a psychometric curve is given; it gives the frequency of seeing a small flash as a function of the flash energy. This plot shows the relation between the subjective percept and the physical parameters of the stimulus. In Fig. 2.2 this curve is approximated by a cumulative Gaussian distribution. As a rule, the visual threshold is defined as the energy that corresponds to a frequency of seeing of 50 %. The slope of the curve is characterized by the Crozier coefficient which is defined as the standard deviation of the distribution, divided by the threshold energy. The Crozier coefficient is a measure for the variance of the threshold (see e.g. Roufs, 1974).

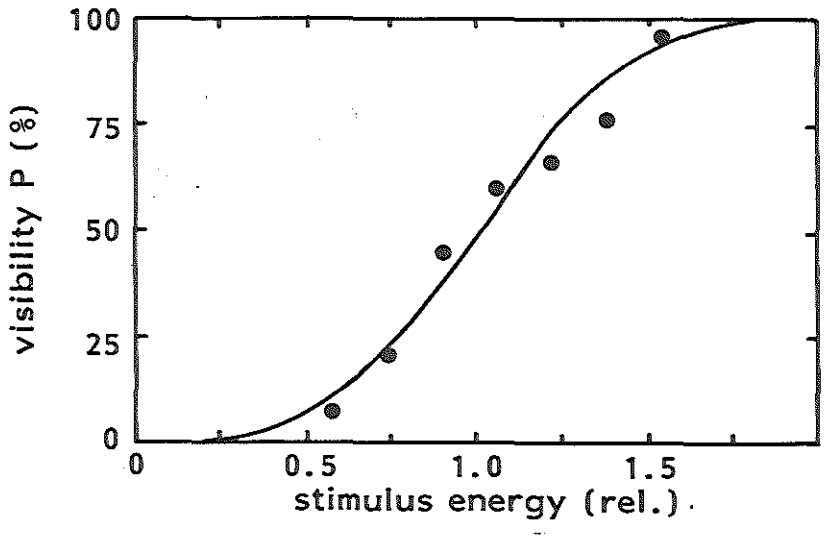

Fig. 2.2 The psychometric curve.

In the experiments, the luminance of the stimulus was kept at a fixed value and the frequency of seeing was estimated by presenting the same stimulus a number of times and determining the relative fraction of positive responses. Throughout this thesis this relative fraction will be called visibility.

A frequency of seeing curve is determined by the threshold and the Crozier coeficient. The visibility as defined above, however, is also due to the statistical spread of the data

which depends on the number of presentations on which it is based. The standard deviation of the visibility can be expressed by

$$s = \sqrt{\frac{p\ (1\ -\ p)}{n}}$$

in which p stands for the visibility and n for the number of presentations. In most experiments p is about 50 %, so 100 presentations have to be used in order to obtain a standard deviation of approximately 5%.

When two flashes are presented, there may be interaction between them, this depending on the stimulus onset asynchrony (hereafter referred to as the interval time) and distance between the stimuli. The visibility can be influenced by the interaction in different ways. The following interactions are possible:

-Complete summation for interval times shorter than about 10 ms and spatial separation of less than about 2 min arc. In that case, the visibility of the complex is equal to the visibility of a single flash which has an energy equal to the sum of the individual energies.

-Probability summation for large interval times or spatial separation. When both flashes have no mutual interactions, the visibility of the complex can be obtained by

$$P = 1 - (1 - p)^2$$

when both flashes separately have a visibility p.

-Partial summation for intermediate interval times and distances. Partial summation may be described as a transition between complete summation and probability summation.

-Inhibition. When either of the flashes is inhibited, the visibility of the complex will be lower than the value expected on the basis of summation. When complete inhibition of one of the flashes occurs for separations larger than the summation areas, the visibility drops from the value corresponding to probability summation to the value for single flash visibility.

-Facilitation. When a supraliminal effect is present in the retinal image, it can facilitate neighbouring subliminal activity (van den Brink and Reijntjes, 1966). In that case, the visibility would be higher than the value expected on the basis of summation.

In most experiments using two flashes as a stimulus, the luminance of the flashes is chosen so that the visibility of each of the flashes is about 30 % . The probability summation visibility is then 51 % which is unfortunately very near the visibility which gives the maximal standard deviaton in the results. It can be calculated that for flashes against a dark background a single flash visibilty of 30 % corresponds to an average number of quanta absorbed by the receptors in the retina which is 1.1 (according to Van der Velden, 1946; Bouman and van der Velden, 1947; and Bouman, 1949). In this study, however, our primary interest is to detect the presence or absence of inhibition. Therefore it is desirable to maximize the difference between the probability summation visibility and the single flash visibility. It can easily be shown that this is the case when the single flash visibility is 50 % (which is when, according to the quanta hypothesis, on the average, 1.7 quanta are absorbed). When the difference between the probability summation visibility and the single flash visibility is called the signal and the standard deviation of the single flash visibility is denoted as noise, the signal to noise ratio is at a maximum for a single flash visibility of 50 %.

For the above reason, most results were gathered using a single flash visibility of about 50 % which gave a probability summation level of about 75 %. No corrections were made for small variations in the single flash visibilities due to day to day variation of the threshold (see e.g. Le Grand, 1968).

Each visibility was determined from 25 presentations with an interstimulus interval time chosen at random between 2 and 4 seconds. When the observer noticed the stimulus at all, he responded by pushing a button. With another button he could interrupt the procedure. After each run, the frequency with which the stimulus was seen was printed out, the interval time and/or the distance between the flashes was changed and the whole procedure was repeated. Finally, the results

were automatically plotted in a graph. The results are generally given as the mean of 4 runs.

When the subject has no occupation apart from occasionally pressing a button, we always found that his performance gradually decreased during the session. This decrease proved to be very stable (namely a 5 % decrease in the visibility of a single flash per minute measuring time) and was remarkably independent on the stimulus parameters. In Fig. 2.3 examples of such results are given for two subjects, one unexperienced (RP, open circles) and one trained (PV, filled symbols). The results plotted show the visibility of a single flash presented at a 10 cd/m^2 background as a function of the time (the stimulus was not changed during this time). The effect was only influenced by the complexity of the stimulus; with a double flash, the decrease appeared to be 2.7 % per minute. A similar effect was reported by Schober (1966) for the detection of targets on a radar screen. Singer et al. (1977) reported that threshold increases as a function of the time can be eliminated by instructing the subject to make large eye movements between the presentation of

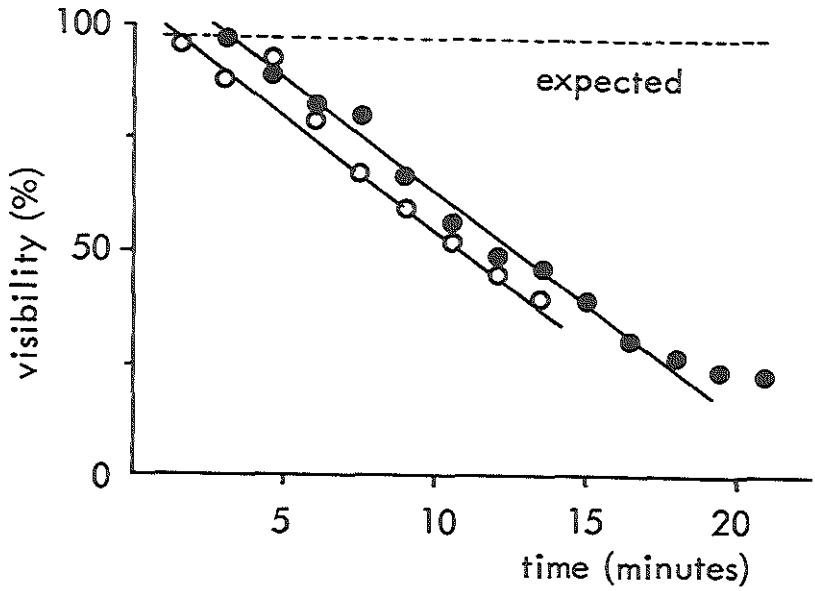

Fig. 2.3 The visibility of a single flash as a function of the length of time after the start of the measurements, for subject RP (open symbols) and subject PV (filled symbols). The dashed line is what would generally be expected.

the stimuli. We found that the drift effect can also be avoided by limiting the duration of a session to half an hour and by giving the observer something to do after each run.

2.1.2 THE METHOD OF ADJUSTMENT. A reliable way of measuring the effect of one stimulus on another is to determine the amount by which one of the stimuli has to be changed in order to compensate for the interaction. The criterion for this method is equality in one aspect or another of the stimuli. This is usually quite straightforward and it does not require much training to give reproducable results.

In the experiments described in the Chapters 8 and 9 two flashes are presented, one of which (the second one) has a fixed (suprathreshold) luminance; the luminance of the other (the first one) being adjusted by the subject so as to equalize the brightness of both flashes. The interval time and the distance between the flashes are then the parameters. The subject operates a button with which he can change the luminance of the flash. The flashes are presented regularly with an interstimulus interval time of about 2 seconds. This procedure is similar to that described by Saunders (1977), but in that case he adjusted the luminance of the second flash. We used a fixed luminance for the inhibition generating flash (it will be shown that this is the second flash) in a given run in order to avoid manipulation of the inhibition generating stimulus.

Based on his judgement the subject increases or decreases the luminance of the flash to achieve equality. In each trial it was usual for some overshoot to occur which was compensated by small changes back and forth (in fact, each trial represents a determination by the so-called staircase method).

To avoid effects of habituation the trials were started with a luminance which was alternately too high or too low, the values of the luminance being chosen at random. In the experiments, 10 trials were performed with each set of stimulus parameters. The arithmic mean of the adjusted values was taken as the brightness match. The standard deviation of this mean is about 5 %.

The adjustment method has some advantages compared to the method of constant stimuli. Firstly, the adjustment method

gives a quantitative measure (be it indirectly) for the strength of the effect of one flash on the other whereas the method of constant stimuli indicates little more then the presence or absence of interactions. Secondly, the adjustment method is much less sensitive to variations in the subject's sensitivity or criterion: his assessment of equality is quite stable whereas the threshold varies from day to day.

On the other hand, the method of constant stimuli is good in other things: firstly it enables the determination of mutual interactions which would not be observed in the adjustment method. Secondly it is not necessary to be able to distinguish between the two stimuli as it is in the adjustment method. This enables measurements with smaller spatial distances and temporal intervals between the two flashes, which is of especial importance when the stimuli are presented to the peripheral field of vision.

Some pilot experiments in which the stimuli were presented at 3 degrees nasal showed that it was almost impossible to equalize their brightness. Thus, in the peripheral experiments the method of constant stimuli was employed. In the foveal experiments both methods were used, although mainly the method of adjustment.

2.2 APPARATUS

In this section the apparatus used in the various experiments is described. The experimental set-up to generate the jumping flashes against a homogeneous background is illustrated in Fig. 2.4.

Unless otherwise stated, the flashes were presented near the centre of a homogeneous background with luminance 10 cd/m^2 and diameter 3.7 degrees. Except for the foveal measurements, a fixation mark with a diameter of 1 degree was used which had some fine details on it which disappeared if the accommodation was not correct. In order to avoid interactions between the stimuli and the fixation marker, no such marker was used in the foveal experiments. Further details are given in the description of the results.

The background was presented in Maxwellian view (Maxwell, 1860; Westheimer, 1966), and the flashes were imaged at infinity. The light sources A, B, and C were light-emitting

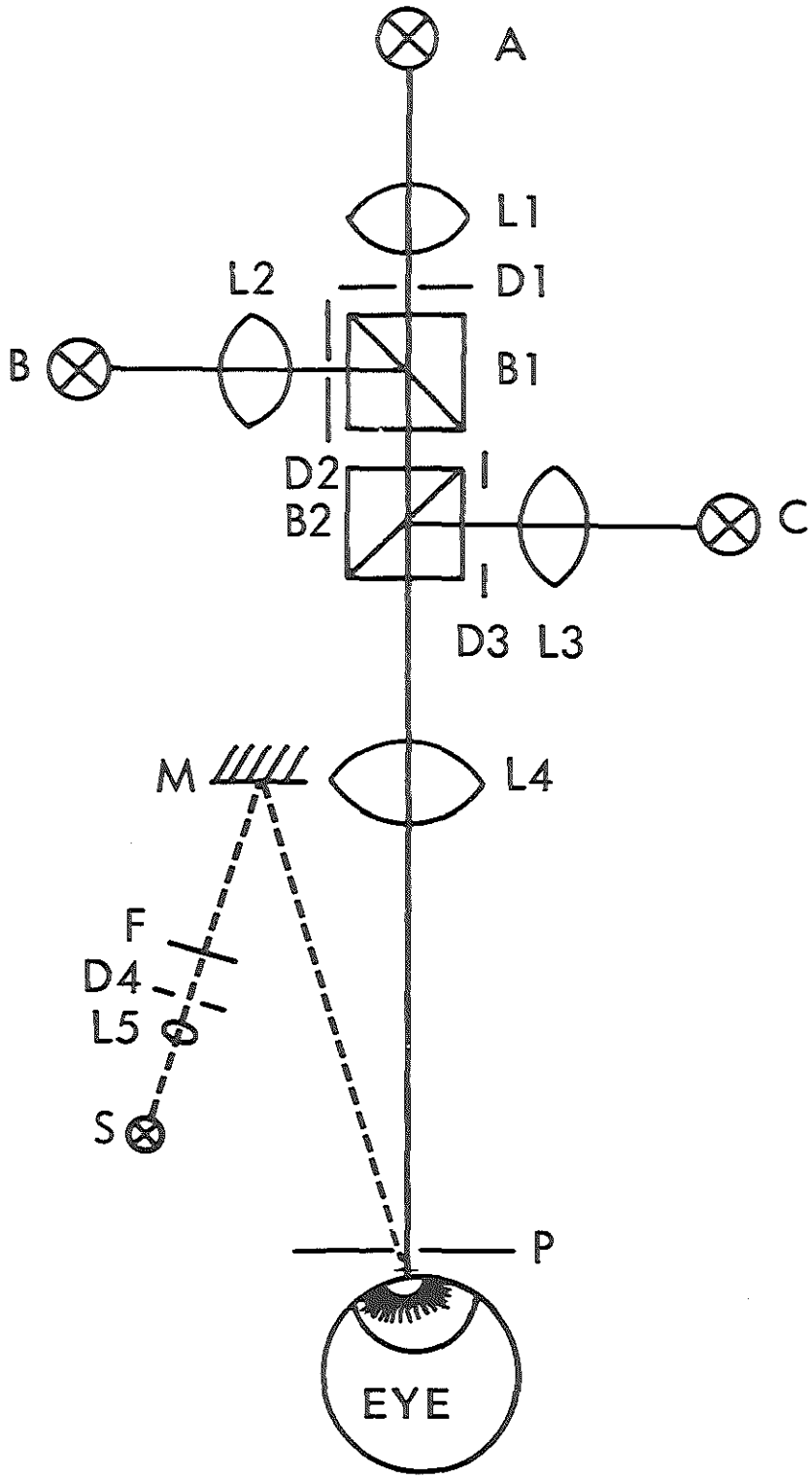
A
L1
L2
D1
B
B1
D2
B2
C
D3
L3
M
L4
F
D4
L5
S
P
EYE

Fig. 2.4 The experimental set-up. Diaphragm D3 determines the background diameter. Bulb S (in the focal plane of lens L5), lens L5 (f=50mm), diaphragm D4 and red filter F generate the fixation stimulus, which is presented to the eye via mirror M.

diodes (LED's, Monsanto type MV 5752, wavelength 635 nm), the light output of which was controlled by adjusting the repetition frequency of a pulsed current (pulse duration 40 micro sec) through the LED's. The background luminance was about 10 cd/m^2. The LED's were situated at the foci of the lenses L1, L2, and L3 (f=120 mm). The diameter of the flashes was approximately 1 min arc, their duration about 10 ms and the diameter of the background was 3.7 degrees arc. The flashes were presented near the centre of the background. To change the distance between the flashes, the position of the diaphragm D2 could be varied by motor control in two perpendicular directions. The delay between the flashes was controlled by a microprocessor (Motorola M6800), which in fact governed the entire measurement procedure. The diaphragms D1, D2 and D3 were all effectively at the focus of lens L4 (f=600 mm) and an artificial pupil P (diameter 2.4 mm) was placed 600 mm in front of lens L4. An illuminated fixation mark D4 with some detail on it was used to maintain the observer's attention during the peripheral measurements. A biteboard and a forehead rest were used to fixate the position of the observer's head.

3.

SPATIOTEMPORAL INHIBITION DETERMINED WITH ELEMENTARY STIMULI

Chapter 3 SPATIOTEMPORAL INHIBITION DETERMINED WITH ELEMENTARY STIMULI

3.1 INTRODUCTION

The spatiotemporal properties of inhibition were studied by measuring the visibility of a jumping flash as a function of the interval time and distance between the flashes. Results are given for elementary point flashes at eccentricities of 3 and 7 degrees and an attempt is made to show the association between the inhibition results and the spatial and the temporal summation areas.

3.2 RESULTS

Temporal or spatial summation measurements have often been made (Van den Brink, 1957; Hallet, 1963; Ikeda, 1965; Roufs, 1973). Values ranging from 10 to 60 ms have been reported for the temporal summation area, while for spatial summation areas values between 2 and 8 min arc have been found.

These results show such a variation that, in order to compare the summation areas quantatively with results obtained using jumping flashes, we carried out spatial and temporal summation measurements for one subject.

Unless otherwise stated, the diameter of both flashes was 1 min arc and their duration was 10 ms in all experiments described in this chapter. The results of the temporal summation measurements at 3 and 7 degrees nasal are given in Fig. 3.1, while Fig. 3.2 gives the results of the spatial summation measurements for vertically and horizontally jumping flashes at 3 degrees nasal and for vertically jumping flashes at 7 degrees nasal. Each point is based on the presentation of 100 stimuli in 4 runs. The standard deviation of the mean is about 5 % . The subject in all measurements was PV, unless mentioned otherwise.

When the jumping flash was presented with both temporal and spatial separation, results as given in Fig. 3.3 were obtained. The visibility of a vertically jumping flash at 3 degrees nasal for 5 different distances between the first and second flash is plotted as a function of the interval time. Straight lines were drawn by eye through the experimental points.

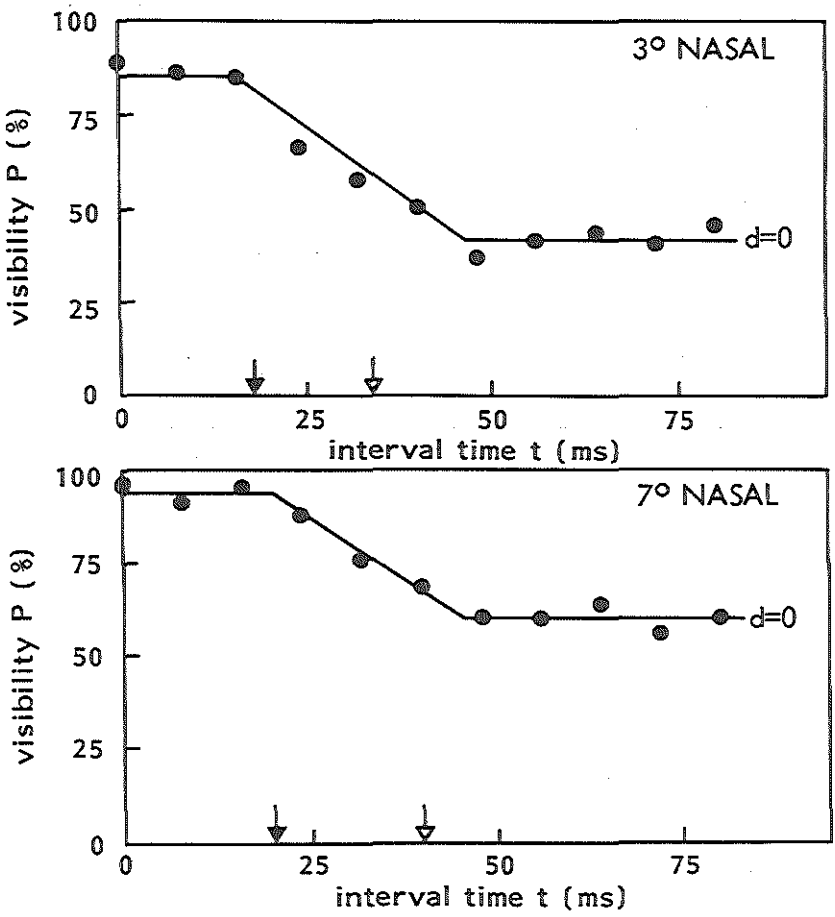

Fig. 3.1 Temporal summation measured with jumping flashes without spatial separation (d=0) at 3 degrees and 7 degrees nasal. The visibility P is plotted as a function of the interval time t. For the arrows on the horizontal axis, see text.

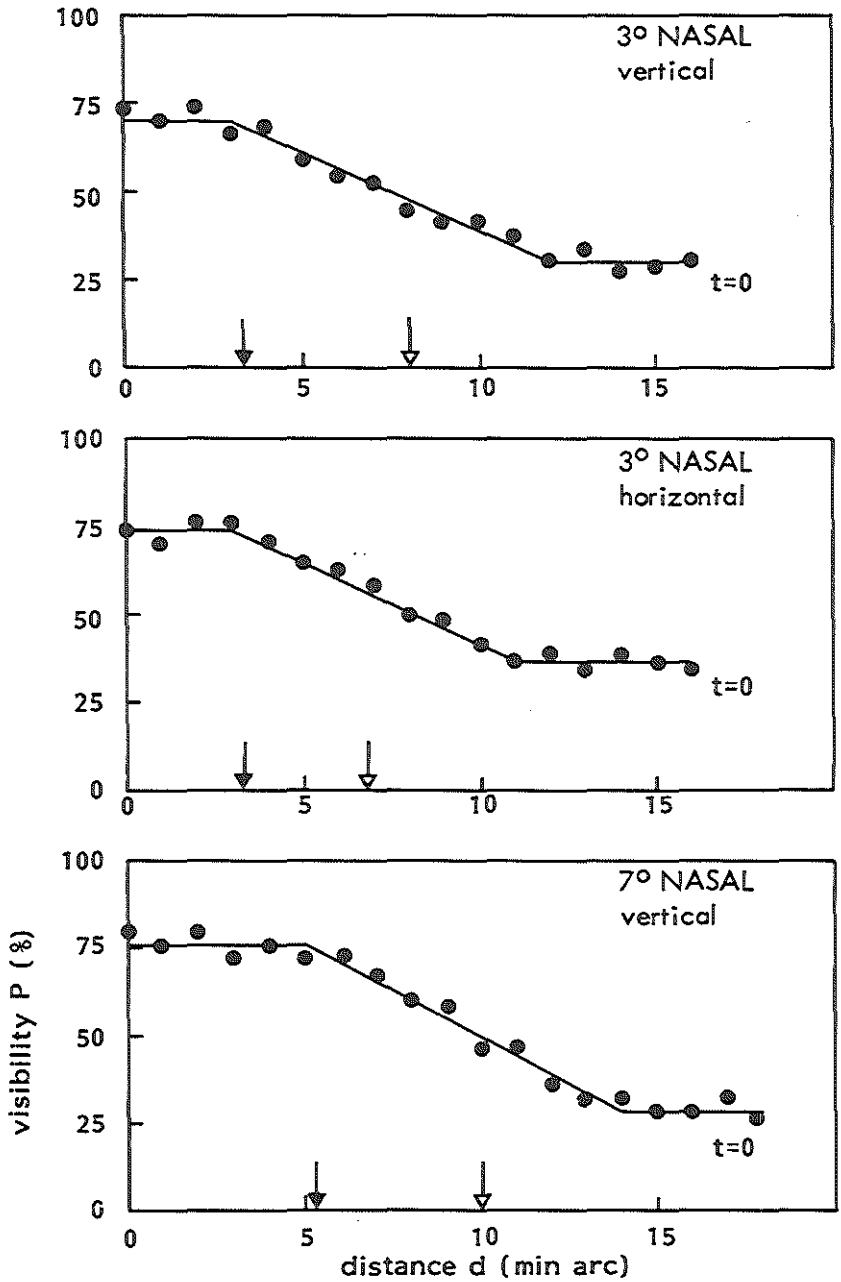

Fig. 3.2 Spatial summation measured with jumping flashes without temporal separation (t=0) at 3 degrees nasal vertical and horizontal and at 7 degrees nasal vertical. The visibility P is plotted against the flash distance d.

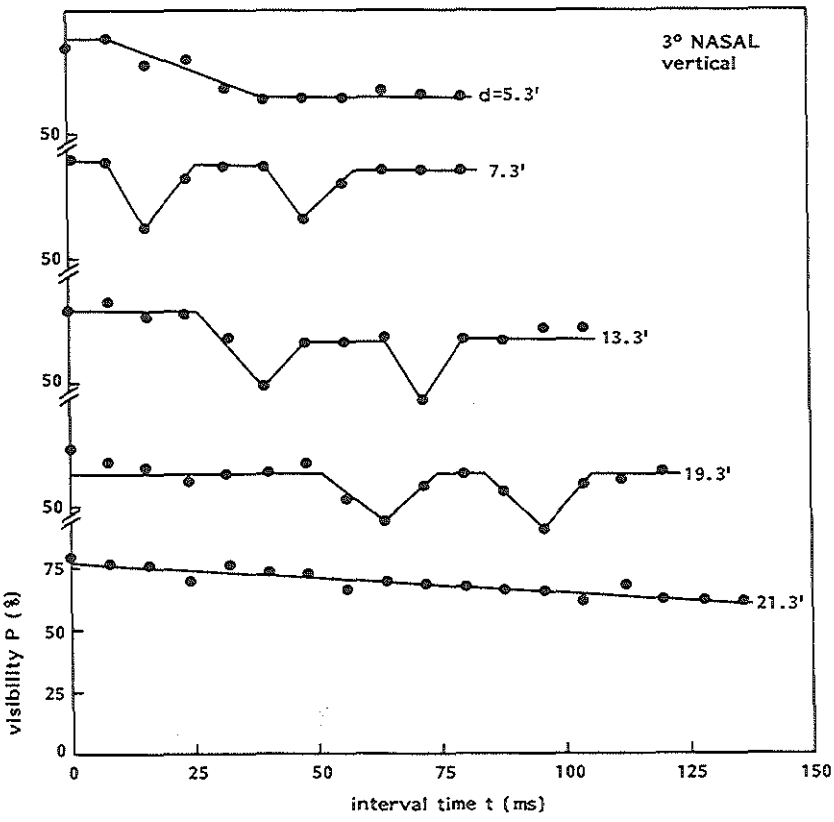

Fig. 3.3 Visibility P of a vertically jumping flash at 3 degrees nasal as a function of the interval time t for 5 distances d between the flashes. For the sake of clarity each curve except the lowest is displaced upwards over a distance equivalent to 50 % detection probability with respect to the curve below it.

The most striking feature of these results is that for distances d between 5.3 an 21.3 min arc we found a drop in visibility over two small ranges of t. Figure 3.4 gives the results for d = 9.5 min arc as measured with an inexperienced and unpaid volunteer J.R. In Fig. 3.5 results are given as measured on RvdR, a slightly trained and paid subject. For these results horizontally jumping flashes were presented at 3 degrees nasal. Each point is based on the presentation of 150 stimuli. The curves are drawn free-hand, allowing generous margins.

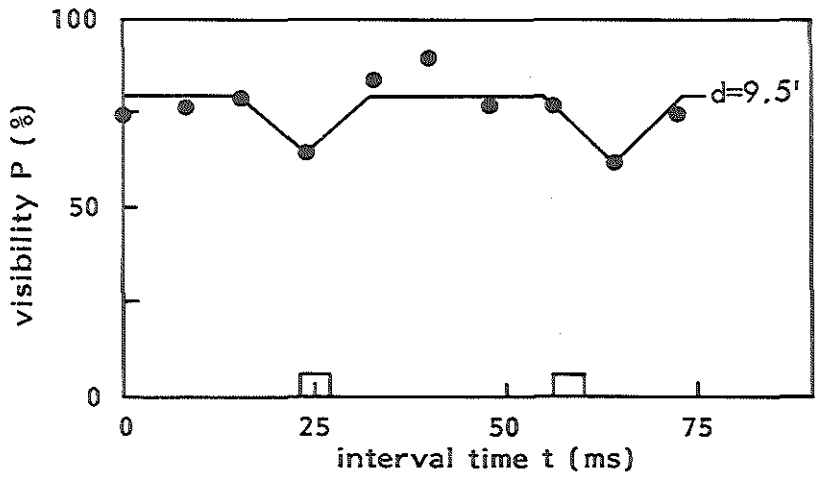

Fig. 3.4 Visibility P of a vertically jumping flash at 3 degrees nasal as a function of the interval time t for subject J.R. The interval times at which the dips were found for subject P.V. are indicated on the time axis.

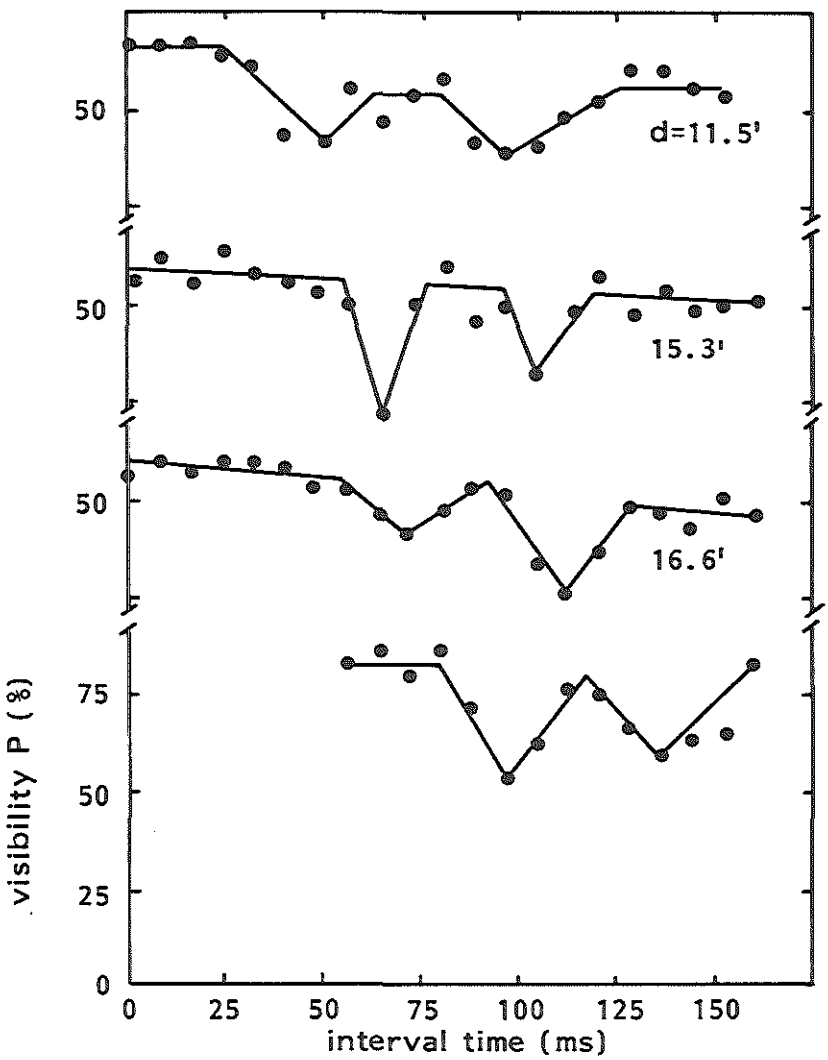

Fig. 3.5 Results as in Fig. 3.3, obtained with subject RvdR for horizontally jumping flashes. For the lowest curve, the flashdistance was 19.3 min arc.

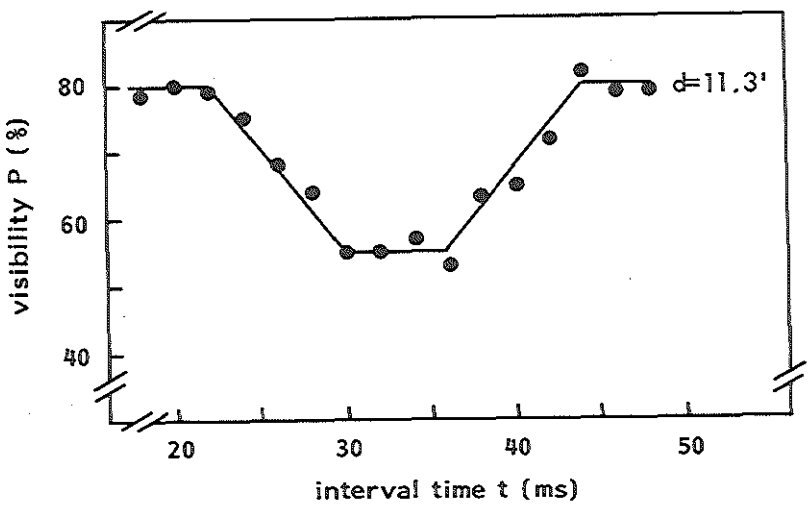

Fig. 3.6 The shape of a dip as measured for d = 11.3 min arc using more flashes per point than usual (200 instead of 100) and smaller time interval steps (2 ms instead of 8 ms).

