ON VISUAL PERCEPTS RELATED TO RECEPTIVE AND PERCEPTIVE FIELD PROPERTIES

An investigation of insensitivity percepts, size illusions and fading

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"Physics is not the key to the minds
of men; neither is physiology."
M.H. Pirenne: "Vision and the eye"
(1948)

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Chapter 1. INTRODUCTION

Chapter 1. INTRODUCTION

1.1. Introduction

The work presented in this thesis was performed at the Laboratory of Medical Physics and Biophysics as a continuation of the work of Stassen (1980). The object of his work was to measure natural eye movements and to determine the importance of drifts and saccades for the preservation of vision. It was an extension of investigations concerning the "artificial" movement of a stabilized image. A stabilized image is a constant retinal illumination pattern that remains when the influence of eye movements is abolished. A stabilized image results in the complete fading of the corresponding percept (Gerrits, 1967). It was found that artificial movements of the stimulus (once the percept had faded) did not result in a complete restoration of the former percept when amplitudes and frequencies were used encountered in normal eye movements (Gerrits,1970a; 1974). After measurement and analysis of drifts and saccades, a stabilized stimulus was moved with recorded eye movements as well as with signals mimicking these movements as close as possible (Stassen,1980). But also under these conditions a faded percept could not be brought back to its original brightness and form at stimulus onset.

Proceeding on the ideas about the importance of the different components found in the eye movements, the influence of different other movements was investigated, hoping to reveal the cause of the failure of the foregoing attempts. This part of the research concerning the eye movements is published elsewhere (Gerrits et al., 1984) and is presented as an appendix to this thesis. It suffices to state that the main problem still was to decide what are in fact "normal eye movements" and what had to be the criterion for a satisfactory restoration of a formerly faded percept. The investigation to reveal the function of eye movements for visual perception was not continued as it was also felt that too much knowledge about the basic functions of the brightness and darkness information processing was still lacking. Therefore the studies described in this thesis were undertaken.

In chapter two a summary is given of the electrophysiological and anatomical data that will be used in the chapters three, four, five and six. The aim of chapter two is not so much to give a full and detailed description of all elements, functioning in the visual system and concerned with processing of brightness and darkness, but it is rather a global presentation of various elements. Only those concepts that form the basis for the hypotheses describing insensitivity percepts, size illusions and differences between fading time constants will be described in detail.

In chapter three experiments are described in which a part of the retina is made insensitive as a result of very intense illumination. The percepts seen against a diffuse background have been described before by Carpenter (1972) and they resemble effects observed in stabilized condition by Gerrits (1977). In a number of preliminary experiments the method employed by Carpenter (1972) was used. Then it was found, however, that the experimental conditions determine the resulting insensitivity percepts. A new method was presented as well as a new hypothesis, which states that the occurrence of the insensitivity percepts can be explained by considering only those ganglion cells of which the receptive field centres are located adjacent to the edge of the insensitive area.

In chapter four experiments are described investigating the classical size illusion, i.e. a light object against a dark background seems to be larger than an equally large dark object against a light background. Gerrits had already carried out a number of preliminary experiments and a hypothesis had been given. The continuation and elaboration led to the rejection of the preliminary hypothesis. A better and more comprehensive explanation of the results could be given by considering the properties of ganglion cells having different receptive field centre sizes.

In chapter five a transition from the receptive fields to their psychophysical correlates: perceptive fields (Jung and Spillmann, 1970) is made. In the foregoing years a number of stabilization experiments have been performed leading to a model that explained the outcomes in a qualitative way (Gerrits, 1967; 1970b; 1978). This model incorporated also electrophysiological, anatomical and psychophysical data from the literature. The need for a quantification of this model was heavily felt and therefore it was tried to quantify the dynamics of fading. It was known that the fading time of percepts within the foveal area is shorter than for percepts located more peripherally, but exact values of the fading time as a function of eccentricity were unknown. Analogous to the increase in the centre size of receptive fields with eccentricity an increase in centre size is found for perceptive fields.

A hypothesis is presented about the fading time constant of perceptive elements (Gerrits, 1978). A small fading time constant for perceptive elements with small field centres and a large fading time constant for elements with large field centres is found experimentally.

The result of this study is the extension of the properties of perceptive fields based on the known properties of receptive fields and data from psychophysical experiments. Elaborating on the concept of the perceptive fields (Jung and Spillmann, 1970) it was possible to build a model which accounts for typical visual effects such as encountered in some illusions, in insensitivity percepts following afterimages and in the percepts resulting from image stabilization. The model is based on electrophysiological, anatomical as well as psychophysical data. The method may be indicated as a forward model approach when perceptual effects are predicted based on well-known properties of neural elements in the visual system. It has to be considered as a reversed model, however, when perceptual phenomena predict the properties of postulated elements. These forward and reversed models have been adopted in turn. This seems to us the most efficient approach of the investigation of this problem.

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Chapter 2. BASIC FACTS OF ELECTROPHYSIOLOGY AND PSYCHOPHYSICS REGARDING BRIGHTNESS- AND DARKNESS INFORMATION PROCESSING.

- 2.1. Introduction
- 2.2. The receptive field concept
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Chapter 2. BASIC FACTS OF ELECTROPHYSIOLOGY AND PSYCHOPHYSICS REGARDING BRIGHTNESS- AND DARKNESS INFORMATION PROCESSING.

2.1. Introduction.

This chapter gives a description of the properties of a number of neural elements that are used in the model of brightness- and darkness information processing described in this thesis. The basis of the model was developed by Gerrits (1967). The model has continuously been adapted as a consequence of both new electrophysiological and psychophysical data from the literature and new results from experiments in stabilized condition since then (Gerrits, 1969; 1970a,b; 1978; 1979). In this thesis the use of the receptive field concept was elaborated still further and the difference in fading time of foveal and peripheral stimuli quantified.

A percept of brightness and darkness is thought to result from a hierarchy of many levels of concatenated interactions, some inhibitory, some excitatory and some still more complex (e.g. a combination of both). In this chapter we will stepwise consider the different elements and indicate the specific properties that are important in the model (see figure 2.1).

The light of a visual stimulus is transformed at the receptor level into a potential. According to their anatomical and functional properties receptors can be classified as rods and cones, the rods being used principally at low illumination levels. As long as we are only dealing with uncoloured stimuli and are only reflecting upon the brightness and darkness system no distinction needs to be made between the three types of cones. Characteristics of receptors have been described extensively by Dowling (1970), Rodieck (1973), Whitten and Brown (1973a,b,c), Valeton (1983) and many others. Of receptor responses both increments and decrements have a signal function. The vertebrate photoreceptors are depolarized in the dark and hyperpolarized by illumination. This means that the increase as well as the decrease of the hyperpolarization of the receptor membrane are important as they signal the increments and decrements of light, respectively. This is in contrast with stages beyond the retinal level in the brightness and darkness system where decrements have no signal value (Walls, 1954; Baumgartner, 1961b; Virsu and Lee, 1983). The decrease of the receptor hyperpolarization results in a darkness signal provided the rate of depolarization is fast enough. For steady high illumination levels the rod response potential returns gradually to a lower level. This return is too slow to generate a darkness signal. Sakitt and Long (1979) found,that the subjective onset and offset of brief photopic stimuli must be attributed to the cone system, whereas subjective persistence of the same stimuli is mediated by the rod system. For rods and cones the time course of dark adaptation ranges from a few minutes up to thirty minutes if

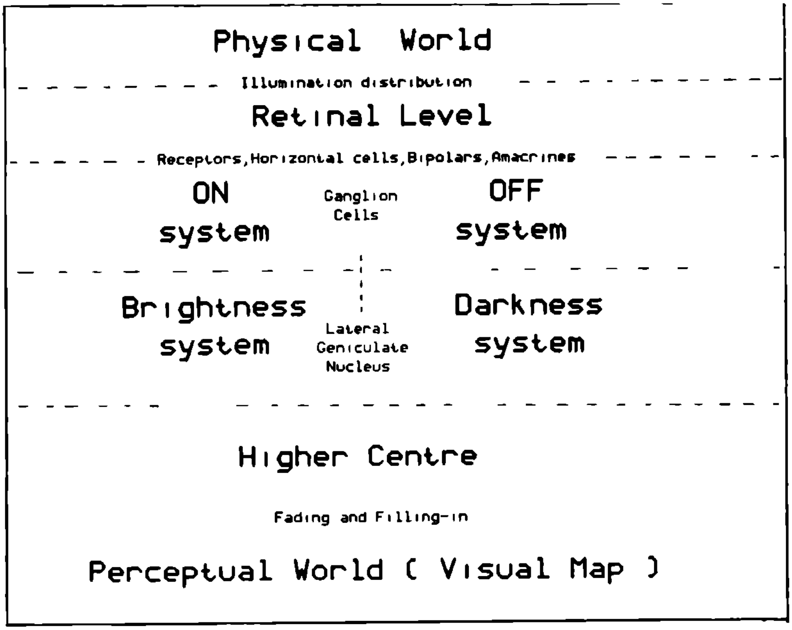

Figure 2 1 The building blocks of the Brightness/Darkness system

retinal illumination was high. This fact will be used when discussing the insensitivity percepts in chapter three. Although there is evidence that a mutual interaction of rods and cones may exist this is still being discussed. The retinal elements (horizontal-, bipolar-, amacrine- and ganglion cells) that are activated by the receptor potentials have a rather tight interaction. From the receptors the signal is transmitted to the bipolar cells. They constitute the only signal path that brings information from the outer to the inner plexiform layers of the retina (Uttal, 1978). The signal generation in bipolar cells is achieved by means of depolarization and hyperpolarization. Already at the bipolar cell level a certain retinal area exists determining the behaviour of one single bipolar cell. This implies that not only one but a number of receptors influences the bipolar's response.

Also the horizontal cells contribute to the response of the bipolars by means of their dendritic fields. Horizontal cells may gain information from all receptor types as a type of horizontal cell was found that responded to all wavelengths equally well (Copenhagen and Leeper, 1979). The signal generation of the horizontal cells is mediated by hyperpolarization. The area from which the bipolar cell receives its information, i.e. its receptive field, can be divided into two parts. They influence the bipolar's response in an antagonistic way. The division is most often accomplished by having a circular central area (the centre) and an area surrounding it as an annulus (the surround). At the bipolar cell level the separation into a channel for brightness and a channel for darkness (see section 2.2) starts. An on-centre bipolar cell depolarizes at light-on in its central zone while an off-centre bipolar cell hyperpolarizes (Rodieck, 1973).

Up to now all signal transmission was achieved by decremental conduction. The next level is the first level in the visual system where signal transmission is mediated by a slow graded potential as well as action potentials (Rodieck, 1973). This is done by the amacrine cells, which are probably concerned with gradient detection as they influence ganglion cell behaviour. Ganglion cells form the last retinal stage in the direct pathway of the visual information processing, i.e. the shortest way the signal can go from the receptor up to the more higher centres of the visual system. Ganglion cells have receptive fields just like the bipolar cells. Depending on the illumination in their receptive field and the properties of the receptive field, a response in the form of action potentials results. There are on-centre / off-surround and off-centre / on-surround cells. An on-centre/off-surround ganglion cell increases its spike activity when the illumination in the central area of its receptive field is increased and decreases its spike activity when the illumination in the surround is increased. An off-centre/ on-surround cell shows a behaviour which is the reverse. This is also true if decremental light stimuli are used instead of light-off (Jacobs, 1965). The activity range of the off-centre neurons is, however, considerably smaller than that of the on-centre neurons.

For a general review of ganglion cell properties we refer to Lennie (1980) and Witkowsky (1980). Studies have shown that in the dark adapted cat and in stringently dark test conditions, a large difference exists in the ongoing (steady state) dark discharge of on- and off-centre units, in the sense that off-centre unit activity exceeds that of on-centre neurones (Barlow and Levick, 1969). Under "normal" conditions the on- and off-systems may be acting in exactly the opposite way. These data will be used in the discussion of the insensitivity percepts (chapter three) and the apparent size effect (chapter four). In chapter three it is supposed that after desensitizing the receptors within the centre, diffuse illumination leads to a "surround" response. The surround influence may indeed become stronger than the centre contribution. This can be deduced from the explanation of Bonds and Enroth-Cugell (1979) of the fact that response of the ganglion cell becomes more transient in the period after bleaching the receptors in the cell's receptive field.

Another important fact stated in the article of Bonds and Enroth-Cugell is the difference between the time course of the recovery of the cell's sensitivity and the amount bleached. In the explanation of Carpenter (1972) about the origin of insensitivity percepts the amount of rhodopsin bleached was the important factor. From our experiments it is clear , however, that the effects described by Carpenter (1972) are caused by differences in sensitivity at the ganglion cell level and thus cannot be uniquely attributed to the amount bleached.

Returning to the description of the retinal signal processing it can be concluded that the first signal processing is thus mediated by the retinal elements(receptors, horizontal-, bipolar-, amacrine- and ganglion cells) and interactions between various groups. These interactions lead to "receptive fields" at the ganglion cell level. The receptive field may refer either to an area within the visual field that influences the cell's response or to the retinal area (see section 2.2). Generally it can be said that the properties of the receptive fields at this level enhance luminance gradients. As there are different receptive field sizes at every location associated with various ganglion cells, a visual stimulus results even at this level in a rather complex activity distribution. On the basis of the receptive field concept an explanation of a number of psychophysical observations can be given. For instance, the square-root law found in psychophysics can be explained by the behaviour of single retinal ganglion cells (Barlow and Levick, 1967). For stimuli larger than the largest receptive field centres the psychophysical threshold will depend upon the most sensitive units (Lennie, 1979). In chapter four an analogous reasoning will be applicated to explain the apparent size effects.

After this discussion of a number of aspects of the retinal signal processing a description is given of the next processing stage. From the retina the signal is transmitted to the lateral geniculate nucleus and further on. Receptive field sizes may increase as several ganglion cells converge upon a cell in the succeeding levels (Hubel and Wiesel, 1968).

The next stage is called "the higher centre" which may be located besides Brodman's area 18 and 19 but anyhow beyond area 17 (Gerrits, 1970b). From the on- as well as from the off-activity only the increments of the instantaneous activity are transmitted to this higher centre (Walls, 1954; Baumgartner, 1961b; Virsu and Lee, 1983). The higher centre is a direct projection of the retina apart from the blind spot. Due to lateral connections the activity at a certain location is also influenced by surrounding activity. The higher centre is the structure in which the combination of brightness- and darkness-producing activity, the fading of it and the effectuation of barriers is thought to take place (Gerrits, 1970b). Here the percept of the retinal image originates. The concept of Baumgartner (1961a,b) and Jung (1961a,b; 1964) in which the electrophysiological responses are correlated with the different properties of the percept, is applied. The activity of retinal on-centre cells excites in area 17 brightness (B) cells, the output of which activates the perceptive elements. In the same way darkness is defined to result from retinal off-centre cells activating area 17 darkness (D) cells and subsequently perceptive elements.

During the "normal" situation, which is a stationary dynamic situation resulting from the activities generated by our continuous eye movements, a percept is formed by activity of both the brightness and the darkness system. The bright and dark areas are separated by barriers. Barriers are formed by adjacent antagonistic activities of the brightness and darkness system preventing their mutual spreading within the projection of the visual field in the darkness and brightness system, respectively. So besides the generation of brightness-producing activity by the brightness system and the generation of darkness-producing activity by the darkness system, these systems confine the spread of their mutual activities within the barriers set up by the contour.

The final stage in the brightness/darkness system is supposed to be a level at which the neural activity is "transformed" into the percept of the actual visual scene. The perceived brightness results from the difference between the corresponding brightness- and darkness-producing activity. This implies that the perceptual result of a change in retinal illuminance not only depends on the actual retinal stimulus but also on the amount of brightness-or darkness-producing activity that may still be present at the higher centre level. The perception of a certain brightness may result from an activation of the brightness system (increase of stimulus luminance) as well as from a deactivation of the darkness system.

2.2. The receptive field concept

2.2.1. Definition

The responses of visual neural units are partly determined by the fact that every cell "looks at a part of the world". This part forms the visual stimulus that is located in its receptive field. The concept of the receptive field (receptive area) was introduced into neurophysiology by Adrian et al. (1931). Hartline (1938; 1940) used the term "receptive field" to describe the area in the frog's retina from which he could obtain a response in a single optic nerve fibre. Jung (1973) used the term "the receptive field of a neuron" for the retinal projection of the area within which photopic stimuli elicit responses that can be recorded objectively from neurons at various levels of the visual system.

Within this so called receptive field two mutual antagonistic regions can be discerned. The centre part of the receptive field, the centre for short, is often a circular patch contributing to excitation for an on-centre cell and inhibition for an off-centre cell. The activity from the region surrounding the centre, inhibits an on-centre cell and excites an off-centre cell (see figure 2.2.) (Barlow, 1957). How this antagonistic behaviour of centre and surround is accomplished and where the site of the interaction is located anatomically is not exactly known for the mammalian visual system, but horizontal cells seem to be involved. The antagonistic output of

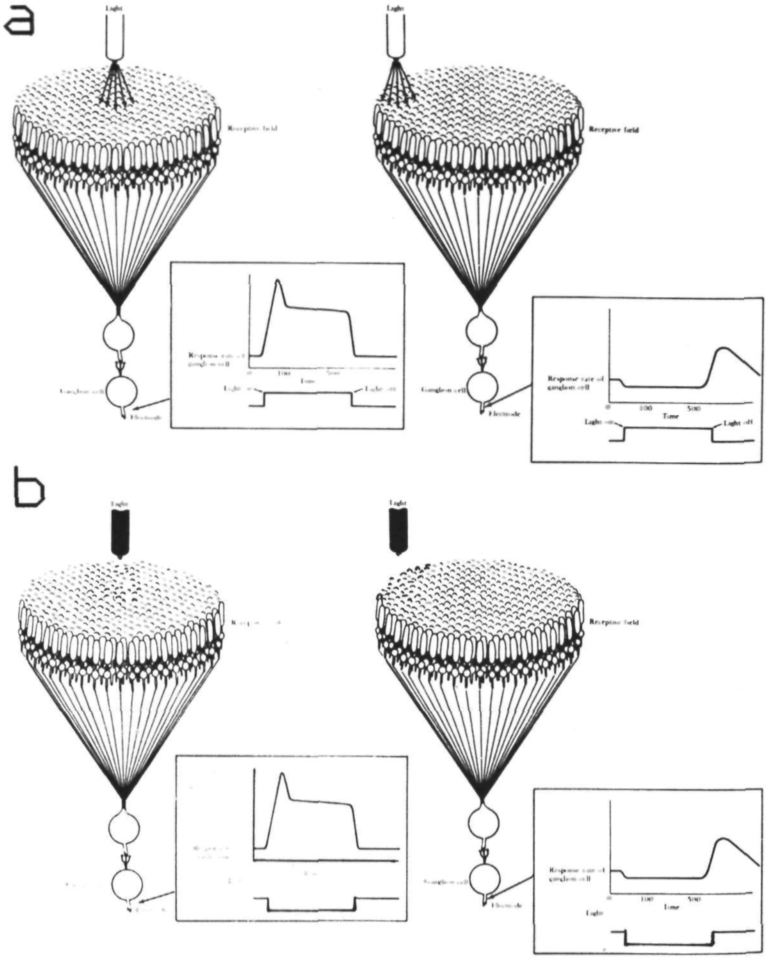

Figure 2.2 The receptive field concept for an on-centre and off-centre cell. a) Illumination of the centre area excites an on-centre cell. Illumination of the surround inhibits the cell. b) For an off-centre cell the reverse is found. An off-centre cell is excited when the centre illumination is switched off or the surround illumination is increased (free after Lindsey and Norman,1980).

the centre and surround depends on the ratio of centre and surround illumination (Freund et al., 1977). The characteristic effects of the surround mechanism appear only when the field centre receives some suprathreshold amount of light. The antagonistic surround responses disappear within a few seconds after the field centre is in complete darkness. At very low illumination levels the surround influence decreases or even disappears (Barlow et al., 1957; Rodieck and Stone, 1965a,b; Sindermann and Pieper, 1965). If the illumination of the centre is much less than that of the surround area on-centre cells may be excited at light-on in their surround while off-centre cells may be inhibited. This is a reversal of the normal behaviour. A comparable situation will be encountered in chapter three due to a partial desensitization of the centre and/or part of the surround.