Figure 3.6 gives the results (for subject PV) of a more accurate measurement (200 flashes per run) with a distance of 11.3 min arc and with small interval steps (2 ms). The visibility found in the dip is 55 % which is roughly equal to the single-flash visibility. The half-height width of the dip is approximately 15 ms. It follows that a time-interval step of 8 ms (as used in all further experiments) is small enough to locate a dip.

In Fig. 3.3 the dips occur at larger values of t when the distance d is greater. To study this effect in more detail, we measured one dip for seven values of d between 5.3 and 21.3 min arc. The results are given in Fig. 3.7, and, for flash distances in this range, show a quite remarkable linear variation in the interval times at which the dips are found.

At a distance d of 21.3 min arc, a small dip can be seen at t = 112 ms. However, this reduction is so small as to be hardly significant.

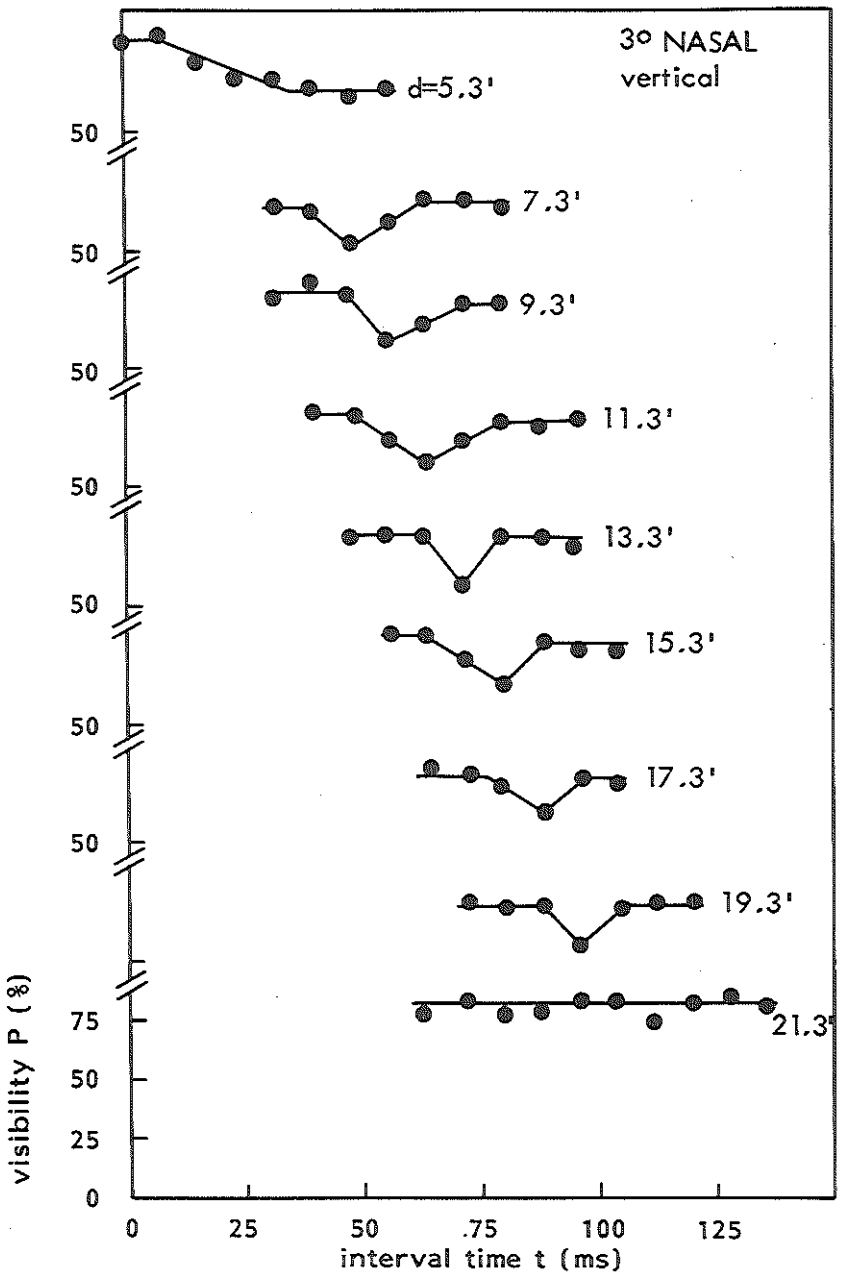

Fig. 3.7 Visibility curves at 3 degrees nasal with vertically jumping flashes for 9 flash distances d ranging from 5.3 to 21.3 min arc. These measurements were performed under the same conditions as for Fig. 3.3, but only for one of the two dips.

3 degrees nasal vertical				
flash distance (min of arc)	7.3	13.3	19.3	
dip interval times (ms)	16 48	40 72	64 96	
3 degrees nasal horizontal				
flash distance (min of arc)	10.0	15.3	21.3	
dip interval times (ms)	36 72	64 96	100 132	
7 degrees nasal vertical				
flash distance (min of arc)	9.3	13.3	17.3	
dip interval times (ms)	16 56	32 72	48 88	
7 degrees nasal horizontal				
flash distance (min of arc)	9.3	13.3	17.3	21.3
dip interval times (ms)	20 68	40 88	64 112	80 128
3 degrees below the fovea vertical				
flash distance (min of arc)	9.3	13.3	17.3	
dip interval times (ms)	32 72	56 96	72 112	
3 degrees below the fovea horizontal				
flash distance (min of arc)	9.3	13.3		
dip interval times (ms)	24 56	40 72		
3 degrees oblique vertical				
flash distance (min of arc)	9.6	18.0		
dip interval times (ms)	24 64	72 104		
3 degrees oblique horizontal				
flash distance (min of arc)	9.6	18.0		
dip interval times (ms)	28 64	72 104		

Table 3.1 The interval times at which dips are found in the visibility curves (referred to as dip interval times) for vertically and horizontally jumping flashes at 3 degrees eccentric (nasal, below the fovea and oblique) and at 7 degrees nasal.

The same measurements were also performed with horizontally jumping flashes at 3 degrees nasal. Two dips were found here as well. The interval times at which dips were found in the visibility curves are given in Table 3.1. With flash distances of 5.3 and 25.3 min arc, no dips were found under these conditions.

Table 3.1 also gives the interval times at which a dip was found using horizontally and vertically jumping flashes at 7 degrees nasal, 3 degrees below the fovea and at 3 degrees eccentric at an angle of 45 degrees with the horizontal meridian (this position is indicated as 3 degrees oblique).

All the measurements show two dips, which occur at values of t which increase with the distance d. The separation of the two dips is independent of the value of d, but does depend on the relative orientation of the two flashes in the stimulus and on the eccentricity at which the observations were made.

3.3 DISCUSSION

The temporal and spatial summation areas for subject PV were determined by measuring the visibility of a jumping flash without spatial separation (d=0, temporal twin flash) or no time interval (t=0, spatial twin flash) respectively. The results are shown in Figs. 3.1 and 3.2. No dips were found in these measurements, which is in accordance with the literature. In general we see areas of constant visibility for low and high separations respectively and a gradual decrease in visibility between these two values.

When however the jumping flashes were presented with both a spatial separation and an interval time between them, the results (see Fig. 3.3) show a reduction in the visibility of the stimulus complex, despite the very small, short flashes which were used. So it seems that elementary flashes yield an inhibition effect, not at the place and time of excitation itself, but separated by a certain distance and interval time from the excitation.

Two dips in the visibility curves were also found with other subjects, see Figs. 3.4 and 3.5. The ranges of t corresponding to the minima of the dips for subject PV are indicated by blocks on the time axis in Fig. 3.4 (these interval times are determined for d = 9.5 min arc by interpolation from Fig. 3.8). Although the dips found in the curve of JR (Fig. 3.4) are less pronounced and the results found with subject RvdR (Fig. 3.5) have more noise, it will be seen that the results resemble those for PV. Two dips were also found at corresponding interval times with subject GW (not illustrated).

On the basis of their determination of the response to twin flashes as a function of the flash diameter, Meyer et al. (1978) concluded that an inhibition effect from a small excited retinal area can only be found beyond a certain minimum

distance from the point of excitation and after a certain time. The measurements with jumping flashes seem to confirm this.

The results in Fig. 3.3 (and those in 3.4 and 3.5) are interesting for a number of reasons. Firstly, the inhibition effect observed is not a single phenomenon, but consists of two short dips in the visibility curve. These dips are completely separate and have a half-height width of approximately 10 ms. This is very small compared with the width of the temporal pulse response, which is about 100 ms, according to various authors (see e.g. Meyer et al., 1978).

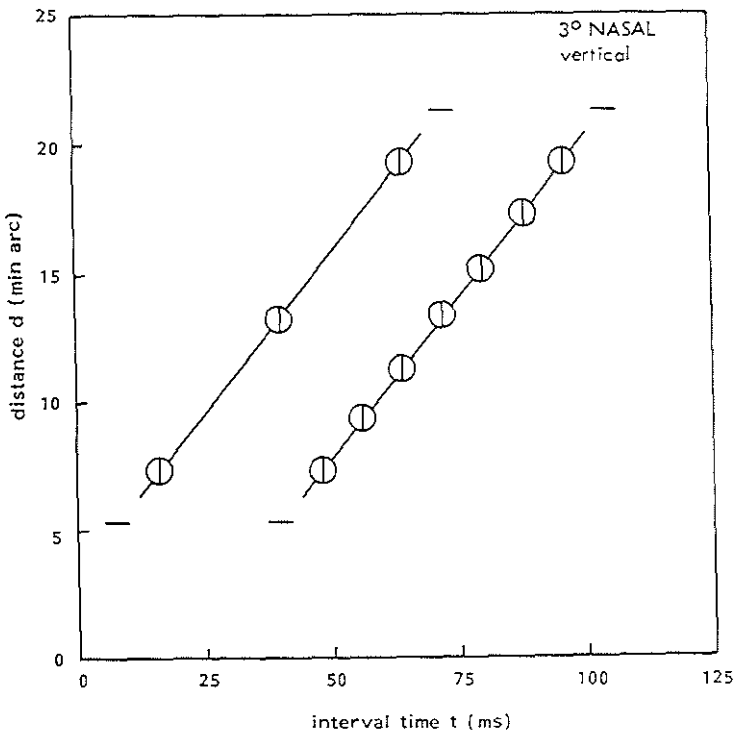

Fig. 3.8 The flash distance d vs the interval time t at which the dips were found at 3 degrees nasal with vertically jumping flashes. The data are taken from Figs 3.3 and 3.7. The small horizontal bars mark the flash distance d at which no dips were found.

If we plot our results as a function of the distance d with the interval time t as parameter, we find dips with a spatial half-height width of roughly 2 min arc, which is very small compared with the point spread function of 10 min arc (see e.g. Krauskopf, 1962). We will return to the dual nature of the inhibition later on in this discussion.

A second point worth to be mentioned is the depth of the dips in the visibility curves. The inhibition is found to reduce the visibility of the stimulus complex from the value given by probability summation to that corresponding to the visibility of each flash separately. This can be interpreted as being due to the complete disappearance, in effect, of one of the flashes.

Thirdly, the interval times t at which the dips are found increase with the spatial separation d between the flashes. This suggests that the inhibition effect is propagated from the area of excitation. To get a better impression of this propagation, the distance d can be plotted against the value of t at which the inhibition effect is measured. When this is done for the results measured with a vertical jumping flash at an eccentricity of 3 degrees nasal, (see Figs. 3.3 and 3.7), the curves in Fig. 3.8 are obtained.

All data points lie on two parallel straight lines, which indicates that the inhibition effects are propagated away from the place of excitation with a constant velocity which is the same for both dips. The value of this velocity (the slope of the lines) in the vertical flash direction is 4.2 degrees per second.

The excellent fit between the experimental points and lines is partly due to the fact that we measured with constant changes in d of 2 min arc and constant changes in t of 8 ms, so departures from linearity of less than 4 ms would not show up in the results.

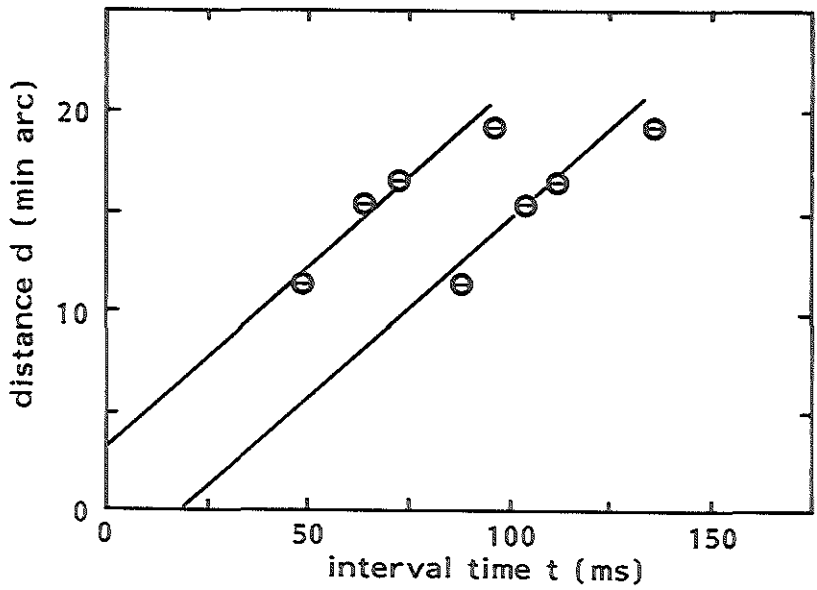

Fig. 3.9 The same as Fig. 3.8 for the results obtained with subject RvdR, as given in Fig. 3.5. The lines are replotted from Fig. 3.10.

In Fig. 3.10 all results presented in Table 3.1 are plotted in a similar way as in Fig. 3.8. Velocities of 3.1 and 4.2 degrees per second are found at 3 and 7 degrees nasal and 3 degrees below the fovea, while at 3 degrees oblique velocities of 3.5 degrees per second are found.

In Fig. 3.9 the results determined with subject RvdR are plotted. Although the lines are the same as those used for the results with subject PV (see Fig. 3.10), they fit the data from RvdR quite closely.

A schematic representation of the velocities found at the different positions on the retina is given in Fig. 3.11. The propagation velocities are represented as vectors. Assuming an elliptical distribution of the propagation velocities with direction and circular symmetry round the fovea, we see that the same ellipse (with a short axis of 3.1 degrees per second and a long axis of 4.2 degrees per second) can be constructed for the four locations studied. From the mea-

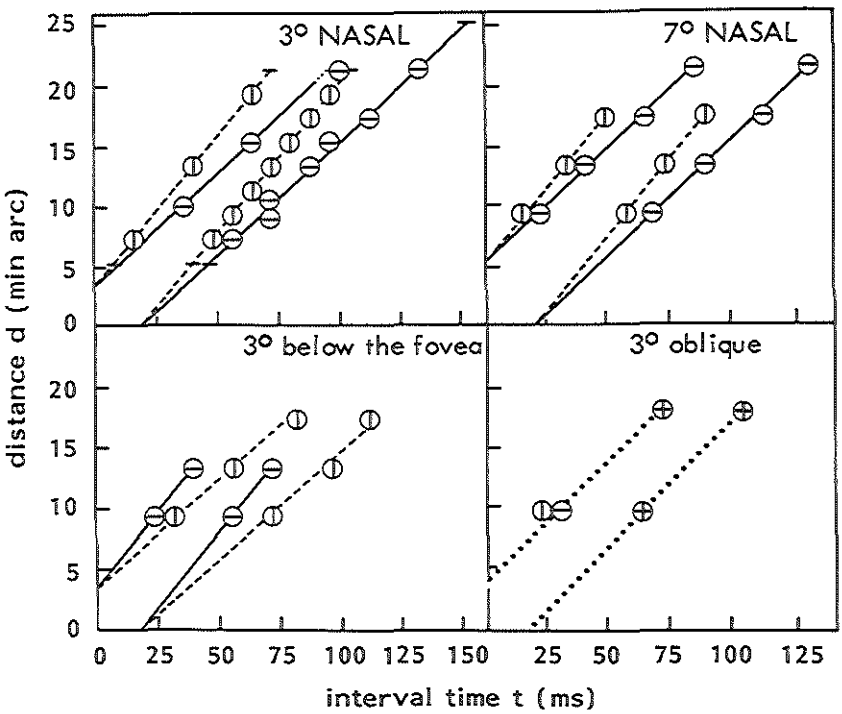

Fig. 3.10 Flash distance d vs the interval time t at which dips are found with vertically (circles with vertical bar) and horizontally (circles with horizontal bar) jumping flashes at 3 and 7 degrees nasal , 3 degrees below the fovea and 3 degrees eccentric on the 315 degree meridian. A circle with a cross in it means that at that point dips are found with both horizontally and vertically jumping flashes. The lines are extrapolated to the axes although no inhibition has been observed with short interval times and small distances. The data are taken from Table 3.1.

surements at 3 and 7 degrees nasal we can conclude that, in this range, the velocities are independent of the eccentricity. The measurements at 3 degrees nasal, 3 degrees below the fovea and at 3 degrees eccentric at the 315 degrees meridian indicate that there is circular symmetry around the fovea for the distribution of the propagation velocities over the flash direction. This distribution seems to be elliptical.

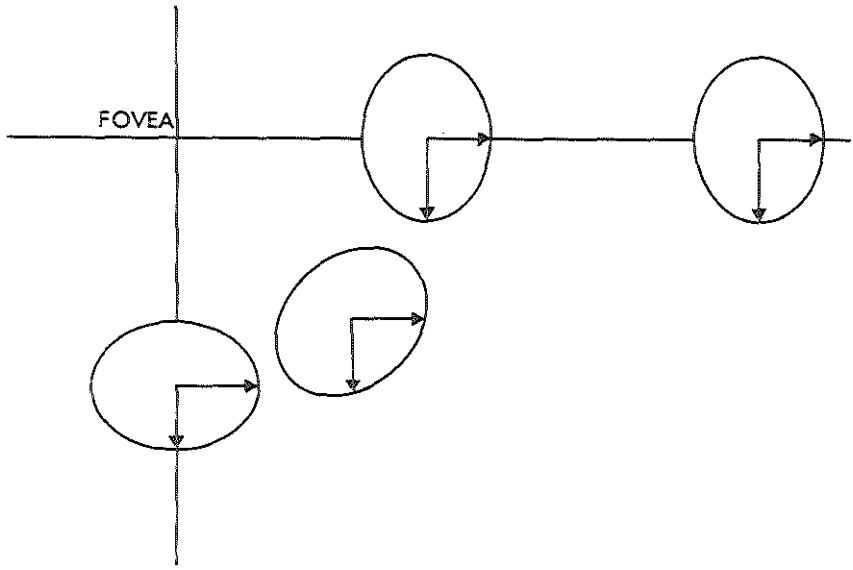

Fig. 3.11 A schematic representation of the propagation velocity distribution over the retina.

All measured velocities can be described with the same elliptical distribution. This means that the slope of the lines in Fig. 3.10 is independent of the eccentricity. But some of the lines through the data measured at 7 degrees seem to be shifted with respect to those determined at 3 degrees eccentric. This can be seen at the intersection of the extrapolated lines with the axes, which depend on the eccentricity but appear to be independent of the jumping flash direction. (Although the lines are extrapolated, we detected no inhibition at values of less than approximately 6 min arc).

Measurements corresponding to points on the time axis come down to use of jumping flashes with d = 0 ("temporal twin flashes"), while points on the position axis correspond to jumping flashes with t = 0 ("spatial twin flashes"). These measurements are the temporal or spatial summation measurements, results of which were given in Fig. 3.1 and 3.2.

The black arrows in Fig. 3.1 and 3.2 indicate the points of intersection of the extrapolated lines with the axes. They seem to coincide fairly well with the boundary of the total summation area, both for spatial and temporal summation. This suggests that the origin of the inhibition coincides with

the boundary of the total summation areas. The point of intersection with the time axis is independent of the eccentricity (for all places where measurements were performed at about 18 ms), while for 3 degrees eccentric the lines cut the position axis at 3.3 min arc and at 7 degrees at 5.2 min arc. The corresponding summation areas show qualitatively the same dependence on the eccentricity as reported by van den Brink (1957).

The open arrows depict another characteristic value obtained with the jumping flashes and represent the vertical or horizontal distance between the two straight lines (see e.g. Fig. 3.8), that is the spatial or temporal dip separation. The open arrows correspond reasonably well with the points halfway between total summation and non-summation. (We may call the area defined in this way the partial summation area.)

Thus, it seems that the propagating inhibition is very closely related to the static summation areas. The summation areas in their turn are closely related to the spatial and temporal point spread function of the visual system (which have no negative values for small stimuli of short duration). It would thus not be surprising if the inhibition behaviour were also dependent on these positive pulseresponses. One possibility is that the inhibition effects originate at the flanks of this response.

One way to obtain two effects is to differentiate the pulse response, as this would give a function with two extremes. A similar line of reasoning was given by Van den Brink and Keemink (1976) and Van der Wildt et al. (1976) in terms of gradient detection. They claimed that the luminance gradient (the derivative of the luminance distribution) is very important for perception. When edge detectors are used to describe the response to a stimulus, two effects are found too.

In view of the small size (1 min arc) and short duration (10 ms) of our flashes, the observed dips may well be assumed to originate on the flanks of the pulse response. In that case, firstly, effects (inhibition dips) smaller than the pulse response itself are possible. Secondly, assuming a Gaussian point spread function, the separation of the two dips should

be equal to half the width of the pulse response. Thirdly, as the spatial and temporal summation area depends on the dimensions of the pulse response, the two observed dips should also be related to these summation areas.

Thus, as the propagation velocity is by definition the ratio of the spatial and temporal dip separations, this velocity should also be equal to the ratio of the summation areas.

Table 3.2 gives the dimensions of the summation areas at two locations on the retina, measured in horizontal and vertical directions. It can be seen that the ratio of the spatial and temporal summation areas is in reasonable agreement with the measured propagation velocity for the inhibition effects.

	dip separation	partial summation area	total summation area	intercept on axis
3 degrees nasal horizontal				
place (min of arc)	6.8	7	3	3.3
time (ms)	37	32	16	18
ratio (degrees per second)	3.1	3.7	3.1	3.1
3 degrees nasal vertical				
place (min of arc)	8.0	7.5	3	3.3
time (ms)	32	32	16	18
ratio (degrees per second)	4.2	3.9	3.1	3.1
7 degrees nasal vertical				
place (min of arc)	10.0	8.5	5	5.2
time (ms)	40	33	20	20
ratio (degrees per second)	4.2	4.3	4.2	4.3

Table 3.2 Comparison of the results of the jumping flash experiments and the temporal and spatial summation measurements. The ratios of the spatial and temporal values are given (by definition, the ratio of the spatial and temporal dip separation equals the propagation velocity).

If the inhibition effect originates at the flanks of the pulse response, we may expect to get such effects at two points which are symmetrical with respect to the centre of the excitation area. The intercepts on the axes should thus be equal to half the flank separation and hence half the dip separation. These relations between summation areas, dip separations and intercepts can also be verified in Table 3.2.

All results described in this chapter were obtained with elementary flashes. It is interesting to determine whether the ideas suggested are generally valid or only relevant under the present conditions. Smith (1967) noted that the high frequency parts of the spatiotemporal contrast sensitivity function expressed as a function of the spatial or temporal frequency (as determined by Robson, 1966) can be interchanged using a ratio of 0.85 degrees per second between the temporal and spatial frequencies. This value is smaller than the propagation velocity we found.

However, when we divide the temporal and spatial frequency at which maximal sensitivity is found (Van der Wildt and Rijsdijk, 1979; Van der Wildt et al.,1976) a value of 10 cycles/second per 3 cycles/degree, which equals 3.3 degrees per second is obtained. This value is roughly the same as the propagation velocity of the inhibition found here. Thus there could be some relation between the transfer functions on the one hand and the propagating inhibition on the other hand. This relation between the inhibition effects found with elementary stimuli and the perception of stimuli of greater extent will therefore be described in the following chapters.

3.4 SUMMARY

Visual spatiotemporal inhibition effects were investigated with the aid of jumping flashes (pairs of point flashes, separated in time and space). Plots of the visibility of the jumping flashes against the interval time produced visibility curves in which two dips representing inhibition effects were observed. These inhibition effects were propagated away from the area of excitation at a constant velocity. Different velocities were

found along meridians and at right angles to them. There seems to be a link between these inhibition effects and the spatial and temporal summation areas. The ratio of the summation areas equals the propagation velocity of the inhibition.

4.

SOME FURTHER ASPECTS OF INHIBITION

Chapter 4 SOME FURTHER ASPECTS OF INHIBITION

4.1 INTRODUCTION

In the previous chapter all results were obtained with monocular presentation of monochromatic (red) stimuli. In this chapter measurements on the propagation of inhibition will be described for stimuli of different wavelength and for dichoptically presented stimuli. These measurements were performed in order to be able to locate the origin of the described inhibitory effects.

At present it is generally assumed that the output signal of the red, green and blue cones of the retina are combined into three visual channels (Hering's theory): two opponent colour channels (yellow-blue and red-green) and one achromatic black-white channel (Kaufman, 1974). These channels have already been found at the retinal level of the horizontal cells. There is evidence that they still exist at the level of the lateral geniculate body. Stimulation of a channel with monochromatic light results in an increase in the firing rate, whereas stimulation with the opponent colour gives a decrease in the firing rate. If inhibition were to act in the colour channels, special effects might be expected when the stimuli, or the stimuli and the background are of different wavelength. Therefore, pilot experiments were carried out with stimuli of different wavelengths.

4.2 RESULTS

The apparatus and the procedure were the same as in the previous chapter, except that LED's of different wavelengths were used. LED's with dominant wavelengths of 565 nm (green), 585nm (yellow), and 635 nm (red) were used for stimuli and background. The combinations used are listed in table 4.1.

Table 4.1. The colour of the stimuli used.

	exp 1	exp 2	exp 3	exp 4	exp 5
First flash	red	green	green	green	green
Second flash	red	red	green	green	red
Background	red	red	red	green	yellow
Fixation	red	green	green	green	green

Prior to each experiment the single flash visibilities were measured for a number of flash luminances and then the flashes were given the estimated increment threshold luminance (that luminance giving rise to a visibility of 50 %). The flash distance was 15.3 min arc in all experiments. The stimuli were presented at 3 degrees nasal and "jumped" towards the fovea. The results are given in Fig. 4.1. All further experiments were carried out with green stimuli, background and fixation.

One easy way of testing the dichoptic aspects of inhibition is presenting the jumping flashes to one eye and the background field to the other eye. In that case inhibition is found as can be seen in the lower part of Fig. 4.2. When no background luminance is presented, see Fig. 4.2 upper part, no inhibition can be detected.

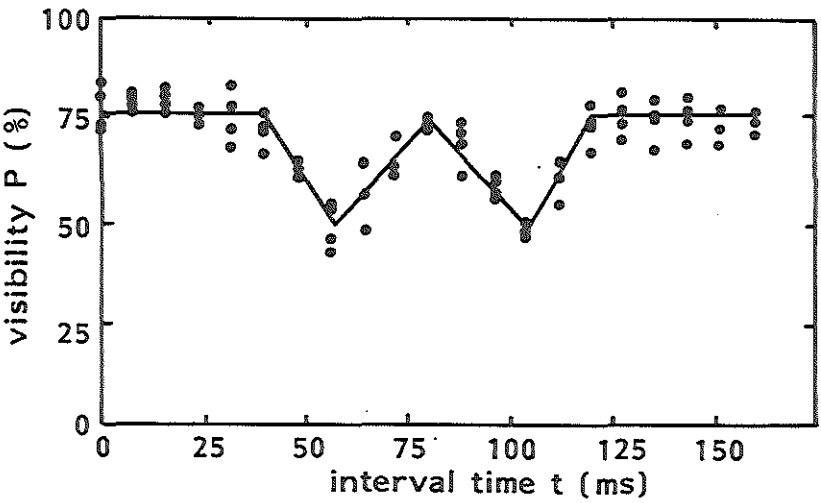

Fig. 4.1 The visibility P of a jumping flash as a function of the interval time t. Several combinations of colours were used (see Table 4.1) for the first and second flash and the background.

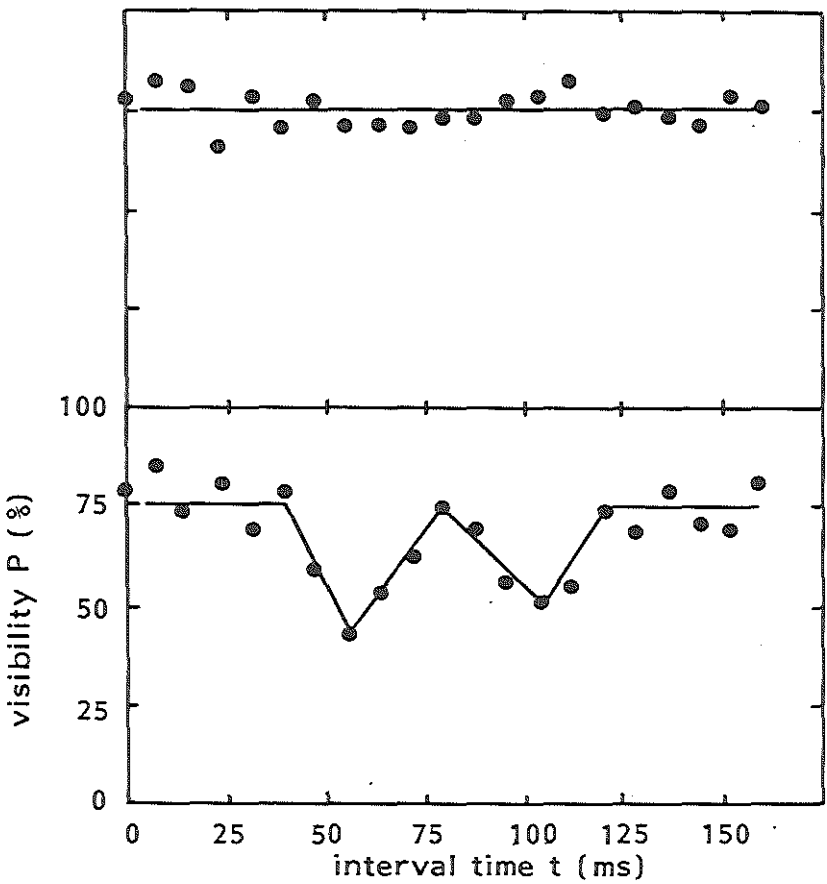

Fig. 4.2 The visibility P of a jumping flash as a function of the interval time t. The flashes were presented against a dark surround. For the lower curve, a background field was presented to the opposite eye.

For the dichoptic presentation of the jumping flashes the experimental set-up was changed. Two LED's were used for stimulus generation. They were placed at 4 m from the observer. A third LED was continuously on as a fixation marker. The stimulus was located 3 degrees to the right of the fixation spot; the first flash was the farthest away from it. Thus the flashes were presented 3 degrees nasal for the right eye and 3 degrees temporal for the left eye. It was possible to ensure that the right eye only saw the first flash and the left eye only the second flash by using

crossed polaroids in front of the LED's and in front of the eyes. A background field with a diameter of 3 degrees was provided for both eyes using a beamsplitter. The flash disparity was 15.3 min arc. The mean of four runs, each consisting of 25 presentations of each interval time is given in Fig. 4.3. The standard deviation of the means is about 5 %.

4.3 DISCUSSION

Hering's theory of colour perception suggests three different mechanisms by which information from the retina could be transferred to the more central processing areas in the brain. The results presented in this chapter indicate that the wavelength of the stimuli does not influence the inhibition behaviour, so it can be concluded that it does not take place in one of the colour channels. This is in agreement with conclusions that may be drawn from experiments with gratings which are not modulated in luminance but in colour (Van der Horst and Bouman, 1969; Noorlander, 1981). In that case, low pass transfer characteristics were found which indicate that there is no inhibitory action in the colour channels.

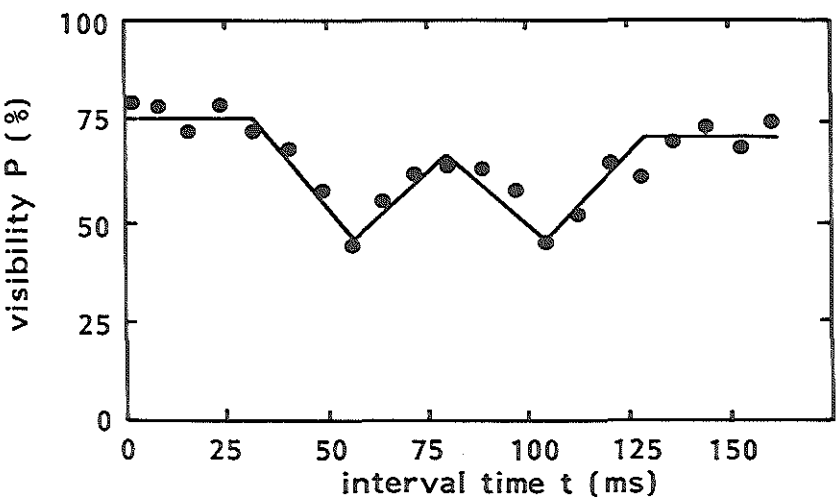

Fig. 4.3 The visibility P of a jumping flash as a function of the interval time t between the flashes. The first flash was presented to the right eye, the second flash to the left eye.