In some cases receptors may still be signalling "illumination" while the physical illumination is removed. This occurs if a sufficiently strong stimulus saturates the receptors, which are not adequately adapted (Whitten and Brown, 1973c). The effects of local adaptation of the receptive field centre have been studied by Bishop and Rodieck (1965), Maffei et al. (1971) and Enroth-Cugell and Pinto (1972) among others. In general it can be said that the centre type response decrease if the centre-surround ratio of illumination decreases.

The receptive fields of cells in the visual system are often described by a sensitivity profile which is a composition of two Gaussian functions (Rodieck, 1965). A graphical representation of the combined function is given in figure 2.3. So the receptive field is to be interpreted as a weighted integration of the visual stimulus, which determines the cell's response. The visual system consists of a great number of cells all with their own receptive field but partly overlapping other receptive fields. At any location different receptive field sizes can be found, i.e. fields with approximately the same surround diameters but different centre diameters (Wiesel, 1960; Enroth-Cugell and Robson, 1966; Hammond, 1974). The size of the receptive field determines the sharpness of the contours to be perceived. Several authors suggest that receptive field size increases as a linear function of eccentricity. Receptive field sizes can be classified in a number of ways. Considering one specific receptive field one is dealing with the centre size as well as the surround size. Wiesel (1960) found that the centre size changes considerably more than the surround area. The sizes of the surrounds of the receptive fields are approximately the same for all cells. It is the size of the centre that changes from small in the central region to large in the peripheral region. Wiesel made already a remark about the importance of the dimension of receptive fields in that the size of the centre portion determines the acuity. Using the Rodieck and Stone (1965b) model the centre-surround ratio σ_c/σ_s must vary. At a certain location within the visual field a range of receptive field sizes exists (Fukuda, 1971; Peichl and Wassle, 1979). According to Rowe and Stone (1980) this is called the residual variation. The average of this range increases with eccentricity (Cleland and Enroth-Cugell, 1968). This is called the systematic variation. Virsu (1976) states that the spatial sensitivity characteristics of single neurons vary considerably from cell to cell over a wide range of visual space as well as within a single retinal location.

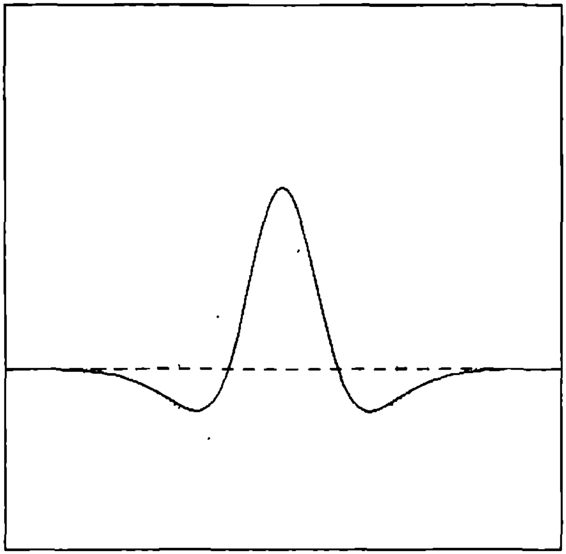

Figure 2 3 Graphical representation of the receptive field concept The function is formed by the difference of two Gaussian functions For centre and surround the parameters are g_c, σ_c, g_s, σ_s, respectively The Gaussian function is described by

$$f(x)=\frac{g}{\sqrt{2\pi}\,\sigma}\,e^{-\left(\frac{x^2}{2\sigma^2}\right)}$$

Apart from the fact that a cell has a receptive field size within a range of sizes characteristic for its retinal location, the receptive field size of a specific cell itself may also vary. Four conditions are known to increase the size that evokes a maximum response from a retinal ganglion cell: dark adaptation, change from cone vision to rod vision, temporal modulation (flicker) and short stimulus presentation (Virsu, 1976). Wiesel (1960) found that the smaller the centre, the larger the threshold elevation due to the surround illumination. This implies that for small contrast gradients (nearly diffuse light) the cells with large receptive field centres are activated most effectively. For large contrast gradients this may be different. It is clear that the cells with small receptive fields adjacent to the contours are activated more strongly by eye movements than the cells with large fields. The eye movements move the stimulus pattern continuously over the small receptive fields with their steep sensitivity profiles. The activity of the larger cells along the contour should be discarded in some way or another because the increasing "sharpness" due to smaller receptive fields would be rather ineffective if information of larger and smaller receptive fields would be simply summated. As a result of various stabilization experiments it has to be concluded that there exists an inhibition of cells having a large receptive field by cells having a small field. If we consider for instance the cells having small on-centre and off-centre receptive fields adjacent to a sharp high contrast contour then it is clear that at the side of the lowest illumination an on-centre cell with a large centre still might generate too much brightness activity because its centre can be located on the side with the highest illumination. As no extra brightness is seen, however, one must assume that the cell with the large centre is suppressed by the cells with the small field centres. By topographical correspondence the small on-centres are located near the large on-centres. Therefore it is expected that they cause the inhibition . An inhibition due to the small off-centre cells cannot be excluded, however (Gerrits, 1978).

It seems worth mentioning here that in the lateral geniculate nucleus inhibitory connections seem to exist between both synergistic (Burke and Sefton, 1966a,b,c; Coenen, 1971) and antagonistic (Singer and Creutzfeldt, 1970) cells. The way in which this dominance of cells with small receptive fields over cells with large fields is achieved, is still unknown but the fact will be accepted for the moment. In chapter four the different characteristics of cells with different receptive field sizes will be used to explain the changes of apparent size as local contrast varies. According to Hubel and Wiesel's model (1962, 1968) several spatially overlapping simple cell receptive fields converge on a receptive field of a complex cell in the striate cortex and thus define its stimulus selectivity. Overlap implies that part of receptive fields are associated with the same retinal area or part of the visual field. According to Fisher (1973) and Drasdo (1977) the overlap factor is constant, i.e. it is independent of retinal eccentricity. The various sizes of the receptive fields at a certain location are found in electrophysiological as well as anatomical studies (Stone and Johnston, 1981). The existence of several receptive field sizes at a certain location enables the visual system to adapt optimally to the actual acuity requirements at different illumination levels. Besides the differences mentioned above, differences between the mean size of the receptive field of on-centre and off-centre cells at a certain location are also found in electrophysiological as well as anatomical studies. Fisher and May (1970) and Fukuda (1971) have presented data indicating that the off-centre cells have, on the average , larger receptive fields than the on-centre cells at the same location in the visual field. Coenen (1971) has pointed out that in the cat the inhibitory receptive fields (surrounds) of off-centre units extend between 10 and 20 degrees, while the inhibitory receptive field surrounds of most on-centre units measure between 5 and 10 degrees. On the basis of latency of the primary excitation it was found that also the excitatory receptive fields (centres) of optic tract off-centre units are, on the average, greater than those of on-centre units.

The differences between the on- and off-centre receptive fields may very well be reflected by some psychophysical phenomena. The well-known phenomenon of Mach bands (Ratliff, 1965), after Ernst Mach who first reported them in 1865, shows a dark band that is wider than the bright band (Remole, 1977; Ratliff, 1984). This indicates a difference between the sizes of the receptive fields of on-centre and off-centre cells. In our study this observation is important for the explanation of the difference in size effects between bright and dark squares (chapter four). In stabilized vision it is observed that the percept of a stimulus displaces when it is turned on or off. It seems as if darkness does not come into the same place as was occupied by the preceding brightness.

Anatomical evidence shows that on- and off-centre cells are organized in a kind of lattice. Both lattices are displaced with respect to each other. They are located in two laminae (about 10 µ apart) within the inner plexiform layer (Peichl and Wassle, 1981).

In conclusion of this part, which contains the electrophysiological and anatomical literature data, a method is indicated that will be used in analysing the responses of the retinal ganglion cells to specific stimulus conditions. It is important to remark that every visual stimulus will excite or inhibit a large number of cells.

Several investigations (e.g. Stone and Freeman, 1973) of the contribution from the different parts of the receptive fields to the activity of the ganglion cells reveal that the incorporation of other positions of receptive field centres other than those close and adjacent to a luminance step do not have any influence on the effects that result from it. On-centre cells will be maximally excited on the light side and most strongly inhibited on the dark side (Baumgartner, 1961a). For off-centre cells the responses are (within wide limits) opposite to those of on-centre cells. In figure 2.4. an example of different ways of representing this approach is given. The degree of overlap determines the "spatial resolution" in terms of representation of the stimulus or in other words the extent to which the stimulus is sampled.

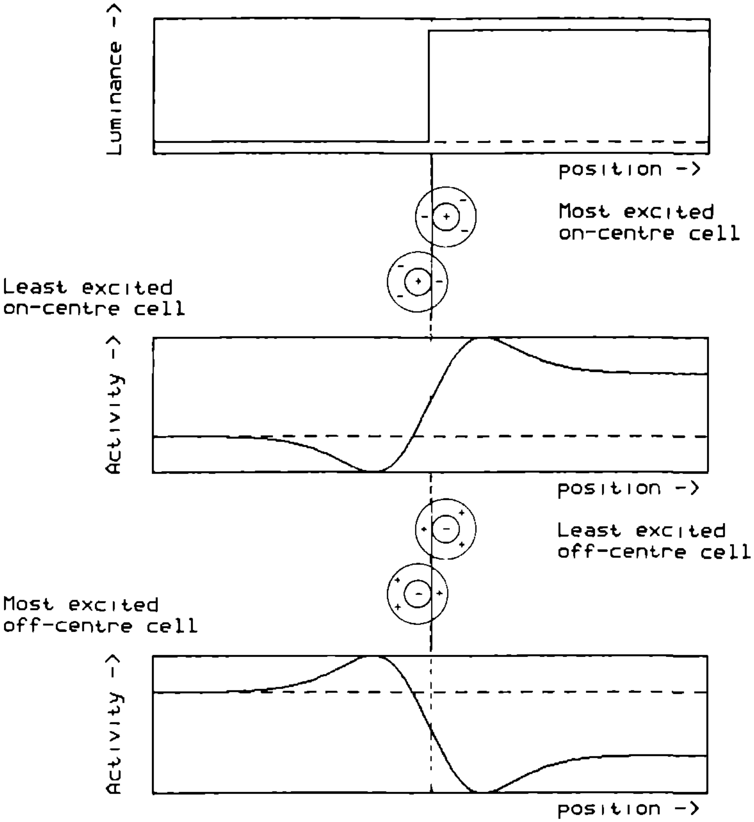

Figure 2 4 A schematic representation of the activity contributions of on- and off-centre cells having their receptive fields in the vicinity of a luminance step

2.3. The higher centre

In the foregoing part an extensive description of the receptive field, a concept that describes electrophysiological phenomena is given. Now will be described what is perceived of the illumination within a receptive field and of the activities thereby elicited. The perception is supposed to come about in the "higher centre" (Gerrits, 1970b). The"higher centre" is the structure in which the electrophysiological correlates of the psychophysically observed phenomena of fading, filling-in and the combination of brightness- and darkness-producing activities to form a percept, are located. Gerrits (1970b) states that in the higher centre two main classes of cells function: Brightness perception cells connected to retinal on-centre cells and darkness perception cells connected to retinal off-centre cells.

It is believed (Barlow et al., 1957; Baumgartner, 1961 b, but particularly Jung, 1961a,b; 1964; 1973) that the on-centre and off-centre systems are the neural channels that signal brighter and darker, respectively; the Jung's (1961a,b) brightness (B) and darkness (D) systems. The existence of two opposing systems in a reciprocal relationship - the B system excited by light increment, and the D system excited by light decrement - is according to Jung (1973) a necessary antagonism. With this the visual system is able to measure very slight deviations from the mean luminance level by signalling the increment as well as the decrement at the edges.

Information processing from the retina to the higher centre is achieved by transmitting only the increments of the actual information level. Electrophysiological experiments show that only changes and not the actual level are signalled. Recent electrophysiological data of Virsu and Lee (1983) confirm the earlier observations of Marocco (1972) that the steady state hyperpolarization of the receptors is not transmitted to the lateral geniculate nucleus cells. Steady white background luminances within a range of 4 log units did not alter the sustained activity with more than 10 spikes per second. In addition it may be noted that the same frequencies of spike activity are found for different brightnesses as the ganglion cell "shifts" its sensitivity curve. This implies that the spike frequency does not encode the absolute illumination level.

Psychophysically there are also a number of indications that constant illumination is not transmitted to the brain. E.g. a stabilized image fades from view notwithstanding the presence of the sustained activity mentioned above. Also in the perception of colour it was found that the absolute level is not transmitted (Walraven, 1981). This was called discarding the background. Pinneo at al., 1967, Enroth-Cugell and Jones (1963), Hansteen (1965) found that when the rate of change of light intensity is sufficiently slow there are no on- and off-bursts at all. So it appears that it is the rate of change of the spike activity that forms the signal as a consequence of transient light intensity changes (Ogawa et al., 1966). This is also found in psychophysical experiments. Gerrits (personal communication) observed that when the rate of change of the illumination of an object, which has faded from view in stabilized vision, is below a threshold value, no renewed perception occurs. The foregoing indicates that only changes of illumination, eliciting on- and off-activity increments of sufficient magnitude , are observed. These illumination changes can be brought about by the shifts of the image across the retinal cells by means of the normal eye movements.(1)

So it is thought that in the higher centre only the incremental changes of the activities of on- and off-centre cells are used to contribute to the perception of brightness and darkness, respectively.

Within the higher centre two separate independent mechanisms play a part: fading, which causes activity to diminish gradually with a specific time constant and filling-in, which enables elements within the higher centre, that were not activated directly, to be activated by neighbouring elements. But now the perceptive field will be discussed first.

2.3.1. The perceptive field

In an analogous way to the receptive field, i.e. the area in the visual world that brings about a response of a cell in the visual system, the perceptive field, i.e. the psychophysical equivalent of the receptive field, is defined (Jung and Spillmann, 1970). Properties of receptive fields are determined by electrophysiology while properties of perceptive fields are estimated indirectly in human vision and measured psychophysically. The centre of a perceptive field is the smallest patch observable with the brightness- or darkness-system in normal vision. The two concepts are schematically indicated in figure 2.5.

Although the perceptive field concept is used in many articles the only explicite properties that have been proposed up to this moment are in regard to their size. Th localization of perceptive fields with respect to receptive fields is supposed to be in a lined up direct projection into visual space.

A percept is thought to result from a mosaic of perceptive elements, which produce brightness- of darkness-pixels, so-called perceptive pixels. Perceptive fields gain input from one or several perceptive elements. In this way a localization of perceptive fields with respect to receptive fields is achieved, which implies the possibility of a back projection into visual space. In this thesis a strict distinction is made between properties of elements connected to a receptive field and those connected to a perceptive field. In the literature this distinction has not been made so strictly thusfar

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1) Note: Remarkably a percept that has disappeared as a result of stabilizing the image cannot be restored to its full brightness by artificially moving the image (Gerrits et al., 1984).

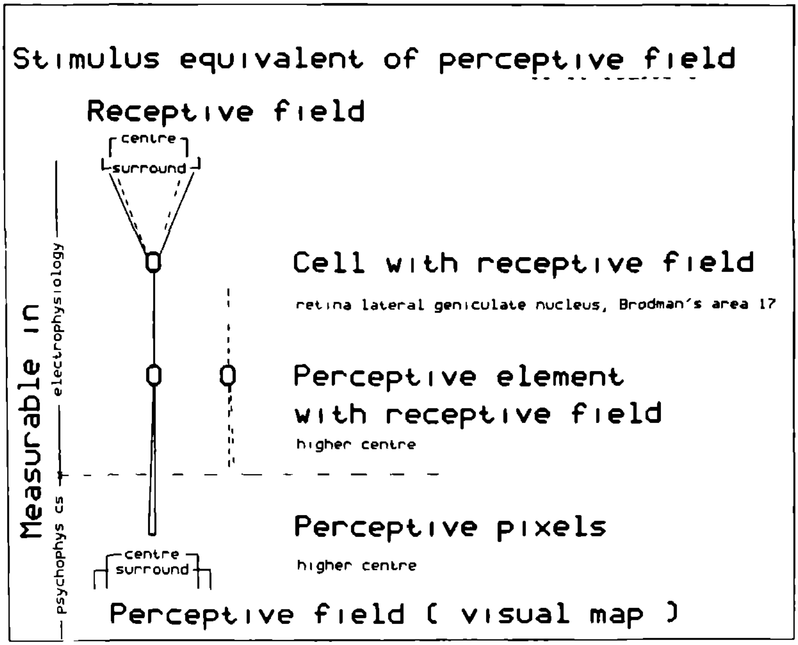

Figure 2 5 The receptive field perceptive element perceptive pixel and perceptive field A schematic representation of the way these concepts are related is given in this figure

In an analogous way to the receptive field model of Rodieck and Stone (1965a,b), Wilson and Bergen (1979) have specified a spatial sensitivity profile for perceptive fields. They indicated at the same retinal location the existence of several receptive fields where infact they meant perceptive fields.