When both flashes are presented to the same eye and no background field is presented, there is no evidence of inhibition. This finding is discussed in Chapter 7 where is stated that inhibition is only generated when the stimuli are presented against a background luminance. The presentation of the background field to the opposite eye again leads to inhibition activity. If the generation of inhibition is purely determined by the activity being presented to one eye, it would not be expected that presenting the background field to the other eye would lead to inhibition.

Inhibition is also found when the first flash is presented to one eye and the second flash to the other eye. In that case the retina cannot possibly be the location where this inhibition takes place; the interaction can only take place at a site where the signals from both flashes have come together, which must at least be beyond the optical chiasm.

4.4 SUMMARY

The propagation of inhibition has been measured for elementary stimuli of different wavelengths. The wavelength was found to have no effect on the spatiotemporal properties of inhibition. With both dichoptic and monochoptic presentation of the stimuli, similar results were found, indicating that the interactions occur somewhere beyond the optical chiasm.

5.

THE INFLUENCE OF THE DIAMETER AND DURATION OF THE STIMULI ON THE PROPAGATION OF INHIBITION

Chapter 5 THE INFLUENCE OF THE DIAMETER AND THE DURATION OF THE STIMULI ON THE PROPAGATION OF INHIBITION

5.1 INTRODUCTION

The response of the human visual system to spatial gratings with exposure times longer than about 100 ms, can be described in terms of line spread functions (Wilson and Bergen, 1979) or point spread functions (Kretz et al, 1979) which are determined with stimuli of long duration. It is not yet possible to describe these spread functions (which all include inhibition) with the results measured with stimuli of short durations (order of magnitude 10 ms) as these do not include inhibition (see e.g. van den Brink, 1957).

The same applies to the temporal domain: Roufs (1972) showed relations between flicker and flash threshold for stimuli of 1 degree diameter, both involving inhibition. Measurements with small diameters (about 1 min arc) did not show inhibition (see e.g. Meijer et al., 1978).

So there seems to be a missing link between the results obtained with stimuli of short duration and small diameter on the one hand and the results obtained with either extended or prolonged stimuli on the other hand. An attempt to bridge the gap is described in Chapter 3 where it was shown that inhibition is propagated away from the area of excitation and that inhibition can be observed with the aid of elementary flashes (duration 10 ms, diameter 1 min arc) provided there is both a spatial separation and a temporal separation.

The relation between the transfer functions and the point spread functions is not completely clear. One of the assumptions implicit in the Fourier transformation is that each part of a stimulus gives rise to a similar excitation pattern and the final pattern is the sum of all parts (linearity). It has not been established that this holds for the inhibitory parts of the responses. This was tested and the results are described in this chapter: measurements on the propagating inhibition for flashes which last longer than 10 ms and are larger than 1 min arc will be given and discussed.

The results of Chapter 3 were all gathered with identical

flashes. From those results it could not be decided whether the first flash inhibits the second one, vice versa, or both. This can be done by using non-identical flashes to give asymmetry.

5.2 METHODS

With two identical flashes, it was found that the distribution of the inhibition propagation velocity over the various directions can be represented by an ellipse. To enhance the strength of the effect, an elliptical flash was used as a probe to measure the inhibition starting from a small flash placed in the centre of the ellipse. The method is the same as that used in Chapter 3, apart from the distinction which is made between the two stimuli by giving them different luminances, durations and/or diameters.

In the experiments described the ellipse was presented first and the small flash followed after an interval time t. Unless mentioned otherwise, an ellipse was used with axes of 14.5 and 11.0 min arc, a line thickness of 3 min arc and a duration of 10 ms. The duration and the diameter of the second flash and the duration and the size of the ellipse were varied in the experiments. When size or duration was changed, the luminance was adjusted to maintain the same visibility of the flash.

5.3 RESULTS

Measurements were done on the visibility (defined as the frequency of seeing) of a stimulus, consisting of a flashed ellipse followed, after an interval t, by a small flash presented in the centre of the ellipse. The visibility as a function of the interval time t is shown in Fig. 5.1. The parameter is either the luminance of the ellipse (Fig. 5.1a) or the luminance of the small flash (Fig. 5.1b). The single flash visibilities of the small flash and the ellipse are indicated respectively on the left and on the right of the figure. For Fig. 5.1a the luminance of the small flash is 0.4 times as high as its threshold value (50 % frequency of seeing) and the ellipse luminances are 0.9, 1.0, 1.2 and 1.3 times as high as the ellipse threshold. For the results in Fig. 5.1b the ellipse luminance was kept constant at 1.2 times its threshold and luminances of 0.4, 0.7, 1.0 and 1.4 relatively

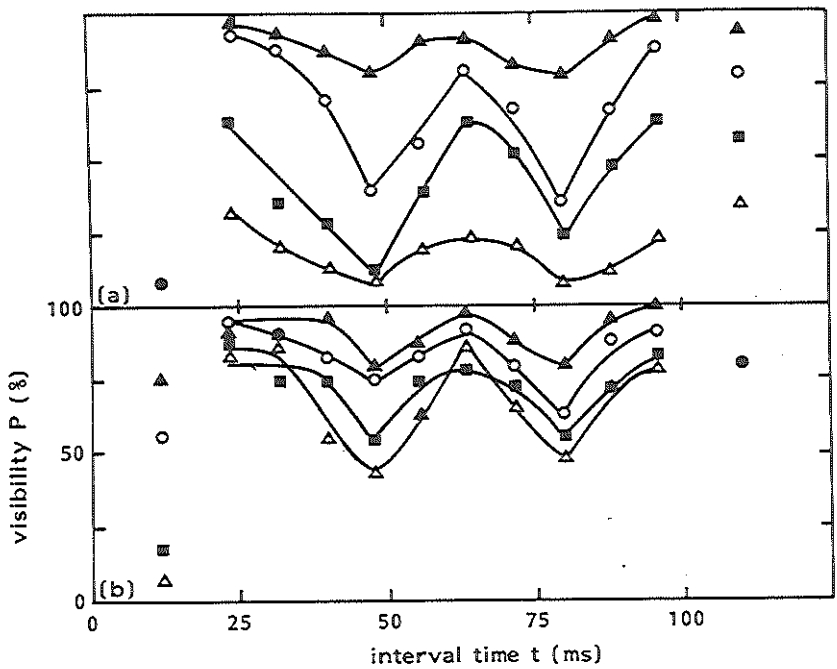

Fig. 5.1 The visibility of a stimulus consisting of an ellipse and a small flash as a function of the interval time t, for various ellipse (Fig. 5.1a) and flash (Fig. 5.1b) luminances. The ellipse is presented before the small flash which is presented in the centre of the ellipse. The single flash visibilities of the small flash and the ellipse are indicated by the symbols on the left and on the right, respectively. All measurements were performed at 3 degrees nasal (right eye), with the longer axis of the ellipse being vertical.

to the threshold for the small flash were used. The results given are the mean of 25 presentations. Lines were drawn by eye through the data points. Under all circumstances, dips are found at interval times of 48 and 80 ms, irrespective of ellipse or flash luminance.

To check the influence of the ellipse size, measurements were also performed with a similar but larger ellipse. The results are shown in Fig. 5.2. For both ellipse sizes, there are two dips in the visibility curves, but they do not occur at the same interval times. In Fig. 5.3 these dip times are plotted against the length of the vertical axis of the ellipse. It can be seen that with larger ellipse sizes the inhibition occurs at longer interval times. This indicates that there

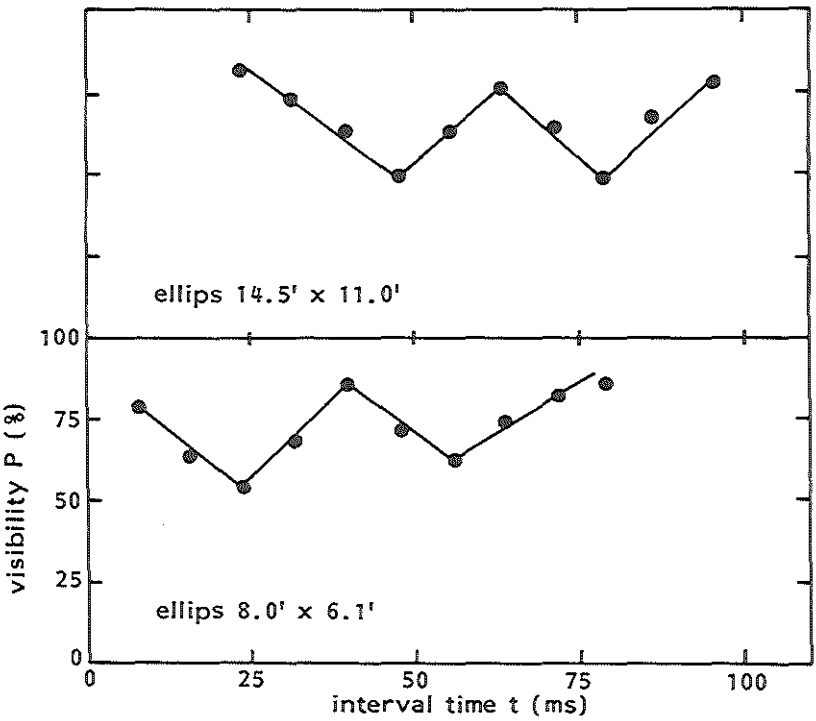

Fig. 5.2 The visibility of an ellipse-point stimulus as a function of the interval time for two ellipse sizes (longer axes respectively 14.5 and 8.0 min arc).

is propagation of the inhibition, as was found before with jumping flashes. For comparison the lines representing vertically propagating inhibition as determined with two elementary flashes at 3 degrees nasal (see Chapter 3) are drawn in this figure.

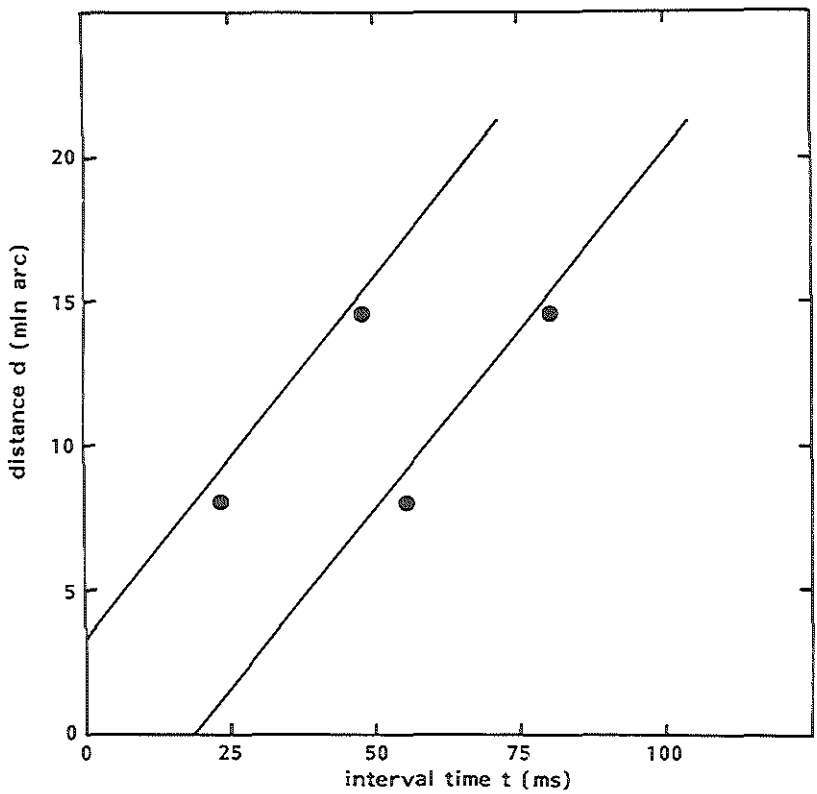

Fig. 5.3 The interval times at which dips are found in the Fig. 5.2 curves are plotted against the length of the vertical axis of the ellipse. The lines represent the vertically propagating inhibition detected with two elementary stimuli and are drawn from Fig. 3.10.

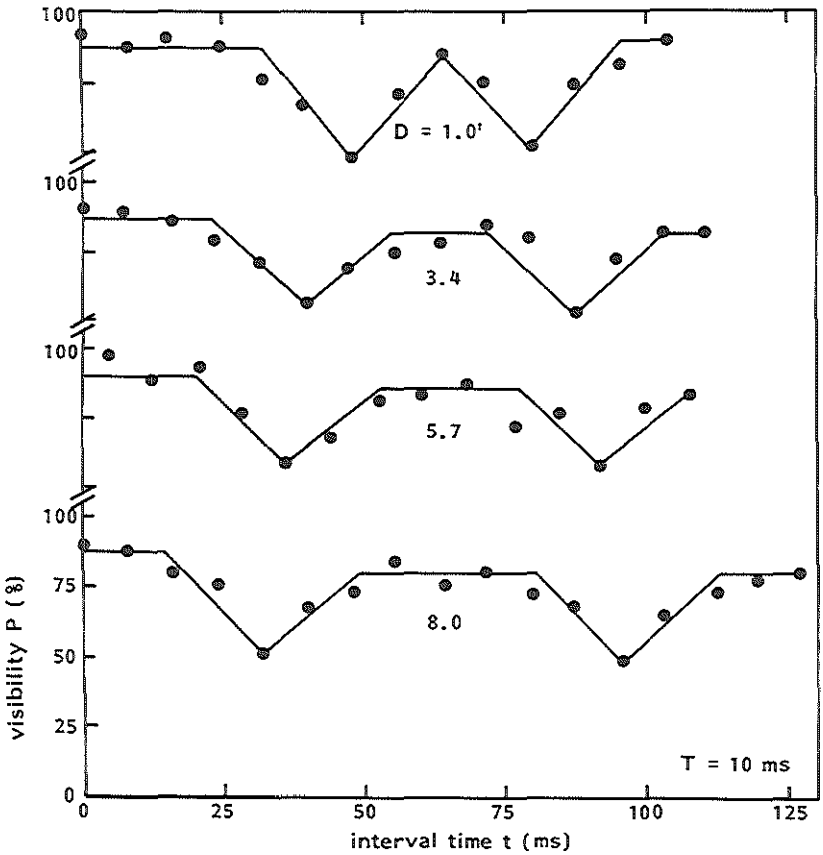

Fig. 5.5 The visibility of an ellipse-point stimulus as a function of the interval time with diameter D of the second flash of 1.0, 3.4, 5.7, and 8.0 min arc.

Varying the diameter of the second flash instead of its duration results in an outward shift of both dips, as shown in Fig. 5.5. The dip times are plotted against the diameter in Fig. 5.6(b).

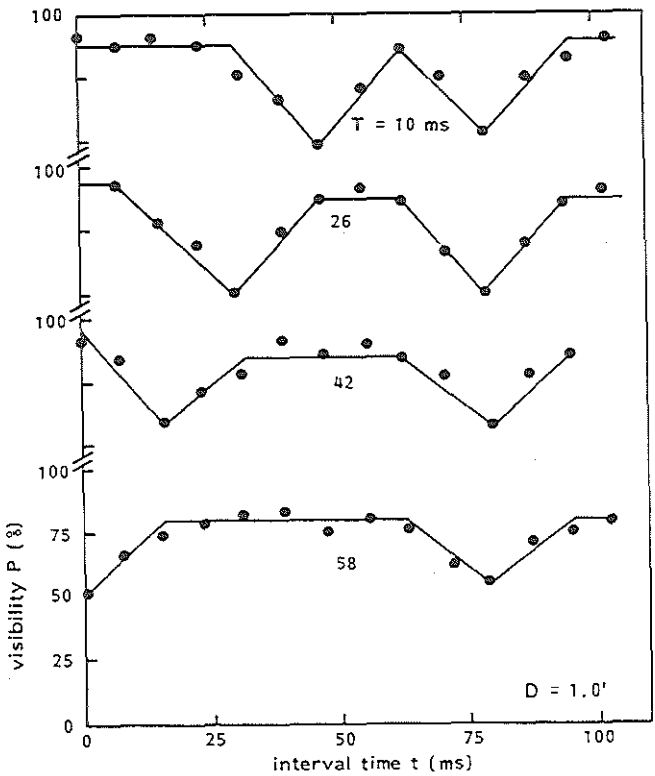

Fig. 5.4 The visibility of an ellipse-point stimulus as a function of the interval time, for durations of the second flash equal to 10, 26, 42 and 58 ms. The diameter of the second flash is 1 min arc.

To begin with, a duration of 10 ms was used for the small flash and for the ellipse. Fig. 5.4 shows the results that were obtained when the duration of the second flash was varied. An increase in its duration results in a shift of the first dip to a lower interval time, whereas the second dip occurs at the same time for all durations used. These dip times are plotted against the point duration in Fig. 5.6(a). An explanation of the lines is given later in this chapter in the discussion.

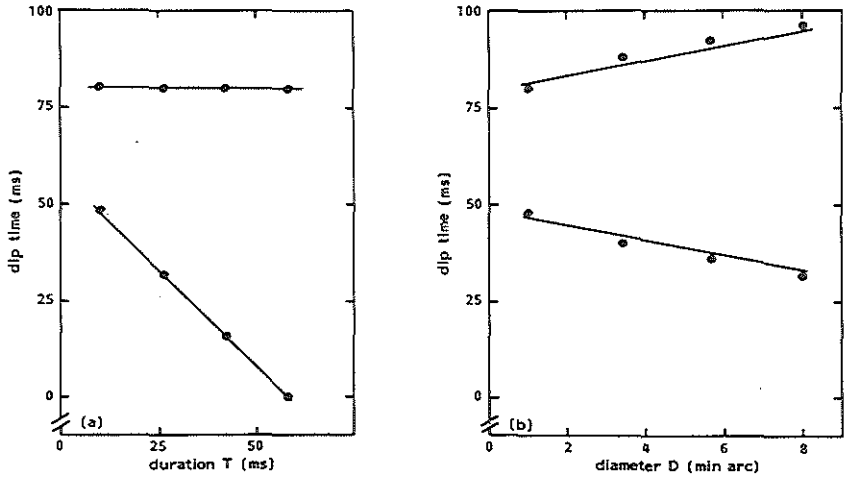

Fig. 5.6 The interval times at which dips are found (a) as a function of the duration T of the second flash (using data from Fig. 5.4) and (b) as a function of its diameter D (using data from Fig. 5.5). The slopes of the lines are calculated on a basis of the model, see discussion.

The experimental data given in Fig. 5.7 were obtained using several different combinations of diameter and duration for the second flash. The arrows point to the dip times that were predicted from the model.

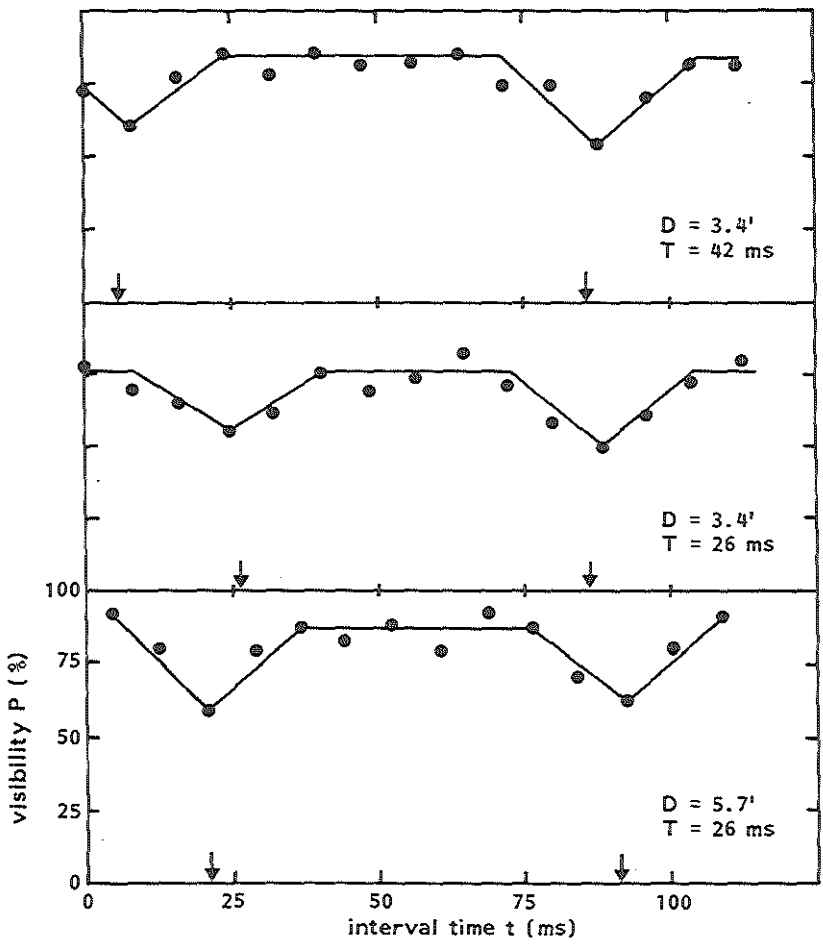

Fig. 5.7 Visibility of the ellipse-point stimulus as a fucntion of the interval time for flash diameter-duration combinations of 3.4 min arc 42 ms, 3.4 min arc 26 ms and 5.7 min arc 26 ms. The arrows indicate the interval times at which inhibition is expected on a basis of the model.

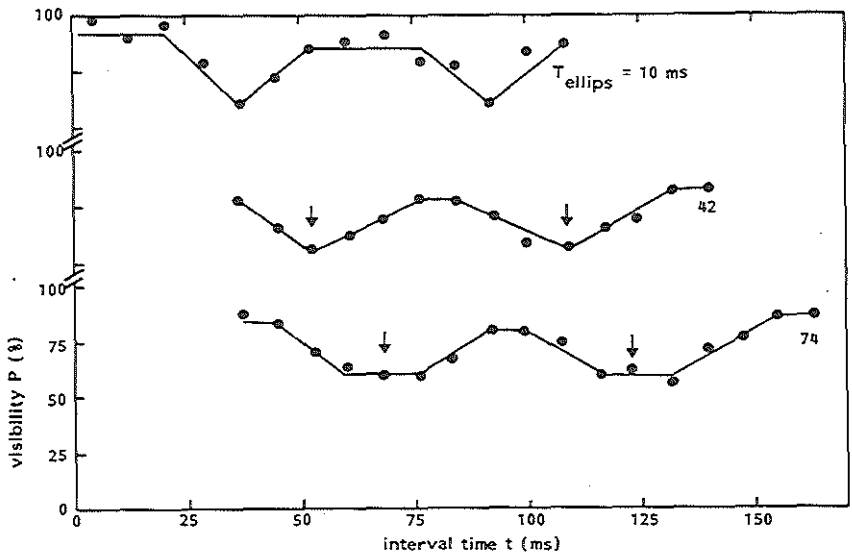

Fig. 5.8 Visibility measurements of an ellipse-point stimulus for ellipse durations of 10, 42 and 74 ms. The diameter of the second flash was 5.7 min arc and the duration was 10 ms. The arrows indicate the places where dips are expected according to the model.

The results shown in Fig. 5.8 were obtained by measuring with several different ellipse durations. An increase in ellipse duration results in a shift to a longer interval time for both dips and in a broadening of the dips. The expected dip times are again marked with arrows.

5.4 DISCUSSION

In this chapter measurements are given for the visibility of stimuli, somewhat more complex than elementary. In order to check if relations exist between the effects found with these stimuli and those found earlier using elementary stimuli, the results will be discussed with reference to the model described in the previous chapter.

The advantage of using an elliptical probe in which the ratio of the axes equals the ratio of the vertical and horizontal propagation velocity of inhibition, is that all the inhibition generated by the small flash arrives at the ellipse at the same time, resulting in a strong inhibition, even when the small flash has a small increment luminance.

In the first experiments, the ellipse flash was preceeding the small flash. If the inhibition originates at the ellipse, it would be expected that the small flash is inhibited under all inhibition circumstances, while the ellipse flash would not. In that case, the visibilities measured in a dip should at least be equal to the single ellipse visibility (when the small flash is completely inhibited). The results in Fig. 5.1a, however, show that the measured visibilities are far below the single ellipse visibility.

If on the other hand, we assume that the inhibition originates at the small flash and acts on the ellipse, no visibilities below the single small flash visibility can be expected although it is possible for the results to be lower than for the single ellipse visibility. The results in Fig. 5.1 (a and b) support this assumption.

Thus it can be concluded that the small flash (the second one) inhibits the ellipse (the first flash), which means backward inhibition. Therefore the inhibition described in this chapter and the propagating inhibition with jumping flashes described in Chapter 3 should be interpreted as backward inhibition. This does not mean, of course, that the inhibition acts before a flash is presented. It is more likely that the second flash shades the processing of the first flash which thereby becomes subthreshold.

In the further experiments, different single flash visibilities were chosen for the ellipse and for the second flash (about 80 and 40 % respectively) in order to ensure that influence of the ellipse on the visibility of the small flash (if any) did not lead to large variations in the visibility of the complex. So, only influences of the small flash on the visibility of the ellipse was measured. In addition, the difference between the visibility given by probability summation and the visibilty of the single small flash (the 'signal' for the detection of inhibition) is larger when the small flash and the ellipse have different single flash visibilities.

The propagating inhibition found with elementary jumping flashes is represented by the lines in Fig. 5.3. The fact that the experimental data obtained with an ellipse and a small flash almost coincides with these lines is a fairly reliable

indication that using an ellipse as a probe for the inhibition neither changes the velocity nor the separate dip times.

The results measured with various durations of the second flash (Fig. 5.4) show that one dip time is independent of the duration while the other dip time decreases with increasing durations. The model presented in an earlier chapters suggests that inhibition occurs on the flanks of the spatial and/or temporal pulse response. As the inhibition is backward, the flanks of the response to the second flash must be taken into account. The model predicts that the temporal separation of the two dips increases in direct proportion to the duration of the second flash.

To detect inhibition of the probe (i.e. the ellipse) there must be a certain time interval between the ellipse and a flank of the inhibition generating flash (the second flash). As the interval time is defined as the onset asynchrony of the ellipse and the small flash, the duration of the small flash has no influence on the interval time at which inhibition from the "on" flank is to be expected. However, to obtain a constant time between the ellipse and the "off" flank of the second flash, the onset of the second flash must be earlier when its duration increases. Thus, inhibition of the "off" flank is to be detected at smaller interval times when longer durations are used.

In Fig. 5.6(a) the dip times found are plotted as a function of the duration. It can indeed be seen that the inhibition of the onset flank is constant (horizontal line) and the inhibition of the "off" flank decreases in direct proportion to T (line with slope -1).

The effect of increasing the diameter of the second flash (Fig. 5.5) can be predicted in a similar way. The spatial flanks of the flash shift symmetrically as the diameter increases. This implies that for one flank the distance to the probe decreases, while for the opposite flank the distance to the same point of the probe increases.

As a result of the propagation of the inhibition (see Fig. 5.3) a change in distance will result in different dip times;

the dip time shift equals the distance shift divided by the propagation velocity. Thus, as the distance shift equals half the diameter changes, the model predicts two lines for the dip times as a function of the diameter, with slopes of + and - v/2, where v stands for the propagation velocity. Lines with these slopes are drawn in Fig. 5.6(b) and coincide fairly well with the data points.

Both the effects of increasing the duration or of increasing the diameter can be described by the flank model. However, when describing duration effects, we must consider the temporal flanks, whereas for the diameter effects we must consider the spatial flanks. The fact that both effects can be described successfully, suggests that the displacement of the inhibition dips is the cumulative effect of both duration increase and diameter enlargement. If this is correct, the effect of increasing both duration and diameter should be the sum of both effects taken separately.

One can examine this hypothesis by comparing the values given in Fig. 5.4, Fig. 5.5 and Fig. 5.7; the first dip in the measurements with a 3.4 min arc 42 ms second flash (see Fig. 5.7) should be displaced over 32 ms to lower interval times, with respect to the first dip measured with a 1.0 min arc 10 ms second flash, owing to a duration increase (see Fig. 5.6a). The diameter enlargement should result in a shift of 6 ms to lower interval times (see Fig. 5.6b). Thus a total shift of 38 ms can be expected which leads to a dip time of 10 ms. For the second dip, the duration has no influence (upper curve of Fig. 5.6a) while the diameter enlargement results in a shift of 6 ms to higher interval times, so a dip time of 80 + 6 = 86 ms can be expected.

The expected dip times for the other diameter duration combinations are determined in the same way and are indicated by arrows in Fig. 5.7. It can be seen that the measured dip times are in agreement with the expected inhibition interval times within the experimental error.

If we assume that the inhibition acts on the maximum of the response to the inhibited flash (the ellipse) it is possible to understand the results with various ellipse durations (Fig. 5.8). This maximum is to be found near the middle of the temporal distribution and, as the interval time is defined

as the stimulus onset asynchrony, an increase in the duration of the ellipse flash should result in a increase in the dip time by half that amount. The expected dip times are indicated by arrows in Fig. 5.8. The measured results are in reasonable agreement with this prediction.

The fact that the dips for longer ellipse flash durations appear to be smoothed out is caused by a reduction in the resolving power, which is due to measuring with a coarse probe.

It can be concluded that a model describing inhibition as phenomena arising on the flanks of the pulse response and acting backwards on the response to the probe, gives a correct description of the results, at least up to stimulus durations of 58 ms, diameters of 8 min arc and probe durations of 74 ms.

An effect which could be related to the propagating inhibition is metacontrast: i.e. above-threshold masking for spatially and temporally non-overlapping stimuli. It has been found (Alpern, 1953; Weisstein, 1972; Growney and Weisstein, 1972) that maximal masking is obtained about 70 ms before the presentation of a maskstimulus, which indicates backward suppression, while we found backward inhibition for interval times ranging from 20 to 120 ms.

For the propagating inhibition at threshold level a model has been designed involving inhibition arising at the flanks of the response. Metacontrast is sometimes described as the result of an interaction between the edges of the test and the mask stimulus (Lefton, 1973; Shapley and Tolhurst, 1973), which means that flanks also seem to be important. As large adjacent stimuli are normaly used for the metacontrast measurements no specific propagation velocity can be expected to appear.

It appears that there might be a relation between propagating inhibition and metacontrast. The differences in stimulation, however, are too large (diameter 1 min arc or 1 degree, adjacent or separated, at or above threshold, etc.) to allow comparison of the results in greater detail. To do this, the propagating inhibition should be studied for stimuli which are more similar to the ones used in metacontrast experiments. In Chapter 8 and 9 we will return to this.

5.5 SUMMARY

The propagation of inhibition is studied for flashes of longer duration and/or larger diameter. A model in which inhibition arises on the flanks of the response to the second flash and acts on the first flash, gives a good description of the results. When non-identical flashes are used, the inhibition proves to be backwards.

6.

FLASH DIMENSIONS AND LUMINANCE

Chapter 6 FLASH DIMENSIONS AND LUMINANCE.

6.1 INTRODUCTION

In Chapter 5 measurements on inhibition, which was generated by a flash of various durations and diameters, were described. However, these experiments actually involved three parameters, not two: in order to maintain a constant visibility level for the flash, the luminance had to be adjusted when another duration or diameter was used. In this chapter the duration and diameter are varied independently of the increment luminance.

6.2 RESULTS

The visibility of a stimulus consisting of an ellipse followed after a delay t by a flash presented at the centre of the ellipse, is given in Fig. 6.1 as a function of the delay time t for a flash with a diameter of 5.7 min arc and a duration ranging from 10 to 138 ms. Lines were drawn by eye through the experimental points. The curves thus obtained were found to comprise horizontal parts with a visibility level of about 90 %. This is the visibility which can be expected on the basis of probability summation (in these areas, the flashes do not interact) and dips (the fall and rise times of which are taken as constant at 12 ms) where inhibition may be assumed to be operative. The single flash visibilities were 80 and 40 %.

It was found further that the delay time at which the dips are found (the "dip time") depends on the duration of the second flash. At short durations, an increase in the duration results in a lowering of the first dip time while the second dip time remains constant. When, however, durations longer then 26 ms are used each increase in the duration results in both dips moving close together, until only one dip remains at a delay time of 64 ms (for durations longer then about 122 ms). Extensive measurements with a flash duration of 122 ms and interval times ranging from -200 to +200 ms showed that no other dips could be detected with this stimulus.