It is now generally assumed that perceptive fields have a "Mexican hat" profile, corresponding to a difference between two Gaussian functions of different widths (Troscianko, 1982).

That various perceptive field sizes exist at a certain location in the visual field can be concluded from psychophysical data of Spillmann (1971) and Troscianko (1982). They found that a range of critical bar widths could be indicated for the Hermann grid illusion. The moment the bar width reaches the diameter of the smallest perceptive field centres locally present, the illusion appears. The illusion disappears as soon as the bar width becomes so much wider than the largest perceptive field centre, that the latter is almost diffusely illuminated.

For receptive fields it was found that the increase of receptive field size was mainly achieved by an increase of the centre diameter. For perceptive fields the same may be assumed. According to Ransom-Hogg and Spillmann (1980) the centre/surround ratio increases with eccentricity as the centre size of the perceptive fields increases also with eccentricity. This implies that the surround remains almost constant. From the data of Wilson (1978) it follows that centre as well as surround diameter increase with eccentricity. The model they fit to the data starts, however, with a constant centre / surround ratio.

To what extent the differences between the perceptive fields at a certain location reflect the properties of the corresponding receptive fields is not fully clear at this moment. Any experiment in which the perception of a central area is influenced by the surrounding retinal illumination arises the question of what is seen of a perceptive field. In the interpretation of the perceptions when inspecting a Hermann grid it is assumed that the observable effect corresponds to the centre of a perceptive field. Note that this is rather difficult to conceive because there are various overlapping perceptive fields at each location and excited simultaneously. If only one centre would be "seen" the others have to be inhibited. The final percept at each location in the visual field seems to be built up from the co-operation of a number of perceptive elements of different sizes (Gerrits, 1978). He stated that future investigations may result in the conclusion that a perceptive element is related to the centre of a perceptive field. According to his latest view the percept described as the perceptive field centre presumably results from the activation of a number of perceptive elements as indicated in figure 2.5. The filling-in, i.e. the lateral activation of neighbouring elements, is the cause that the perceptive elements can only be observed separately in certain stabilization experiments. The receptive field of a perceptive element has, in fact , no limit in the visual field. Based on various experiments in stabilized condition it has to be assumed that the elements connected to large perceptive pixels can be inhibited by elements connected to small perceptive pixels. Small elements seem to be more dominant in het generation of brightness or darkness than cells with a field with a large centre (Magnussen and Glad, 1975). This dominance also follows from the apparent constancy of contrast, which implies that as long as contrast is above the threshold value for the highest spatial frequency in a stimulus, no apparent contrast change occurs as spatial frequency changes (Woodhouse and Barlow, 1982). According to the optical modulation transfer function of the human eye there is a progressive loss of modulation in the image as the spatial frequency is increased. Thus the apparent constancy of contrast presupposes that the cells with small centres (high spatial frequencies) must signal the brightness or darkness more effectively than cells with large centres.

2.3.2. Fading

Fading is the gradual decrease of brightness and/or darkness caused by the loss of brightness- and/or darkness-producing activity. When brightness-producing activity fades the percept becomes less bright (darker), when darkness-producing activity fades the percept becomes less dark (brighter).

Fading is a mechanism, that is continuously active. In normal vision it is compensated for by the continuous retinal image movements in addition with filling-in. Filling -in is the spreading of activity within the higher centre from activated elements to less activated elements in the brightness or darkness system. Filling-in will be thoroughly discussed in section 2.3.3. Only when the input of brightness- or darkness-producing activity is too small or is stopped fully, the effects of fading will be perceived. The eye movements normally present cause a continuous input of brightness- or darkness-producing activity. Schematically the fading has been indicated in figure 2.6a. Fading may be described as a gradual loss of information which occurs with time.

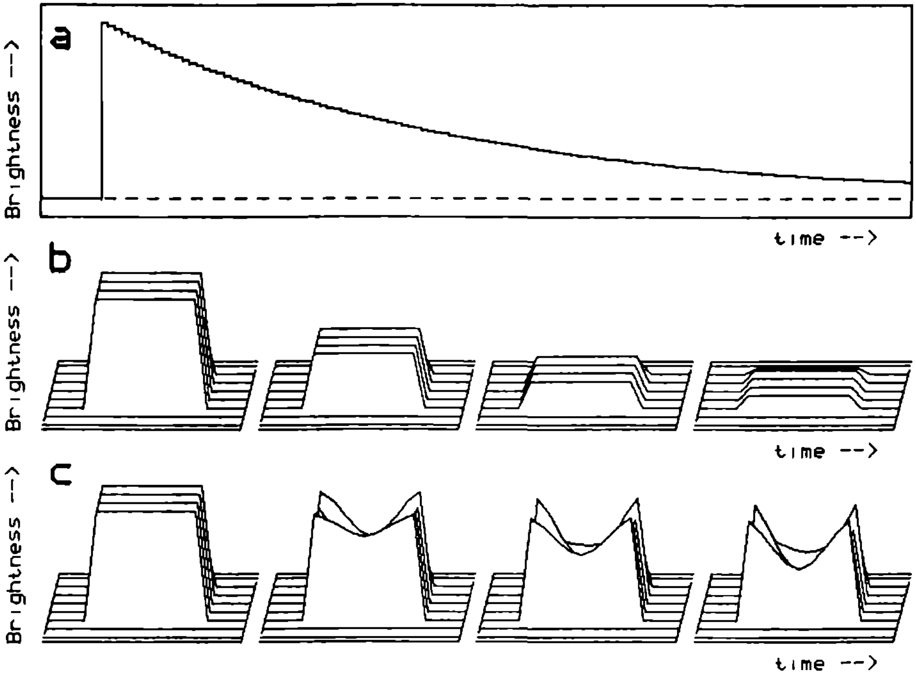

Figure 2 6 Functional representation of fading
- a The time course of the brightness-producing activity of a higher centre element The activity fades within a few seconds
- b An example of fading of 128 elements each having the same time constant
- c An example of fading of 128 elements having smaller time constants in the foveal projection

In experimenting with this dynamic phenomenon, measuring the exact moment of total disappearance is impossible. As soon as the empty field (Yarbus, 1967) is observed it still takes some time before the lowest brightness level is reached. The very slight brightness that can be observed from that moment on will not disappear. It is called the residual brightness (Gerrits, 1978) and it is caused by the very small variations in neural activity that always remain. Nevertheless it has been tried to measure a fading time in various experiments while the stimulus parameters luminance, contrast, spatio-temporal structure, the degree of retinal image stabilization and the location within the visual field were varied (e.g. Sparrock, 1969). In this thesis (chapter five) it is suggested to determine a fading time constant rather than a fading time. The fading time constant is a system parameter, describing the rate at which a higher centre element loses its activity and depending only on the localization in the visual map. From earlier stabilization experiments (Gerrits, 1978; Gerrits et al., 1984) it was determined in a qualitative way that fading proceeded faster in the foveal than in the peripheral projection of the visual field. From experiments, to be described in chapter five, the fading time constant was quantitatively determined . It appeared that higher centre elements associated with the centre of the foveal area have the smallest time constant. As will be seen in the next part about filling-in this does not imply, however, that the activity of these elements will be the first to disappear. For the hypothetical situation that only fading is present it is schematically indicated in figure 2.6 how fading proceeds. When the fading time constant is equal for every element, activity decreases as indicated in figure 2.6b. When the fading time constant varies with space, being smallest in the "fovea", the decrease proceeds as indicated in figure 2.6c.

The fading of brightness and darkness should be distinguished from the neutralization of only partially faded brightness or darkness by darkness or brightness, respectively. Normally only brightness- or darkness-producing activity is present at a certain location. However, activity may spread around due to filling-in. So also an area where darkness was signalled at first may be filled-in with brightness-producing activity although the darkness has not yet fully faded. Thus the perception of the brightness-producing activity will be less than in the case of all darkness having disappeared and filling-in having been completed. A part of the brightness-producing activity will therefore be called to be neutralized by the darkness-producing activity. So neutralization is the mutual reduction of the perceptual result of brightness- and darkness-producing activity simultaneously present. As a consequence neutralization is instantaneous.

From various experiments it has become clear that different fading time constants also exist for the different modalities: contours, colours and brightness. Regardless the colour or object chosen, the sequence of disappearance of the perception is always the same: firstly the contours, secondly the colour, thirdly the brightness (Gerrits, 1966).

Can the origin of fading be found at the retinal level? The response of the on- or off-centre ganglion cell consists of a change of the instantaneous spike rate. An increase is signalled to the higher centre a decrease is not. But even if the decrease of the spike rate, i.e. the decay of the burst response to a steady level was signalled, it is not at all compatible with the slow decay of the brightness or darkness percept in stabilized condition. This can also be deduced from an experiment by Nakagawa (1962). He reported that the presentation of a regular series of electrical pulses to a patient's optic nerve resulted in fading within a few (2-5) seconds of the brightness percept elicited by the stimulus onset. Also the response of the pupil does not change while the subject's percept fades (Gerrits, 1966). As the pupillary sphincter is controlled by nerves coming from the nucleus of Edinger-Westphal, which, in its turn receives information from the pregeniculate nucleus where a part of the optic tract arrives, it is clear that the sustained activity of the ganglion cells supplies the signal of steady retinal illumination. Thus fading has to occur at a higher level in the system. It is found that in the various stages following the retina (lateral geniculate nucleus, superior colliculus, visual cortex) it is even more true that the mean level of the retinal illumination is not signalled. Clarke and Belcher(1962) suggested that fading might be located in the lateral geniculate nucleus because a binocular experiment indicated that it does not arise in the visual cortex. The overall picture is that the further one goes up the visual pathway, the more successfully the effect of the mean level of illumination is cancelled (Levick, 1972). Up to now nobody has found a nucleus containing cells that show a decay of activity which parallels the slow fading of the brightness or darkness observed in stabilized condition. This is the reason why fading, an effect that is clearly observed in the experiments but has not yet been localized anatomically, is placed in a hypothetical centre, called the "higher centre " for the time being.

2.3.3. Filling-in

The concept of filling-in was introduced by Walls (1954). It was incorporated in a qualitative model of information processing in man's visual system by Gerrits and Vendrik(1970b). Filling-in is defined as the activation of a brightness- or darkness-producing element by neighbouring elements. Filling-in occurs when two conditions are fulfilled: firstly the receiving element obtains less direct input than its neighbours and secondly it is not impeded by antagonistic activity. Filling-in is the activation by lateral inputs (Gerrits, 1979), which implies interconnections between perceptive elements. Due to the filling-in mechanism brightness- or darkness-producing activity spreads out within an area bounded by barriers. A barrier is set up by brightness- and darkness-producing activities at both sides along a contrast boundary. The level of activity obtained by filling-in is determined by the surrounding activity as well as the presence of barriers. The rate of fading of barrier forming brightness- or darkness-producing activity determines the rate at which filling-in is seen to proceed. In cases where no barrier is generated filling-in is seen to proceed almost instantaneously. In figure 2.7 the filling-in process is schematically illustrated. The filling-in process will be considered for a stabilized situation and the onset of a bright area surrounding a dark disk is indicated. At the borders of the bright area more brightness will be generated (Mach bands) than elsewhere due to the unilluminated surrounds of the corresponding on-centre cells.

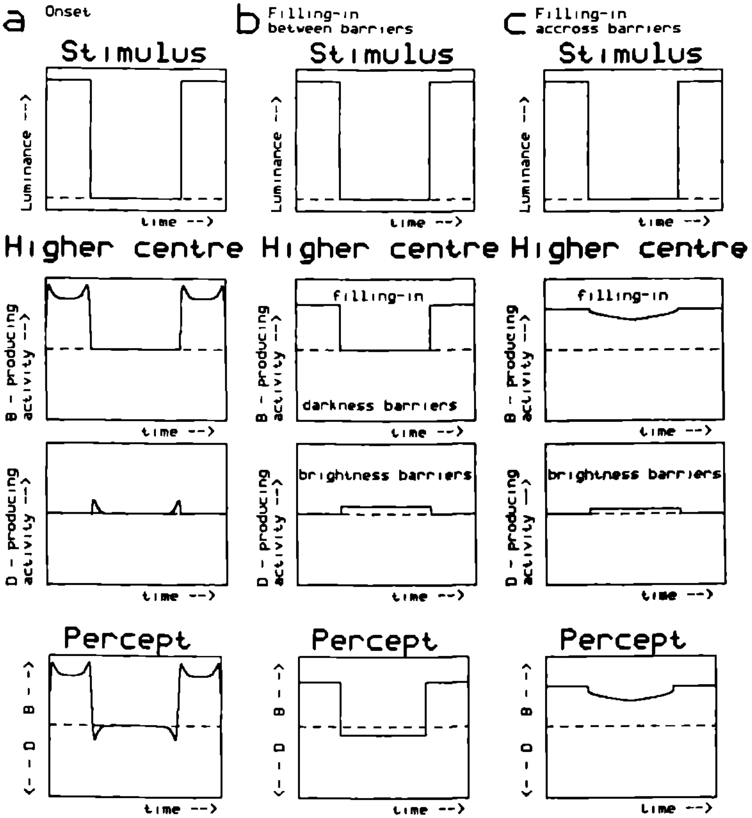

Figure 2 7 Functional representation of filling-in in a stabilized condition

a Onset of the area surrounding a black square, i e locally the brightness is increased A cross-section is made through the luminance profile of the stimulus, the brightness- and darkness-producing activity and the perceived' brightness and darkness pattern

b Filling-in of the dark area with darkness-producing activity because no barriers are present at the inside At the outside brightness-producing activity equalizes the outside area, i e the bright Mach band disappears, because of the absence of a darkness barrier

c Filling-in of the black square as the darness barriers at the inside of the square decrease in strength As a consequence the central area is seen to be filled-in with the brightness

This locally higher extent of brightness does not exceed the barrier caused by darkness activity but will only spread out over the bright area (filling-in, figure 2.7b). On the side of the dark area a barrier is encountered, however, and filling-in is prevented. Within the dark area the same situation occurs. The darkness will spread out over the entire dark area but will be prevented going any further because of the barrier formed by the brightness, surrounding the dark area (figure 2.7b). In the third column it is shown how the filling-in starts to bring brightness in the central area as soon as the darkness, and as a consequence the barrier, has faded (figure 2.7c).

The function of filling-in is thought to compensate for the fact that the system does not possess the same sensitivity throughout the retinal area. Only the on-set of a homogeneous stimulus might reveal these inhomogeneities but as soon as the first burst of activity is passed filling-in prevents preserving them (Walls, 1954). Within the homogeneous area every receptive field will be diffusely illuminated and as a consequence the corresponding cells will maintain their sustained activity, which apart from small random increments is not transmitted to the higher centre. When irregular retinal image movements are present (normally resulting from eye movements) changes of illumination will occur within receptive fields located at the edge of the homogeneous area. This will result in a continuous generation of on- and off-activity.

For an unstabilized homogeneous area the perceived brightness or darkness is determined by the elements subserving the perception of the contour of the area. The contributions from the boundaries, that result from the continuous eye movements, cause brightness or darkness of a light or dark homogeneous area to be maintained after its onset, while a continuous inflow of brightness- or darkness-producing activity is generated. An extensive discussion about the necessity of the signal being irregular can be found in Gerrits and Vendrik (1974) and Gerrits et al. (1984).

For the preserved perception of a homogeneous bright stimulus area this implies that the brightness-producing activity originating at the edge will not meet a barrier and as a consequence "spreads out", thus compensating for the fading. An analogous situation is described by Fischer et al. (1975) in their brightness restoration hypothesis. They suggest a signal, which continuously reactivates the brightness of the enclosed area and originates at the edge .

As was mentioned in the previous part of this chapter, activity fades with a different time constant for elements which are located in various positions within the visual field. In complete stabilization the activity of an element is determined by the amount faded as well as the filled-in activity. It is clear that the location of the stimulus in the visual field determines which boundary element dictates the activity within the stimulus area. So perception of brightness or darkness within a large stabilized homogeneous area is determined by elements with the largest fading time constant. The area is only seen to be homogeneous during fading when these elements are positioned symmetrically with respect to the elements that have smaller time constants.

Filling-in does not proceed in a specific direction, e.g. from peripheral to foveal parts. A higher centre element that receives "filling-in activity" may be located anywhere adjacent to a higher centre element activated by direct input. From earlier stabilization experiments it was concluded that filling-in has to proceed in the direction of the foveal area. Observations revealed that this was not a property of filling-in but of the smaller fading time constant of the foveal region. Filling-in proceeds in a direction that is determined by the actual levels of brightness- or darkness-producing activity. Areas up to 32 degrees in diameter can be filled-in (Gerrits, 1970a).

2.4. Adaptation

In this part a few remarks about adaptation will be made. The concept of adaptation is used in various ways often applying to very different mechanisms. Sometimes it refers to an active process of the system to suit itself to changing circumstances, but it is also used to describe transient activities dictated by passive elements. As it was tried to define rather precisely the various mechanisms active in the model of brightness and darkness processing, a definition of adaptation could not be omitted here. In this thesis the concept of visual adaptation is defined as the mechanism that describes how the visual system changes its dynamic range in order to "perceive" optimally the specific stimulus. For example: The dynamic range of 1.5 log units of the brightness or darkness channel in the visual system is too small to process the range of natural possible luminances (8 log units) (Barlow, 1982). In normal daily life, however, the system usually processes luminances in a small range around a mean value. By shifting its midpoint of luminance sensitivity, the brightness system is able to use its dynamical range to a full extent. Then the system is adapted to the specific illumination conditions.

Adaptation may be considered with respect to a physical characteristic of the stimulus (luminance, velocity, size) but also with respect to a subjective characteristic (brightness, darkness, colour, apparent size). This is one of the reasons which led to so various definitions of adaptation. Time dependable sensitivity is an overall system characteristic that may result from adaptation of receptors up to an adaptation of higher processes. Adaptation of receptors and neurons can be determined from electrophysiological experiments. Psychophysics always involves the whole system and may also reveal adaptation in the higher processes, for instance habituation. Habituation is a decreasing perceptual effect of a continuing stimulation. Often adaptation is used while habituation is meant.

A good review about the different mechanisms playing a role in adaptation was given by Barlow (1982).

2.5. Concluding remarks

In this chapter data from electrophysiology as well as from psychophysics have been used. Data of animals as well as human beings have been considered. Although the model has still a hypothetical character, as it is partly based on predicted electrophysiological phenomena, it is capable of combining a large number of psychophysical observations with electrophysiological findings. For a number of animals it is clear that a correlation of their neural activities can be correlated to human perception but on the other hand for a large number it should be kept in mind that this is only true for some functional parts of their visual system. The question arises as to what extent the use of such data is allowed.

Baumgartner (1961b) and Jung (1961a,b; 1964) were the first to correlate the neural activity with perception. They correlated the firing of the off-centre cells (darkness (D)-neurons) in the visual cortex with the perception of darkness and that of the on-centre cells (brightness (B)-neurons) with the perception of brightness. Jung used the data of Grusser and Grusser-Cornehls (1962) to correlate the human afterimage with the periodic firing of the B- and D-neurons in the cat after light-off. An investigation that related human verbal report of the perception of intermittent light stimulation to the corresponding electrical activity of the visual system was carried out by Pinneo and Heath (1967). They stated that the close correspondence between the average amount of activity measured and subjective reports of their patient, was not likely to be coincidental. Cleland and Enroth-Cugell (1968) stated, that human and cat data become compatible if one assumes that as the background luminance in psychophysical experiments changes, new ganglion cells with different receptive field sizes are called upon for decision-making - a mechanism suggested by Pirenne and Denton (1952) to explain human visual acuity changes. Coenen and Eijkman (1972) felt justified in assuming that single units in the human visual system behave similarly to single units in the cat as the responses after a flash in cat and monkey do not show much difference with respect to the time course of the activity (Hubel and Wiesel, 1960). Also Magnussen and Glad (1975) found, where parallel experiments make comparisons possible that generally there is a good agreement between neuronal recordings and human perceptual data.

However that may be, the correlation of electrophysiological and psychophysical data encourages thinking about new electrophysiological as well as psychophysical investigations. As long as it is possible to explain psychophysical phenomena in terms of properties of retinal, lateral geniculate nucleus, area 17 and higher centre cells this correlation should be done. After all these cells are the basic components that subserve animal and human perception.

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Chapter 3. INSENSITIVITY PERCEPTS AND RECEPTIVE FIELDS.

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3.1. Abstract

An afterimage (AI) is a well-known phenomenon. It may be generated by exposing a part of the retina to a very strong light source. By using a very short exposure, for instance from a photoflash it can be prevented that the image of the source smears out due to eye movements. A true afterimage is a fluctuating brightness that remains visible for some period after the luminance that brought it about was switched off. A percept is considered to be a true afterimage as long as it is visible in complete darkness. However, in the area in which the afterimage was seen it is possible to generate a so-called insensitivity percept (IP). IP's are the prolonged dark or light percepts that remain observable against new bright or dark stimuli after a true afterimage has disappeared. The IP's discussed in this chapter were inspected against modulated backgrounds. It was found that the rate of modulation has to be sufficiently fast with respect to the fading time of the percept that is generated. Test stimuli of short duration have to be applied to prevent the percept to fade and to avoid artefacts from adaptation. Only ganglion cells with the centres of their receptive fields along the contour of the flash exposed area are responsible for the IP's. These cells which have an insensitive centre and surround part, respond abnormally. On-centre cells are excited when diffuse background illumination decreases and off-centre cells are excited when it increases.

3.2. Introduction

An image can be fixed in a number of ways on the same retinal location in spite of eye movements (Ditchburn & Ginsborg, 1953; Riggs et al., 1953; Yarbus, 1967, p. 171; Ditchburn, 1973; Gerrits et al., 1984). These so-called stabilization techniques enable the study of visual information processing while the influence of retinal image movement, resulting from eye and/or head movement, is eliminated.

To enable a clear comparison between the percepts resulting from image stabilization and retinal insensitivity the percept of a disk is described when it is presented stabilized on the retina.

Three main stages in the perceptual appearance of a stabilized homogeneous light disk on a dark background can be distinguished (Gerrits, 1966):

a. The contour begins to fade away directly after presentation of the stimulus. It becomes less distinct, while the brightness of the disk decreases gradually. The disk seems to expand.

b. While the processes described under (a.) continue, also the colours (if present) become more and more unsaturated. So after some time only a colourless blurred percept of the disk remains.

c. The brightness difference between blurred disk and background is the last part of the percept that remains. The final percept is formed by a very vague patch of brightness that almost disappears

from view.
From these observations it has to be concluded that the disappearance of the contour, of the colour and of the brightness or darkness proceed with different time constants. Note that although the percept fades totally from view, the image of the disk remains unchanged on the retina.

When a black disk surrounded by a green area is stabilized it also disappears from view. The darkness within the percept of the disk fades and the disk is fully filled-in with the brightness and the colour of the surrounding area. Meanwhile the total percept decreases in strength until only a very faint residual brightness remains.

There is a link between a stabilized image (SI) and an afterimage (AI) because they are both "fixed" on the retina. Generally the term "afterimage" refers to the appearance of a light area in a darker surround after an exposure to a flash of very high intensity. Also the perceived light or dark patch that is seen when inspected against backgrounds of various luminances is called an "afterimage" . In complete darkness any change in retinal illumination can be avoided, but an influence on the perceptual appearance of an afterimage by saccadic suppression cannot be excluded. The afterimage seen in complete darkness is the true afterimage (AI). It disappears after a period of brightness fluctuations. This early or original afterimage (Brown, 1965) is a result of retinal processes. Experiments were done (Craik, 1940; Cibis and Nothdurft, 1948), in which pressure on the eye ball prevented the stimulus that generated the afterimage from being seen.

The perceptual phenomena seem to correlate with the "oscillations" measured at retinal ganglion cell level by various experimenters (Grusser and Grutzer, 1958; Grusser and Rabelo, 1958) and at the cortical level by Jung(1961a) and Grusser and Grusser-Cornehls (1962).

Also studies that analysed the question whether or not percepts of stabilized images completely disappear from view have dealt with afterimages. According to Campbell and Robson (1961) complete stabilization is possible only when the object to stabilize is formed by some internal structure of the eye. Evans (1966) used afterimages as a method of obtaining stabilized retinal images and Magnussen and Torjussen (1974) have put it as follows: " If a brief flash of light is delivered to the eye, an afterimage that mirrors the size, shape and retinal position of the inducing stimulus may be observed. Depending upon changes in the state of the retinal cells themselves (Craik, 1940; Newsome, 1971) an afterimage is a spatially (though not temporally) perfectly stabilized retinal event-an event, moreover, for which there is good reason to believe that it is virtually indistinguishable to the more central parts of the visual pathway from a real light image stabilized on the retina by optical devices (Barlow and Sparrock, 1964)."

It should be noted, however, that the fluctuations seen in an afterimage, which result from retinal processes, are not seen in the percept of a stabilized retinal image, which loses its contrast, brightness and colour in a different way and which does not fluctuate.

The receptors in the flash exposed area have not yet regained their full sensitivity at the moment the afterimage disappears. It is still possible to generate dark and bright "afterimages" that can be observed against bright and dark backgrounds respectively, when the retinal illumination at the edge of the bleached area is changed in the right manner. The luminance of the background has to change with a minimal slope and amplitude as will be seen later. These percepts will be called insensitivity percepts (IP's), also indicated in the literature as the late or secundary stimulus afterimages (Brown, 1965). They are the result of the different receptor sensitivities inside and outside the flash exposed area. IP's have the same dimension as the preceding afterimage and can be interpreted as "simultaneous contrast effects ". IP's may very well be compared to the percepts of stabilized images but the time constant with which the receptors regain their sensitivity is much larger than the fading time constant (see chapter five). It takes the insensitive area about 20 to 30 minutes to regain the same sensitivity as the surrounding area. So for an IP the retinal change of activity at the on- or offset of a diffuse background cannot be distinguished by the brightness- or darkness system from the change of activity that results when a stabilized image is presented. Because the area generating the IP is part of the retina, excluding any effect of eye movements, the IP will fade as soon as illumination becomes constant. As long as the background illumination is changed, an increment in brightness or darkness is signalled from the border and this is sufficient for a percept of the insensitive area to appear.

For a properly chosen background modulation the insensitivity can be seen during a period that is appreciably longer than the period during which the true afterimage was seen. The important parameters are the mean level, the amplitude, the frequency and the wave-form of the modulation.

As only insensitivity percepts will be considered and not afterimages, the changes that take place directly after the bleaching flash will not be discussed. The question of how much photopigment was actually bleached has not been considered. The reduction of sensitivity is not a simple function of the amount bleached (Bonds & Enroth-Cugell, 1979), only the decrease of the sensitivity that results at the ganglion cell level, due to the desensitized receptors in the receptive fields, will be used. It will be shown in this chapter that only cells with part of their receptive field located at the boundary of the desensitized area are responsible for the observed effects.

Summarizing it can be said that the main difference between the percept of a stabilized image, an afterimage and an insensitivity percept (IP) consists of the generation of the phenomenon. For a stabilized image the visual stimulus remains unchanged after the stimulus onset and the percept fades. For an afterimage the visual stimulus is presented only for a limited period (stimulus on- and offset) and the percept disappears after an initial period of fluctuations. It is assumed that the offset response of the receptors is less strong as the receptors are made insensitive by strong illumination. This should also result in a lack of compensation for the brightness (B)-activity generated in the higher centre. We shall come to this later. For an insensitivity percept finally the retinal illumination remains also unchanged (except for the stimulus onset) while the percept also fades. The strength of the insensitivity percept decreases because the receptor insensitivity decreases as time proceeds. So that it is no longer possible to generate an IP. The characteristics of the AI,IP and SI are summarized in table 3.I. The time relations between a SI, an AI and an IP are given in a schematical representation in figure 3.1.

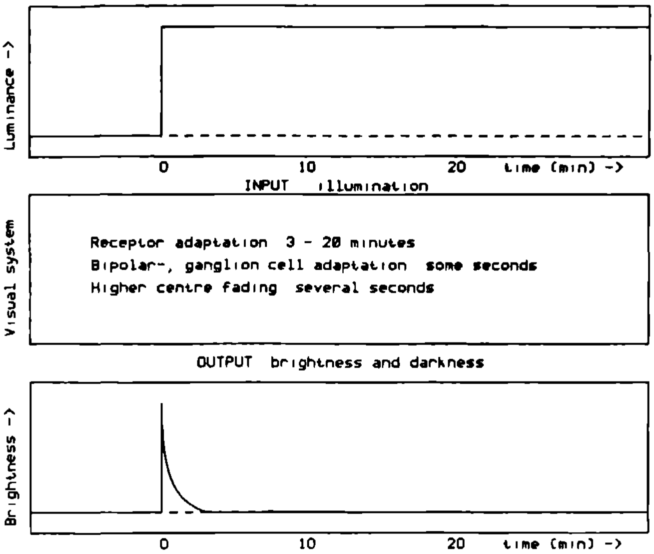
Percept	Stimulus	Illumination	Form	Nervous structure	Duration
		required after generation	determined by	responsible	of the period it can be seen (min)
Afterimage	Strong primary illumination	No	Primary illumination pattern	Retinal network	2 - 3
Insensitivity Percept	Strong primary illumination followed by diffuse secondary illumination	Non-stationary conditions	Primary illumination pattern	Receptors	20 - 30
Percept of stabilized image	Any illumination pattern	Stationary conditions	Actual illumination pattern	Higher centre	02 - 2

Table 3 I Characteristics of afterimages, insensitivity percepts and percepts of stabilized images

As was already pointed out in chapter two, changes in the percept of a homogeneous area can be induced by changes of the illumination within the area as well as changes of brightness- or darkness-producing activity at the border of the area only. This implies that the appearance of the insensitivity percept may be brought about by the cells lying at the inside of the insensitive area but having a receptive field that has a part of its surround located outside the insensitive area. Additionally it is worth noting that the shape of the receptive field is not influenced by the desensitization of the receptors but only the contribution of the exposed parts is reduced (Enroth-Cugell and Pinto, 1972).

The appearance and changes of insensitivity percepts have earlier been investigated by Carpenter (1972). He called them afterimages and explained their behaviour in terms of a diffusion process active at the level of the photopigment. It was found, however, that the time constant for pigment regeneration in man is much smaller than the time constant for recovery of the threshold sensitivity (Pugh, 1975). Carpenter (1972) also suggested that afterimages (here called insensitivity percepts) eclips at a certain illumination level, i.e. they switch from "brighter than the background" to "darker than the background" and that they become

a. Stabilized image



b. Afterimage & Insensitivity percept

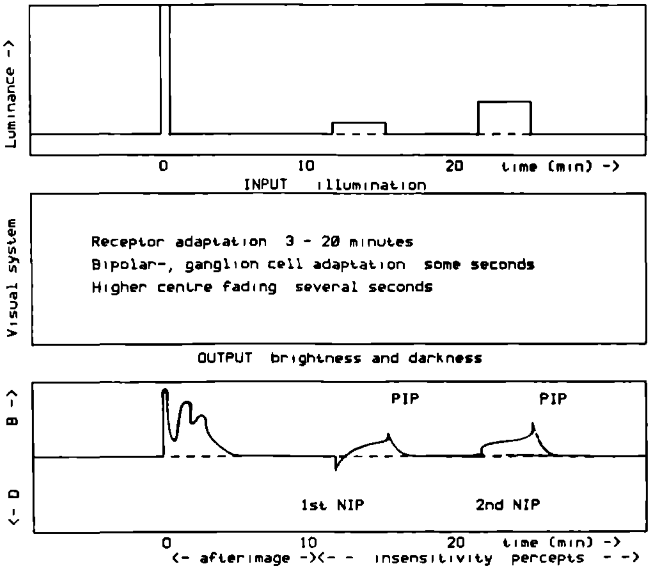


Figure 3 1 Schematic representation of the time course of stimulus and percept in a stabilized image and an afterimage, respectively An afterimage is followed by an insensitivity percept when a modulated homogeneous background is inspected

invisible at the actual level of reversing . When a number of afterimages of various strengths are present he stated that they all eclipse at the same illumination.
In this chapter we will present experiments to investigate whether the insensitivity percepts can be attributed to changes of the activities at the border only. Additionally the eclipse of insensitivity percepts, generated at different intervals of time, will be compared.

3.3. Method

A moderately light-adapted subject looked monocularly towards a diaphragm and a central fixation spot through a 20 diopter lens. The diaphragm diameter was adjustable to span 1.7 to 20.4 degrees in the visual field. After the subject positioned his head by a chin rest and head support, the room light was switched off and a strong photoflash was presented as soon as the subject fixated. A modified Brown Hobby Flash unit (2.10^6 cd/m^2 within 2 msec; temporal distribution measured by a PIN-10 AP silicon photodiode-United Detector Technology: rise time 2 μsec) was used. To prevent any smearing of the image due to eye movements a short high intensity flash was used instead of a source of less intensity that had to be fixated during a somewhat longer period.

After the flash the subject turned towards a second setup equipped with a chin rest, a forehead clamp and adjustable neutral density filters (10 x, 100 x, 1000 x), to look monocularly at a Philips LDN 5006 video monitor for pulsed illuminations. On this monitor light disks, adjustable in luminance and diameter (4 up to 30 degrees), were presented to elicit the insensitivity percepts. A fixation spot (36 x 36 min arc) in the centre of the disk was continuously present on the screen. All adjustments of luminance increments, decrements and stimulus sizes were registered continuously as a function of time. One naive (WR) and a highly trained (HG) subject participated in these experiments. In an experimental session, the subject, continuously looking at the fixation point, triggered the presentation of a low luminance disk of 4, 8, 12, 24 or 30 degrees in diameter, which lasted up to about half a second. If no IP was observed he increased the luminance amplitude and repeated the short presentation of the disk.

3.4. Results

In the first series of experiments it was found that during the first few minutes after presentation of a foveally centred flash, of e.g. 15 degrees in diameter, reliable adjustments to determine the IP thresholds could not be made. This was due to the strong interference of the fluctuating (true) afterimage, which showed up. After that, however, the outcomes became reliable and three clearly different percepts could be distinguished. These percepts have been sketched in figure 3.2.a, b and c. At a certain threshold luminance the first negative IP (the first NIP) was soon detected. It was defined negative because it was seen as a dark disk against a dim light background (figure 3.2.a).

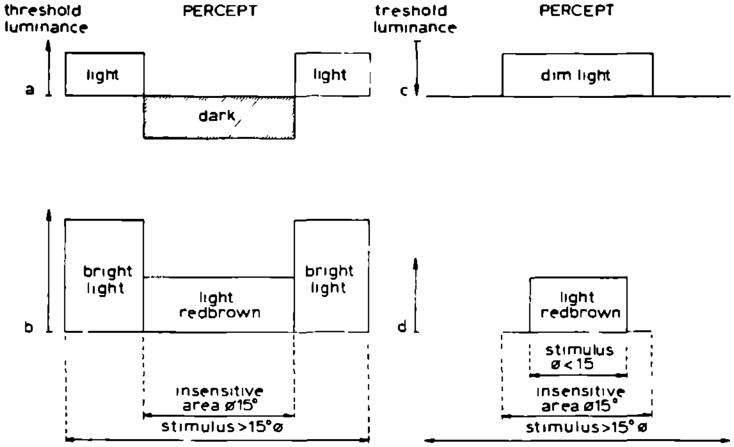


Figure 3 2 The different percepts at their threshold luminances (not drawn on scale), elicited by disks larger and smaller in diameter than the insensitive area
a The first negative insensitivity percept (1st NIP)
b The second negative insensitivity percept (2nd NIP)
c The positive insensitivity percept (PIP)
d The percept elicited by a disk smaller than the insensitive area

A small further increase of the test stimulus luminance elicited a confusing percept: the insensitive area looked neither dark nor bright and had no sharp contours.

The second negative IP (the second NIP) was observed when the subject increased the test stimulus still more and has been sketched in figure 3.2.b. A low brightness and a reddish-brown color was now observable in the insensitive area while the background was bright and colourless. It is called a negative insensitivity percept, because the insensitive area looked darker than the background. As the retina regained its sensitivity in the course of time the first NIP and, later on, also the second NIP could no longer be elicited.