The convergence of the dips is not in agreement with the model proposed in Chapter 5. Based on that model it would

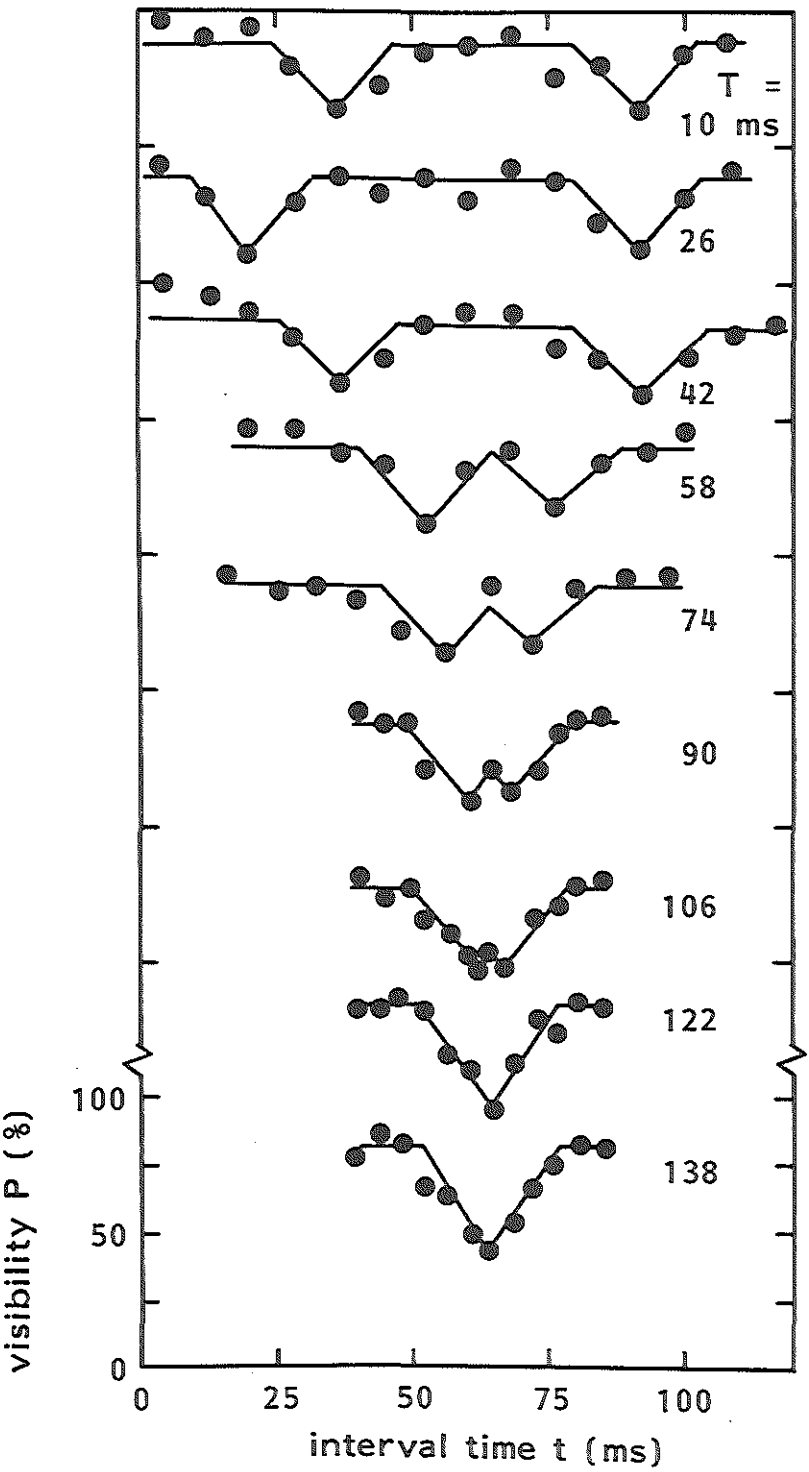
T =
10 ms
26
42
58
74
90
106
122
138
visibility P (%)
100
50
0
0
25
50
75
100
interval time t (ms)

Fig. 6.1 The visibility of a stimulus consisting of an elliptical flash followed by a small flash as a function of the delay time t, with the flash duration T as parameter. The small flash is presented at the centre of the ellipse. Each curve except the lowest is displaced upwards over a distance equivalent to 50 % detection probability with respect to the curve below it. Straight lines are drawn by eye through the experimental points. In each case the probabilities plotted are the averages of the results for 25 flashes.

DIAMETER (MIN OF ARC)

DURATION (MS)	1.0	3.4	5.7	8.0	10.3
10	48 80 (0.90)	40 88 (0.078)	36 92 (0.023)	32 96 (0.011)	48 80 (0.0076)
26	32 80 (0.34)	24 88 (0.033)	20 92 (0.013)	48 76 (0.0057)	56 72 (0.0036)
42	16 80 (0.20)	8 88 (0.018)	36 92 (0.0066)	56 72 (0.0030)	60 68 (0.0020)
58	0 80 (0.15)	16 88 (0.015)	52 76 (0.0045)	60 68 (0.0027)	62 66 (0.0016)
74	24 80 (0.13)	44 84 (0.0075)	56 72 (0.0036)	62 66 (0.0019)	64 (0.0011)

Table 6.1 The dip times found with various flash durations and diameters. The data are based on experiments similar to those the results of which are given in Fig. 6.1. The flash luminance relative to the increment threshold luminance of a 10 ms, 1 min arc flash is given between brackets for each combination of flash duration and flash diameter. The luminances were chosen so that the single flash visibility was about 40 % in all cases.

be expected that increasing either the diameter or the duration, or both, would result in the inhibition dips moving further apart. Measurements were therefore also performed with other flash diameters and durations. The luminance of the ellipse was kept the same (resulting in a single flash visibility for the ellipse of about 80 %), while the flash luminance was adjusted when the duration or diameter was changed to maintain a single flash visibility of about 40 %. The dip times found with flash durations ranging from 10 to 74 ms and diameters ranging from 1.0 to 10.3 min arc are given in Table 6.1. The luminance of the flash is also given, relative to the threshold of a 10 ms, 1 min arc point flash.

All the measurements show the same trend as the results presented in Fig. 6.1. The dip times found with the various durations and diameters of the second flash are plotted in Fig. 6.2 as a function of the duration with the diameter

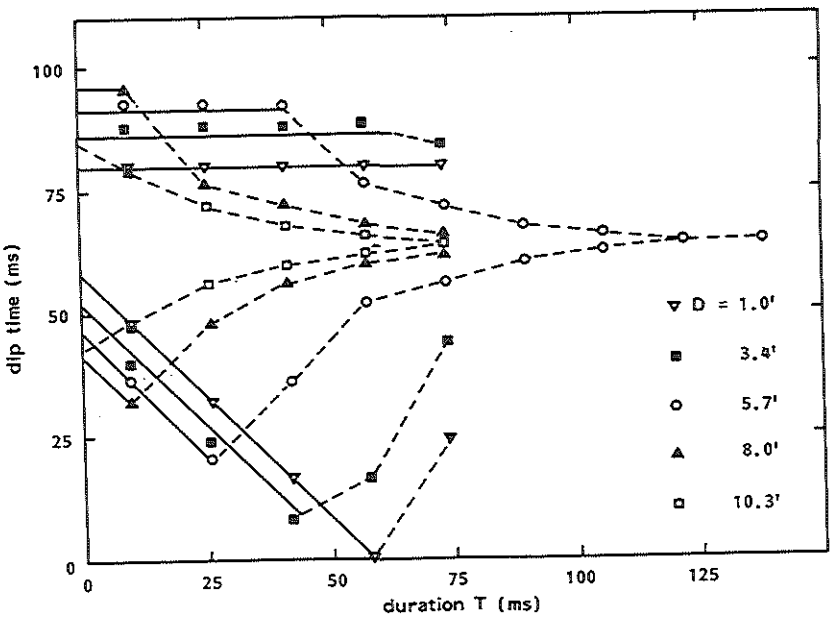

Fig. 6.2 The dip times as a function of the flash duration, with the flash diameter as parameter. The data are taken from Fig. 6.1 and Table 6.1. The straight, solid lines are calculated on a basis of the model; see text.

as parameter. It will be seen that for short durations the data agree well with straight lines calculated on the basis of the model presented in Chapter 7 (the mathematics are given in the last part of Chapter 9). At longer durations, however, the two dips approach each other until only one dip remains at a delay time of 64 ms, which seems to be independent of the diameter used. If the data are plotted as a function of the diameter with the duration as parameter, similar conclusions may be drawn: the data lie on straight lines when the diameters are small, but not when they are larger.

Measurements were also performed with a second flash of duration 122 ms and diameter 5.7 min arc (dimensions which result in one dip, see Fig. 6.1), presented within a smaller ellipse (axes 8.0 and 6.1 min arc). Figure 6.3 shows that under these conditions too, a sinlge dip is found at a delay time of 40 ms. The arrow in Fig. 6.3 indicates the interval time at which the inhibition would be expected if the propagation velocity was the same as determined with two elementary flashes (see discussion).

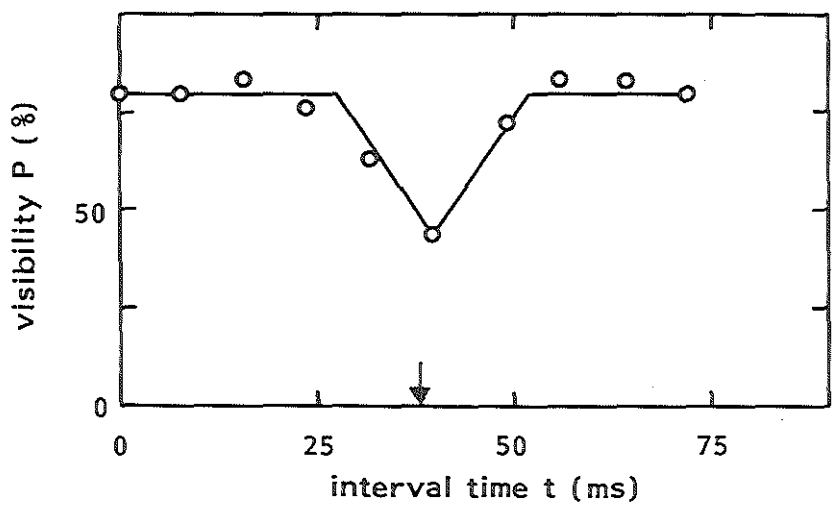

Fig. 6.3 The visibility of a stimulus consisting of an elliptical flash with axes of 8.0 min arc and 6.1 min arc followed after a delay time t by a 122 ms, 5.7 min arc flash, as a function of the delay time t. If the propagation velocity for this case is equal to that determined for elementary stimuli, a dip will be expected at the delay time indicated by the arrow.

As can be seen in Fig. 6.4, measurements with a 122 ms, 5.7 min arc flash, which gives rise to only one dip, show that the increment luminance of the second flash has no influences on the dip time. For the three curves in this figure the flash had half, once, and twice the luminance of the 40 % visibility flash (the corresponding single flash visibilities are shown by symbols at the left in the figure).

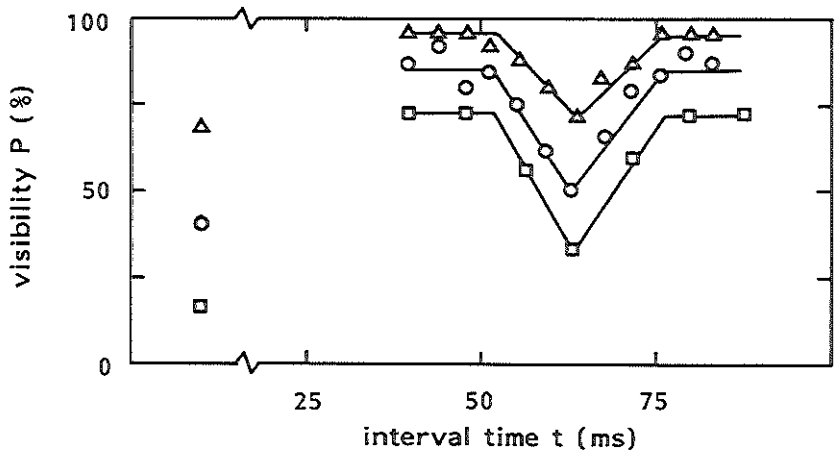

Fig. 6.4 Visibility curves for a 122 ms, 5.7 min arc flash in combination with the ellipse used for Fig. 6.1, with the flash luminance as parameter. The single flash visibilities are indicated by the symbols on the left of the figure.

Similar experiments with a 5.7 min arc flash of 58 ms duration gave quite different results, as can be seen in Fig. 6.5. Measurements with luminances of 0.6, 0.9, 1.1, and 1.4 times the 50 % visibility luminance show that for this stimulus the dip times are strongly influenced by the luminance, even though the flash duration and diameter are kept constant. The separate curves in the figure are shifted over 50 %.

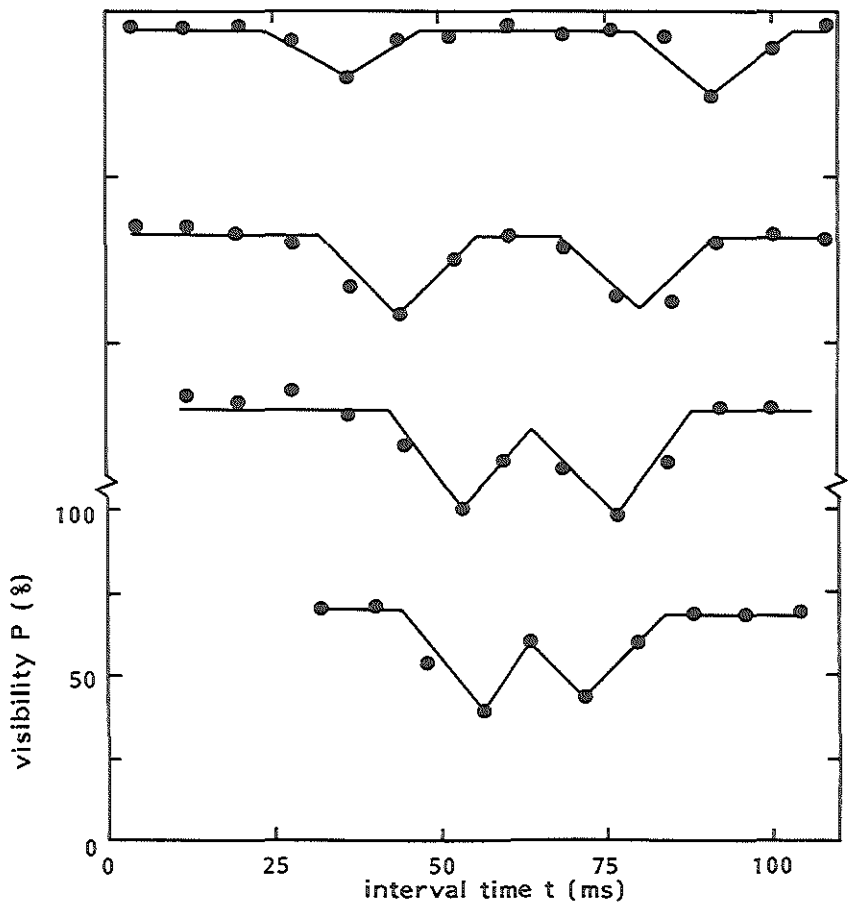

Fig. 6.5 Visibility curves for a 58 ms, 5.7 min arc flash presented in the ellipse used for Fig. 6.1. Reading from top to bottom the flash luminance is successively 1.4, 1.1, 0.9, and 0.6 times the increment threshold value.

The dip times found as a function of luminance using a constant flash diameter and duration (taken from Fig. 6.4 and Fig. 6.5) are plotted as triangles in Fig. 6.6. The luminance is expressed relative to the increment threshold luminance of a 10 ms, 1 min arc point flash. The results found with variations in both the luminance and the flash diameter and/or duration which did not lie on the straight lines in Fig. 6.2. are also plotted, as dots, in Fig. 6.6 (these data are taken from Table 6.1 and Fig. 6.1). The flash diameter and duration ranges covered by these dots are 3.4 min arc - 10.3 min arc and 10 - 74 ms. The oblique lines in this figure are fitted to the experimental points by a least-square method.

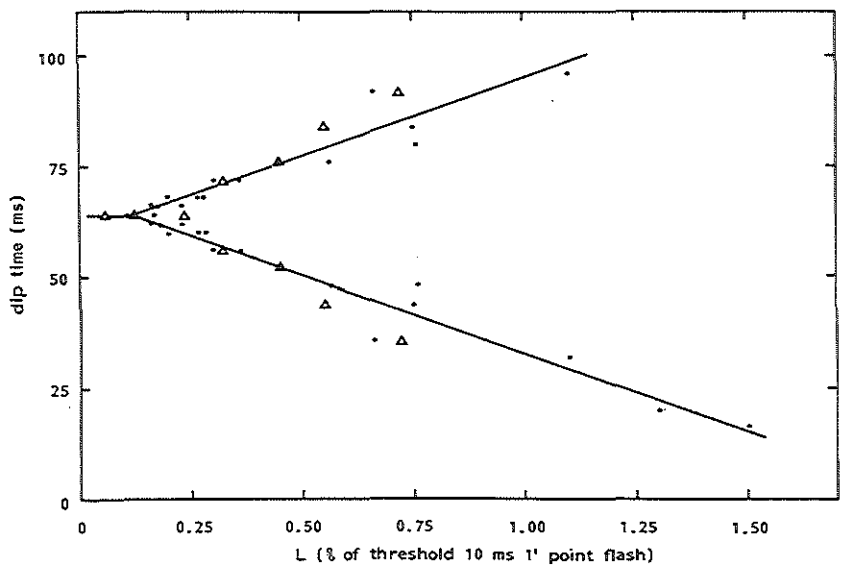

Fig. 6.6 The dip times as a function of the increment luminance relative to the threshold of a 10 ms, 1 min arc point flash. The triangles represent dip times determined by varying the luminance at constant duration and diameter (using data taken from Figs. 6.5 and 6.4). The dots represent results measured with various flash diameters and durations; these are the data which are not fitted by the straight solid lines in Fig. 6.2. The oblique lines give the best fit curve as determined by a least-squares procedure.

For reasons to be described in the discussion, measurements were also performed with a second flash of diameter 5.7 min arc and durations of 26, 58, and 90 ms, without changing the luminance when the duration was varied. The three curves obtained in this way, shifted vertically to facilitate comparison, are drawn in Fig. 6.7. They show that under these conditions, the dip times are not influenced by the duration of the flash. The arrows indicate the expected dip times, as derived in the discussion.

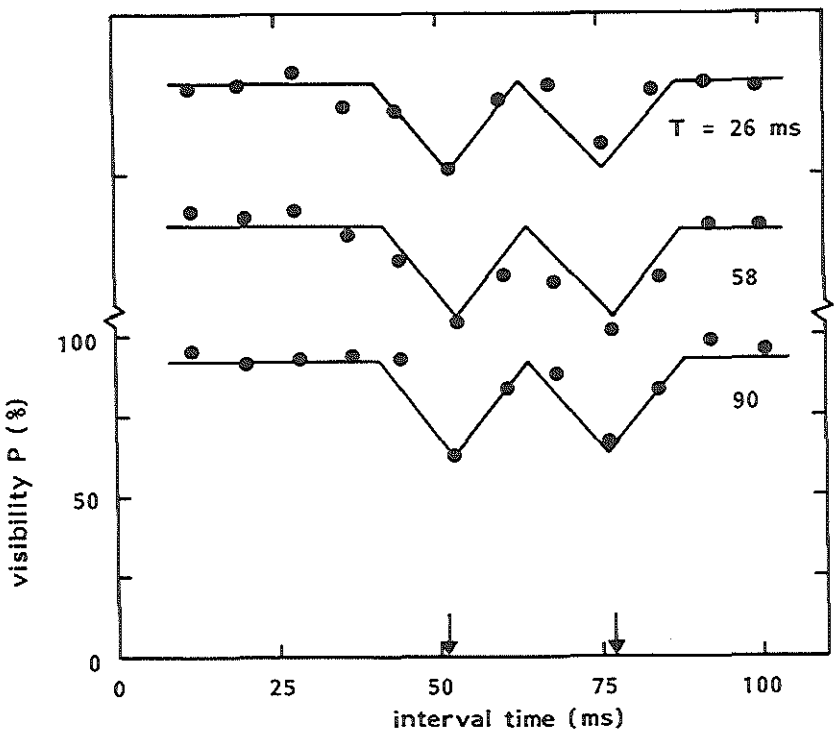

Fig. 6.7 Visibility curves determined with a 5.7 min arc flash of three durations. The flash luminance is the same for all three curves. An identical curve is drawn through each set of points. The arrows mark the dip times expected from interpolation of Fig. 6.6.

6.3 DISCUSSION

In this chapter the results are described using stimuli for which the diameter and duration are increased further than was done in the previous chapter. The objective was to increase the understanding of inhibition for complex stimuli, by slowly increasing the complexity of the stimuli. It will appear that the effects of luminance overrule those of diameter or duration changes, in which we are primary interested.

The straight lines in the left-hand part of Fig. 6.2 were constructed on the basis of the model described in the previous chapter. In the region where these lines fit the data, it can be concluded that the model is valid. In this section attention will be concentrated specifically on the region where the straight lines do not fit the data.

The results in Fig. 6.2 indicate that when long flash durations are used, an increase in the duration no longer results in an increase in the dip separation, but on the contrary in a decrease. This deviation occurs at smaller durations when larger diameters are used. The two dips converge to a single dip at a delay time of 64 ms; this value appears to be independent of both the duration and the diameter of the second flash.

The main conclusion drawn from previous studies was that inhibition is propagated. As the results with long flash durations or large flash diameters do not fit the model, it is interesting to test whether some form of propagation can still be detected. To do this a flash which gives only one dip was used together with a smaller ellipse as probe flash. It was found (see Fig. 6.3) that a single dip also occurs under these conditions, but at a different time. If the propagation velocity of the single dip is the same as determined with the elementary flashes, it may be expected that the shifts in dip time will equal the change in the long axis of the ellipse divided by the vertical propagation velocity (or the changes of the short axis of the ellipse divided by the horizontal propagation velocity). The expected dip time calculated on this basis is indicated by an arrow in Fig. 6.3. There is close agreement between theory and experiment. It may thus be concluded that under these circumstances the inhibition is propagated with the same velocity as that

determined with elementary flashes.

It has been found that the increment luminance of elementary point flashes has no influence on the dip time. The single flash visibility was varied in these experiments, so the visibility in a dip and the probability summation visibility level also changed. Measurements with a flash giving rise to only one dip showed the same effect: the luminance only affects the visibility levels (see Fig. 6.4). When, however, similar measurements were performed with a flash of 5.7 min arc diameter and 58 ms duration, the luminance affected not only the visibility level but also the dip times (see Fig. 6.5). It will be seen that at high luminances the dip separation is larger then at low ones. It can be seen from Fig. 6.2. that the model does not fit the results found with this combination of flash diameter and duration, while moreover the dips have not yet converged to a single dip. Thus in this region the dip time depends on the luminance.

Because the single flash visibility was kept constant in the experiments with various flash diameters and durations, the luminances used vary widely; see Table 6.1. It has been shown that the luminance can influence the dip times. For example, with long duration or when large diameters are used, the luminance has to be kept low to give 40 % visibility and the dips are found to approach one another; see Fig. 6.2.

Moreover, when the luminance is lowered without changing the diameter or duration of the second flash, the dips also converge; see Fig. 6.5. It might thus be possible that the departure from linearity seen in Fig. 6.2 is entirely due to changes in the luminance, and that the actual diameter and duration have no influence here.

To test this, all dip times connected by broken lines in Fig. 6.2 (i.e. the data which the model does not fit) were plotted as a function of the luminance, as shown in Fig. 6.6. It can be seen that all these points lie on two lines, despite the wide range of flash duration and diameter involved. The dip times caused by luminance variation without any change in the dimension of the flash (see Fig. 6.5) are plotted as triangles. The agreement between the triangles and the other points indicates that the dimensions of the second flash do not have much influence on the dip times in this range.

If this is so, duration should not have any effect on the dip time, when the luminance is kept constant. This should enable the dip times to be predicted by interpolation in Fig. 6.6. The data of Fig. 6.7 show that, in this case the dip times agree well with the predictions (marked by arrows).

It may thus be concluded that the dip times for flashes of long duration and large diameter are determined by the luminance instead of by the flash dimensions. The boundary between the region where the model is valid and that where the luminance predominates seems to be at a luminance of 1.5 % of the increment threshold luminance of a 10 ms, 1 min arc point flash; all results determined at lower luminances, plotted in Fig. 6.6 are satisfactorily fitted by the straight lines. The results measured at higher increment luminances can all be predicted by the model. A plot of these results against the luminance gives a broad band of points in which no particular trend can be found.

Even though it is clear that at low luminances the actual dimensions of the flashes do not determine the dip times, it is interesting to speculate that the dip times (and in particular the distance between the two dips) may still be correlated with the subjective dimensions of the flash. This agrees with the finding that the apparent duration of a flash at very low luminances is much shorter than the actual duration. In these terms, the straight lines in Fig. 6.6 would simply mean that lowering the luminance results in a decrease in the dimensions as seen by the observer. If this is so, the single dip found at very low luminances should be bound to that part of the stimulus which is seen. The fact that neither the flash duration nor the flash diameter influences the delay time at which this single dip is found indicates that this part of the stimulus is located at the spatial centre of the flash near the temporal onset.

This agrees with the finding that the temporal response for flashes with a duration of about 50 ms shows overshoot, which indicates self-inhibition. Twin flashes with diameters of up to about 10 min arc do not show self-inhibition (Meijer et al., 1978), indicating the absence of spatial self-inhibition. The maximum response should thus be near the temporal onset, at the spatial centre.

It would thus seem that even though the dip times at low luminances are not correlated with the physical duration and diameter of the flash, they may still be correlated with the perceived dimensions of the stimulus.

6.4 SUMMARY

The propagation of inhibition is studied for stimuli of longer durations and larger diameters then the ones used in the previous chapters. It is shown that for those extended stimuli the interval times at which inhibition is detected is mainly determined by the increment luminance of the stimuli rather than by the duration and the diameter.

7.

THE INFLUENCE OF THE BACKGROUND ON THE GENERATION OF INHIBITION

Chapter 7 THE INFLUENCE OF THE BACKGROUND ON THE GENERATION OF INHIBITION

7.1 INTRODUCTION

The behaviour of the human visual system strongly depends on the luminance level. Amongst the many effects which illustrate this, are the temporal and the spatial contrast transfer functions of the system. At moderate and high luminances, the visual system generally acts like a band-pass filter (spatially as well as temporally) for stimuli of long duration and large diameter, while at low luminances low-pass filter characteristics are found (De Lange, 1958; Kelly, 1971; Roufs, 1972; Van Nes, 1967). Inverse Fourier transformation of the contrast transfer functions shows that at high luminances the pulse response consists of a positive (excitatory) and a negative (inhibitory) region. The transforms of the results at low luminances, however, are completely positive, indicating the absence of inhibition. Measurement of the point spread function as a function of the background luminance yields similar results (Krauskopf, 1962; see also Westheimer, 1967). The conditions determining whether or not inhibition arises have not yet been completely elucidated.

Although it has not yet been fully established that the inhibitory effects which are described in the previous chapters are based on the same mechanisms as those found with gratings or flickering light, it is interesting to apply the elementary jumping flash technique to the study of how inhibition effects depend on the background luminance.

In the present chapter, the results of elementary flash experiments using several background luminances and patterns will be described. The main objective is to find out what demands have to be met by the background luminance pattern in order to permit the generation of propagating inhibition.

The stimulus consists of two small flashes (diameter 3 min arc, duration 10 ms, wavelength 635 nm). The horizontal distance between the centres of the flashes is 15.3 min arc. The flashes are presented near the centre of a stationary background field of diameter 3.7 degrees. The visibility of this flash complex is measured as a function of the interval

time between the two flashes. In the first series of experiments, the uniform background luminance was the parameter. In the second series, part of the background field was covered by a dark vertical bar, the width and position of which relative to the position of the flashes were taken as parameters. In the final series, the background field was replaced by a stationary thin line of light, whose position with respect to the flashes was varied. In all experiments, the flashes were presented to the right eye at 3 degrees nasal.

7.2 RESULTS

Measurements were performed with jumping flashes presented against a homogeneous background. The background luminance was 2.3 log units above threshold (which is about 0.01 cd/m^2) and the distance between the two flashes was 15.3 min arc. Every result given is the mean of three determinations each with 25 presentations. The standard deviation of the mean is about 5 % . Since each flash on its own has a visibility of about 50 % probability summation would lead us to expect a visibilty of about 75 % for the jumping flash, as the distance between the flashes exceeds the summation area. In Fig. 7.1 the visibility P of a jumping flash is given as a function of the interval time t. The results indeed show a 75 % visibility over part of the interval time range, but also two dips where the visibility drops to 50 % i.e. the value for one single flash. Such results were discussed in Chapter 3; it was argued there that dips as seen in Fig. 7.1 are due to inhibition of the first flash by the second.

The results obtained at various background luminances, are plotted in Fig. 7.2. The background luminances Lb are given in log units above threshold. Straight lines were drawn by eye through the points in these graphs. As mentioned above, the jumping flashes were always presented at increment threshold luminance. It may be noted that we found that the increment threshold luminance divided by the background luminance (the Weber fraction) decreased by about 0.2 log units per log unit increase in the background luminance. This value is about the same as reported in the literature (see e.g. Le Grand, 1968).

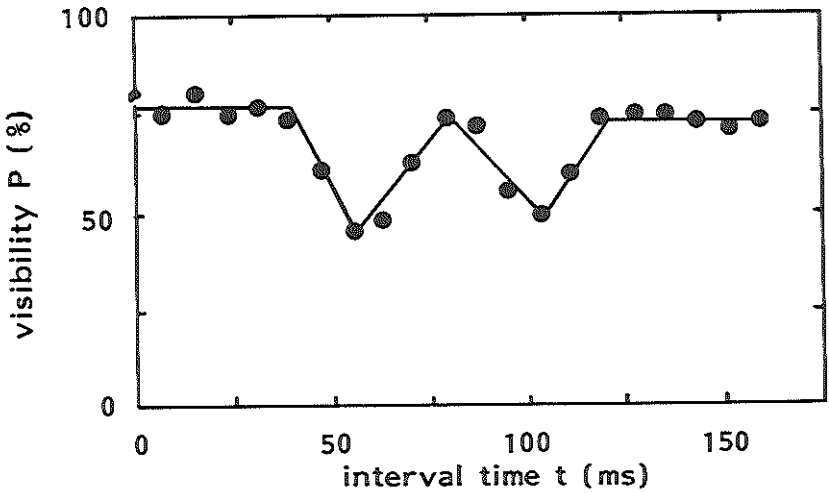

Fig. 7.1 The visibility P of a jumping flash as a function of the interval time t. The distance between the two flashes is 15.3 min arc. Each point in this graph represents the mean of 75 presentations. The standard deviation of the mean is about 5 %. Straight lines are drawn by eye through the experimental points.

The measurements were also performed using other flash distances and a homogeneous background of luminance 3.5 log units (see Fig. 7.2 bottom right). The range of interval times where the visibility of the jumping flash is reduced to about 50 % by inhibition is given in Fig. 7.3 for three flash distances d as three horizontal lines. The broken lines in Fig. 7.3 were replotted from Fig. 3.10 for the sake of comparison, and indicate the distance at which inhibition is found as a function of the interval time, when point flashes of diameter 1 min arc and duration 10 ms are displayed against a background luminance of 2.3 log units. The slope of these lines is 3.1 degrees per second.

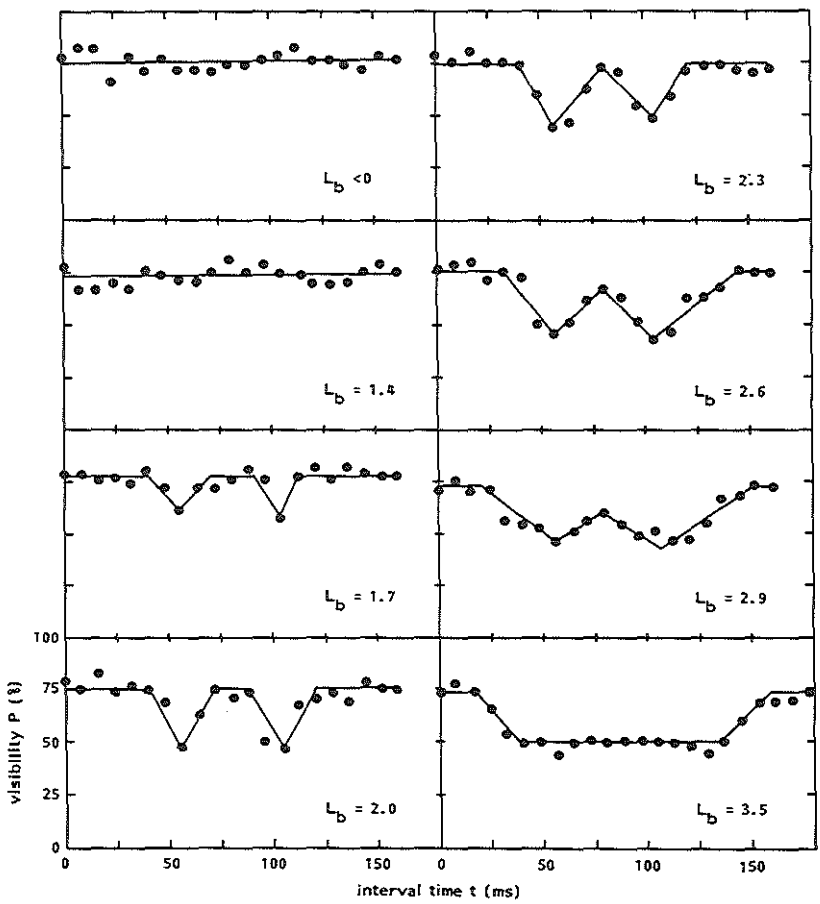

Fig. 7.2 The visibility P of a jumping flash as a function of the interval time t, with the background luminance Lb as parameter. The background luminances are given in log units above threshold. The top left-hand graph gives the results with a dark background. Each flash has a luminance equal to the increment threshold luminance; when the background luminance was changed, the flash luminances were also changed to keep the flashes at threshold. Further details as in Fig. 7.1.