A bright, positive IP (PIP) was generated by decrements from adjustable background levels (see figure 3.2.c.). It was only observable if the subject waited long enough to get rid of all remnants of the foregoing dark NIP, generated by the onset of the background.

In the second series of experiments it was investigated whether the IP's were generated by activities of cells located in the sensitive area, the insensitive area or in both. For this purpose disks with both larger and smaller diameters than that of the insensitive area were presented repeatedly in a mixed sequence within the 20 minutes it took the retina to regain its sensitivity. For an insensitive area of e.g. 15 degrees in diameter disks measuring 4, 8, 12, 18, 24 and 30 degrees in diameter were used. A typical result from a naive subject (WR) is shown in figure 3.3. The two groups of curves diverge at first to meet each other again after about 16 to 20 minutes. The three lower curves represent the threshold versus time functions when the larger (18, 24 and 30 degrees) disks are presented, the three upper curves result from the presentation of the smaller (4, 8 and 12 degrees) disks. As the threshold of the small disk was reached it showed up with a low brightness and a redbrown color (figure 3.2.d). The threshold luminance eliciting a small light redbrown disk was always higher than the threshold of the first NIP (see figures 3.2a and 3.3) but much lower than the threshold of the second NIP (figure 3.2.b). This implies that the first NIP cannot be generated by on-centre cells in the bleached area which respond less than the surrounding ones in the normal, unbleached area.

When a small disk, presented at its threshold luminance, was increased in diameter its percept changed from a low brightness reddish-brown disk into a dark disk, i.e. into the first NIP, as soon as its diameter overstepped the diameter of the insensitive area.

If the luminance remained constant after the step the first and second NIP, as well as the PIP disappeared. This had to be expected as the contour between the sensitive and insensitive area was, in fact, stabilized on the retina. However, the light redbrown disk (figure 3.2.d) did not disappear because of the stimulus was continuously displaced within the insensitive area by the fixational eye movements.

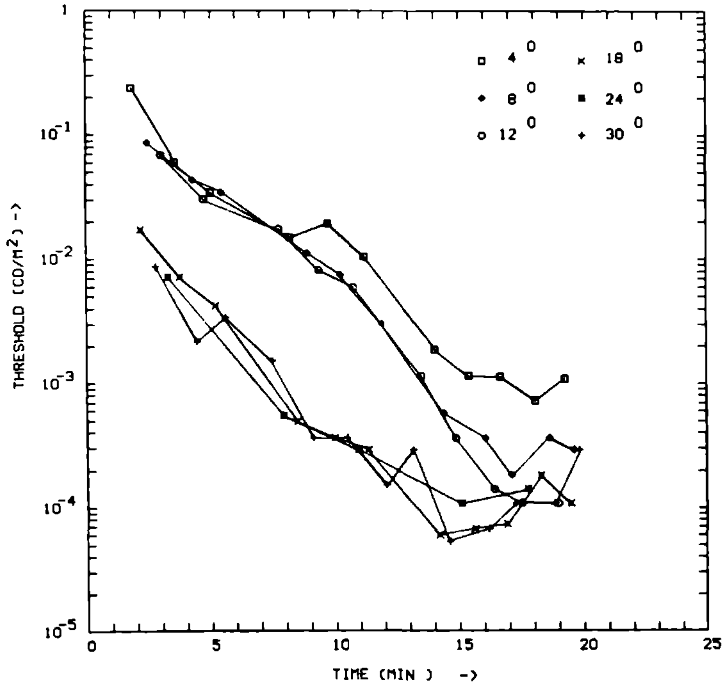
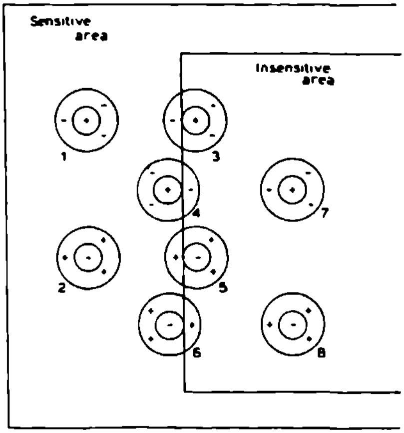


Figure 3 3 Luminance thresholds as a function of time for disks (backgrounds) larger (three lower curves) and smaller (three upper curves) in diameter than the insensitive area (15 degrees) At the lower threshold the first negative insensitivity percept was observed, at the higher threshold a light redbrown disk was seen Data from subject WR

3.5. Discussion

To understand the origin of the insensitivity percepts we restrict ourselves to the brightness and darkness system only and we apply the wellknown properties of receptive fields to these specific stimulus conditions. For simplification we start to suppose that the retinal insensitive area is sharply demarcated and that the percepts are determined by the activity of the classes of ganglion cells whose receptive fields have been sketched in figure 3.4. We will make corrections for this supposition later on.

It is known that most receptive fields consist of a concentrically organized centre and surround structure (Kuffler, 1953; Barlow et al. 1957; Rodieck, 1965; Rodieck and Stone, 1965; Cleland and



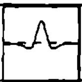
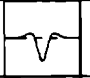
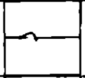
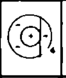
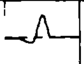
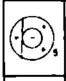
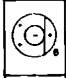
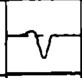
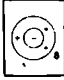
RECEPTIVE FIELD		RESPONSE AT DIFFUSE LUMINANCE	
TOP VIEW	SENSITIVITY PROFILE	INCREMENT	DECREMENT
		EXCITATION = BRIGHTNESS R_{on1}	INHIBITION
		INHIBITION	EXCITATION = DARKNESS R_{off2}
		INHIBITION	EXCITATION = BRIGHTNESS $R_{on3} \ll R_{on1}, R_{on4}$
		EXCITATION = BRIGHTNESS $R_{on4} > R_{on1}$	INHIBITION
		EXCITATION = DARKNESS $R_{off5} \ll R_{off2}, R_{off6}$	INHIBITION
		INHIBITION	EXCITATION = DARKNESS $R_{off6} > R_{off2}$
		ONLY EXCITATION AT A LARGE INCREMENT	ONLY INHIBITION AT A LARGE DECREMENT
		ONLY INHIBITION AT A LARGE INCREMENT	ONLY EXCITATION AT A LARGE DECREMENT

Figure 3.4 Eight classes of ganglion cells have to be considered in the explanation of the occurrence of insensitivity percepts

Enroth-Cugell, 1968; Cleland et al., 1973; Enroth-Cugell and Pinto, 1972; Enroth-Cugell and Lennie, 1975). A receptive field belonging to an on-centre cell, has a centre that excites the cell as it is illuminated and a surround that inhibits the cell when illuminated. The receptive field belonging to an off-centre cell, has a centre that inhibits the cell when illuminated and a surround that excites when illuminated. A full description of these properties was given in chapter two. We will restrict ourselves to the differential response formulas in case of increase or decrease of a diffuse illumination.
For an on-centre cell:

$$\Delta R_{on} = \Delta I \ (K_c - K_s) \qquad 3.1.$$

and for an off-centre cell:

$$\Delta R_{off} = \Delta I \ (K_s - K_c) \qquad 3.2.$$

where ΔR_{on} = the differential response of the on-centre cell (spikes/sec)
ΔR_{off} = the differential response of the off-centre cell (spikes/sec)
K_c = the gainfactor of the centre
K_s = the gainfactor of the surround
ΔI = the increase or decrease of the intensity of the illumination.

The gainfactors depend on the degree of insensitivity within the receptive field resulting from the previous exposure. The influence of the surround part of the receptive field can be considered to modulate the response elicited by illuminating the centre. In normal conditions, i.e. when all the receptors of the receptive field are equally sensitive, the centre mechanism is stronger than the antagonistic surround mechanism and determines the cell's response to diffuse illumination. In figure 3.4. we have cells with receptive fields that were not desensitized at all (cells 1 and 2), some had only a part of the surround insensitive (cells 4 and 6), others had an insensitive centre and an insensitive part of the surround (cells 3 and 5) and there are cells that had a fully insensitive receptive field (cells 7 and 8).

An increase of the on-centre cell activity conveys the message "brighter" and will therefore be called its brightness-activity; an increase of the off-centre cell activity signals "darker" and will be called darkness-activity (Baumgartner, 1961; Jung, 1961a,b; Magnussen and Glad, 1975; Jung, 1973).
The fact that only increases of the spike activity carry information from the retina to the brain is incorporated in the information processing model of Gerrits and Vendrik (1970). This model is backed up by anatomical and electrophysiological evidence (Gouras, 1970, 1971; Brooks and Jung, 1973; chapter two of this thesis). The relative contributions from parts of the receptive fields of some cells were changed strongly by the given flash. It is supposed that exposure to intense illumination, results in a reduction of the gain factor of the sensitivity of centre and surround.

This leads to the sensitivity profiles as given in figure 3.4. The receptive fields of only those cells are considered that are located along the edge of the bleached area. The amount of sensitivity reduction influences the cell's response in the case of diffuse illumination.

The response of the cells 3, 5 and 7 (see figure 3.4.), which determine the percept of the insensitive area at the onset of a diffuse light, have been sketched schematically in figure 3.5.

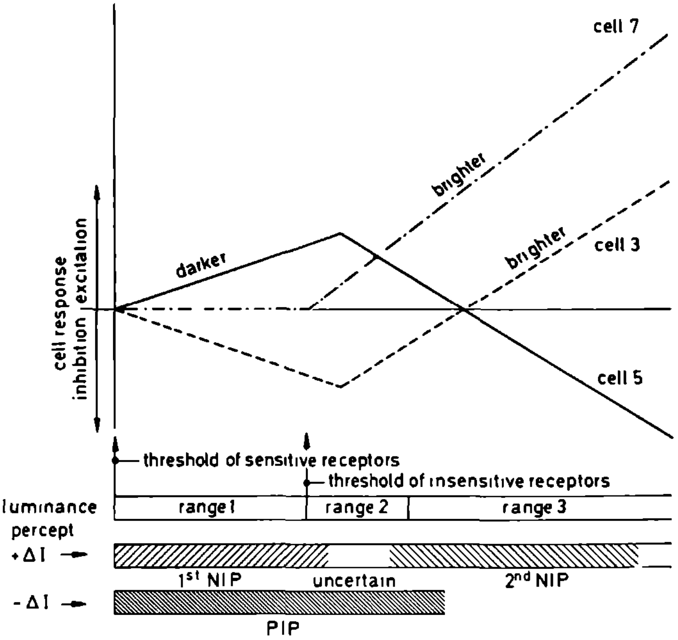


Figure 3 5 A schematic diagram indicating the relative luminance levels at which on-centre cell 3 (see figure 3 4) and off-centre cell 5 reverse their responses (from excitation to inhibition and vice versa) and the threshold of on-centre cell 7 is reached. Further explanation in the text

On-centre cell 7 does not respond to stimuli of any luminance level (range 1 as indicated in figure 3.5.) below the threshold of its insensitive receptors. The onset of a supra-threshold diffuse stimulus (range 2 and 3) elicits an excitatory response from this on-centre cell, meaning "brighter".

On-centre cell 3 exhibits a reversed to normal response when a diffuse stimulus of a low luminance (range 1) is presented. This luminance is subthreshold for its insensitive receptors but supra-threshold for the receptors in the sensitive part of its receptive field. As a result cell 3 is inhibited by the inhibitive contribution of the sensitive part of its surround instead of being excited from the centre at the onset of this stimulus. It is clear that the response of cell 3 to stronger diffuse luminances (range 3), supra-threshold for the insensitive receptors, will be almost normal. This is the consequence of the fact that the gain factor of the centre mechanism is always greater than that of the surround mechanism. An intermediate luminance level can also be found for which the response of cell 3 is nil. At this level the sum of the inhibitory contributions, relatively strong from the sensitive part and weaker from the insensitive part of the surround, is equal to the excitatory contribution from the insensitive but preponderant centre. Note that the threshold luminance to elicit an excitatory response is higher for cell 3 than for cell 7 because cell 3 possesses a partly sensitive inhibitory surround.

According to an analogue reasoning it can be explained that cell 5 responds with an excitation instead of an inhibition to the onset of diffuse stimuli in range 1, which are sub-threshold for its insensitive receptors but supra-threshold for the sensitive part of its surround (see figure 3.5.). This excitation conveys the message "darker". Also this cell changes its response into its normal mode, i.e. from excitation into inhibition, when the diffuse luminance level is increased sufficiently (into range 3) and it becomes unresponsive at a certain intermediate luminance level.

The first NIP, observed at low luminances, originates from the activity of the cells 1 and 4, generating the brightness-producing activity in the sensitive background area, and the cells 5, generating the darkness-producing activity along the contour. That the activities are not elicited in the centre of the insensitive area has to be concluded from the measurements in which only a small area inside the insensitive area was illuminated. There it was found that the threshold to elicit a brightness percept (on-activity) was higher than the level for the first NIP to be observed. So this proves that the first NIP results from off-activity and not from a reduced on-activity in the insensitive area. After reaching the brain the darkness-producing activity fills-in (Walls, 1954; Gerrits and Vendrik, 1970) and , as a result the whole disk is seen as dark.

When the luminance is increased the threshold of the on-centre cells 7 is reached but the off-centre cells 5 still respond with an excitation at the stimulus onset. Thus the darkness-producing activity, generated along the inside contour of the disk, upon reaching the brain keeps trying to darken the whole disk by filling-in. However, at the same time, brightness (and a redbrown color) is generated on the inside of the disk by all the cells 7. These opposite influences, their strengths depending on the exact luminance level, are responsible for the confusing percept in this range of luminances (see section 3.4. Results).

The luminance of the stimulus is again increased. As a result the excitation of cell 7 becomes stronger and the excitation of cell 5 diminishes. Cell 5 becomes finally inhibited at about the same luminance level at which cell 3 starts contributing with an excitatory response. From the luminance level at which the brightness-producing activity from cell 7 surmounts the darkness-producing activity from cell 5 a brightness is observed which is described as the second NIP. This brightness is , of course, much less than that generated by the activities of the cells 1 and 4.

To observe a disk with a diameter smaller than that of the insensitive area (figure 3.2.d.), the luminance level has to reach the threshold of the cells 7. The disk is observed as light redbrown. When this threshold luminance is kept constant but the size of the disk is increased, the light redbrown percept changes into the first dark NIP (see section 3.4 Results), as soon as the contour of the insensitive area is overstepped. This is understandable as, at this moment, the cells 5, signalling darker, are activated. The cells 3 are not involved in this percept as they respond with inhibition at the threshold luminance of the cells 7.

The generation of the positive insensitivity percept (PIP) is also explained with the help of figure 3.4. and 3.5. The onset of a low luminance stimulus generates the first NIP by the excitation of the cells 5; meanwhile the cells 3 are inhibited and remain inhibited as long as the stimulus lasts. When the stimulus is switched off the inhibition of cell 3 is released and the cell responds with an excitation, signalling brightness to the brain. This brightness is only well observed, however, if the darkness, generated before by the cells 5 in response to the preceding increment, has disappeared. Otherwise this brightness only neutralizes the darkness. In order to get rid of this darkness the stimulus is presented for a longer period, allowing the perceived darkness to disappear by fading.

IP's originate from the activities of the cells along the border of the insensitive area. The determinant contribution of these cells is also directly observable when a square flash is presented and only along a part of the contour of the insensitive area a background is presented (unreported experiments). Imagine that the retinal area, indicated by "insensitive area" in figure 3.4 did not represent the image of a strong flash but the image of a stabilized or unstabilized disk of steady luminance on a background of a variable luminance. Now consider again the responses of the "sensitive" and "insensitive" parts of the receptive fields. When the background luminance is increased or decreased darkness or brightness is observed at the locus of the faded stabilized image (Barlow and Sparrock, 1964; Gerrits and Vendrik, 1970). These percepts originate from the responses of the cells along the contour between the background and the disk. In case a light or dark disk is unstabilized it becomes less bright or less dark by increments or decrements of the background luminance, respectively. These perceptual changes, observed in the image of the invariable stabilized or unstabilized disk, are elicited by the responses from the "sensitive" parts of the receptive fields of the cells 5 and 3 (see figure 3.4), generating darkness or brightness, respectively. They are known as simultaneous contrast effects. The neural origin of the effects seen in the insensitive area after a flash has been presented is exactly the same. The receptors located in the image of the flash do not respond to low luminance steps of diffuse backgrounds. The observed IP's are, therefore "simultaneous contrast" effects.

The insensitivity of the bleached area was used to eliminate the influence of the eye movements, as in stabilized images (Lennie et al., 1982). There exist, however, fundamental differences between the percept and origin of a true afterimage, an insensitivity percept and the percept of a stabilized image, respectively. A true afterimage, resulting from a short-lasting high intensity flash, disappears in a few minutes in complete darkness and ends in "Eigengrau". A constantly illuminated stabilized image loses its sharp contours, its colour fades and, finally its brightness disappears for the larger part. A faint, stimulus dependent level of residual brightness remains visible, however, even after many minutes (Gerrits, 1978). It is thought that this brightness results from fluctuations of the sustained activity of the on-centre ganglion cells, as the stimulus is continuously present.

As a result of the recovery of the receptors in the insensitive area the strength of the IP diminishes and, finally, the IP cannot be elicited any longer. Changes in the background illumination continue, however, to effect the percept of a stabilized image. The generation of the true afterimage and IP can be explained by retinal processes, the observed fading and filling-in reflect cortical processes (Gerrits and Vendrik, 1970; Crane and Piantanida, 1983).

As was already mentioned in the introduction it was stated by Carpenter(1972) that insensitivity percepts, generated at different moments in time, eclipse all at the same luminance level. This was investigated in an additional experiment in which two insensitivity percepts were inspected against a diffuse background of 36 degrees wide. The background was illuminated by a Ferranti cathode ray tube (CL 63) of which the luminance was triangularly modulated with a frequency of 0.1 Hz. Two afterimages were generated at an interval time of sixty seconds. They had a diameter of 6 degrees and were centred at the vertical meridian at a distance of 4.5 degrees above and below the centre of the foveal area. Two naive (AB and JK) and one trained (LvE) subjects participated in the experiments. In figure 3.6. a representative measurement is given.

During the decreasing phase of the background luminance the subject signalled alternatingly for the upper and for the lower area the level at which the insensitivity percept became brighter than the area surrounding it, i.e. when a PIP was seen. Three important time phases may be distinguished. In the first period the fluctuation due to the true afterimage are still present. It is not possible then to detect a PIP in the most recently generated insensitive area.

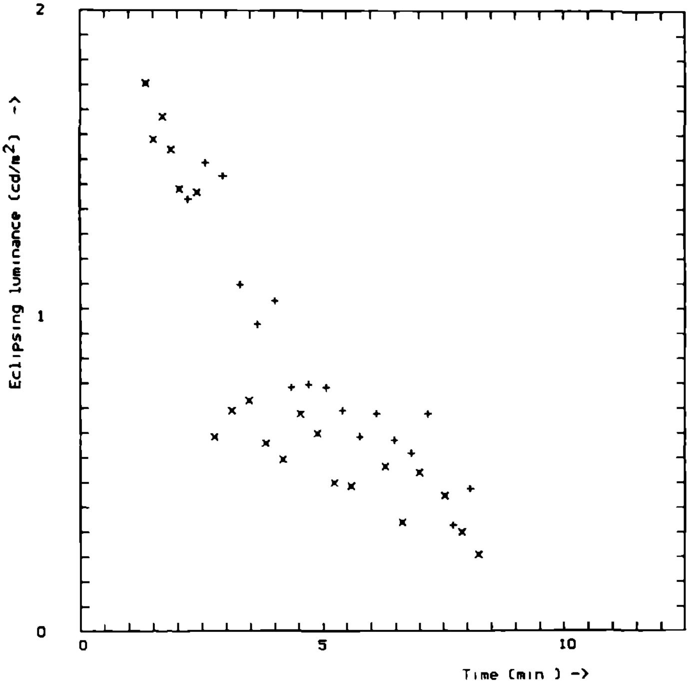


Figure 3 6 The eclipsing luminance as a function of time for two insensitivity percepts that resulted from two afterimages generated at an interval time of sixty seconds. Data from subject JK

In the second period two PIP's can be distinguished eclipsing at clearly different background levels. This contradicts the statement of Carpenter (1972) that the level of the eclipsing luminance is independent of the time elapsed since the afterimage was generated. In the third period the difference levels off and the PIP's are detected at the same luminance level. This occurs already within about eight minutes. The period in which significant differences between the sensitivity inside and outside the afterimage area could still be measured was found to be twice as long in the threshold experiment (figure 3.3). So it is obvious that light adaptation due to the average luminance level in the case of a continuously modulated background considerably influences the illumination level at which the PIP can be seen. This adaptation can also account for the fact that according to Carpenter (1972) the eclipsing luminance shifted in the direction of a luminance level of the background which remained constant for some time and to which the sensitive receptors adapted.

The appearance of a PIP is in the case of a continuously modulated background (0.1 Hz) presumably also influenced by the residual darkness of the preceding NIP, which has not fully faded. Both an insensitivity percept and a percept of a stabilized image, seen against an unstabilized background is sufficiently changed in time. IP thresholds should, therefore not be determined by too slowly increasing or decreasing background luminance levels. In preliminary experiments with a continuously modulated background it was found that no insensitivity percept was generated when luminance varied too slowly. Obviously at a low frequency no darkness can be generated, which would have made the insensitive area look darker. For these low frequencies the darkness fades as quickly as it is generated. At higher frequencies of the background modulation darkness is generated, however, and the first NIP appears. Therefore insensitivity percepts can best be seen with stepwise luminance changes of short duration to avoid light adaptation.

When the magnitude of the light increments was slowly increased from zero level, the insensitivity percept appeared as a very faint patch of darkness. This patch had an indefinite contour which exceeded the insensitive area. Thus the IP appeared to be larger than the preceding afterimage. A possible explanation for this observation is that cells with large receptive fields located outside the insensitive area have a lower threshold than the cells with small receptive fields. In the explanation it is supposed that the IP is determined by the cells with receptive fields along the sharply demarcated image of the flash. True this may be another explanation of the very faint patch exceeding the insensitive area may be found in the fact that in a certain area next to the bright sharply contoured image some stray light will reach the retina. This stray light slightly lowers the sensitivity of the cells in this area. The decrease of the sensitivity of these cells depends on their proximity to the contour. As a result an attentive observer may detect a vague patch, only slightly darker than the remainder of the field, considerably larger than the image of the flash and with an indefinite contour. This inhomogeneity in the field is due to the smaller on-responses, i.e. brightness-signals from these somewhat less sensitive cells and is only seen at illumination levels below the threshold of the first NIP. This implies that the perceptual effects caused by the stray light are negligible with respect to the IP's and this justifies our supposition that the retinal insensitive area is sharply demarcated.

Theoretical analyses as well as direct electrophysiological investigations (Stone and Freeman, 1973) of the contribution from the different parts of the receptive fields to the activity of the ganglion cells, reveal that the incorporation of other positions of receptive field centres along the contour (figure 3.4.) has principally no influence on the explanation. The presence of different sizes of receptive field centres in any location (Wiesel, 1960; Enroth-Cugell and Robson, 1966; Fukuda, 1971; Hammond, 1974; Peichl and Wassle, 1979; Stone and Johnston, 1982), enables us to obtain IP's with a sharpness which is optimized by the dominance of the smallest centres operational at the actual luminance level present.

3.6. Conclusion

It was shown that insensitivity percepts, popularly called "afterimages" result from a fundamentally different origin than the true afterimages. By varying the area of illumination it could be shown that the insensitivity percepts result from an uncommon response of some ganglion cells when diffuse light falls on their partly insensitive receptive fields. IP's have to be classified as percepts due to simultaneous contrast. IP's have to be studied with short lasting increments of luminance to avoid additional light adaptation. The rate at which the background luminance is changed is very important, as it determines the effectivity of the generation of the insensitivity percept. If the rate is too slow fading, filling-in and adaptation prevent the activity generated from being seen.

Various insensitive areas resulting from a sequential generation of afterimages show time shifted curves of regaining sensitivity.

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Chapter 4. APPARENT SIZE AND RECEPTIVE FIELD PROPERTIES

4.1. Abstract

A light square against a dark background besides an equisized dark square against a light background shows a difference in apparent size such that the light square seems larger than the dark one. This illusion was studied for squares of 109 x 109 min arc. Their centres were located 90 min arc out of the centre of the fovea. The apparent size is dependent on the contrast between the square and the background and not on the mean luminance. In the contrast range investigated the apparent size changed within a range of 2 to 13 min arc for light squares and from 1 to 14 min arc for dark squares. Although apparent size has also been studied as a function of retinal eccentricity, a number of complications prevent conclusions to be drawn from these results which describe how perceived size is influenced by eccentricity.

The addition of a small white or dark line to the luminance step that constituted the border of the square changed the illusion dramatically. It is argued that this explains the observations of Weale (1975), who found an inversion of the illusion for very small contrast values.

The results are explained on the basis of a model based on the presence of a number of receptive fields of different sizes located at the same retinal location.

4.2. Introduction

In this chapter a new application of the receptive field concept is presented. Here it will be considered, how it can influence apparent size in some conditions. For demonstration purposes figure 4.1 can be used. Although in this figure the white and the black square have exactly the same physical size, the apparent size is different, as the white square looks larger than the black one. This illusion is often referred to as the "irradiation illusion" (Helmholtz, 1909; Kravkov, 1950; Yarbus, 1967; Weale, 1975; Coren and Girgus, 1978) or the "classical size illusion. The example given here is only one of the many different forms that can be found in the literature.

Our interest in size phenomena has arisen from the observations of a change of the apparent stimulus size in stabilized vision and during the inspection of an afterimage (AI) and an insensitivity percept (IP, see chapter three). In stabilized vision it is clearly seen that a thin line passing through the foveal area and extending into the periphery looks smaller in the foveal than in the peripheral area. During the fading of the percept the size seems to increase.

For the explanation of these effects the following model was studied. At the outside of the contour of a bright stimulus small darkness elements are activated. At the inside of the contour large brightness elements are located which overlap the contour.

Figure 4 1 The " irradiation " or " classical " size illusion
The light - and dark square have physically the same size

The latter would generate brightness outside the contour if they were not masked or suppressed by the small darkness or brightness elements. Gerrits (1978) has put forward strong indications that these small elements fade the first releasing the suppression of the larger elements and as a consequence brightness appears outside the stimulus causing its apparent increase in size.

When inspecting an AI as well as an IP against backgrounds held at different distances it is seen that its apparent size changes although the retinal size remains constant (Emmert's law; Emmert, 1881). In this study distance was not varied so that this effect could not play a role. Besides the distance the luminance of the background too determines the apparent size of an IP. So in the case of percepts of a stabilized image and IP's a dynamic apparent size effect was seen as a consequence of a changing brightness in adjacent regions. This is a case of a successive comparison of apparent sizes. In the illusion described hereafter a comparison of apparent sizes is made simultaneously.

The experiments in this chapter involve apparent size comparisons by means of a stimulus configuration in which a test stimulus is compared to a standard that can be adjusted in physical size by the subject. Surprisingly one is not directly aware of changes in size when they are not important in the scene. In the experiments presented here, the changes in apparent size could be reproduced throughout all measurements and by all subjects.

Based on earlier observations in stabilized as well as non-stabilized vision a hypothesis was developed, which explained the changes in apparent size in terms of the activities in the brightness and darkness system. This may be in contrast with theories about frequency channels, although one can hold an intermediate view that an organization of several receptive fields determines a complex receptive field which can functionally act as a spatial filter (Glezer et al., 1978). The early hypothesis implied that the apparent size was determined by the location of the receptive fields of the activated off-centre cells. For a light stimulus on a dark background this meant that off-centre cells outside the contour determine the apparent size. For a dark stimulus on a light background the off-centre cells at the inside of the contour determined the apparent size. The aim of the present investigation was to quantify this hypothesis.

The first quantitative study to determine the apparent size was done by Weale (1975). For high contrast values he confirmed that a light square is seen larger than a dark one of the same physical size. For small values he found, however, an inversion of the effect. The light square looked smaller than the dark one. He used pieces of polaroid to make up his stimulus. We know, however, from our own experience that dark edges produced by the cutting of the polaroid will introduce other effects. Such an edge of the square is not determined by a single luminance step only. So it was decided to undertake a series of experiments in which for a single luminance step at the edge of the square the contrast, the mean luminance and the retinal eccentricity could be varied. In additional experiments a white or black line was added to the luminance step, that made up the edge of the square.

The influence of temporal aspects on the apparent size was not investigated.

4.3. Method

The stimulus was a light square on a dark background (negative contrast) or a dark square on a light background (positive contrast) in the left half of the display. Stimuli were generated by a programmable video generator connected to a Philips LDN 5006 Video Monitor. The square always measured 109 x 109 min arc. The centre of this standard stimulus was located 90 min arc to the left of a fixation spot. The mean luminance (L_m) was defined as:

$$L_m = \frac{L_{BG} + L_{FG}}{2}$$, where L_{BG} = the luminance of the background cd/m^2

and L_{FG} = the luminance of the foreground (the square) in cd/m^2.

Contrast (C) is defined as:

$$C = \frac{L_{BG} - L_{FG}}{L_{BG} + L_{FG}} \times 100\%$$

The mean luminance was always 35 cd/m^2. The contrast values used were ± 2, ± 5, ± 8, ± 10, ± 15, ± 25, ± 50 and ± 82%. To the right of the fixation spot a test stimulus was displayed against a constant background (35 cd/m^2) and symmetrically with respect to the standard. It was a line figure (a frame), that could be adjusted in size by a potentiometer setting. The lines that formed the frame were 3 min arc wide. Subjects adjusted the frame size by changing the length of the frame sides. The size of the frame is defined as the mean value of the inner and outer side length. The viewing distance was 150 cm, while the subject's head was positioned by having had him place his chin on a support and rest his forehead against a restraining bar. All viewing was monocular, the unused eye was occluded. Subjects were free to determine the time they needed to adjust the size of the test stimulus in order to match the standard stimulus. The centre of the stimulus configuration was at the same height as the subject's eyes. Two naive subjects (AB, ND) and two experienced subjects (LvE, HG) served as observers.

In a number of control experiments the effects of the symmetry of the stimulus configuration, the influence of fixation or free inspection and the test stimulus (a square instead of a frame) were investigated. The size of the test stimulus was matched as a measure of the apparent size of the square. Each experiment consisted of six runs. For each contrast value randomly selected from a number of eight, two observations were made. Subjects started their first match at the smallest attainable size of the test stimulus and their second at the largest size. For each contrast value at least twelve measurements were made and a total of 16 x 12 datapoints resulted from an experiment.

4.4. Results

In figure 4.2 two typical matches of the contrast experiment are given. The physical size of the test stimulus was plotted as a function of the contrast of the standard square. The luminance and background of the test stimulus were kept constant. The size of the test stimulus, matching the apparent size of the light or dark standard stimulus, indicates how apparent size changes with contrast. For the light as well as the dark square the apparent size is a function of contrast. For the higher contrast values the light square is always seen larger than the dark square. For small contrast values the apparent size differences between the light and dark

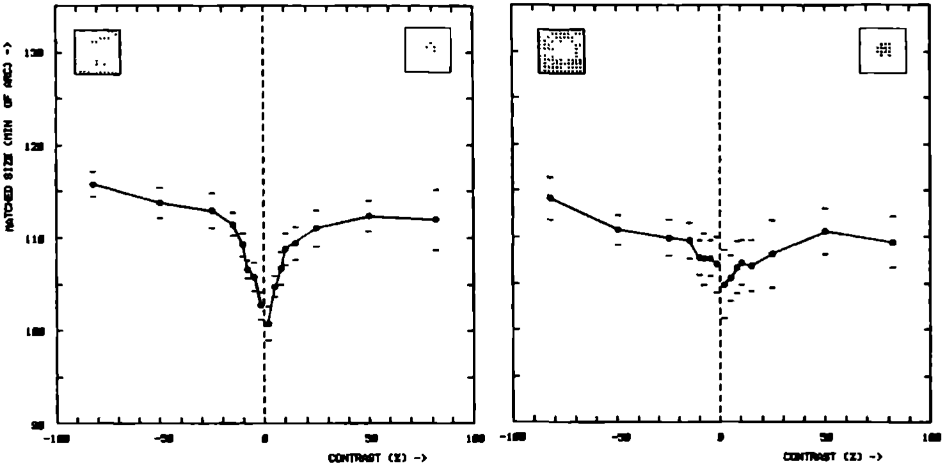


Figure 4 2 Two typical matches of the contrast experiment in which a frame was used as a test stimulus Left graph for subject AB, right graph for subject LvE

square are smaller. On the average it was found that for all subjects apparent sizes were 1.6 - 4.4 min arc larger for negative contrast (light square) than for positive contrast. Note that this result was found in a stimulus situation in which the light and dark square were not presented at the same time. In het normal form of the size illusion two objects of opposite contrast are presented simultaneously (figure 4.1). In the experiments presented here, only one of the squares was presented besides a test stimulus of constant luminance and adjustable in size. Thus the apparent size determined is an aspect of the square itself and not an effect of opposite contrasts being presented simultaneously.

Although the form of the function was nearly the same for all subjects, its position and range in the vertical direction varied considerably. Possible explanations for this will be given in the discussion of this chapter. To extract some quantitative results from the overall data the following parameters were defined:

P, the highest level for negative contrast (light square)
Q, the highest level for positive contrast (dark square)
R, the lowest value reached at -2% contrast (light square)
S, the lowest value reached at +2% contrast (dark square)
T, the difference between P and Q, indicating the maximal strength of the size illusion
U, the range of apparent size changes for negative contrast (light square)

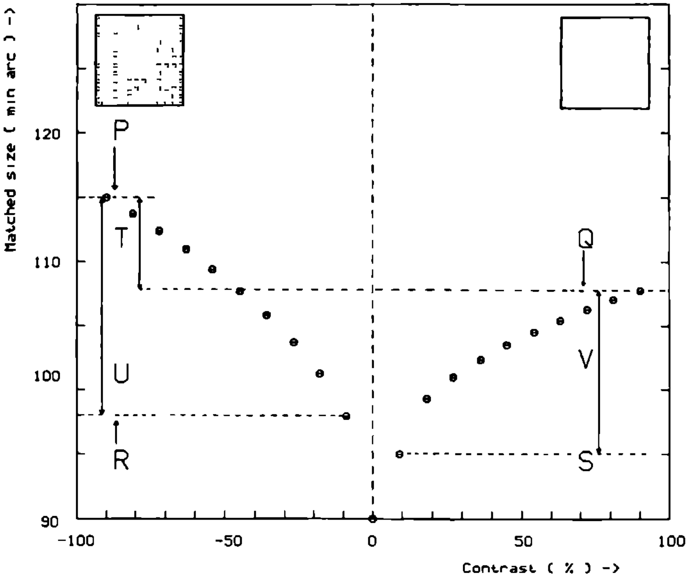


Figure 4 3 A smooth curve was fitted by eye through the data of the size matching experiments This curve is characterized by the paramaters indicated in the text

	Parameter values (min arc)							
	Subject	P	Q	R	S	T	U	V
1	AB	114.2	108.9	101.7	94.9	5.3	12.5	14.0
	ND	110.8	107.0	100.6	96.1	3.8	10.2	10.9
	LvE	114.9	106.3	-	98.2	8.6	-	8.1
	HG	-	103.7	-	94.5	-	-	9.2
2	AB	111.8	109.1	99.7	97.8	2.7	12.1	11.3
	LvE	109.4	107.0	104.1	101.8	2.4	5.3	5.2
	HG	105.1	101.8	98.4	95.3	3.3	6.7	6.5
3	AB	110.6	108.0	96.7	94.0	2.6	13.9	14.0
	ND	111.8	107.0	105.1	99.2	4.8	6.7	7.8
	LvE	112.3	104.9	-	100.3	7.4	-	4.6
	Averages (min arc)							
4	AB	112.2	108.7	99.4	95.6	3.5	12.8	13.1
	ND	111.3	107.0	102.9	97.7	4.3	8.5	9.4
	LvE	112.2	106.1	104.1	100.1	6.1	5.3	6.0
	HG	105.1	102.8	98.4	94.9	3.3	6.7	7.9

Table 4 1 Parameters from apparent size matches with a frame (3 min arc wide) as a reference The parameters P, Q, R, S, T, U and V were estimated after a smooth curve had been fitted through the data by eye (see figure 4 3)

V, the range of apparent size changes for positive contrast (dark square)

The values of these parameters (indicated in figure 4.3.) are given in table 4.1. A smooth curve was fitted through the data by eye and the defined parameters were estimated from the fitted curve.