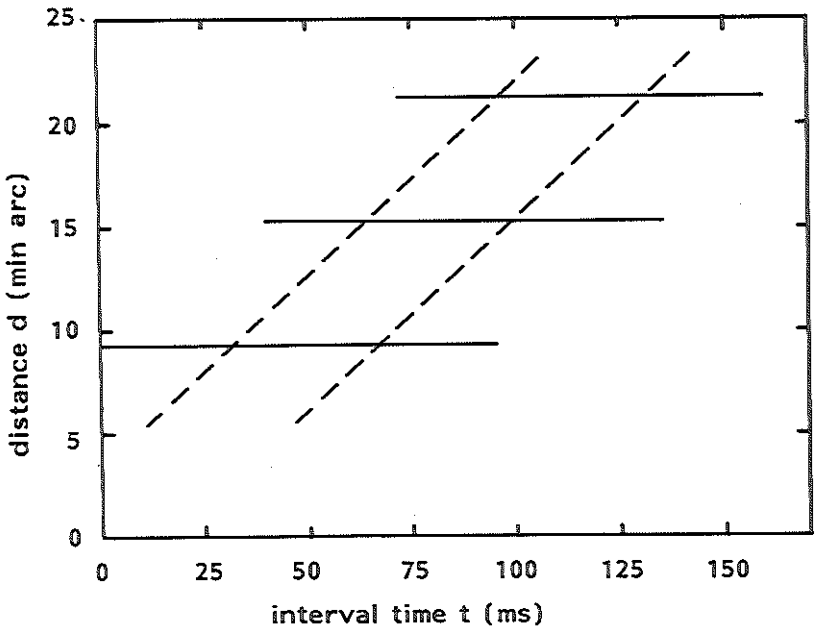

Fig. 7.3 The range of interval times at which the visibility of the jumping flash is 50 %, for three flash distances d and a background luminance of 3.5 log units (as in the bottom right-hand curve of Fig. 7.2), are indicated by the three horizontal lines. The broken lines (replotted from Fig. 3.10) represent the distances at which inhibition was found, with jumping flashes presented against a background luminance of 2.3 log units above threshold, as a function of the interval time.

To determine the demands that have to be met by the background pattern in order to enable the detection of inhibition, measurements were made with a background which was not homogeneous. The results in Fig. 7.4 were obtained with jumping flashes presented against a background of luminance Lb = 2.3 log units, split into two parts by a vertical dark bar. The width W of this bar and its position relative to the flashes (which jump to the right) are indicated in Fig. 7.5; each diagram in this figure relates to the graph in the corresponding position in Fig. 7.4. It will be noted that for all values of W up to 47 min arc the same curve may be drawn through the experimental points and it gives a good fit in each case. At W = 47 min arc, however, the position of the bar relative to the jumping flash has a crucial effect on the results (see Figs. 7.4 and 7.5, top right and right just above the middle).

Finally, the background was replaced by a thin bright vertical line of width 2 min arc (height 2 degrees) and brightness corresponding to a background luminance of 2.3 log units (in fact, the background field was set at a luminance of 2.3 log units and most of it, except the line, was shielded). Instead of determining the whole curve in Fig. 7.1. for each position of the line, we only explored three interval times: those corresponding to minimum visibility (inhibition) of the jumping flash with uniform background luminance (viz 56 and 104 ms; see Fig. 7.1) and 80 ms as an intermediate value which does not give rise to inhibition. Figure 7.6 shows the results obtained under these conditions, plotted as a function of the distance of the bright line from the centre of the jumping flash. (For example, distance 0 corresponds to placing the bright line exactly half-way between the two flashes.) In addition, the whole visibility curve (corresponding to Fig. 7.1) was determined for distances of 0, -18, and +32 min arc between the bright line and the centre of the jumping flash. These results (not shown here) confirm that no dips occur at other interval times than those ones used for Fig. 7.6.

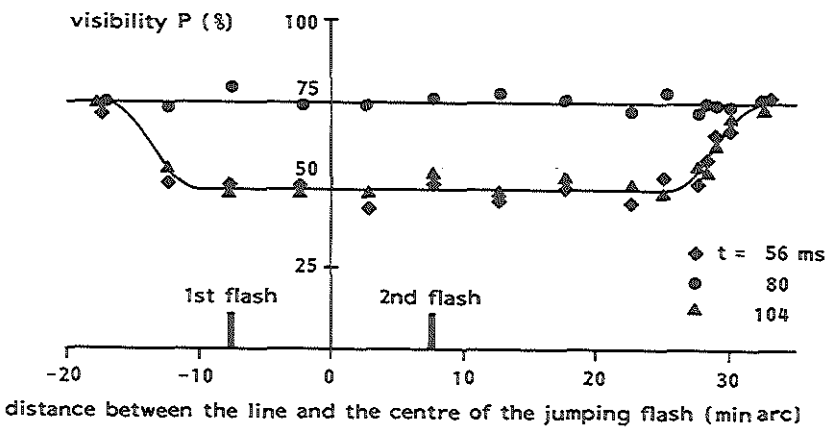

Fig. 7.6 The visibility P of a jumping flash for three interval times t, as a function of the position of a bright vertical line with respect to the centre of the jumping flash. The flashes were presented against a dark background.

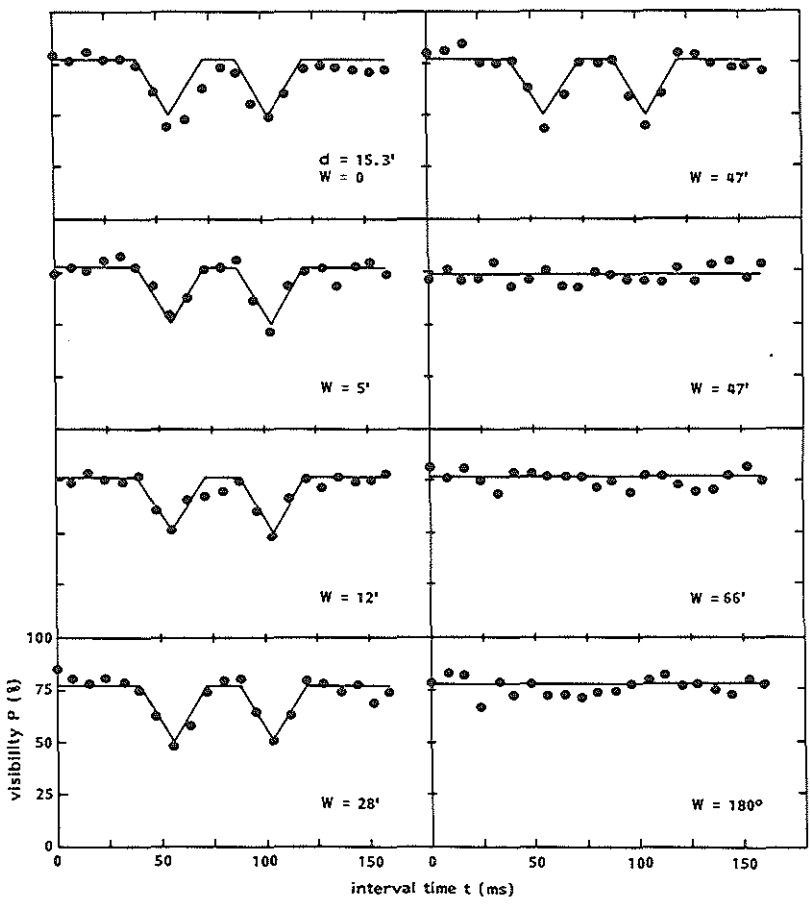

Fig. 7.4. The visibility P of a jumping flash as a function of the interval time t, with the width and position of a vertical dark bar in the background field as parameters. The flashes were presented against a background of luminance 2.3 log units above threshold. The width and position of the bar with respect to the flashes are depicted in Fig. 7.5. Each diagram in Fig. 7.5 relates to the graph in the corresponding position in Fig. 7.4. The same curve is drawn through the experimental points for all widths up to 47 min arc.

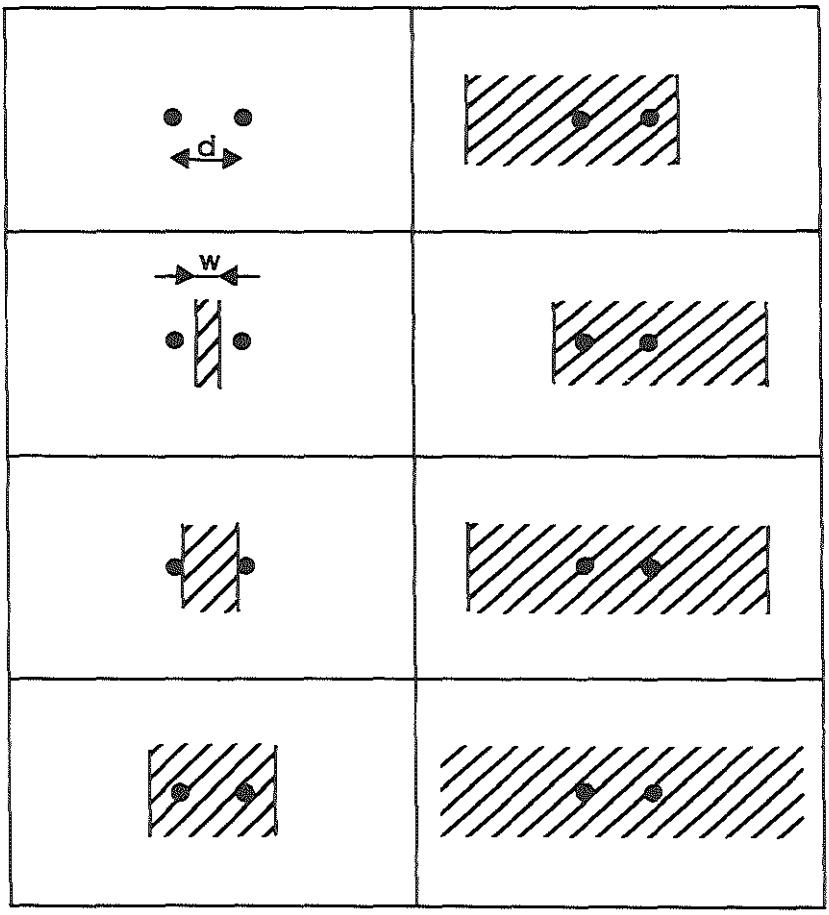

Fig. 7.5 Schematic representation of the stimuli patterns used to obtain the results in Fig. 7.4. The position of each elementary flash is indicated by a black point. The left-hand point represents the first flash, the right-hand one the second. The position and the horizontal width W of the dark bar are indicated to scale with respect to the position of the flashes. The vertical extent of the bar is unlimited. The bottom right-hand diagram represents a 'bar' covering the entire background field.

7.3 DISCUSSION

A remarkable aspect of the results in Fig. 7.2 is that at each luminance at which inhibition occurs, it is found at the same interval times. This is despite the strong influence that the luminance has on the width of the inhibition dips; we shall return to this point below. This indicates that the velocity at which the inhibition is propagated does not depend on either the background luminance or the increment threshold luminance. This was tested for stimuli with flash distances between 7 and 22 min arc, viewed against a background of luminance 3.5 log units. The results (see Fig. 7.2 and 7.3) show that despite the broad range of background luminances and increment threshold luminances tested, the inhibition can still be described as propagating with the previously found constant velocity of 3.1 degrees per second (the dashed line in Fig. 7.3).

It is known from the literature that the width of the spatial and temporal pulse response depends on the luminance level. In Chapter 3 we argued that the velocity of propagation of inhibition should be equal to the spatial summation area divided by the temporal summation area. On that occasion, the constancy of the propagation velocity would imply strong relations between spatial and temporal summation. Van den Brink (1956) measured the temporal and spatial summation areas as a function of the background luminance. He found that the summation areas decreased with increasing luminance. However, the ratio of the spatial and temporal summation areas remains constant within 10 % when the background luminance is varied from 1 to 4 log units above threshold. So, the constancy of the propagation velocity of the inhibition would seem to be confirmed by the known properties of summation.

The width of the inhibition dip varies widely: at a background luminance of 1.7 log units the dips are quite narrow, while at a luminance of 3.5 log units, they are so wide that they merge into one, yielding quite a wide range in which the visibility is constant at 50 %. This constant low level is not necessarily the result of a constant strength of inhibition: if one of the flashes is inhibited, the visibility of the jumping flash is 50 % (due entirely to the visibility of the remaining flash) and any further increase in the inhibition of the first-mentioned flash will not change the matters appreciably.

Increase in the background luminance above 3.5 log units has no further effect on the shape of the curves: for example, a background luminance of 4.1 log units above threshold yields results (not given here) similar to those in the bottom right-hand curve in Fig. 7.2.

When the stimuli are presented against a dark background, no inhibition is detected (see Fig. 7.2); the visibility remains constant at the probability summation level. There could be several reasons for this. On the one hand, there might be a threshold luminance for the background below which no inhibition is generated. Alternatively, the inhibition may be unable to travel across areas not undergoing visual excitation. On the other hand, why should there be inhibition when flashes are viewed against a dark surround; there is nothing to be inhibited.

If there is a background luminance level below which no inhibition is generated, it may be concluded from the results in Fig. 7.2 that this level would be between 1.4 and 1.7 log units above the threshold luminance. However, the experiments with a thin bright line between the flashes (see Fig. 7.6) show that inhibition can be detected using flashes presented against a dark surround. Hence, it is not exclusively the luminance of the background which determines the presence or absence of inhibition.

To check whether inhibition effects can cross unilluminated areas, a dark bar was presented between the two flashes. Figure 7.5 shows that for bar widths W of 5, and 12 min arc, the flashes were still presented against a light background but there was a dark gap between them. It may be seen from Fig. 7.4 that the results for these bar widths do not differ significantly from those obtained with W=0; it may thus be concluded that a dark area between the stimuli is no obstacle to the propagation of inhibition. Similar results were even obtained with a bar width of 28 min arc, which means that the flashes were presented against a dark area. This demonstrates that neither the presence of a light background at the site of the stimuli is a necessary condition for the generation of inhibition.

No inhibition was found when the flashes were presented against a totally dark surround (denoted as W= 180 degrees in Fig. 7.4; see also Fig. 7.2 for Lb 0) or against a bar of width W=66 min arc. The critical range for the occurrence of inhibition must thus be for bar widths between 28 and 66 min arc. The most curious results are those represented by the top two graphs on the right-hand side of Fig. 7.4: in both cases the bar width was 47 min arc, but in the first case the bar was shifted 9.5 min arc to the left with respect to the centre of the flashes and in the other case the same distance to the right. When the bar is positioned to the left, inhibition is found; when it is positioned to the right, however, there is no inhibition.

The crucial parameter in this case appears to be the distance between the second flash (the right-hand one in Fig. 7.5) and the nearest edge of the background field: with the shift to the left, this distance is 6 min arc, the same as with W=28 min arc (bottom left-hand curve in Fig. 7.4) and in both cases inhibition is found. With the shift to the right, the above mentioned distance (25 min arc) is the same as with W = 66 min arc and in both cases no inhibition is found. Hence, when a light background is present within 6 min arc of the second flash, inhibition is found, and when the light background is further away than 25 min arc no inhibition is found. The fact that the distance to the second flash is critical agrees with the previous conclusion that it is the second flash which generates the inhibition.

To determine the position of the boundary between inhibition and no inhibition with greater accuracy, measurements were performed with the two flashes against a background which was dark except for a thin vertical bright line situated at various positions. The results in Fig. 7.6 show that there is a difference between the visibility of the jumping flash with the 80 ms interval time on the one hand and the 56 and 104 ms interval times on the other (indicating the presence of two separate inhibition dips) for a range of positions of the bright line which is asymmetrical around the centre of the jumping flash. These results can be summarized by saying that inhibition is found when the distance between the second flash and the line is less than 22 min arc.

It might be possible that the effect of the thin line is operating via stray light at the location of the test flash. Heinemann (1961) has determined the amount of stray light for a stimulus of somewhat larger dimensions than the ones used in this chapter. He found a value of about 5 %. In the present situation with a line of luminance 2.3 log units, this value can be taken as an overestimation. In that case, the amount of light at the site of the flashes would be 1 log unit at most. In Fig. 7.2 it can be seen that a background field with this luminance does not give rise to inhibition. So, it is unlikely that the inhibition is generated as a result of stray light from the line.

In Chapter 3 where the flashes were presented against homogeneous backgrounds it was found that the inhibition propagation range is about 20 to 25 min arc. Combining this with the present findings we may conclude that a flash only generates inhibition when background illumination is present within the inhibition propagation range (even though the illumination may be of very limited extent - e.g. a vertical bright line). It is possible to speculate that the inhibition is only generated when there is the possiblity of enhancing the visibility of the generator.

7.4 SUMMARY

The influence of the background on the generation of inhibition has been investigated. The use of elementary point flashes as probes makes it possible to detect both the site and the time of inhibition with a high degree of precision. The background luminance is found to influence the extent of inhibition. When no background illumination is present, no inhibition is detected. When only part of the background is illuminated, inhibition is sometimes found, and sometimes not, depending on which parts are illuminated. Experiments involving systematic buildup and breakdown of a background luminance field showed that inhibition only occurs when luminance is present within the range within which the inhibition effects operate (about 25 min arc).

8.

FOVEAL INHIBITION MEASURED WITH SUPRATHRESHOLD STIMULI

Chapter 8 FOVEAL INHIBITION MEASURED WITH SUPRATHRESHOLD STIMULI

8.1 INTRODUCTION

All experiments described so far concern peripheral vision at increment threshold luminance levels. A backward inhibition effect has been found and the influence of a number of parameters has been studied. However, the inhibition has not been observed directly; all conclusions are based on variations in the frequency of seeing the stimulus. It might be wondered whether it is possible to demonstrate the inhibitory effects more clearly. If the inhibition were also to occur with suprathreshold stimuli, it might for instance be possible to prove that the first stimulus is being inhibited, just by saying which of the two is seen. Therefore, measurements were carried out using suprathreshold stimuli which were presented to the fovea. The data collected with such stimuli will be described and discussed in this chapter.

Three series of experiments will be described. In the first, the elementary jumping flashes were presented to the fovea at increment threshold luminances, in order to check whether or not the eccentricity influences the inhibition behaviour. In the second series, we still used jumping flashes; however, the stimuli were presented at suprathreshold luminances and the experimental criterion was equality in the brightness of the two flashes. This series allowed us to compare the results with previously determined inhibition data. In the third series, the diameter and the duration of the second flash were increased in steps in order to test whether or not the model developed in Chapter 5 also holds for foveal suprathreshold inhibition.

In experiments 1 and 2 each flash had a diameter D of 1 min arc and a duration T of 10 ms. Measurements were performed as a function of the interval time t, for several flash distances d. In experiment 3 the diameter D and the duration T of the second flash were varied while those of the first flash were kept constant at 1 min arc and 10 ms.

8.2 RESULTS

The subject was instructed to fixate at the centre of the background field where the first flash was presented. No separate fixation marker was used. With a small fixation mark there is the inherent danger of interactions between the test stimuli and the marker. A large fixation mark, however, cannot ensure foveal presentation of the stimuli. Therefore, the eye movements of subject PV were determined using the after-image method described by Duwaer (1982). With a stationary 3 min arc diameter fixation stimulus, it was found that the standard deviation of his eye movements is about 1.5 min arc. According to Rattle (cited by Ditchburn, 1973) the standard deviation for a 3 degree disc is less than double the value for a 4 min arc disc. The background field used in the present study can thus serve as a fixation mark, resulting in a standard deviation of the eye movements of about 3 min arc.

8.2.1. ELEMENTARY STIMULI AT THE INCREMENT THRESHOLD LEVEL. The frequency of seeing the jumping flash is determined in the same way as was done in the previous chapters, except that the stimuli were presented foveally. The frequency of seeing a jumping flash is plotted as a function of the interval time t in Fig. 8.1. The second flash was presented 17 min arc vertically above the first flash. The results given are the mean over 10 runs, which represents a total of 250 presentations. The standard deviation of the visibilities is about 5 %. Each flash has a visibility of about 45 % on its own, so if the flashes do not interact, a visibility of about 70 % would be expected on the basis of probability summation. The results do indeed show a 70 % visibility level at high and low interval times, but also two dips where the visibility drops to a visibility of 45 % which is just the visibility of a single flash. These dips were ascribed to inhibition (see Chapter 3) and the main goal of this part of the study is to determine the foveal properties of this kind of inhibitory effect for suprathreshold stimuli.

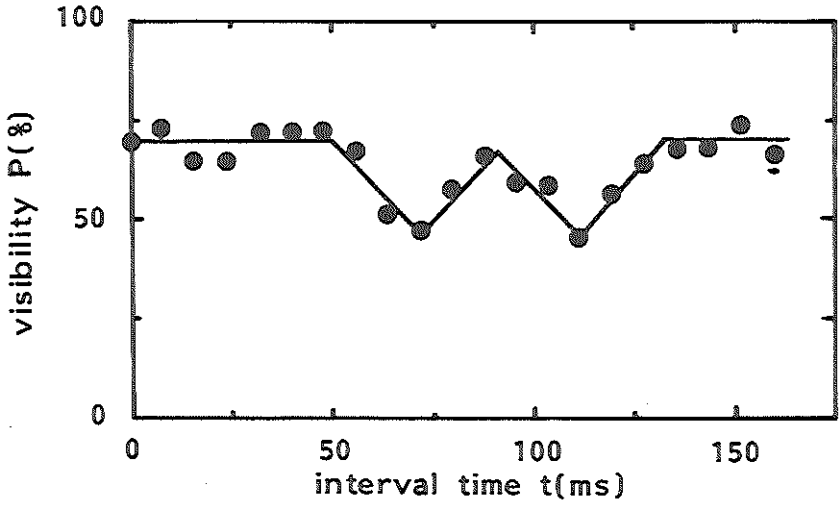

Fig. 8.1 The visibility of a foveally presented jumping flash (i.e. the frequency of seeing) as a function of the interval time t between the flashes. Straight lines are drawn by eye through the experimental points.

8.2.2. ELEMENTARY STIMULI AT SUPRATHRESHOLD LUMINANCE LEVELS. For the suprathreshold experiments the subject varied the increment luminance of the first flash to obtain equal brightness for both flashes. The luminance of the second flash was kept constant at 17 dB above its increment threshold level. This procedure proved to be much more pleasant and stable than the one used for experiment 1: only 10 adjustments were necessary to obtain a standard deviation of the mean of about 5 % . In Fig. 8.2 the results are plotted as a function of the interval time t, for three flash distances d, the second flash being presented vertically above the first one. The straight lines in the figure are drawn by eye through the data points. The adjusted luminance L is given along the ordinate. It is defined as the increment luminance of the first flash relative to the increment luminance of the second flash when, according to the subject, both flashes look equally bright. Thus, when L = 1 both flashes have the same brightness when their luminances are the same. It is evident that for two regions of interval times there has to be a remarkable difference between the luminance of both flashes (up to almost a factor 2) if they are to appear equally bright. The existence of the effects measured on the first subject were confirmed with four other

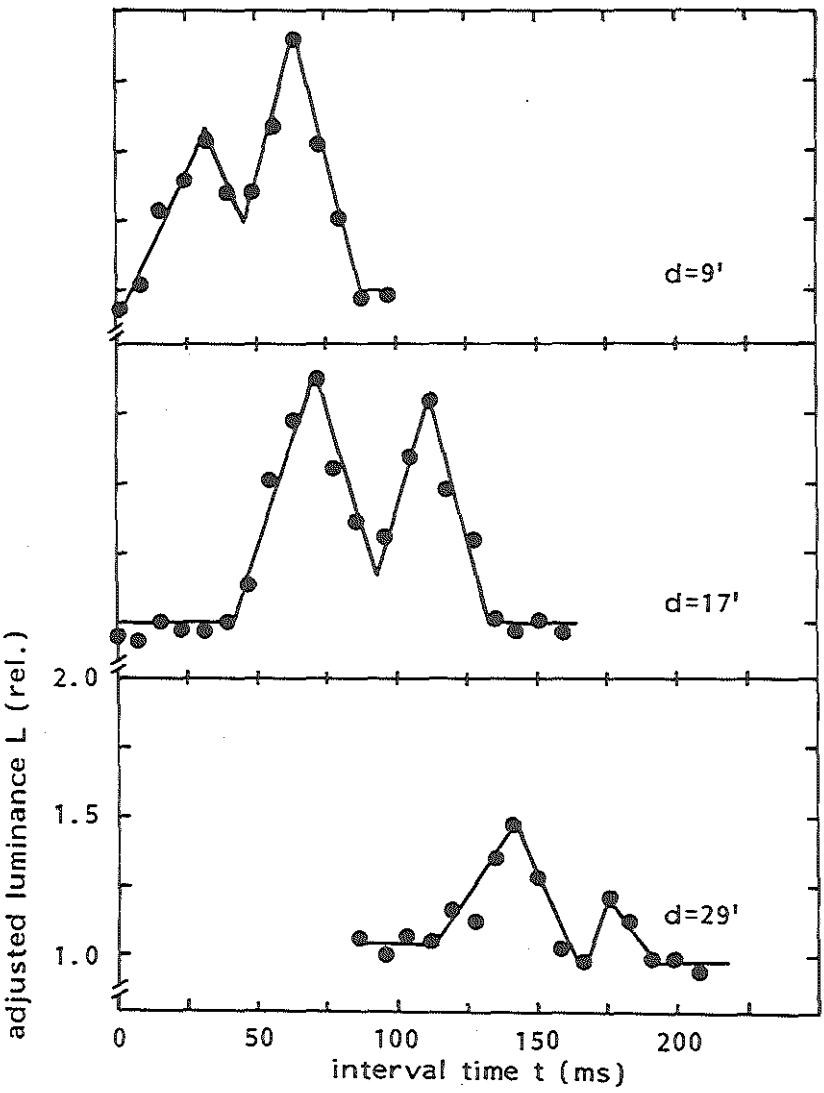

Fig. 8.2 The adjusted luminance L of the first flash, which is required to obtain the same brightness as the second flash, as a function of the interval time t, for three flash distances d. The vertical scale is the same for each plot.

subjects. One other subject was also tested for the attributes measured in Fig. 8.1 and Fig. 9.2; his results do not differ significantly from those presented here.

The interval times at which the peaks are found in Fig. 8.2 (the peak times) increase with the distance between the two flashes. This indicates that the inhibition which presumably causes the peaks, is propagated. To show this more clearly, the interval times at which the highest adjusted luminance were found are plotted in Fig. 8.3 (as circles with a vertical bar in) against the distance d. These data are taken from Fig. 8.2 and from similar experiments with other flash distances ranging from 3 to 40 min arc (those results are not shown here, but apart from a shift of the peaks and variation in their height they resemble those in Fig. 8.2).

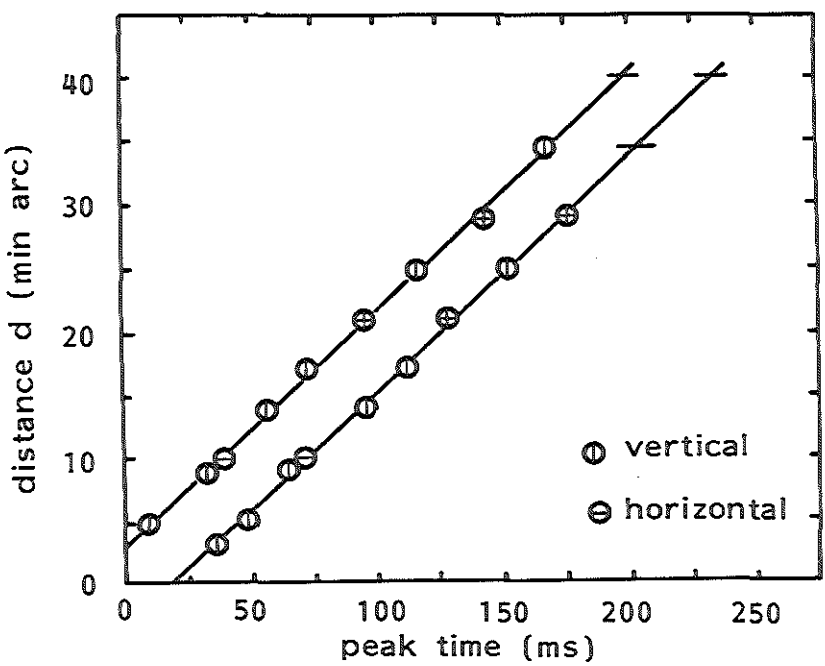

Fig. 8.3 The flash distance d as a function of the interval time t at which peaks are found in Fig. 8.2 and in plots for similar experiments using other flash distances and directions. The direction of the bars in the circles indicates whether the results are obtained with horizontal or vertically jumping flashes. The diameter of the circles approximates the accuracy of the results.

Results obtained with horizontally jumping flashes are also indicated (by circles with a horizontal bar in); they show substantially the same trends as those obtained with vertically jumping flashes. The plot of flash distance against peak times (Fig. 8.3) indicates that the propagation is very regular: both peaks are propagated at the same constant velocity of 3.1 degrees per second (the slope of the least-square fit lines in Fig. 8.3).

The results in Fig. 8.2 show that not only the position of the peaks but also their height varies with the experimental conditions. The peak luminances (determined in the same experiments as the data in Fig. 8.3) are plotted as a function of the peak time in Fig. 8.4, irrespective of the spatial aspects.

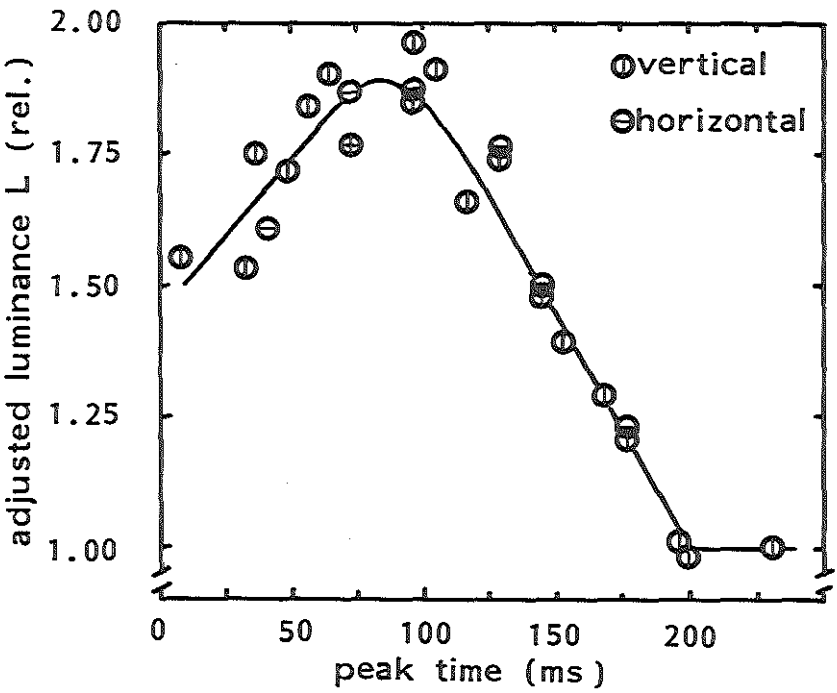

Fig. 8.4 The peak values of the adjusted luminance L as a function of the interval time at which the peaks are found, for the experimental results in Fig. 8.3. The standard deviation of the results is about 5 %.

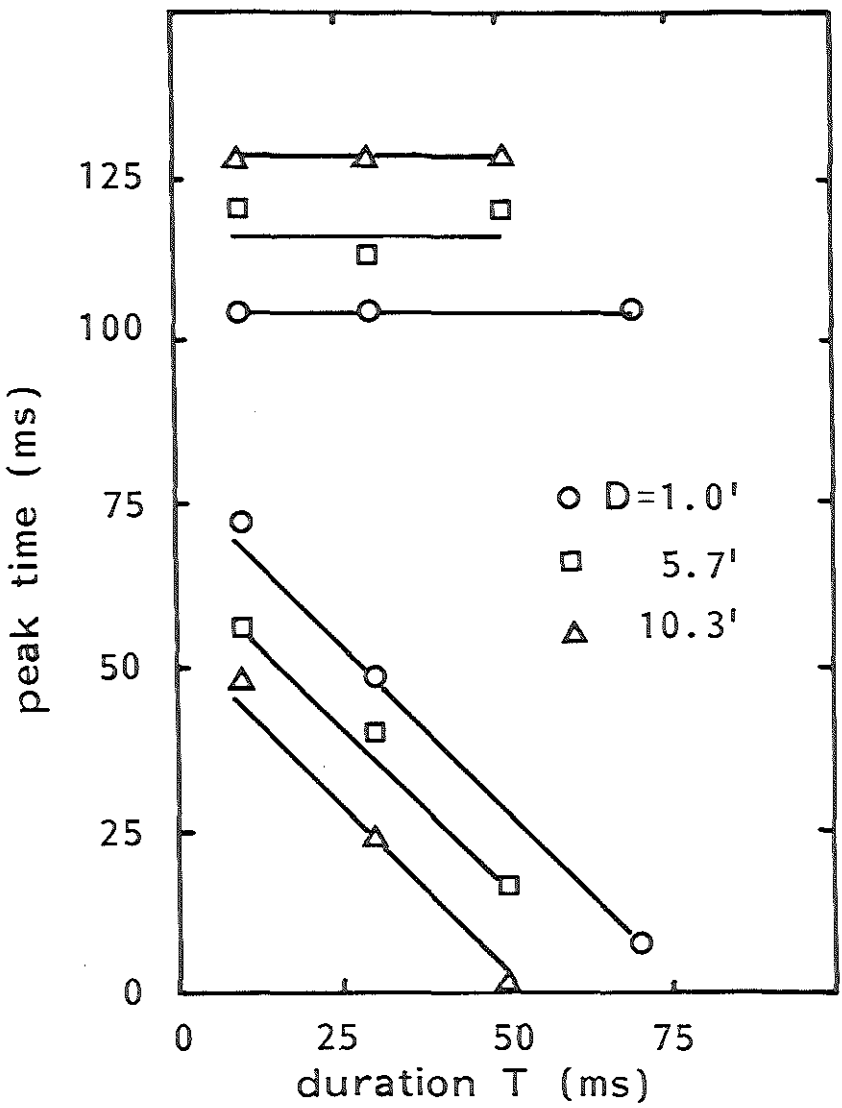

Fig. 8.5 The peak time as a function of the duration T of the second flash with its diameter D as parameter. The lower curves relate to the first peaks, the upper ones to the second peaks. The resolution in the peak times is 4 ms, since they are taken from plots in which the interval times are increased in steps of 8 ms. The lines are calculated on the basis of the model described in the discussion.

8.2.3 SUPRATHRESHOLD EXTENDED STIMULI. All the data presented sofar were obtained using the same dimensions for both flashes (diameter 1 min arc, duration 10 ms). It was found in the case of peripheral vision that experiments with jumping flashes consisting of two non-identical flashes were able to throw some light on the nature of the inhibition effect. It was therefore decided to perform similar measurements with foveal suprathreshold stimuli. The dimensions of the first flash (which serves as the probe for detection of inhibition) were kept constant at 1 min arc diameter and 10 ms duration, while the diameter and duration of the second flash were varied. These factors have an influence on the brightness of the second flash. In order to keep the results comparable to those obtained with the elementary stimuli, this brightness effect was undesirable. Therefore, the luminance of the second flash was changed when the diameter or duration were varied, so as to keep the brightness the same as that of a 10 ms 1 min arc flash of 17 dB above threshold. The luminance required for this was found to be inversely proportional to the flash duration; the diameter had hardly any influence.

The centre-to-centre distance between the flashes was kept constant at 17 min arc. The results resemble those in Fig. 8.2, apart from shifts of the peaks to other interval times. They are summarized in Fig. 8.5 where the peak times are plotted as a function of the duration T with the diameter D as parameter. The lines are calculated on the basis of the model described in the discussion.

8.3 DISCUSSION

Series of experiments are described in which the stimulus consists of two small flashes of short duration. The advantage of this kind of stimuli is that it permits the determination of interactions between stimuli with a high resolving power in space as well as in time, showing effects which cannot directly be seen when larger stimuli are used. In the present chapter, results obtained with stimuli presented foveally at suprathreshold luminance levels are compared with the previous findings.

8.3.1 FOVEAL INHIBITION AT INCREMENT THRESHOLD LUMINANCE LEVELS. To test whether inhibition effects occur in the fovea in the same way as in the periphery, the foveal results in Fig. 8.1 were determined, using the same procedure as in the previously reported peripheral studies.

To obtain a 5 % standard deviation of the mean, the results had to be averaged over 250 presentations - as compared with 25 or 100 presentations in the peripheral experiments. This lower foveal accuracy might well be due to the fact that near the fovea the threshold is more strongly dependent on the eccentricity than in the periphery (see e.g. Blommaert and Roufs, 1981). The subject's eye movements lead to a certain spread in the eccentricity at which the stimuli are perceived, which in its turn results in a threshold variation which is much higher foveally than at the periphery.

The results in Fig. 8.1 look much like those obtained with peripheral presentation of the stimuli (see Chapter 3). From those results, it was deduced that the dips in the visibility curves are the result of inhibition of the first flash by the second one. This explanation might also account for the foveal results, for the visibility measured in the dips is 45 % which is exactly the same as the visibility of one single flash. Thus, it seems that the foveal inhibition effects are similar to those at the periphery.

The interval times at which maximum inhibition is detected are the same for stimuli at threshold luminance levels and for suprathreshold stimuli when the distance between the flashes is the same (compare Fig. 8.1 and the middle curve of Fig. 8.2).

8.3.2 FOVEAL INHIBITION MEASURED WITH SUPRA-THRESHOLD STIMULI. When the stimuli are presented at the increment threshold luminance level, the subject cannot tell whether the inhibition effects observed relate to the first or to the second flash. When the stimuli are presented foveally at suprathreshold luminance levels, it is possible to say which flash inhibits which. This would then be a direct, straight forward indication for the backward nature of the inhibition. In a qualitative test, 10 subjects all reported

that the first flash was markedly dimmer than the second one when the flash distance and interval time were suitably chosen. So, the second flash generates the inhibition which acts on the first flash, in the same way as described for peripheral inhibition at the threshold level.

To study foveal inhibition, suprathreshold stimuli are much more suited than threshold stimuli; with the suprathreshold stimuli there is a quantitative measure for the intensity of the interaction, whereas the visibility measurements with threshold stimuli indicate little more than the presence or absence of inhibition. When the stimuli are presented at the periphery, the subject cannot discriminate between the two flashes, so the adjustment method cannot be used.

The effects found with suprathreshold stimuli are regarded as being due to inhibition. This may not be strictly correct, but for the sake of clearity we will refer to the effect which gives the peaks as inhibition.

The above mentioned propagation velocity of 3.1 degrees per second, and the intercepts of the lines in Fig. 8.3 with the axes (viz 3.5 min arc and 18 ms) agree well with the values found at the periphery with flashes jumping both towards and away from the fovea (radial jumping flashes): measurements at 3 degrees nasal, 3 degrees oblique and 3 degrees below the fovea all yield an inhibition propagation velocity of 3.1 degrees per second for radially jumping flashes and intercepts of 3.3 min arc and 18 ms.

While the experimental conditions used here differed appreciably from those used previously to study the effects at the threshold increment level, the results showed quite similar effects. This indicates that the suprathreshold inhibition reported here behaves in the same way as the threshold inhibition and might thus be based on the same mechanism.

The peripheral experiments indicated that the velocity of propagation depends on the direction of the jumping flash. This velocity appears to exhibit circular symmetry around the fovea, with a radial component of 3.1 degrees per second and a tangential component of 4.2 degrees per second. The apparent isotropy of the foveal inhibition (both horizontally

and vertically jumping flashes resulted in an inhibition propagation velocity of 3.1 degrees per second) might be due to the fact that no matter in which direction the flashes are jumping, the foveal stimulus seems to be jumping in a radial direction without any tangential component, since the first flash itself is presented to the fovea.

The great advantage of the suprathreshold adjustment method is that it gives a quantitative measure of the intensity of the interaction involved; the height of the peaks in Fig. 8.2 is a direct measure of the amount by which the luminance of the first flash must be increased to compensate for the supposed inhibitory effects. Assuming linearity, this amount gives an estimate for the strength of the inhibition in the absence of compensation. When the peak height is plotted as a function of the peak times (see Fig. 8.4), all points lie more or less on a single curve; the peak height increases up to a peak time of about 90 ms and then decreases gradually to zero at about 200 ms. A plot (not given here) of peak height against flash distance, on the other hand, seems to yield two curves of similar shape but slightly different position; one for the first and another one for the second peak. This can also be seen from Fig. 8.2: when comparing the three curves, it can be seen that the maximum peak height is found at a distance of 17 min arc while for the second peak the maximum is found at a shorter distance, namely 9 min arc. Thus the peak at the lower interval time reaches its maximum height at a larger flash distance than the second peak. However, at a certain interval time, the peak height does not depend on the flash distance. This seems to indicate that the intensity of the inhibition is determined more by the temporal than by the spatial separation of the elementary flashes.

The peripheral experiments at threshold level revealed no dips at interval times longer than about 125 ms (or separations larger than 20 min arc). In the present (foveal) experiments, however, peaks are found up to interval times of 175 ms and separations of up to 35 min of arc (see Fig. 8.3). This finding may indicate some form of inhomogeneity, but may equally well reflect differences in experimental procedure and in the luminance used. The adjustment method permits the determination of even weak interactions (see e.g. the portion of the curve in Fig. 8.4 for long interval

times) which would not show up in the plots of data measured at threshold luminance levels.

8.3.3 FOVEAL INHIBITION WITH EXTENDED STIMULI. Measurements in the peripheral field of vision using stimuli at the threshold level showed that increasing the duration and/or the diameter of the second flash caused changes in the interval times at which inhibition is detected. These results could be explained by assuming that the inhibition propagates away from the edges of the excitation pattern and acts on the first flash (Chapter 5). This accounts for the excistence of two peaks in the curves in Fig. 8.2; one from the nearer and one from the further edge.

As a further test of the similarities between peripheral inhibition and foveal effects, the measurements were also performed foveally with a number of different flash diameters and durations using suprathreshold stimuli.

The results as shown in Fig. 8.5 yield very similar effects to those found with peripheral presentation of the stimuli at threshold luminances. A complete description of this effect is not given here, since it does not differ significantly from that given previously in Chapter 5. The basic argument is that if inhibition is to be detected, the distance between one of the flanks of the second flash and the centre of the first one, divided by the time between the first flash and the start or end of the second one must be equal to the inhibition propagation velocity. So, increasing the diameter of the second flash results in a shift to lower interval times for the first peak and to higher interval times for the second peak. Essentially the same happens when the duration of the second flash is increased. However, as we defined the interval time as the onset-asynchrony, the duration of the second flash does not influence the interval time at which the inhibitory effect from the onset is to occur.

The straight lines in Fig. 8.5 were constructed on the basis of the above assumption (see Chapter 9); the good fit between these lines and the experimental points indicates that the description used for peripheral inhibition is also valid for the results obtained with foveal presentation of the stimuli.

All these findings indicate that the results found with foveal presentation of suprathreshold stimuli resemble the peripheral inhibition at increment threshold luminance levels in many respects. This indicates that the visual system is spatially unexpected homogeneous as far as the propagation of inhibition is concerned, much more than would be expected from a comparison with e.g. spatial summation effects (Van den Brink, 1957) or line spread functions (Hines, 1967; Limb and Rubinstein, 1977).

8.4 SUMMARY

Foveal inhibition has been studied using both elementary stimuli presented at increment threshold luminance and suprathreshold stimuli. Both kinds of stimuli yield a similar kind of propagating inhibition. The results are compared with the data on peripheral inhibition; equal propagation velocities are found. The inhibition produced with spatially extended stimuli is described on the basis of the hypothesis derived from measurements on elementary stimuli.

9.

METACONTRAST

Chapter 9 METACONTRAST

9.1 INTRODUCTION

In Chapter 5 it has been suggested that there might be a relation between the propagation of inhibition and a special form of masking known as metacontrast, that is the phenomenal reduction of the brightness of a visual stimulus followed after a certain delay by an adjacent, non-overlapping second stimulus. Ever since the articles of Alpern (1952, 1953) there has been a wide interest in metacontrast. The literature on this subject has been reviewed by Raab (1963) Kahneman (1968) and Lefton (1973).

The basic mechanisms giving rise to metacontrast are not yet entirely clear. It might be related to lateral inhibition networks (Weisstein, 1968, 1975; Bridgeman, 1971) or to the transient inhibition of sustained activity (Breitmeyer and Ganz, 1976). However, interactions that are associated with similarities between Fourier components of the target and of the mask (White and Lorber, 1976) or interactions between edge detectors (Shapley and Tolhurst, 1973) have also been proposed as the underlying mechanisms.

Both the inhibition described in the previous chapters and metacontrast are associated with the reduction in the effectiveness of the energy of a stimulus when it is followed after a certain delay by another stimulus presented in the spatial surroundings of the first. Hence, it would not be at all surprising to find that these two effects are related in one way or another. However, there are large differences between the types of stimuli so far used in the investigation of these two effects: most of the inhibition experiments make use of jumping flashes presented peripherally at threshold luminance levels, whereas metacontrast is usually studied with stimuli of fairly large spatial extension, well above threshold luminance. In the previous chapter however, it was shown that propagating inhibition effects can also be found whit suprathreshold stimuli which are presented foveally. Using these data, an attempt is made in the present chapter to bridge the gap between the inhibition and metacontrast experiments.

In order to test whether the ideas deduced from experiments with elementary and small stimuli can be used as a basis for the description of results obtained with extended stimuli, we carried out a series of measurements using a stimulus borrowed from the metacontrast studies, viz a disc followed after a certain delay by an annulus surrounding it.

It is common in the literature to use the term "metacontrast" only to describe the effects observed when two stimuli are presented to adjacent retinal areas. We will retain this convention throughout this study, distinguishing between "metacontrast" as just defined and "inhibition", which is produced when there is a spatial separation between the two flashes.

9.2 RESULTS

Instead of using two identical elementary flashes, the first flash was replaced by a circular flash (in which the diameter was a parameter ranging from 3.4 to 33.4 min arc, duration 10 ms) and the second flash was a ringshaped flash (inner diameter 34 min arc, ring thickness 4 or 16 min arc, duration 10 ms) surrounding the first flash. The measuring method and the other experimental conditions are the same as for the suprathreshold measurements described in Chapter 8.

The subject adjusted the luminance of the disc to make it look just as bright as the annulus. Two series of measurements were made with annuli of internal diameter 34 min arc and width 4 or 16 min arc. The diameter of the disc, taken as parameter in these measurements, ranged from 3.4 to 33.4 min arc (hence, the largest disc used just fits in the annulus). The results are given in Fig. 9.1 for an annulus width of 4 min arc and in Fig. 9.2 for 16 min arc. The lines in these figures represent predictions derived from the model given in the discussion, with the aid of data obtained with elementary stimuli.

9.3 DISCUSSION

9.3.1 PREDICTIONS FOR THE DISC-RING STIMULUS. Now that the spatiotemporal properties of propagating inhibition have been established for elementary flashes in the foregoing chapters, it is tempting to examine how well these ideas also apply to extended stimuli. We therefore tried to use

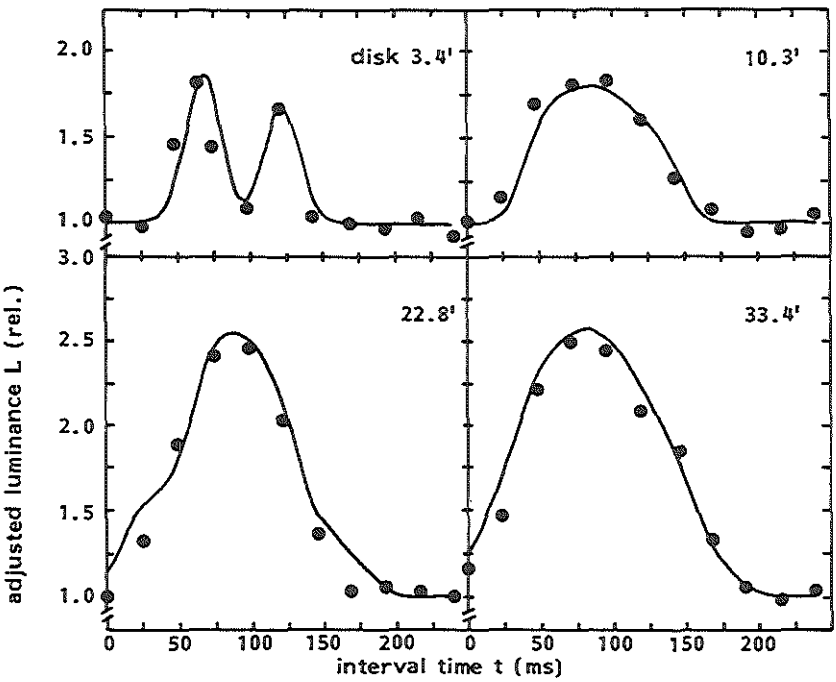

Fig. 9.1 The adjusted luminance L of the first flash required to obtain the same brightness as the second flash as a function of the interval time t for four diameters of the first flash. The second flash had the form of a ring (internal diameter 34 min arc, width 4 min arc) surrounding the first, so the largest first flash fills the ring completely. Each point is based on 10 adjustments, the standard deviation of the mean is about 5% . The lines are calculated on the basis of the results measured with two elementary point flashes.

data derived from elementary stimuli for the prediction of the results for an extended stimulus: a disc followed after a certain delay by an annulus around it. This stimulus was chosen since it is a complex stimulus consisting of two parts which are spatially and temporally separated (compare the jumping flashes), and because this stimulus is frequently used in metacontrast experiments. This enables comparison with published data.

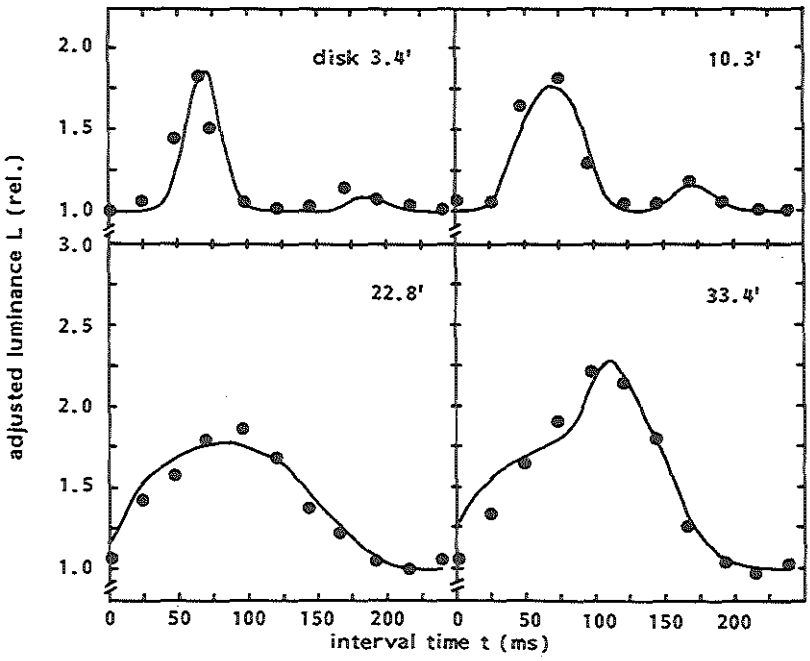

Fig. 9.2 Results obtained with a width of 16 min arc for the second flash, other experimental conditions being as for Fig. 9.1.

On the basis of the experiments with elementary flashes, we may expect the inhibition produced with such extended stimuli to arise at the inner and outer edges of the ring, to be propagated with a velocity of 3.1 degrees per second, and to reduce the brightness of the disc by an amount that depends on the time that the inhibition is being propagated. In addition, it is assumed that the overall extent to which the brightness of the disc is reduced is equal to the inhibition effects from the ring, summed over the entire area of the disc. The mathematics are given in detail in an appendix to this chapter, and the calculated results are given as the lines in Fig. 9.1, 9.2 and 9.3.

The essential feature of the model is that it assumes a strongly non-linear generation of inhibition: only the edges of the ring should give rise to propagating inhibition, the

parts between the edges would not. This accounts for the occurrence of the two dips and for the way in which the relation between the dips changes with the ring thickness.

As far as the detection of inhibition is concerned, the model makes use of integration to bridge the gap between point-shaped probes and extended probes. The concept of integration is often used in the literature to relate the results of point spread functions to contrast sensitivity functions (see e.g. Wilson and Bergen, 1979) or to predict disc thresholds from point thresholds (see e.g. Blommaert and Roufs, 1981).

It is also assumed in the literature that multiple pointspread functions exist at each retinal location (see e.g. Koenderink, 1976). The essence of the present model, however, is that the choice between a point spread function with inhibition and one without inhibtion is made upon considering the neighbouring locations.

In order to facilitate the use of experimental data obtained with elementary stimuli as a basis for the calculation, a Gaussian function with a standard deviation of 15 ms is used to describe the form of the first peak of the middle curve in Fig. 9.3. This function fits the experimental points reasonably well. Its contribution to the overall results is not very critical: particularly with larger discs, errors of approximation introduced by this function will largely average out.

The values for the propagation velocity on the other hand, are very critical; the horizontal scale of the calculated curves in Figs. 9.1, 9.2 and 9.3 vary in direct proportion to this parameter.

The time variation of the intensity of inhibition (Fig. 8.4) has a great influence on the calculated results: if it were not taken into account and it were assumed that when inhibition is present it has the same strength over the whole range, the curves obtained would have a (slightly smoothed) block shape.

9.3.2 COMPARISON WITH EXPERIMENTAL RESULTS. The model was first used to describe the results for two elementary point flashes. Those results were given and discussed in Chapter 8 (see Fig. 8.2). In Fig. 9.3 the same results are plotted again, but in this case the lines are calculated on the basis of the model. The reasonable fit obtained here is not so surprising, since the model is based on these results. It may be noted that a much better fit would be obtained with the results found for a flash distance of 29 min arc (bottom curve of Fig. 9.3) if the flash distance were taken as 30 min arc instead of 29. This would cause the calculated curve to shift 5 ms to the right and the peaks to be a little lower. It almost looks as if fitting the model to the experimental points gives a more accurate estimate of the flash distance than direct measurement (the difference of 1 min arc involved corresponds to a shift of 175 micrometer in the apparatus).

It is even more interesting to compare the expected and measured data for the disc-ring stimulus. The theoretical lines fit the experimental points in Fig. 9.1 and 2 reasonably well; this indicates that the results found with stimuli of diameters up to about 1 degree can indeed be described in terms of the results obtained with elementary stimuli, provided that the propagative aspects of the inhibition are taken into account.

The smallest disc used (diameter 3.4 min arc) is small enough to separate the effects of the inner and outer edge of the ring. (The resolving power of a larger disc is lower, as the effects of the two edges of the ring tend to get spread out over the disc, so that they can no longer be distinguished.) Comparing the upper left-hand curves of Fig. 9.1 and 9.2, we see that the first peak (inhibition generated at the inner edge of the ring) is found at the same interval time for the wide ring and the narrow one (the internal diameter being the same in both cases). The second peak is found at longer interval times for the wider ring, which can be seen as a clear demonstration of the propagation of the inhibition. (Again, a better fit would be obtained if the internal radius of the ring were taken as 1 min arc less than the set value).

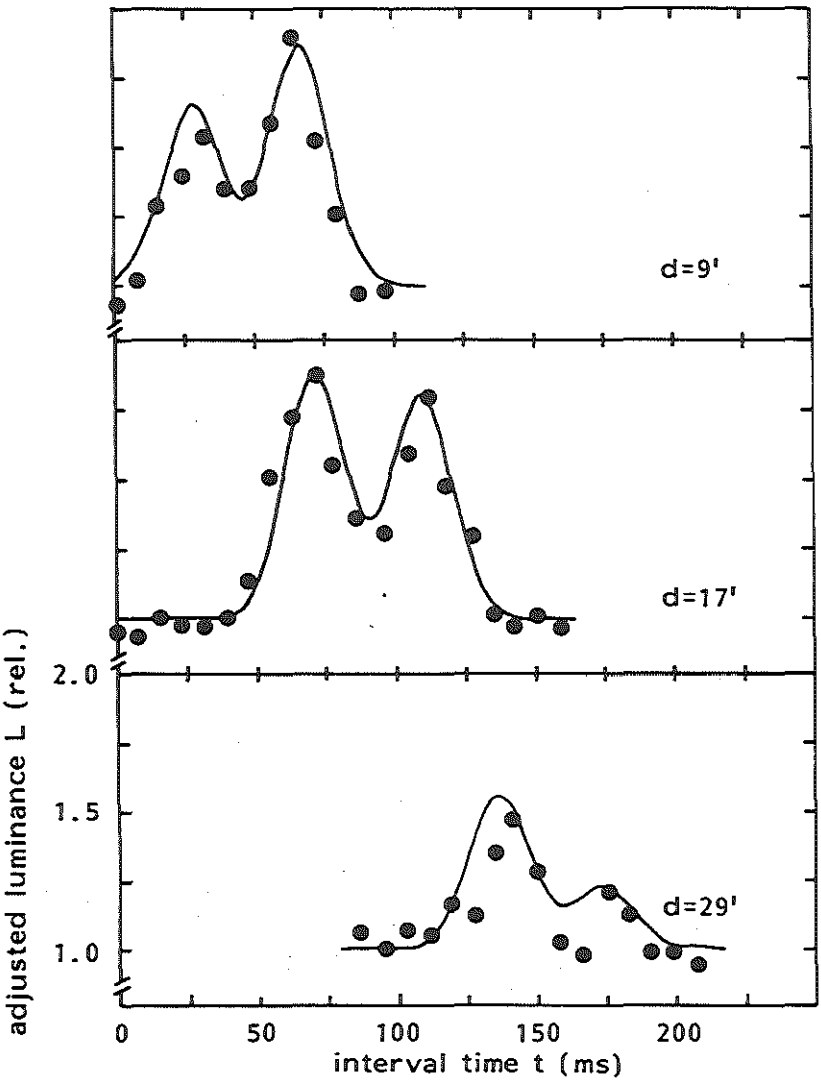

Fig. 9.3 The adjusted luminance L of the first flash required to obtain the same brightness as the second flash as a function of the interval time t for three distances between the flashes. Both flashes have a diameter of 1 min arc and a duration of 10 ms. The data points are the same as those in Fig. 8.2. The lines are calculated on the basis of the model explained in the discussion.

At low interval times with large discs, there are significant discrepancies between theory and experiment. It is likely that the two stimuli, when presented simultaneously, influence each other in the same way, so that the adjusted luminance will have a value of 1. The model, however, only takes account of the influence of the second flash on the first one.

The results found with the largest discs can also be interpreted in another way: when the first flash (which acts as a probe) is so large that it covers the whole range of distances at which inhibition is active (0 to 35 min arc; the range of the effects seen in Fig. 8.3), the spatial aspects of the propagation of the inhibition need not be taken into account. The plot of the inhibition intensity as a function of time (Fig. 8.4) can then be used to estimate the results that would be obtained with a disc of diameter 33.4 min arc. The curve of Fig. 8.4 does indeed give a reasonable fit with the data from the bottom right-hand curve in Fig. 9.1.

It may be noted in connection with the bottom right-hand curve in Fig. 9.2 (the largest disc in the wide ring) that the inhibition generated at the outer edge of the ring cannot act on the first flash at interval times shorter than about 90 ms, since it will take about 90 ms to be propagated as far as the first flash (see Fig. 8.3). Hence, at short interval times only the inhibitive effect of the inner edge is detected, and only for larger interval times can the inhibition from both edges be active. Comparing these results with those for short interval times and large discs, we do indeed see that the adjusted luminance increases faster with increasing time interval for the thin ring than for the wide ring.

9.3.3 COMPARISON WITH METACONTRAST DATA. The stimuli used for the experiments of Fig. 9.1 and 2 were typical metacontrast stimuli, especially the ones with a disc diameter equal to the inner diameter of the ring. The results for the largest discs follow the pattern often reported in the literature for metacontrast measurements: an increase in the intensity of the interaction up to an interval time of 70 to 90 ms and a decrease for larger interval times. To the best of our knowledge, a relation between metacontrast effects and those observed using elementary stimuli has never

before been suggested in the literature. However, the considerations presented in this chapter indicate clearly that the model used to describe the inhibition effects for elementary stimuli may also be used to describe metacontrast-like effects. Since these elementary stimuli are found to give rise to propagating inhibition, it is tempting to suggest that similar propagating inhibition plays a role in metacontrast.

9.3.4 COMPARISON WITH METACONTRAST THEORIES. There is an extensive body of literature on metacontrast, which has led to the development of a number of models for this phenomenon. The most widely held theories can be divided into two groups; those presupposing sustained-transient inhibition and those involving lateral inhibition networks. If the propagation of inhibition as described in this thesis forms the general basis of metacontrast, this will have important implications for the theories.

The neural network explanation suggested by Bridgeman (1971) makes use of a network proposed by Ratliff (1965) for simulation of the responses to a metacontrast stimulus. It is found that the simulated response after presentation of both stimuli looks more like the response to the second stimulus presented than to the first one. Bridgeman suggested that this would form the basis for metacontrast effects. However, this neural network is essentially based on forward propagation of inhibition: "at any time t a neuron is being inhibited by signals which originated from its immediate neighbors at t-1, from twice as far away at t-2, etc." (Bridgeman, 1971, p.530). It is not clear how these effects can be related to the backward propagation of inhibition.

Another neural network proposed by Weisstein and her co-workers (Weisstein, 1968; Weisstein et al., 1975) is based on the assumption that units with a fast response inhibit units whose response is slower. It follows that the stimulus for the fast-responding units would have to be delayed in order to have them interfere with a prior stimulus (in other words, this model implies backward masking). Neurophysiological evidence for such a view has been presented. The idea of the propagation of inhibition can be fitted into this model quite easily: the combination of a number of these

networks (such as that in Fig. 11.5 in Weisstein et al., 1975) in series would clearly result in backward propagation of inhibition.

The idea that metacontrast is based on a "transient-sustained" mechanism meets with widespread acceptance nowadays. There is a considerable body of psychophysical evidence for this view, which does not assume any direct link between neural networks and metacontrast effects (Breitmeyer and Ganz, 1976; Breitmeyer, 1978, Matin, 1975; Mitov et al., 1981; Breitmeyer and Rudd, 1981). It is assumed in such models that the sustained (slow responding) activity of certain cells or groups of cells is inhibited by the transient (fast responding) activity of others. It is interesting to compare the ideas presented in this thesis with this description. We found that the inhibition arises on the spatiotemporal flanks of the response to the stimulus. Now transient channels are known to be involved in signalling the spatial location or motion of a stimulus (Breitmeyer and Ganz, 1976); it follows that their operation must involve some kind of edge effects. Furthermore, we found that inhibition acts over the whole area stimulated by the probe. This may be considered to be analogous to inhibition of the sustained channels which are involved in the processing of structural or figural information.

Inhibition of the signals passing through sustained channels by those in transient channels, as suggested by Breitmeyer, might thus be applicable to the present situation. However, the sustained-transient hypothesis as currently presented does not include any propagation of the inhibition.

The overall conclusion to be drawn from the above discussion is that foveal inhibition (which, like peripheral inhibition, can be described as being propagated in time) offers a reasonable explanation for many features of metacontrast, though certain aspects remain to be clearified.

9.4 SUMMARY

The hypothesis formulated from measurements with elementary jumping flashes are used to describe the results found for a metacontrast stimulus consisting of a disc which is followed after a certain delay by a ring surrounding the disc. Mathematical expressions are given for the model. It is suggested that the propagation of inhibition is the mechanism underlying metacontrast; the data do not seem to contradict this.

9.5 APPENDIX

In this section the derivation will be given of an expression for the inhibition produced with extended stimuli in terms of data for elementary stimuli.

The peak times found using two elementary point flashes of diameter 1 min arc and duration 10 ms can be described by the following expressions

$$t_{\text{peak},1} = \frac{d - 3.5'}{v} \quad \text{and} \quad t_{\text{peak},2} = \frac{d + 3.5'}{v} \qquad (1)$$

where d (in min arc) represents the centre-to-centre distance between the two flashes, v the propagation velocity (in min arc per ms) and 3.5 min arc is the intercept with the distance axis of the plot of the peak times against the flash distance, see Fig. 8.3. (The peak times could equally well be described with reference to the intercept with the time axis, 18 ms; this choice would lead to a course of argument essentially identical with that developed below).

If the diameter D of the second flash changes by ΔD (=D-1') then one of the edges of this flash approaches the first flash by 1/2 ΔD, while the other edge recedes by an equal amount. As a result of the propagation of the inhibition, the peak times now become

$$t_{\text{peak},1} = \frac{d - 3.5' - \frac{1}{2}\Delta D}{v} \quad \text{and} \quad t_{\text{peak},2} = \frac{d + 3.5' + \frac{1}{2}\Delta D}{v}$$

Increasing the duration T of the second flash by an amount ΔT (=T - 10 ms) only influences the lower peak time (see text), so

$$t_{peak,1} = \frac{d - 3.5' - \frac{1}{2}\Delta D}{v} - \Delta T$$

$$\text{and} \quad t_{peak,2} = \frac{d + 3.5' + \frac{1}{2}\Delta D}{v} \qquad (2)$$

The lines in Fig. 8.5 are calculated with these expressions for a number of durations T and diameters D.

For the calculation of the results for extended stimuli we now introduce a time function which has a maximum of 1 at t = 0. This function is meant to describe the form of the inhibition peaks, such as, for example, the first peak in the middle curve of Fig. 8.2. Actually a Gaussian function is used with a standard deviation of 15 ms. The results measured with elementary point flashes can then be described by

$$R(t) = a \sum_{j=1,2} G(t_{peak,j}) f(t - t_{peak,j}) \qquad (3)$$

where R(t) is the amount by which the luminance of the first flash has to be increased to obtain equal brightness of the two flashes (if R(t) = 0 the brightness of both stimuli is the same when their luminance is equal), G(t) is the height of the peaks as a function of the time at which they are found (the curve of Fig. 8.4), f(t - tpeak) is a time function having a peak at t = tpeak and a is a constant.