For all subjects it was found that the change in apparent size as a function of contrast was nearly the same for a light as well as for a dark square. The second group of data in table 4.1 came from a repetition of the first group of experiments (mean luminance is constant at 35 cd/m^2). The third group resulted from an experiment in which the contrast and the mean luminance were both varied. For a light square the foreground was kept constant at 100 cd/m^2, for a dark square the background was kept at 100 cd/m^2. In this way mean luminance varied from 55 up to 98 cd/m^2. In all series nearly the same kind of function was found. These results were expected because some additional experiments in which only the mean luminance was varied, did not reveal an influence of the mean luminance on apparent size in a range measured from 3 up to 140 cd/m^2.

The influence of the test stimulus

In the experiments presented so far a rectangular frame was used as a test stimulus. It can be argued that different subjects used either the inside or the outside edge of the lines for their size adjustments. To investigate any

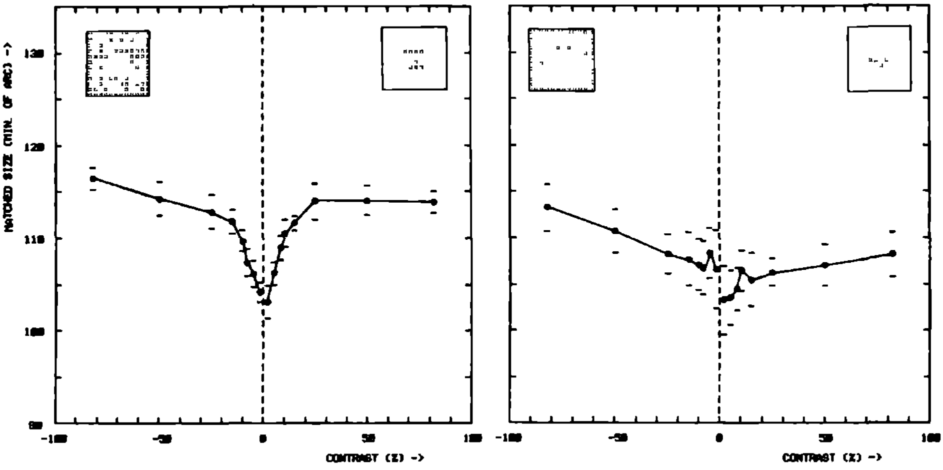


Figure 4 4 Two typical matches from the contrast experiment in which a square was used as a test stimulus The contrast between test square and background was held at approximately 100% Left graph for subject AB, right graph for subject LvE influence of the frame used to match the apparent size, a few experiments were done with a square of constant contrast instead of the frame. As we can see from figure 4.4 no difference in the shape of the curve is found. The level of the apparent size is, however, shifted in vertical direction (compare with figure 4.2). This shift can satisfactorily be understood by considering the stimulus characteristic used to judge the stimulus size. When a test square is used, there is no discussion about what is indicated as its size. With a frame, however, the size can be defined in different ways. Generally we can speak of an effective side length $l_e = a\,l_i + b\,l_o$ (figure 4.5). The inner side length is l_i, the outer l_o and a,b are constants between zero and one. The width of the frame ($w = (l_o - l_i)/2$) has always been 3 min arc in the experiments. Using the frame as the test, the value of the size (as indicated in figure 4.4) is taken as the mean value of the inner and outer side length ($a = b = 0.5$).

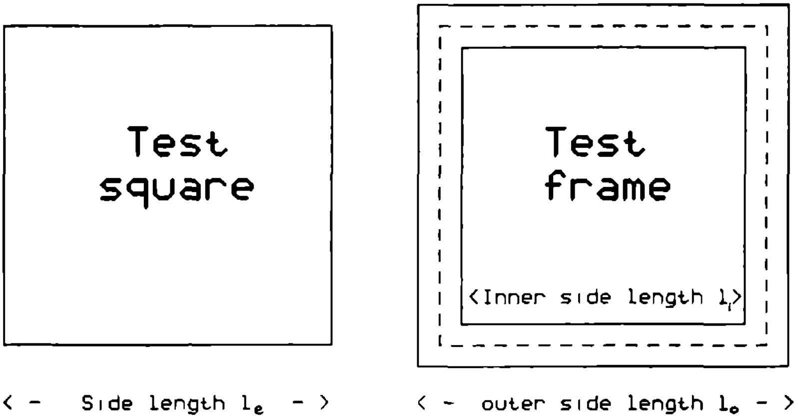


Figure 4 5 An illustration of the effective side length For a test square it's size is determined by the side length l_e which is also the size resulting from a match experiment for each subject When a test frame is used the inner as well as the outer side length may be used to determine the size Subjects may match the size of a frame by " looking " at the effective side length $l_e=[l_i+l_o]/2$

For all four subjects the difference between the overall mean for the frame and square data has been calculated. These values are given in table 4.II. The estimated size for the square is always greater than it is for the frame. This could imply that the subjects made their judgement on the outside edges of the frame lines. As de values registered are the sizes that correspond to the mean of the inner and outer side length, a shift of the data for the test frame over the width of a frame line should result. A difference of 3 min arc should therefore be expected in table 4.II.

Finally it should be noted in this part that when the contrast of the standard and the test square differed only with respect to

Subject	Overall mean (min arc)		Difference (min arc)
	Window	Square	
AB	106.0	110.3	4.3
ND	106.3	108.6	2.3
LvE	105.1	107.1	2.0
HG	100.4	104.2	3.8

Table 4 II Comparison of the apparent size as determined with a reference frame and a reference square

its sign, i.e. when a dark square was matched with a light square or vice versa, the dip at small contrast values was not found. Note that this should be expected as it was found, that for small contrast values a light and dark square were seen to be equal in size.

The influence of the spatial symmetry of the stimulus configuration

In the match experiments with a symmetrical stimulus configuration the subjects could be influenced by the distance of the left test contour with respect to the edge of the half field on which the rectangular frame was presented. They might also have tried to get the upper and lower contours of the standard and test in line. The possible influence of the spatial symmetry was investigated by creating an asymmetrical stimulus situation. The centre of the test stimulus was placed at a distance of 90 min arc from the fixation point under an angle of 45 degrees with respect to the horizontal.The results are given in figure 4.6 in the case of an asymmetrical test frame and test square. For a test frame placed asymmetrically but at the same eccentricity (90 min arc), only a slight increase of the standard deviations of the overall mean with respect to the symmetrical situation was found. Only for subject AB the dip for small contrast values was still clearly present (see figure 4.6). For all subjects the light square appeared larger. For the highest contrast values an illusory size difference of 2.2 - 5.5 min arc was found and the overall mean of the data was 1.4 - 3.5 min arc. The control experiment for subject AB with the asymmetrical test square, again indicated a larger value than determined with the test frame.

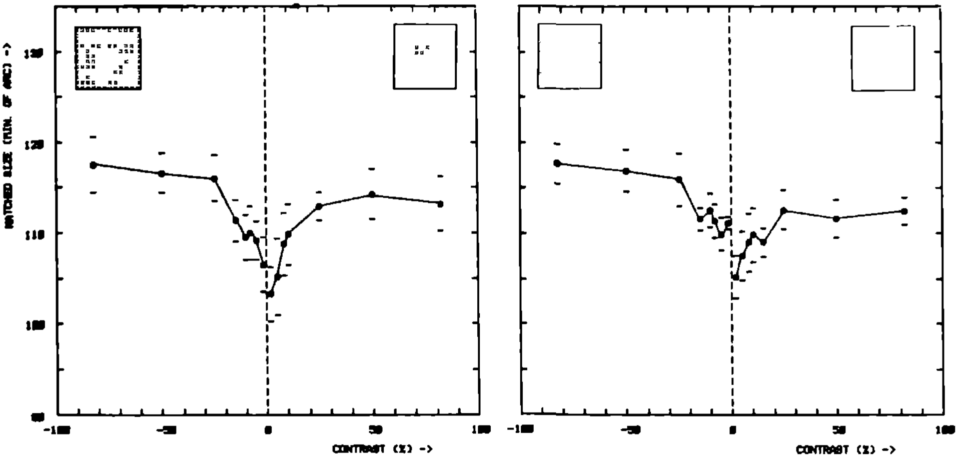


Figure 4 6 Two typical matches of the contrast experiment in which a frame (left part) and a square (right part) were used as test stimuli in an asymmetrical stimulus configuration Both graphs are from subject AB The asymmetrical stimulus configuration was made by a displacement of the test stimulus in the vertical direction while the distance to the fixation point was constant

The influence of fixation

In a number of experiments the subjects were allowed to inspect the stimulus configuration in a free way. This was done because a number of authors (Gregory et al., 1959; Heineman, 1969; Bagrash, 1974; Weale, 1975; Gelb and Wilson, 1983a,b; Skottun and Freeman, 1983) did their experiments in a comparable way and it was tried to obtain results from comparable situations. Moreover it came out that in the experimental conditions where the standard and test stimulus were not symmetrically presented, the subjects had problems in maintaining fixation. By allowing the subjects to look alternatively at the standard and the test stimulus a satisfactory condition could be reached although the subjects had the impression that if the standard and the test stimulus were presented symmetrically in relation to the midline it was easier to balance for size.

The comparison of the results of subjects AB, ND and LvE from an experiment with and without fixation reveals that for the fixation condition the size differences and standard deviations turned out to be larger than for the free inspection condition. This result will be discussed later on and will be related to unreported experiments in which both the standard and the test stimulus were presented at different retinal eccentricities.

4.5. Discussion

For all subjects a clear increase of the subjective size with contrast was found. The effect is independent of mean luminance in the range studied (3 up to 140 cd/m). Also experimental conditions as fixation or free inspection, symmetrical or asymmetrical stimulus presentation, and a square or a frame as match stimulus did not influence the results.

Helmholtz (1909) suggested that the size illusion results from irradiation. In his opinion the colour dispersion and monochromatic aberrations of the eye result in blur-circles, which make the light spread beyond the geometrical edge of the retinal image of the light area. Helmholtz's reference to the blurring of the image cannot be the correct explanation of the origin of the phenomenon as the effect of blurring is much smaller than the effects measured. According to Vos et al. (1976) the blur due to the optical properties of the eye is under normal viewing conditions limited to about 2 min arc. Moreover blur should affect apparent size for negative and positive contrast in the same way.

A relation between apparent size and spatial frequency channels or different size-tuned mechanisms has been suggested by several authors (Blakemore and Campbell, 1969; Bagrash et al., 1974; Beverly and Regan, 1979; Gelb and Wilson, 1983a,b). Here it will be tried to relate the apparent size effect directly to specific properties of elements within the human visual system. An explanation of the size illusion was given earlier by Thomas (1970) on the basis of the receptive field theory, but only in a qualitative way. To describe our quantitative data we come to the following model, which is based on the properties of neural units and their receptive fields.

The model states that the activities in the brightness/darkness system predict the shifts in perceived size as a function of contrast. These activities originate from the on-centre and off-centre cells having a receptive field of a certain size, which for individual cells is invariant for the luminance range studied. The model is based on the following facts:

a) At every location a number of cells each having its own receptive field's centre diameter, are associated with that location (Wiesel, 1960; Enroth-Cugell and Robson, 1966; Cleland and Enroth-Cugell, 1968; Hammond, 1974; Virsu, 1976)

b) For diffuse illumination it is found that cells with a small centre have a higher threshold than cells with a large centre (Wiesel, 1960). This implies that for small contrasts within the receptive field the cells with large centres will be activated at lower levels than cells with a small centre. For large contrasts cells with small centres will also be activated.

c) The mean size of the receptive fields of the on-centre cells is smaller than the mean size of the receptive fields of the off-centre cells at every location (Fisher and May, 1970; Fukuda, 1971; Coenen, 1971; Hammond, 1974).

d) Perceptive fields are the psychophysical equivalents of receptive fields (Jung and Spillmann, 1970). Their position in perceptive

space can be projected back at a location overlaying corresponding receptive field(s) (see chapter two). It is strongly suggested but not yet confirmed that a perceptive field might be "seen" by means of one or an ensemble of the perceptive elements as described by Gerrits (1978). The argument is that the perceptive fields are considerably larger than the perceptive pixels characterizing the perceptive elements. The smallest perceptive pixels only seen in sharply focussed stabilized images and described as "pinpoints of light" in foveally presented 4 - 10 min arc wide lines, have diameters of less than 1 min arc. The smallest perceptive field centres, however, have a diameter of approximately 4 min arc (Spillmann, 1971; Blommaert, 1981).
A more extensive description of the receptive field, perceptive field and perceptive pixel properties can be found in chapter two.

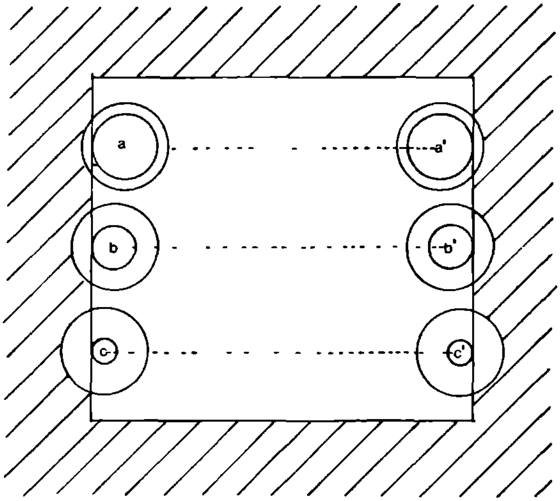


Figure 4 7 In a light square on a dark background receptive fields of a small, medium and large centre size are indicated Note the shift of the location of the midpoint of the centre towards the edge of the square for the optimally excited cells with a smaller centre

In figure 4.7 an example of the explanation is given for a light square presented on a darker background. Three receptive field sizes are indicated. Note that they have the same surround diameter but different centre diameters. For small contrast values the luminance step at the edge of the square is only small. This implies that the illumination of the parts of the receptive field located inside or outside the square is only slightly different and approximates diffuse illumination. So for small contrast values only cells a & a' will respond while cells b & b' and c & c' are not activated yet. As perceptive fields signal the location of the middle of the centre, the distance a-a' will determine the size of the square. If contrast is increased also the cells b & b' and c & c' will start to respond. So the difference in response between cells with a small centre and cells with a large centre of their receptive field will decrease. In the higher centre the brightness- producing activities resulting form the cells with a small centre as well as with a large centre add up. In this way the location at which maximal brightness is generated shifts towards the stimulus contour. This implies that the indication of the size of the square will shift subjectively from a-a' to c-c' resulting in an increase of the apparent size of the square.

Another way of representing the situation is done by making a cross-section through the square (see figure 4.8). From the fact that the maximum of the B-activity as well as the maximum of the D-activity shifts to the contours of the square it has been concluded that the B-activity determines the size of the light square. From figure 4.8 and the data for the dark square it is concluded that for a dark square the D-activity determines the apparent size of the square. When a dark square is presented the maximum of the activation on the inside of the square will shift from the off-centre cells with large receptive fields to those with a small receptive field. This will result in an increase of the apparent size of the dark square. The conclusion is that the apparent size is always determined by the activity of the cells along the edge, inside the square, i.e. the on-centre cells for a light square and the off-centre cells for a dark square. The subjective contour location is obviously determined by the amount of contrast at the edge. Another important supposition is that these size judgements seem to favour the foreground and seem to be related to the interpretation of the square being an object against a background whether it is light or dark. This seems an obvious remark but it is not as one could imagine that a hole in the background could be determined by the same stimulus configuration. Thusfar the shift of the level of activation has been considered to be the same for on-centre as well as off-centre cells. This is sufficient to explain the increasing apparent size of both light and dark squares as a function of increasing contrast.

According to the theory of irradiation a dark square should decrease in size as contrast increases. This is not observed. The experimental results even indicate the contrary. The observation that the apparent size of both a light and a dark square increases with increasing contrast is understandable, however, applying the hypothesis presented.

Theoretical analysis as well as electrophysiological investigations (Stone and Freeman, 1973; chapter two of this thesis) make clear that the cells having their receptive field's centres located adjacent to the contours are activated the strongest and thus determine the location of maximal brightness or darkness. There remains the fact to be explained that the light square appears larger in size than the dark square in the "classical size illusion". This should be expected, however, if it is realized that the apparent size shift results from the fact that the optimally activated cell

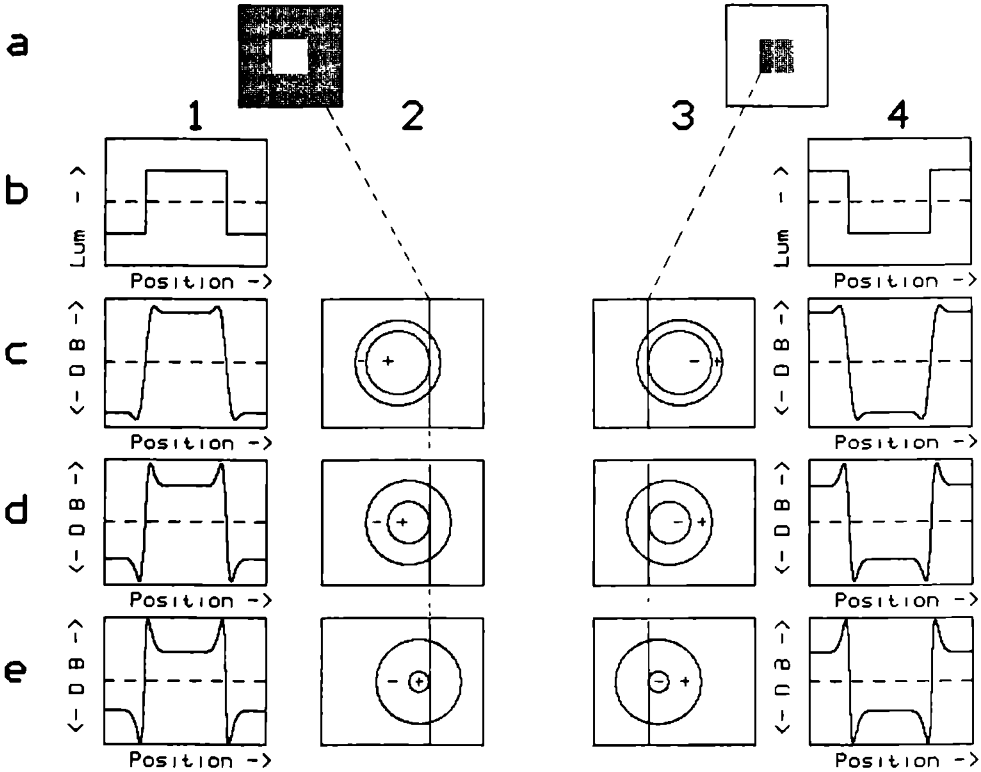


Figure 4 8 A representation of the situation with receptive fields with large, medium and small centres adjacent to the edge of a light or dark square In the first row (a) the light and dark square are drawn In the columns 2 and 3 the edge of one side is shown expanded In row b the cross-sections through the squares are given The brightness and darkness distribution corresponding to this cross-section are given in row c, d and e For low contrast values the cells with a large centre determine the activity distribution (c) When contrast is increased cells with a medium centre become activated too (d) For high contrast values even the cells with the smallest centres are activated will be located closer and closer to the contour as contrast increases. The smallest distance to the contour is equal to the radius of the smallest receptive field centre. This implies that a difference in centre diameter between on-centre and off-centre cells may explain a different size shift between situations in which the on-centre cells or off-centre cells determine the apparent size.