For larger probes, formula 3 has to be integrated over all possible peak times. A first flash of diameter S can be used to the detect the propagating inhibition over a range of interval times equal to S/v, so that the results obtained with an inhibition generating flash of diameter D and duration T, using a probe flash of diameter S, may be described by the following expression:

$$R(t) = a \sum_{j=1,2} \int_{t_{\text{peak},j} - S/2v}^{t_{\text{peak},j} + S/2v} G(t_{\text{peak}}) f(t - t_{\text{peak}}) \, \mathrm{d}t_{\text{peak}} \quad (4)$$

where the peak times are given by equation (2). The curves of Fig. 9.1, 9.2 and 9.3 were obtained by a numerical procedure based on this expression, which was used to calculate the expected results for a series of interval times increasing in steps of 2 ms.

10.

SPATIAL AND TEMPORAL TWIN FLASH RESPONSE

Chapter 10 SPATIAL AND TEMPORAL TWIN FLASH RESPONSE

10.1 INTRODUCTION

All experiments described in the previous chapters have in common that the inhibition is always detected at locations outside the area stimulated by the generator of the inhibition.

Measurements of the twin flash response as a function of the flash diameter (Meijer et al. 1978) showed that the response was subject to an inhibition effect, but only above a certain flash diameter and a certain delay time. This led to the idea that the spatiotemporal point spread function of the human visual system consists of an area of summation surrounded by an interaction-free zone, which in its turn is encircled by an inhibition region.

Measurements with jumping flashes confirmed that the inhibition generated by a small flash of short duration is to be found at a certain distance away from the point of excitation and at a certain interval time. Those results indicated that inhibition is propagated and manifests itself as two dips in the visibility curves. Instead of this, Meijer and co-workers found one dip at a stationary interval time. One of the differences between the two situations is that Meijer used probes which were presented within the spatial area stimulated by the generator, whereas we until now, have only considered measurements outside this area. Therefore, in the present chapter a study is made of whether propagating inhibition effects can be observed within the spatial area covered by the generator.

In addition, we examine whether the high degree of symmetry for the spatial and the temporal properties of the propagating inhibition is also present for twin flashes.

Since in this chapter many combinations of flash diameter and duration are discussed which can also be different for the two flashes, the stimulus in each figure is plotted in a position (vertical) versus time (horizontal) plane.

10.2 RESULTS

Measurements were done on the visibility of a twin flash (two successive flashes presented to the same retinal position) as a function of the interval time between the flashes. The flashes were presented near the centre of a stationary background field of diameter 3.7 degrees. In all experiments, the flashes were presented to the right eye at 3 degrees nasal. Both flashes had a visibility on their own of about 45 %. The results are given in Fig. 10.1 for two diameters of the flashes: 5.7 min arc (upper curve) and 57 min arc (lower curve). The results are the mean of 7 runs of 25 presentations. The standard deviation of the mean is about 5 %. Both curves have in common that for low interval times a high visibility (about 95%) is found and for large interval times a constant visibility of about 68 % is found. With large twin flashes, however, a dip is found at an interval time of about 50 ms which is not present in the results for the small twin flashes. The results indicated with the blocks were obtained using randomized interval times.

In order to investigate the difference between the two curves in Fig. 10.1 measurements were performed in which one flash had a diameter of 5.7 min arc and the other flash 57 min arc, the smaller flash being presented at the centre of the larger one. The results are given in Fig. 10.2 in which the upper curve represents the result found when the smaller flash was presented before the larger one, and the lower curve was obtained when the larger flash was the first. The results are comparable with those in Fig. 10.1: with the small flash presented first no dip is found, with the larger presented first a dip is found at an interval time of 50 ms.

In the next experiments the first flash was the small one and the second flash was the larger (compare upper curve of Fig. 10.2). The position of the first flash with regard to the second flash was the parameter: instead of placing the small one in the centre of the second one it was now placed at different positions. The results in Fig. 10.3 were gathered with the first flash presented within the large flash at distances of 10, 15, and 20 min arc from the edge. The lower right curve is found with the small flash presented 15 min arc outside the larger one.

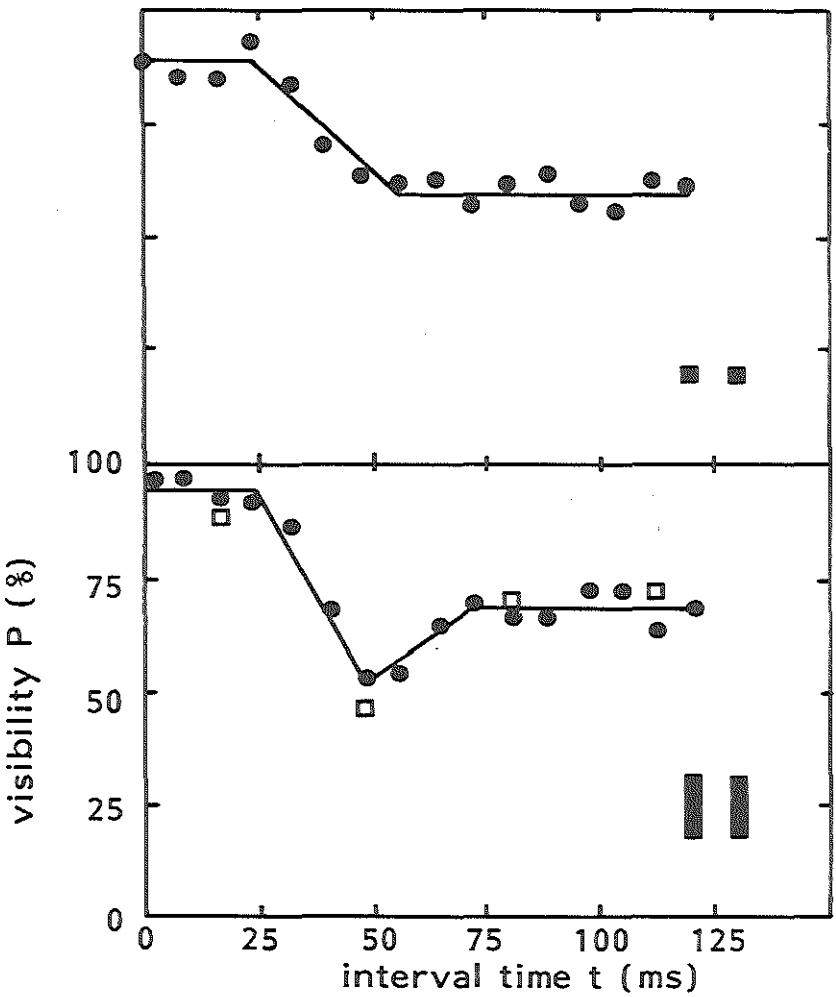

Fig. 10.1 The visibility of a spatial twin flash as a function of the interval time for flashes with two diameters: 5.7 min arc and 57 min arc respectively. In Fig. 10.1 - 10.6 the small plots at the bottom right give a schematic representation of the stimuli used in a position (vertical) versus time (horizontal) diagram.

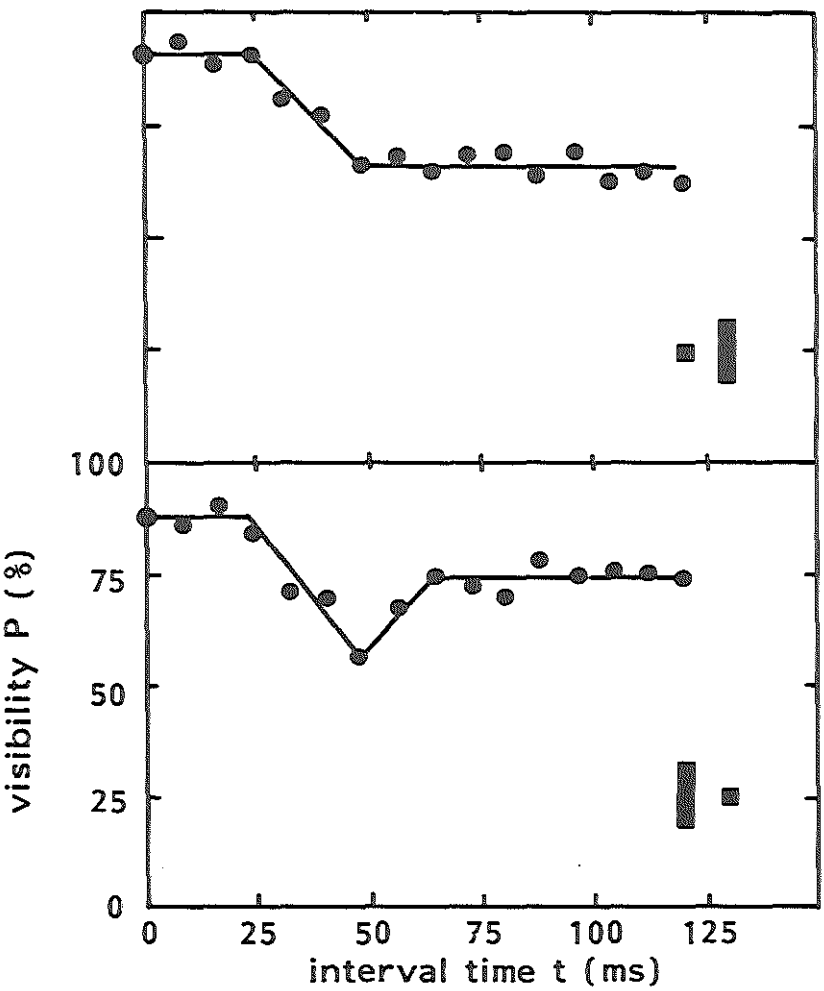

Fig. 10.2 The visibility of spatial twin flashes using different diameters (5.7 or 57 min arc) for the two flashes. For the upper curve the small flash is presented first.

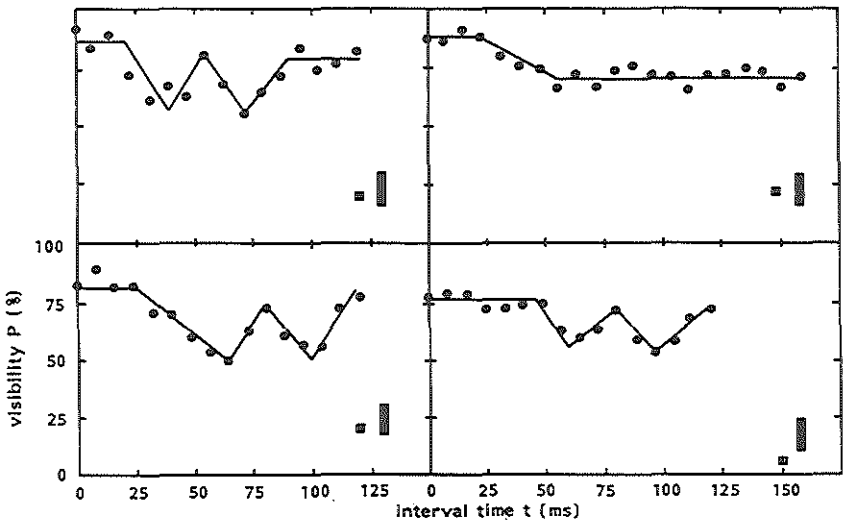

Fig. 10.3 The visibility of a stimulus consisting of a 5.7 min arc and a 57 min arc diameter flash as a function of the interval time. The parameter is the distance between the small flash and the edge of the larger one.

The interval times at which the dips are found in the Fig. 10.3 curves are plotted in Fig. 10.4 against the distance between the smaller flash and the edge of the larger flash. The results found with the small flash outside the large flash are depicted at a negative distance. The small horizontal lines indicate distances at which no dips were found. The line represents the results found with two elementary point flashes and are replotted from Fig. 3.10.

For reasons of symmetry it was expected that the temporal equivalent of the spatial twin flashes would yield similar effects (see discussion). Therefore measurements were performed with temporal twin flashes, i.e. two flashes presented simultaneously, but with a certain distance between them. Measurements were made for temporal twin flashes as a function of the distance between the flashes with the duration of the flashes as a parameter (compare the results in Fig. 10.1 for spatial twin flashes, which are expressed as a function of the interval time between the flashes with the diameter

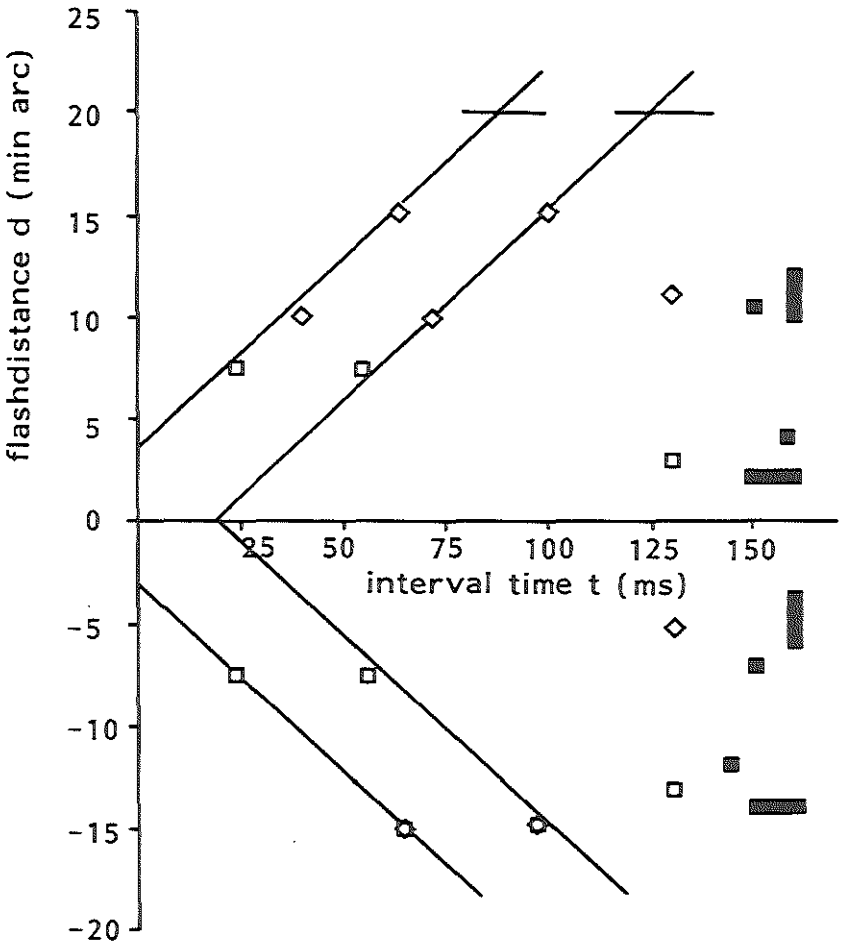

Fig. 10.4 Schematic representation of the distance against the interval time at which dips are found. The results marked (+) are found with a spatially extended second flash, those marked (x) are from measurements with a temporally prolonged flash. The results in the upper part are obtained when the probe is presented within the spatial or temporal area stimulated by the generator, while for the lower part the probe is presented outside this area.

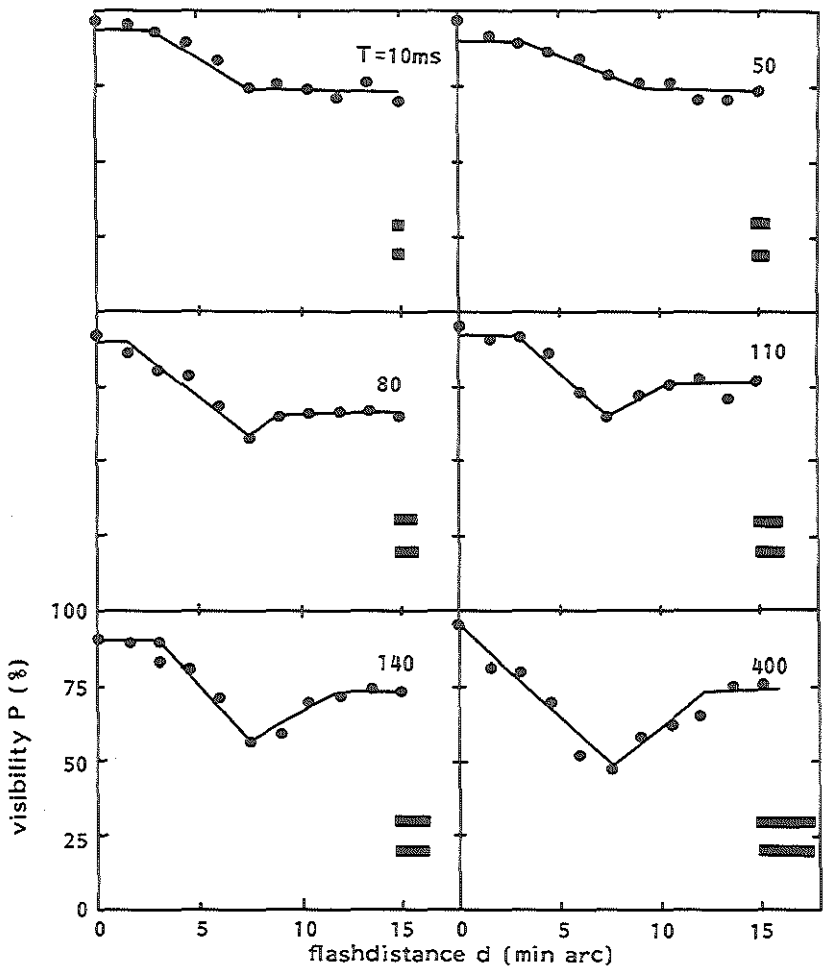

Fig. 10.5 The visibility of a temporal twin flash as a function of the interval time, the duration of the flashes being the parameter.

of the flashes as a parameter). The results are given in Fig. 10.5. For small separations a high visibility is found for all durations, while for large separations the visibility is constant at the value determined by probability summation. For durations of 10 and 50 ms no dip is found while for durations longer than 110 ms dips are found. The 80 ms results show a small dip which is just significant.

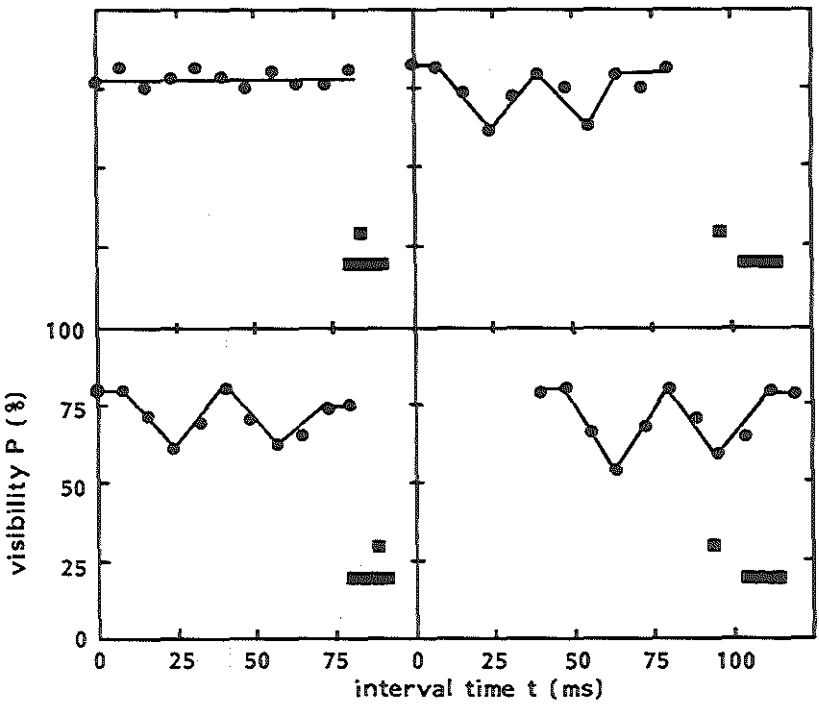

Fig. 10.6 The visibility of a stimulus consisting of a 10 ms and a 400 ms duration flash as a function of the interval time. For the lower left curve, the interval time with regard to the termination of the longer flash is given along the horizontal axis. The distance between the flashes is 7.5 min arc except for the lower right curve, where it is 15 min arc.

In analogy with Fig. 10.3 measurements were also performed with a short, small flash (diameter 5.7 min arc, duration 10 ms) presented within the time range i.e. after the beginning or before the end of another flash of small size (diameter again 5.7 min arc) but of long duration (400 ms instead of 10 ms). The results are given in Fig. 10.6. For all curves the distance between the flashes was 7.5 min arc except for the bottom right one, where the distance was 15 min arc. For the upper left curve, the short flash was presented shortly after the onset of the long flash; for the right two curves the short flash was presented before this onset. The results are plotted against the stimulus onset asynchrony (the interval time between the beginning of the two flashes). For the left lower curve, the short flash was

presented shortly before the termination of the longer flash and the results are given as a function of the interval between the termination of the two flashes.

The dip times found with one flash of short duration and one longer flash are also plotted in Fig. 10.4 (as diamonds) in exactly the same way as the spatial results. Thus, the dip times found with the short flash presented during the presence of the longer flash are plotted in the upper half of Fig. 10.4, and the dip times found with the short flash presented 'out of' the longer flash (in fact, before) are plotted in the lower half of Fig. 10.4.

10.3 DISCUSSION

The main conclusion that Meijer et al.(1978) drew from their experiments was that the point spread function consists of a summation area and a surrounding inhibition region. Each point is assumed to give rise to such a point spread function. Contrary to this, the experiments described in this thesis indicate that the inhibitory activity appears only to be generated at the edges of the stimuli. As this seemed contradictory, the inhibition activity for extended stimuli was measured, using small probes to detect inhibition with high resolution and larger probes to enable comparison with Meijer's results.

The results found with two identical flashes of diameter either 5.7 or 57 min arc (see Fig. 10.1) are comparable to those given by Meijer: with the small flashes no evidence of inhibition is found while with the larger stimuli a clear inhibition effect can be seen. The interval time at which the inhibition is found is different: Meijer reports maximum inhibition for interval times of about 70 ms whereas in the present study maximum inhibition is found at an interval time of 50 ms.

If it were the case that each point of the second flash generates inhibition, it might be expected that using a small probe in the centre of a large generator would give similar results to those found with a large probe (i.e. with two large flashes). The results given in Fig. 10.2a show that this is

not the case: no evidence of inhibition is found with a small probe while with a larger probe using the same size of the generator, there is clear evidence of inhibition (see Fig. 10.1, the lower curve). So it seems that the diameter of the probe is important.

To check the influence of the size of the generator, its diameter was enlarged using a large and a small probe. Under these circumstances inhibition is again found. Moreover, it occurs at the same interval times as found using two large flashes (see Fig. 10.2b). Thus, the difference between the upper and the lower curve in Fig. 10.1 is caused by the dimensions of the probe used; the diameter of the generator is not relevant.

Comparing the upper and lower part of Fig. 10.2 it may be noted that the only difference in the stimuli is the sequence of the two flashes. Remembering that inhibition is generated at the edges of the second flash, the difference in the results found can be understood as follows: with the small generator the inhibition is generated at the edges, the large probe being presented at interval times and distances where the inhibition is active and can be detected. With the large generator and the small probe, the inhibition is generated near the edges of the large flash and cannot reach the centre, where the small probe is presented, due to the limited propagation range of the inhibition.

In the latter case, propagating inhibition should be detectable with the small probe when the probe is placed near the edge of the large generator. The results in Fig. 10.3 show that inhibition can indeed be found when the small flash is presented nearer to the edge, so it is evident that the distance to the edge is the crucial parameter. Inhibition is also found with the probe 15 min arc outside the edge. The interval times at which the inhibition is found are plotted in Fig. 10.4 against the distance to the edge. The results found with the probe outside the edge are plotted at a negative distance. The straight lines have a slope of 3.1 degrees per second; that is the same as the propagation velocity found with elementary stimuli. When the probe is placed 20 min arc inside the generator no inhibition is found. So the assumption of one unique point spread function cannot be maintained.

Although it seems that similar results are found in Fig. 10.3 as were found with elementary flashes (compare e.g. Fig. 3.10) we have to realize that for Fig. 3.10 we explained the dual nature of the inhibition (the two dips in the curves) by reference to the two flanks. But now two dips are found which seem to originate at one edge. Because of the duration of the stimuli, which is still 10 ms, temporal flanks exist which are separated by the same amount as those caused by elementary flashes.

In Chapter 5 complete symmetry was found between the spatial and temporal effects. The inhibition could be described by reference to the spatial flanks, but also by reference to the temporal flanks. For the large generator used here, this symmetry vanishes: if we still retain a description in terms of inhibition arising at two flanks, we have to consider the temporal flanks. This seems to indicate that the temporal flanks of a stimulus are of primary importance in the generation of inhibition. If this is true, one must expect one single dip for a small flash of long duration. But if the symmetry is retained, two dips can be expected. Therefore similar experiments were performed but then translated into their spatiotemporal counterpart: for instance, twin flash measurements for flashed discs (of short duration) with various diameters as a function of the interval time were replaced by measurements on the visibility of two small point flashes of various durations as a function of the distance between the flashes.

The results shown in Fig. 10.5 show a remarkable resemblance to those in Fig. 10.1: with flashes of short duration there is no evidence of inhibition whereas the use of flashes of long duration results in a clear inhibition dip in which the visibility drops to about 50 % at a distance of 7.5 min arc. (Transforming this value into its temporal analogue via the propagation velocity leads to a time of 40 ms, which is close to the dip time found in the experiments in Fig. 10.1).

These results can be understood in terms of the concept of the propagation of inhibition. When the duration of the stimuli is short and they are presented simultaneously, inhibition is generated but cannot be detected. When the duration increases, the flashes are still present when the inhibition from the other flash arrives. The similarities between the

curves in Fig. 10.5 and 10.1 are unexpectedly large. In the spatial case it is clear that one of the flashes is inhibited which results in a visibility equal to that of the remaining flash. For the temporal twin flashes this distinction cannot be made: both simultaneously presented flashes influence each other in the same way. The fact that the visibility in the dips of the curves in Fig. 10.5 also is about 50 % thus cannot be ascribed to complete inhibition of one of the flashes.

The similarities are again found when instead of placing a small flash outside a large flash, a flash of short duration is presented before the onset of a flash of long duration (compare Fig. 10.6 with Fig. 10.3). Increasing the distance between the flashes results in an increase in the dip times, as might be expected on the basis of the spatial experiments. Similar results are found when the probe is presented before the termination of the long flash (the lower-left curve of Fig. 10.6). However, when the probe is presented shortly after the onset, no inhibition is found as the propagation of inhibition is only in one temporal direction (backwards). The measured dip times are plotted in Fig. 10.4 as diamonds and it can be seen that they coincide with the results found with the spatial twin flashes. So it seems that inhibition is found in those circumstances where it can be expected on the basis of propagating inhibition.

Thus, from the temporal twin flash experiments it can be concluded that the inhibition behaviour is again symmetric in place and time and that the inhibition propagates inside a stimulus in the same way as it does outside.

10.4 SUMMARY

The inhibition behaviour is studied for large discs of short duration and for point flashes of large diameter. It is shown that for those stimuli the inhibition is only generated at the edges of the stimuli and not at the inner parts of the stimuli. It is also shown that similar inhibition effects are generated both inside and outside the area stimulated by the inhibition generating flash.

11.

GENERAL DISCUSSION

Chapter 11 GENERAL DISCUSSION

INTRODUCTION

Throughout this study measurements have been carried out to examine various aspects of the propagation of inhibition. The results were discussed for each topic separately. In this chapter more general aspects of the type of inhibition in question will be discussed.

SYMMETRY BETWEEN SPATIAL AND TEMPORAL ASPECTS OF VISION

The visual system is remarkably symmetrical with respect to spatial and temporal effects. The shape of the contrast transfer function, for instance, is almost the same for spatial contrast as it is for temporal contrast. Even the influence of the parameters of the grating or of the flickering light show a high degree of symmetry for spatial and temporal effects. Van der Wildt (1984) showed that, for example, the influence of the width and the presentation time of a grating on the spatial contrast sensitivity curve is comparable to the influence of the duration and the diameter of a flickering light on the temporal contrast sensitivity curve. When a spatial parameter is translated into its temporal counterpart its influence on the transfer function is very much alike.

For an elementary jumping flash the spatial, c.q. temporal counterpart is the same jumping flash: this stimulus is symmetrical to such an extent that exchanging place and time does not influence it at all. This symmetry is also found in the results: the effect of increasing the interval time between the two flashes (at a fixed flash distance) is the same as that of increasing the distance between the flashes (keeping the interval time constant). The influence of the diameter and the duration of the flashes also show this high degree of symmetry for spatial and temporal effects.

A velocity is one of the few parameters which yield a direct relation between spatial and temporal effects. For the inhibition, a constant propagation velocity is found. This propagation velocity might be the basic phenomenon for the spatial/temporal symmetry. In that case, this propagation

velocity is the translator between spatial and temporal aspects of vision. This has been established for summation when it is determined with elementary stimuli: it was found that the ratio of the spatial and temporal summation area equals the propagation velocity. Comparison of the grating and flicker measurements leads to ratio's between 1 and 3 degrees per second (as described in Chapter 3). It is tempting to suggest that the propagation velocity of inhibition is the primary effect resulting in the symmetry between spatial and temporal aspects of vision, but it cannot be excluded that other effects play a role, which might even be of greater importance.

INHIBITION AS AN EDGE EFFECT

With elementary jumping flashes inhibitory effects were found which appeared to be elicited at the flanks of the response to the stimuli. For more complex stimuli, the results can still be described as being tied to the edges of the response to the stimulus; an increase of the diameter or the duration of the flashes results in a shift of the interval times at which the inhibition effects are measured. This shift is linearly related to the shifts in diameter and/or duration. When there is a discontinuity in the luminance distribution, inhibition is generally assumed to result in a magnification of that discontinuity. As such, inhibition may serve to enhance the appearance of borders and contours. The merit of the explanation of inhibition being generated at the flanks of the response is its simplicity. Nevertheless, it enabled us to describe metacontrast measurements with extended stimuli, quantitatively.

The description involves, however, a strongly non-linear generation of inhibition: concerning the inhibition, it is certainly not correct to describe a large stimulus as a number of neighbouring small ones, as often is done. In the literature there is, indeed, a discrepancy between the experimental data for thresholds for extended stimuli and the predicted values on the basis of data obtained with small stimuli. When the point spread function for a small stimulus of long duration is measured, evidence is found for inhibition. When the response to extended stimuli is described as a linear summation of a number of these point spread functions, large deviations are found between theory and experiment (see Blommaert

and Roufs, 1981). On the occurrence of inhibition only being generated at the edges of the stimuli, the point spread function including inhibition only holds for the elements near the edge of an extended stimulus. The central parts of such a stimulus would give rise to a point spread function without inhibition. Since the amount of edge relative to the amount of inner part decreases rapidly with the flash diameter, it might be expected that for the description of threshold data for large stimuli, the influence of the inhibition is negligible and need not be taken into account at all. This agrees with the findings of Ricco (1877) who reported that within certain limits of the diameter of a test stimulus the effect produced by the absorption of light in the receptors depends only on the product of intensity and surface of the test area. In the literature it has been suggested that at each location on the retina more than one point spread function exists (Koenderink and van Doorn, 1978; Wilson and Bergen, 1979). These point spread functions would all exist at each spatial location; the most sensitive for a specific stimulus would determine its threshold. However, once the choice is made, the further elaboration is principally linear. The essence of inhibition being bound to the edges of a stimulus is that the choice for a specific point spread function (with or without inhibition) is made upon considering each part of a stimulus in connection with its neighbours.

INHIBITION VERSUS FACILITATION

It has been shown that the inhibitory effects are only effective when background light is present within the range of the effects. Without a background no inhibition is to be found. Even if there were inhibitory activity, it would not be profitable since there is no activity that is bound to be suppressed. A study by van den Brink and Reijntjes (1966) at the absolute threshold level (i.e. against a dark surround) showed that there is evidence for the inverse effect, facilitation: as soon as a suprathreshold effect is present, the subthreshold activity in other parts of the retina can be enhanced and become suprathreshold. Evidently, with a background, the visibility of details can be improved by suppression of the surrounding activity, whereas overall visibility can be improved by facilitation, when there is no background activity. Combining these findings thus seem to lead to an optimal performance of the system for all luminance levels.

THE POSSIBLE EFFECTS OF EYEMOVEMENTS ON THE RESULTS

It was mentioned in Chapter 3 that the dips as found in the curves like Fig. 3.3 have a half-height width of about 10 ms, or in the spatial analogue, 2 min arc. One may wonder whether these small values are likely to be effective because of a subject's eye movements. Eye movements can be divided into two groups, the saccades (fast changes in eye position during short times) and drift (which is much slower). When the subject's eye makes movements in between the presentation of the two flashes that form the jumping flash, the retinal distance of the flashes may not be equal to the presented distance. The chance that a saccade occurs between the presentation of the flashes is, however, rather small, since the interval time between the flashes is at most 200 ms. Thus saccades are unlikely to have a significant influence on the results. Saccadic suppression due to an eye movement which is evoked by the first flash can be excluded as the origin for the dips. Because the latency for such an eye movement is already in the order of 200 ms.

In Chapter 8 it has been stated that the standard deviation of the subject's eye movements during fixation is about 1.5 min arc for a stationary target with a diameter of 3 min arc. This value can be taken as an (over-) estimate of the eye movements between the presentation of the two flashes. The fact that we found such small widths for the minima in our data may be due to the foregoing reason.

FORWARD OR BACKWARD INHIBITION

Throughout this thesis the inhibition found has been referred to as backward inhibition. This was based on the observation that the first flash is being inhibited by the second one. No reaction, however, can take place before an action. In Chapter 3 it was stated that we assume that the processing of the first flash is shaded by the presentation of the second flash, but this can be expounded further. On the basis of experiments in which the stimuli were presented dichoptically, it has been established that this type of inhibition is likely

to take place at a high level in the processing of visual information. Other investigators (see e.g. Breitmeijer and Ganz, 1976) have reported that the response to a stimulus can be divided into two parts: one fast responding with low spatial resolution (the transient response) and one slow responding with a high spatial resolution (the sustained response). If it is assumed that the transient response to the second flash inhibits the sustained response to the first flash, no problem exists with regard to causality. It would then be more correct to refer to forward propagation rather than backward propagation. The transient response would in that case be propagated in the cortex. When the flashes are presented near each other the propagation only has to be over a short range, so inhibition is found for small interval times. With larger separations, it takes longer to reach the sustained response to the first flash, so the inhibition is only to be found at longer interval times. This description assumes that the imaging from the eye to the cortex is retinotoop, (separate parts of the retina give rise to response at separate parts of the cortex), and the 'distance' within the cortex should be proportional to the distance at the retina. There is physiological evidence for such a system. The fact that the propagation velocities are independent of the eccentricity is however not what would be expected on the basis of known aspects of the physiology: it has been found that the ratio of 'cortex distance' and retinal distance decreases with the eccentricity (Koenderink, 1978: Rovamo and Virsu, 1979). For the temporal aspects of vision, such an eccentricity dependency does not exist (van den Brink, 1957; Rovamo and Raninen, 1984). The constancy of the velocity found thus implies that when the inhibition takes place in the visual cortex, the 'cortical velocity' (expressed in mm cortex per second) depends on the place within the cortex.

INHIBITION AS AN IMAGE-CONTROLLED SHUTTER

Generalizing the results, it can be said that when changes occur in the luminance distribution somewhere in the visual field, the surrounding activity is suppressed before the new part is filled in. This may be analogous to the procedure used when one wants to write on a full blackboard: firstly an area is cleaned and successively the new information is put on it. By cleaning the spot before the presentation of the new information and erasing the previous information,

attention is drawn to that location. In this paradigm the function of inhibition can be that of a image-controlled shutter: changes in the image on the retina lead to suppression of the old scene. This clearance prevents the perception of blurred images, and as such it would be an effective way of preserving the visus for moving images. The experience in daily life, that the appearance of changes somewhere in the visual field directly draws the attention, might be a similar effect. In addition, it is also more efficient to change only those parts that are different from the previous image. This is in agreement with the general notion that sense organs are more sensitive for changes and inhomogeneities than they are for continuity (see e.g. van den Brink, 1982). Recent developments in video techniques are based on similar considerations: quite often, only a part of the screen changes at a time (e.g. a moving person against a stationary background). By transmitting only the changes in the image, a large reduction of the bandwidth is possible. So, in a system with a certain bandwidth, the information processing capacity can be enlarged by first extracting the things that have to be changed and only transmitting those new things.

CONCLUDING REMARKS

In the literature it has been established that inhibitory effects can only be detected with stimuli of suitable spatial and temporal extension. As a result, the resolution of the determination of the spatial and temporal properties of the inhibition has been limited. In the present study measurements have been described using two small stimuli of short duration which are separated in time and in space. This separation in time and space can be seen as substitutes for continuity in time and of extensiveness in place, respectively. This study shows that by using such a stimulus it is possible to isolate the important properties which are a neccesary condition for the detection of inhibition, without loosing resolution. The measurements with this kind of stimuli enabled us to recognize typical spatiotemporal properties of inhibition occuring in large stimuli of long duration that cannot be found with such stimuli themselves.

ABSTRACT

ABSTRACT

In this thesis measurements are described by which the dynamic behaviour of lateral inhibition in the human visual system is investigated, using psychophysical methods.

When elementary jumping flashes are used as stimuli, the dynamic behaviour of inhibition can be determined with a high resolution for both position and time. (Jumping flashes are two small flashes of light which are presented one after the other and a small distance apart.) When the distance between the flashes is kept constant and the interval time between them is varied, it is found that for two small ranges of interval times, the visibility decreases from the value expected on the basis of probability summation to the single flash visibility. It is shown that under these circumstances only one of the flashes is visible and the other is inhibited. It is apparent that inhibition is not a stationary phenomenon, but that it moves away from its origin. A flash can be inhibited when it is followed after a certain delay by another one. When the distance between the flashes is increased, the inhibition is found at longer interval times, indicating the propagative character of the inhibition. The velocity of propagation is constant.

The two inhibition dips which have been identified and which are propagated at a constant velocity are remarkably independent of the parameters of the stimuli. The eccentricity at which the jumping flashes are presented has an influence on the interval times at which the dips are found, but does not influence the propagation velocity. Similar effects are found with suprathreshold stimuli: there are two ranges of interval times where the brightness of the first flash is reduced by the presentation of the second flash. These measurements again lead to the same propagation velocity as found with stimuli presented at the increment threshold luminance. The same applies to the colour of the stimuli: the inhibition dips occur at identical times for all combinations of red and green for the first and the second flash. Neither the increment luminance of the inhibition-generating flash nor the background luminance has any influence on the dip times. The background luminance does, however, effect the shape of the dips: at a higher luminance the dips become broader until only one large dip remains. No inhibition is

found with a dark background. The only parameter that has an influence on the velocity of propagation is the direction in which the flashes jump. For flashes jumping to or away from the fovea a velocity of 3.1 degrees per second is found, whereas tangentially jumping flashes result in a velocity of 4.2 degrees per second. It is assumed that the distribution of the velocities over the direction of jumping is elliptical.

The fact that two dips were repeatedly found in the measurements led to the idea that the inhibition might be generated at the edges of the response to the stimuli. The width of the response for elementary stimuli is a direct measure of the summation areas. So, a relationship might be expected between the summation areas and the properties of the propagating inhibition. These relationships were sought and found. It became apparent that the distance (or interval time) between the two inhibition dips is equal to the spatial (or temporal) summation area. As a result, the velocity of propagation of inhibition is equal to the ratio between the spatial and temporal summation areas.

The idea that inhibition arises on the flanks of the response was further tested by changing the diameter and duration of the stimuli and studying their influence on the inhibition. It was demonstrated that the second flash inhibits the first one; so the inhibition is backwards. When the duration of the second (inhibition-generating) flash is increased, the inhibition dips move further apart. The shift is linearly related to the increase in duration, as might be expected on the basis of the model. Increasing the diameter of the second flash also results in shifts in the interval times at which the inhibition is found. These shifts are linearly related to changes in the diameter (divided by the propagation velocity). It is thus impossible to distinguish between the temporal and the spatial flanks in the generation of inhibition. When both the diameter and the duration are increased, the shifts in the dip times are equal to the sum of the shifts which might be expected from an increase in either the diameter or the duration.

Measurements with extended stimuli of long duration which are presented at increment threshold luminances give deviations from the model. These deviations are associated

with the increment luminance used. As soon as the increment luminance of the stimuli is less than 1.5 % of the threshold luminance for an elementary flash (with duration 10 ms and diameter 1 min arc), the dip times are no longer determined by the actual diameter and duration, but only by the increment threshold luminance.

When stimuli are presented at suprathreshold luminance levels propagating inhibition effects are found which closely resemble the results found with threshold stimuli. The advantage of the suprathreshold method is that it gives a quantitative measure for the strength of the inhibition as a function of the time, whereas the measurements at threshold level indicate little more than the presence or absence of inhibition.

The results found with elementary stimuli are used to describe metacontrast. Metacontrast is the phenomenal reduction in the brightness of a disc when it is followed after a certain delay by a surrounding ring of light (ring diameter of the order of 1 degree). Assuming that inhibition only arises at the edges of the ring and acts on the disc with a time variation as found with elementary stimuli (diameter of the order of 1 min arc), it is possible to account quantitatively for the results of metacontrast measurements. This suggests that the propagation of inhibition is the mechanism underlying metacontrast.

The luminance of the background against which the flashes are presented has an influence on the results. When no background is present, no inhibition can be detected. Measurements with light or dark bars in the neighbourhood of the jumping flash show that inhibition is only generated when background light is present within the propagation range of the inhibition.

When the inhibition generated by a flash with a large diameter (1 degree) is measured using an elementary probe flash, it is once again found that inhibition is only generated at the edges. Although propagating inhibition is found under these circumstances too, the symmetry between spatial and temporal effects as found with elementary stimuli no longer holds. The dips found are clearly bound to the temporal flanks of the spatially extended stimulus. Transposing this stimulus into its spatiotemporal counterpart (a small spot of light which

has a long presentation time) leads to results which can be accounted for by assuming that the inhibition arises on the spatial flanks of the temporally prolonged stimulus. Thus, the symmetry between position and time is again established.

SAMENVATTING

SAMENVATTING

In dit proefschrift worden metingen beschreven aan het dynamisch gedrag van laterale inhibitie in het menselijke visuele systeem, waarbij gebruik gemaakt wordt van psychofysische meetmethoden.

Met elementaire springflitsen bestaande uit twee kleine, kortdurende flitsen die na en naast elkaar aangeboden worden, wordt het dynamisch gedrag van inhibitie gemeten met een hoog scheidend vermogen in de tijd en in de plaats. Als de afstand tussen de flitsen constant gehouden wordt, dan wordt bij twee intervaltijden een afname van de waarnemingskans gevonden. In plaats van de op grond van kanssommatie verwachte zichtkans wordt dan een zichtkans gemeten die overeenkomt met de zichtkans van een enkele flits. Aangetoond is dat onder deze omstandigheden slechts een van de twee flitsen zichtbaar is; de andere is dan onderdrukt. Het blijkt dat de betreffende inhibitie effecten geen stationaire verschijnselen zijn, maar iets dat zich voortplant. Als de afstand tussen de flitsen groter is, wordt de inhibitie gevonden bij een grotere intervaltijd, hetgeen erop duidt dat de inhibitie een lopend verschijnsel is. Dit voortplanten geschiedt met een constante snelheid.

Het blijkt dat het vinden van twee inhibitieminima opmerkelijk onafhankelijk is van de parameters van de stimuli: de eccentriciteit waarop de stimuli aangeboden worden heeft een invloed op de intervaltijden waarop de dips gevonden worden, maar beinvloed de loopsnelheid niet. Met stimuli boven de drempel worden vergelijkbare effecten gevonden: voor twee intervaltijden wordt de helderheid van de als eerste aangeboden flits verminderd door de aanwezigheid van een tweede flits. Bij deze metingen wordt weer dezelfde loopsnelheid gevonden als met stimuli die op de increment drempel worden aangeboden. Hetzelfde geldt voor de kleur van de stimuli: alle mogelijke combinaties van rood en groen voor de eerste en tweede flits van de springflits resulteren in inhibitie minima op dezelfde intervaltijden. Ook de luminantie van de inhibitie opwekkende flits en de achtergrondluminantie hebben geen invloed op het tijdstip waarop inhibitie optreedt. De achtergrondluminantie beinvloedt wel de vorm van de minima: bij een hogere luminantie worden de dips breder totdat er uiteindelijk een groot minimum bestaat. Bij een donkere achter-

grond wordt geen inhibitie gevonden. De enige parameter die invloed blijkt te hebben op de loopsnelheid is de richting waarin de springflits springt. Voor springflitsen die naar, of van de fovea af springen wordt een snelheid gevonden van 3,1 graden per seconde. Voor tangentieel springende flitsen wordt een snelheid van 4,2 graden per seconde gevonden. Verondersteld wordt dat de verdeling van de loopsnelheden over de flits richtingen elliptisch is.

Het steeds vinden van twee minima in de resultaten heeft geleid tot het idee dat deze inhibitie ontstaat op de flanken van de responsie op een stimulus. De breedte van de responsie is voor elementaire stimuli een direkte maat voor de sommatiegebieden. Op grond hiervan worden dus relaties verwacht tussen de sommatiegebieden en de eigenschappen van de lopende inhibitie. Deze relaties zijn onderzocht en gevonden. Het blijkt dat de afstand (dan wel intervaltijd) tussen de twee inhibitie minima gelijk is aan het spatiele (dan wel temporele) sommatiegebied. Een gevolg hiervan is dat de loopsnelheid van de inhibitie gelijk is aan de verhouding van het plaats- en het tijdsommatiegebied.

Het idee dat deze inhibitie ontstaat op de randen van de responsie is verder getest door de duur en de diameter van de stimuli te veranderen en de invloed hiervan op het inhibitiegedrag te bestuderen. Bij deze metingen is aangetoond dat de tweede flits de waarneembaarheid van de eerst aangebodene onderdrukt: er is dus sprake van achterwaartse inhibitie. Als de duur van de tweede flits (die dus de inhibitie opwekt) vergroot wordt, schuiven de gevonden inhibitiedips uit elkaar. Deze verschuiving is evenredig met de duurverlenging, in overeenstemming met het genoemde flanken model. Wanneer de diameter van de tweede flits vergroot wordt, verandert de intervaltijd tussen de dips. Deze verandering is evenredig met de diameterverandering (gedeeld door de loopsnelheid). Hierdoor kan niet met zekerheid worden vastgesteld of de tijdflanken, dan wel de plaatsflanken bepalend zijn voor het opwekken van inhibitie. Als zowel de duur als de diameter vergroot worden, is de verschuiving van de minima gelijk aan de som van de verschuivingen die verwacht zouden worden ten gevolge van de duurverlenging enerzijds en de diametervergroting anderzijds.

Bij metingen met uitgebreide stimuli van lange duur, die

op drempelnivo worden aangeboden, treden afwijkingen van het model op die toegeschreven kunnen worden aan de gebruikte increment luminantie. Zodra de increment drempelluminantie van de stimuli minder is dan 1,5 % van de drempel voor een flits van 10 ms duur en 1 boogminuut diameter, worden de diptijden niet meer bepaald door de actuele duur en diameter, maar alleen door de increment drempelluminantie.

Wanneer de stimuli aangeboden worden met een luminantie boven het drempelnivo, worden lopende effecten gevonden die veel overeenkomsten vertonen met de resultaten gevonden met stimuli op drempelnivo. Het voordeel van de bovendrempelige metingen is dat deze ook een waarde geven voor de intensiteit van de inhibitie als functie van de tijd, terwijl met de metingen op drempel nivo weinig meer verkregen wordt dan een aanduiding voor de aan- of afwezigheid van inhibitie.

De met elementaire stimuli gevonden resultaten zijn gebruikt om metacontrast te beschrijven. Metacontrast is de reductie van de helderheid van een stimulus wanneer hierna een stimulus bestaande uit een eromheen passende ring (met een diameter in de orde van 1 graad) wordt aangeboden. Met de aanname dat inhibitie ontstaat op de randen van de ring en onderdrukkend werkt op de schijf met een intensiteit, zoals gevonden is met elementaire stimuli (diameter in de orde van 1 boogminuut) zijn de resultaten van metacontrast metingen quantitatief te beschrijven. Dientengevolge wordt verondersteld dat metacontrast een direct gevolg is van de lopende inhibitie.

De achtergrondluminantie waarop de springflitsen worden aangeboden heeft invloed op de gevonden resultaten. Als er geen achtergrond is, wordt er geen inhibitie gemeten. Metingen met donkere en lichte balken in de buurt van de springflits tonen aan dat inhibitie slechts gegenereerd wordt wanneer binnen de dracht van de inhibitie achtergrondluminantie aanwezig is.

Wanneer met een elementaire probe het inhibitie gedrag wordt gemeten dat opgewekt wordt door een flits van korte duur, maar grote diameter (1 graad), dan blijkt dat ook voor deze generator geldt dat de inhibitie alleen ontstaat op de randen.

Ook onder deze omstandigheden wordt lopende inhibitie gevonden. Het blijkt echter dat de met elementaire stimuli gevonden gelijkwaardigheid van tijd en plaats randen niet meer opgaat: de twee gevonden dips lijken nu duidelijk te correleren met de temporele flanken van de spatieel uitgebreide stimulus. Wanneer deze stimulus vertaald wordt in zijn plaats-tijd analogon (dus een kleine lichtstip met een lange presentatieduur) wordt gevonden dat het ontstaan van de inhibitie dan gekoppeld is aan de plaatsflanken van de stimulus. De symmetrie tussen plaats en tijd blijft dus behouden.

REFERENCES

REFERENCES

Alpern M.J. (1952) Metacontrast: historical introduction. Am. J. Optom. 29, 631-646.

Alpern M.J. (1953) Metacontrast. J. opt. Soc. Am. 43, 648-657.

Bekesy G. von (1928) Zur theorie des Horens. Die Schwingungsform der Basilarmembran. Physik. Zeitschr. 29, 793-810.

Bekesy G. von (1960) Neural inhibitory units of the Eye and Skin. Quantitative description of contrast phenomena. J. Opt. Soc. Am., 50, 1060-1070.

Bekesy G. von (1967) Sensory inhibition. Princeton University press.

Bloch A.M. (1885) Experiences sur la vision. C.R. Soc. Biol., Paris, 2, 493-495.

Blommaert F.J.J. and Roufs J.A.J. (1981) The foveal point spread function as a determinant for detail vision. Vision Res. 21, 1223-1233.

Bouman M.A. and Velden H.A. van der (1947) The two-quanta explanation of the dependence of the threshold and visual acuity on the visual angle and the time of observation. J. Opt. Soc. Am., 37, 908-919.

Bouman M.A. (1949) On the quanta explanation of vision. Thesis Utrecht.

Bouman M.A. (1950) Peripheral contrast thresholds of the human eye. J. Opt. Soc. Am. 40, 825-832.

Bouman M.A. and Brink G. van den (1952) On the integrate capacity in time and space of the human peripheral retina. J. opt. Soc. Am., 42, 617-620.

Boynton R.M. (1972) Discrimination of homogeneous double pulses of light. In: Handbook of sensory physiology VII/4, 202-233.

Breitmeyer B.G. and Ganz L. (1976) Implications of sustained and transient channels for theories of visual pattern masking, saccadic suppression, and information processing. Psychol. Rev. 83, 1-26.

Breitmeyer B.G. (1978) Metacontrast with black and white stimuli: evidence for inhibition of on- and off-sustained activity by either on- or off-transient activity. Vision Res. 18, 1443-1448.

Breitmeyer B.G. and Rudd M.E. (1981) A single-transient masking paradigm. Percept. and Psychoph. 30, 604-606.

Bridgeman B. (1971) Metacontrast and lateral inhibition. Psychol. Rev. 78, 528-539.

Brink G. van den and Bouman M.A. (1954) Variation of integrative action on the retinal system: an adaptational phenomenon. J. Opt. Soc. Am. 44, 616.

Brink G. van den (1957) Retinal summation and the visibility of moving objects. Thesis, Utrecht.

Brink G. van den and Keemink C.J. (1976) Luminance gradients and edge effects. Vision Res. 16, 155-159.

Brink G. van den and Reijntjes G.A. (1966) Spatial and temporal facilitation in vision. Vision Res. 6, 533-551.

Brink G. van den (1982) On the relativity of pitch. Perception, 11, 721-731.

Campbell F.W. and Green D.G. (1965) Optical and retinal factors affecting visual resolution. J. Physiol., 181, 576-593.

Campbell F.W. and Robson J.G. (1968) Application of Fourier analysis to the visibility of gratings. J. Physiol. 197, 551-566.

Dawis S., Shapley R., Kaplan E. and Tranchia D. (1984) The receptive field organization of X-cells in the cat: spatio- temporal coupling and asymmetry. Vision Res. 24, 549-564.

Ditchburn R.W. (1973) Eye-movements and visual perception. Clarendon Press, Oxford.

Duwaer A.L. (1982) Assessement of retinal image displacement during head movement using an afterimage method. Vision Res. 22, 1379-1388.

Fiorentini A. and Maffei L. (1970) Transfer characteristics of excitation and inhibition in the human visual system. J. Neurophysiol. 33, 285-292.

Fry G.A. (1948) Mechanisms Subserving Simultaneous Brightness Contrast. Am. J. Optom. and Arch. Am. Acad. Optom., 25, 162-178.

Graham C.H. (Editor) (1966) Vision and Visual perception. John Wiley and Sons Inc. New York USA.

Grand Y. Le (1968) Light, colour and vision. Chapman and Hall, London.

Growney R. (1978) Metacontrast as a function of the spatial frequency composition of the target and mask. Vision Res. 18, 1117-1123

Growney R. and Weisstein N. (1972) Spatial characteristics of metacontrast. J. opt. Soc. Am.62, 690-696.

Hallett P.E. (1963) Spatial summation. Vision Res. 3, 9-24.

Hartline H.K. (1940) The nerve messages in the fibres of the visual pathways. J. Opt. Soc. Am. 30, 239-247.

Hartline H.K. and Ratliff F. (1954) Spatial summation of inhibitory influences in the eye of limulus. Science, 120, 781.

Heijde G.L. van der (1980) Temporal aspects of monocular and binocular vision. Thesis Amsterdam.

Heinemann E.G. (1961) The resolution of apparent brightness to the threshold for differences in luminance. J. Exp. Psychol., 61, 389-399.

Herrick R.M. (1972) Increment threshold for two identical flashes. J. opt. Soc. Am. 62, 104-110.

Herrick R.M. (1974) Foveal light-detection thresholds with two temporally spaced flashes: a review. Percept. Psychoph. Vol 15, No 2, 361-367.

Hines M. (1976) Line spread function variation near the fovea. Vision Res. 16, 567-572.

Horst G.J.C. van der and Bouman M.A. (1969) Spatiotemporal chromaticity discrimination. J. opt. Soc. Am., 59, 1482-1488.

Ikeda M. (1965) Temporal summation of positive and negative flashes in the visual system. J. opt. Soc. Am. 55,1527-1534.

Kahneman D. (1968) Methods, findings, and theory in studies of visual masking. Psychological Bulletin, 70, 404-425.

Kaufman L. (1974) Sight and mind. An introduction to visual perception. Oxford University press.

Keemink C.J. Van der Wildt G.J. and van Deursen J.B.P. (1979) Microprocessor-controlled contrast sensitivity measurements. Med. & Biol. Eng. & Comput., 1979, 17, 371-378.

Kelly D.H. (1971). Theory of flicker and transient responses, I. Uniform fields. J. Opt. Soc. Am., 4, 537-546.

Koenderink J.J. (1976) Current models of contrast perception. In Spatial Contrast (Edt. Spekreijse and Van der Tweel). Amsterdam.

Koenderink J.J. and Doorn A.J. van (1978) Visual detection of spatial contrast: influence of location in the visual field, target extent and illuminance level. Biol. Cybernet. 30, 157-167.

Koenderink J.J., Bouman M.A., Bueno de Mesquita A.E. and Slappendel S. (1978) Perimetry of contrast detection thresholds of moving spatial sine-wave patterns. III. The target extent as a sensitivity controlling parameter. J. Opt. Soc. Am., 68, 854-860.

Krauskopf J. (1962). Light distribution in human retinal images. J. Opt. Soc. Am., 52, 1962, 1046-1050.

Kretz F., Scarabin F., and Bourguignat E. (1979) Predictions of an inhomogeneous model: Detection of local and extended spatial stimuli. J. Opt. Soc. Am. 69, 1635-1647.

Kulikowski J.J. and King-Smith P.E. (1973) Spatial arrangement of line, edge and grating detectors revealed by subthreshold summation. Vision Res. 13, 1455-1478.

Lange H. de (1957). Attenuation characteristics and phase-shift characteristics of the human fovea-cortex systems in relation to flickerfusion phenomena. Thesis Delft.

Lange H. de (1958). Research into the dynamic nature of the human foveal-cortex systems with intermitted and modulated light. I. Attenuation characteristics with white and colored light. J. Opt. Soc. Am., 48, 777-784.

Lefton L.A. (1973) Metacontrast: a review. Perception and Psychophysics, 17, 571-584.

Limb J.O. and Rubinstein C.B. (1977) A model of threshold vision incorporating inhomogeneity of the visual field. Vision Res. 17, 571-584.

Mach E. (1865) Uber die wirkung der raumlichen Vertheilung des Lichtreizes aus die Netzhaut. Sitsungsberichte der mathematisch-naturwissenschaftlichen Classe der kaiserlichen Akademie der Wissenschaften, Wien, 52/2, 302-322. (A translation is given by Ratliff, 1965).

Martinez J.M., Sturr J.F. and Schmalbach N.L. (1977) The luminance difference threshold: evidence for inhibitory interactions in spatial summation. Vision Res. 17, 687-689.

Matin E. (1975) The two-transient (masking) paradigm. Psychol. Rev. 82, 451-461.

Meeteren A. van (1973) Visual aspects of image intensification. Thesis Utrecht.

Meijer J.G. Wildt G.J. van der and Brink G. van den (1978) Twin-flash response as a function of flash diameter. Vision Res. 18, 1111-1116.

Mitov D., Vassilev A., and Manahilov V. (1981) Transient and sustained masking. Percept. and Psychoph. 30, 205-210.

Nes F.L. van (1968). Experimental Studies in spatiotemporal contrast transfer by the human eye. Thesis Utrecht.

Nes F.L. van (1967). Spatial modulation transfer in the human eye. J. Opt. Soc. Am., 57, 401-406.

Noorlander C. (1981) The spatiotemporal line element in colour space. Thesis, Utrecht.

Petry S. (1978) Perceptual changes during metacontrast. Vision Res. 18, 1337-1341.

Raab D.H. (1963) Backward masking. Psychol. Bull. 60, 118-129.

Ratliff F. (1965). Mach bands: Quantitative studies on neural networks in the retina. The Rockefeller institute, New York. Holden-Day, inc. 1965 San Francisco, London, Amsterdam.

Ricco A. (1877) Relazione fra il minimo angolo visuale a l'intensita luminosa. Ann. di Ottalm. 6, 373-479.

Robson J.G. (1966) Spatial and temporal contrast-sensitivity function of the visual system. J. opt. Soc. Am.56, 1141-1142.

Rodieck R.W. (1965) Quantitative analysis of cat retinal ganglion cell response to visual stimuli. Vision Res. 5, 583-601.

Rohler R. and Hilz R. (1966) Physical and physiological factors in visual modulation transfer. Excerpta Medica Foundation, Amsterdam.

Roufs J.A.J. (1972). Dynamic properties of vision-I. Experimental relationships between flicker and flash thresholds. Vision Res. 12, 261-278.

Roufs J.A.J. (1972) Dynamic properties of vision-II. Theoretical relationships between flicker and flash thresholds. Vision Res. 12, 279-292.

Roufs J.A.J. (1973) Dynamic properties of vision-III. Twin flashes, single flashes and flicker fusion. Vision Res. 13, 309-323.

Roufs J.A.J. (1973) Dynamic properties of human vision. Thesis Eindhoven.

Roufs J.A.J. (1974) Dynamic properties of vision-IV. Threshold of decremental flasehs, incremental flashes and doublets in relation to flicker-fusion. Vision Res. 14, 831-851.

Roufs J.A.J. (1974) Dynamic properties of vision-VI. Stochastic threshold fluctuations and their effect on flash to flicker sensitivity ratio. Vision Res., 14, 871-888.

Roufs J.A.J. and Blommaert F.J.J. (1981) Temporal impulse and step response of the human eye obtained psychophysically by means of a drift-correcting pertubation technique. Vision Res. 21, 1203-1221.

Rovamo J. and Virsu V. (1979) An estimation and application of the human cortical magnification factor. Expl. Brain Res., 37, 495-510.

Rovamo J. and Raninen A. (1984) Critical flicker frequency and M-scaling of stimulus size and retinal illuminance. Vision Res. 24, 1127-1131.

Sakitt B. (1971) Configuration dependence of scotopic spatial summation. J. Physiol. 216, 513-529.

Saunders J.E. (1977) Foveal and spatial properties of brightness metacontrast. Vision Res. 17, 375-378.

Schade O.H. (1956) Optical and photoelectric analog of the eye. J. Opt. Soc. Am., 46, 721-739.

Schober H.A.W. (1966) Visual performance on radar screens at scotopic conditions. In: Performance of the eye at low luminances. M.A. Bouman and J.J. Vos (eds.) Excerpta Medica Foundation, Amsterdam.

Scholtens A.M.W. and Bouman M.A. (1977) Psychophysical experiments on spatial summation at threshold level of the human peripheral retina. Vision Res. 17, 867-873.

Shapley R.M. and Tolhurst D.J. (1973) Edge detectors in human vision. J. Physiol., Lond. 229, 165-183.

Sheard C. (1944) Dark adaptation. J. Opt. Soc. Am., 34, 464.

Sidowski J.B. (Ed.) (1966) Experimental methods and instrumentation in psychology. McGraw-Hill, New York, USA.

Singer W., Zihl J. and Poppel E. (1977) Subcortical control of visual threshold in Humans; evidence for modality specific and retinotopically organized mechanisms of selective attention. Exp. Brain Res., 29, 173-190.

Smith R.A. (1967) Space-time symmetry in visual contrast sensitivity. J. opt. Soc. Am. 57, 1425.

Taylor W.K. (1956) Electrical simulation of some nervous system functional activities. In 'Information theory', Colin Cherry, ed., New York Academic Press.

Thomas J.P. (1978) Spatial summation in the fovea: asymmetrical effects of longer and shorter dimensions. Vision Res. 18, 1023-1029.

Velden H.A. van der (1946) The number of quanta necessary for the perception of light at the human eye. Ophthalmologica, 111, 321-331.

Vrolijk P.C. and Wildt G.J. van der (1981) Psychophysical experiments on the dynamics of inhibition. Proceedings 22nd Dutch Federation Meeting, Utrecht.

Vrolijk P.C. and Wildt G.J. van der (1982a) Propagating inhibition as a function of flash diameter and duration. Vision Res. 22, 401-406.

Vrolijk P.C. and Wildt G.J. van der (1982b) Is metacontrast based on the propagation of inhibition? Perception Vol 11, number 1, A32.

Vrolijk P.C. and Wildt G.J. van der (1983a). Propagating inhibition as a function of flash diameter and duration. International Synopsis, Ophthalmology Digest, 3, 12.

Vrolijk P.C. and Wildt G.J. van der (1983b). The influence of the background on the propagation of inhibition. Perception 12, number 1, p A19.

Vrolijk P.C. and Wildt G.J. van der (1985a) Is inhibition an edge effect? Perception 14, nr. 1, pA24.

Vrolijk P.C. and Wildt G.J. van der (1985b) Foveal inhibition measured with suprathreshold stimuli. Vision Res., 25, 1413-1421.

Vrolijk P.C. and Wildt G.J. van der (1985c) The influence of the background on the generation of inhibition. Vision Res., 25, 1423-1429.

Weisstein N. (1968) Backward masking and models of perceptual processing. J. Exp. Psychol. 72, 232-240.

Weisstein N. (1972) Metacontrast. In Handbook of Sensory Physiology, Vol VII/4 Visual Psychophysics (Edited by Jameson D. and Hurvich L.M.), Chap. 4 Springer, Berlin.

Weisstein N., Ozog G., and Szoc R. (1975) A comparison and elaboration of two models of metacontrast. Psychol. Rev. 82, 325-343.

Westheimer G. (1966) The Maxwellian view. Vision Res. 6; 669-682.

Westheimer G. (1967) Spatial interaction in human cone vision. J. Physiol., 190, 139-154.

White C. and Lorber C. (1976) Spatial frequency selectivity in visual masking. Percept. Psychoph. 19, 281-284.

Wildt G.J. van der, Keemink C.J. and Brink G van den (1976) Gradient detection and contrast transfer by the human eye. Vision Res. 16, 1047-1053.

Wildt G.J. van der and Rijsdijk J.P. (1979) Flicker sensitivity measured with intermittent stimuli: II. Comparison between temporal gradient detection and the "de Lange" curves. J. opt. Soc. Am. 69, 666-669.

Wildt G.J. van der and Vrolijk P.C. (1981). Propagation of inhibition. Vision Res. 21, 1765-1771.

Wildt G.J. van der and Vrolijk P.C. (1985) How to combine modulation in space and time. Perception 14, nr. 1, pA5.

Wildt G.J. van der. (1984) Interchangeability of space and time in perception. in Limits in perception. Van Doorn et al. (eds). VNU Science Press.

Wilson H.R. and Bergen J.R. (1979) A four mechanism model for threshold vision. Vision Res. 17, 571-584.

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De schrijver dezes werd in 1956 geboren in Scheveningen. Op 6-jarige leeftijd werd er verhuisd naar Spijkenisse. Aldaar is in 1972 het MAVO en het type diploma behaald hetgeen gevolgd werd door het HAVO en het VWO diploma in respectievelijk 1974 en 1975. In 1975 is begonnen met een studie Technische Natuurkunde aan de Technische Hogeschool Delft. Dit resulteerde in het doctoraal diploma in 1981. Bij het afstudeeronderzoek in de vakgroep Biologische Natuurkunde onder leiding van Prof.dr. G. van den Brink en Prof.dr.ir. F. Bilsen is een basis gelegd voor het in dit proefschrift beschreven onderzoek. Van 1982 tot en met 1985 is de schrijver in dienst geweest bij de Nederlandse Organisatie voor Zuiver-Wetenschappelijk Onderzoek (Z.W.O.) en tewerkgesteld bij de vakgroep Natuurkunde en Technologie onder leiding van Prof.dr. G. van den Brink aan de Medische Faculteit van de Erasmus Universiteit Rotterdam. Gedurende deze periode is in nauwe samenwerking met Dr. G.J. van der Wildt gewerkt aan de totstandkoming van dit proefschrift.