On the average on-centre cells do have a smaller receptive field size than off-centre cells (see chapter two). So the effect of the increasing size is expected to be larger for a light square than it is for a dark one. Actually this is found in the data. If we replot the data we find that for any contrast value a bright square looks larger than a dark square (figure 4.9). We see, however, that for larger contrast values the difference is markedly greater than at small contrast values. This is in agreement with the finding of Georgeson and Reddin (1981)that at low contrast values the tuning curves for light and dark bar widths were almost identical, confirming that, at least at low contrast,

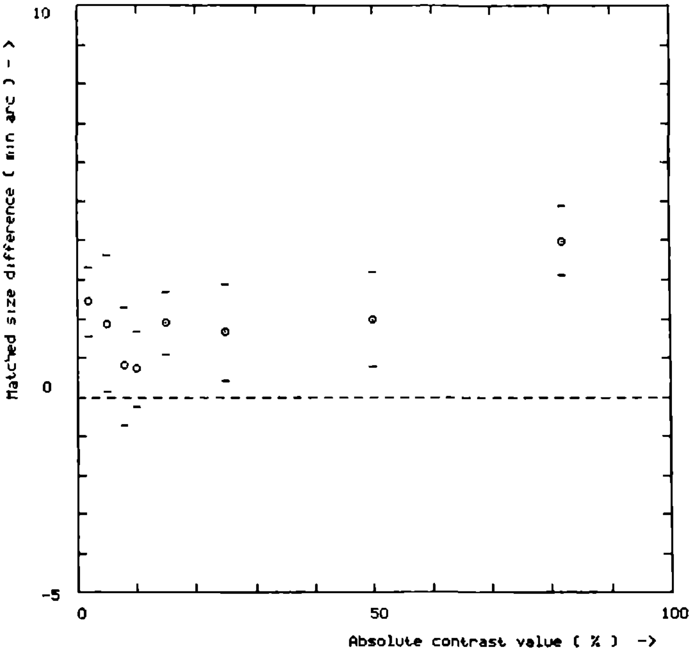


Figure 4 9 The difference between the matched sizes determined for positive and negative contrast as a function of the absolute contrast value This is a replot of the data presented in figure 4 2, 4 3, 4 4 and 4 6 It shows that a bright square on a dark background is always seen larger than a dark square on a light background for contrast values of more than thirty percent That the difference becomes markedly larger at higher contrast values is due to the fact that more and more cells with a small centre become activated and the existence of smaller centres for on-centre cells than for off-centre cells (see text) the visual processing of complementary light and dark patterns is very similar. The same is found in the studies of Remole (1977) and Magnussen and Glad (1975). Remole (1977), in studying Mach bands, showed that for steep slope gradients at the luminance edge the dark band is the broader at moderate photopic luminances. Towards higher luminances bright bands decrease more rapidly than dark bands. Possibly this can also be attributed to the activation of cells with progressively smaller receptive field centres. The mean receptive field size being smaller for on-centre than off-centre cells can account for the asymmetry of the light and dark Mach-bands. Thus a nonlinearity in the brightness system as proposed by Marimont (1963) and Von Békésy (1968) is not necessarily indicated by this asymmetry.

The size differences quantitatively

From the data of the experiments where the apparent size of a light or dark square (109 x 109 min arc) was determined as a function of contrast we calculated an overall change of size of 8 min arc ($\sigma = 4$ min arc) for the light square and 7 min arc ($\sigma = 4$ min arc) for the dark square. This was measured for the squares located with their centres 90 min arc out of the centre of the fovea. These results can be compared to those of Weale (1975), who also used a square of 109 min arc. For three subjects and two illumination levels he found a range of 2 up to 6.5 min arc for the amplitude of the size effect in the classical size illusion. Clearly the order of the magnitude of the results is the same. According to our hypothesis the difference of corresponding diameters of receptive field centres should range from 7 to 8 min arc. This corresponds to data of Hubel and Wiesel (1960), who found in the spider monkey foveal receptive fields up to 8 min arc. Marr et al. (1980) came to a smallest channel or in terms of receptive field centres to a value of 1.3 min arc.

Finally we come to the point of the new size effect as presented by Weale (1975). For small contrast values Weale states that the darker square is seen larger than the brighter one: a reversal of the classical effect. For a square of 109 x 109 min arc Weale found that the apparent size difference (dark square larger than light square) was approximately 3 min arc for two of his subjects and only 1 min arc for a third one. Weale cut his square out of polaroid material. Considering that any stimulus cut out of polaroid is always demarcated by the edge caused by the cutting of it, our measurements were repeated with a thin (2.5 min arc) line generated along the edge of the standard stimulus. The results are given in figure 4.10. For small contrast values the observations of Weale were confirmed for only one subject. This supports the suspicion that the measurements of Weale (1975) suffer from an artefact: the edges of the standard square he presented were not perfectly formed by one luminance step only. In addition a still larger and more conspicuous effect was found by the addition of the thin line along the edge of the square. A very strong movement of the boundary of the square was seen when contrast was modulated continuously. The farther

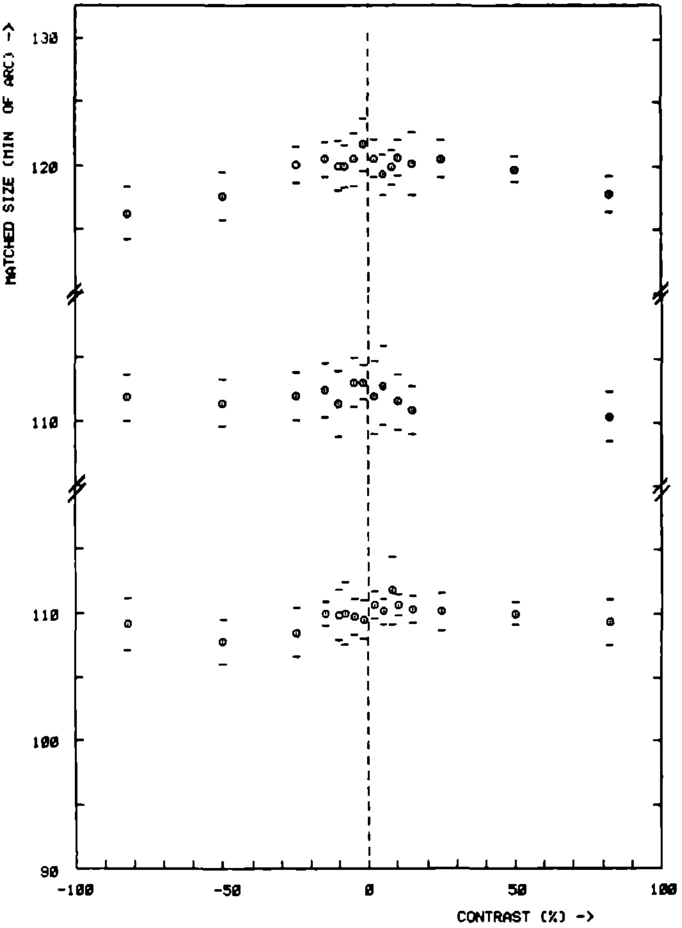
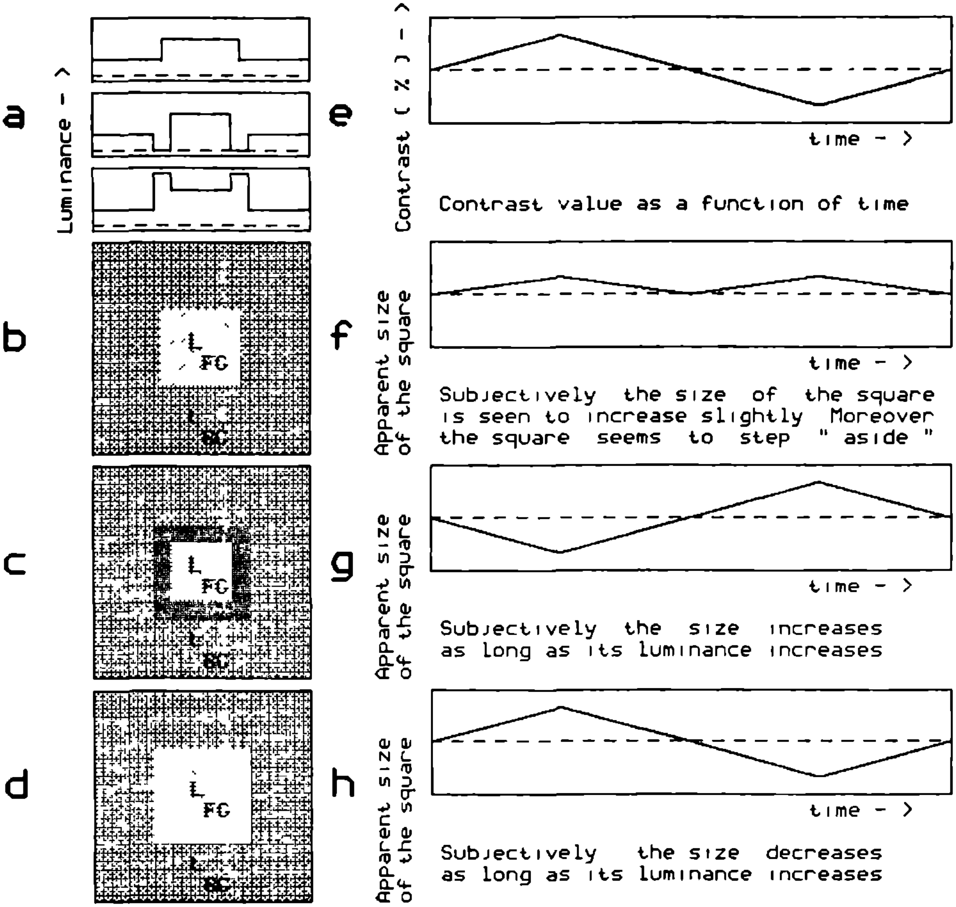


Figure 4 10 Three typical matches of the contrast experiment in which a thin black line (2 5 min arc) was added along the edge of the square A black square was used as a test stimulus The graphs are from the subjects AB (upper), LvE and HG (lower)

peripherally, the larger the amplitude of the movement illusion seemed to be. The apparent movement of the contours gave a remarkably strong impression of a square increasing and decreasing in size. For a black line along the edge: a light square is seen larger than a dark square and for a white line along the edge: a dark square is seen larger than a light square. Schematically these two situations are indicated in figure 4.11e,f,g and h and in figure 4.12. So when contrast between square and background is modulated the size effect



Contrast value as a function of time

Subjectively the size of the square is seen to increase slightly Moreover the square seems to step " aside "

Subjectively the size increases as long as its luminance increases

Subjectively the size decreases as long as its luminance increases

Figure 4 11 An illustration of the contrast modulation of the square with and without a thin line along the luminance step a) The luminance profiles without a line, with a light - and with a black line b) The contrast modulation function c) Only a modulation of the square and background luminance d) The apparent size changes for the situation depicted in c) and the modulation function of b) e) The same as c) but with a black line at the luminance edge f) The apparent size changes for the situation of e) and the modulation of b) g) The same as c) but with a white line along the luminance step h) The apparent size changes for the situation of e) and the modulation of b)

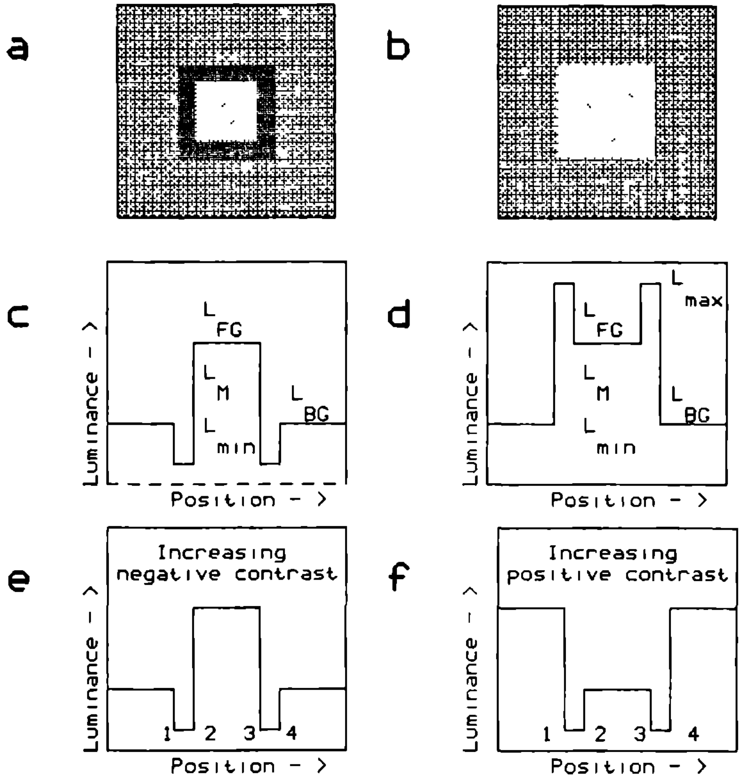


Figure 4.12 a) A light square against a dark background with a black line along the luminance step. b) A light square on a dark background with a white line along the luminance step. c) and d) The luminance distribution in a and b, respectively. e) the situation as indicated in c for increasing negative contrast (square lighter than the background) and f) The situation as indicated in c for increasing positive contrast (square darker than background).
Increasing negative contrast implies that L_{FG} ($>L_M$) increases and L_{BG} ($<L_M$) decreases. Increasing positive contrast implies that L_{FG} ($<L_M$) decreases and L_{BG} ($>L_M$) increases. For further explanation see text.

induces an apparent movement in the situation that the edge of the square is not exclusively formed by only one luminance step. Due of course to the presence of the additional line the percept of a square persists, even when the contrast between the "square" and the background is zero. If contrast is modulated without the additional line being present, there are two different situations: a light square on a darker background and a dark square on a lighter background. At the moment of zero contrast during modulation the square seems to step aside in a direction depending on the transition from light to dark or dark to light. When the line is absent the size is not seen to change during modulation. Contrary to this the presence of the line seems to bring about a much more gradual change of the square size and causes a continuing increase or decrease of the apparent size during modulation. The frequency of the observed size changes is of course the same as the frequency of the contrast changes when a black or white line is present.

With a line along the edge there exist two luminance steps instead of one. In terms of contrast defined earlier this means that only negative or only positive contrast values occur when the square luminance is considered with respect to the luminance of a black or white line respectively (figure 4.12 c and d). So the luminance of the line determines whether the left or right trajectory of the function describing the relation between apparent size and contrast (figure 4.3) is traversed. For instance, if a black line along the edge is present (figure 4.12 c, e and f) the contrast of the square with respect to the line is always negative (the luminance of the square is always higher than the luminance of the line). When this local contrast at the edge of the square increases (becomes more negative) an increase of the apparent size is found according to the left trajectory in figure 4.3.

Now an additional effect occurs, however, as the decreasing luminance in the background activates the off-centre cells in that area. The off-activity generated adjacent to the constant dark line is much stronger than that elicited at larger distances from this line.

In the area enclosed by the constant black line the increasing luminance of the square activates most strongly on-centre cells adjacent to the line. In this way strong on- and off-activities are generated each at one side of the dark line. This causes the impression that the dark line moves as these activities are indistinguishable to the system from activities that would have resulted from a physical displacement of the line (Rodieck, 1965). While the black line seems to displace outwards (figure 4.12e) the square seems to expand. The synchronous action at both sides of the line introduces the apparent movement of the line. An analogous description can be made if the square has a white contour line (figure 4.12 b and d), but the movement is then reversed.

In the experiments and measurements presented at the beginning of this chapter contrast was not modulated while subjects made their size matches and consequently no apparent motion was seen. Some preliminary results indicate that certain combinations of modulation and phase differences between the luminance of the line and the square can generate a percept of a constantly expanding or shrinking square. The induction of apparent movement only occurs if the contour line is thin enough. When the line in the stimulus is given a larger width the induced movement amplitude decreases and the situation of a light or dark square on a background of "opposite" luminance is restored. Of course also other combinations of dark and light constant lines can be presented along the edges of the square. The application of two opposite light and two opposite dark lines, or a light horizontal and a dark vertical line opposite a dark horizontal and a light vertical line leads to amusing apparent movement percepts.

In the introduction it was already mentioned that apparent size may be influenced by various factors. In this chapter only the influence of contrast was studied. It was found that apparent size as a function of contrast varied in the same way for all subjects apart from a shift of the mean value with respect to the physical size. This shift was also found by Virsu (1974) and Weale (1975). Most probably this shift has to be attributed to a higher order mechanism influencing apparent size and responsible for the size constancy effect.

The fact that the size difference as well as the standard deviations decrease when subjects are allowed to inspect the stimulus configuration without fixation may be explained by considering that smaller receptive fields will be involved whenever the edges of the square and the frame are compared by foveal vision. This possible influence of the stimulus location prevents conclusions from the unreported experiments in which the stimulus square as well as the test frame were displaced to more peripheral locations with respect to the fixation point. In these experiments it was found that size matches increased considerably as more peripheral locations were involved.

4.6. Conclusions

The estimated size is a function of contrast. The apparent size of a bright as well as a dark square decreases with decreasing contrast values. For every contrast value the bright square appears to be larger than the dark one. In terms of receptive fields it has to be concluded that the apparent size of the bright square is determined by the on-centre cells and that of the dark square by the off-centre cells. The overall observation that bright squares look larger than dark squares finds its origin in the difference of the sizes of the receptive fields of on- and off-centre cells at the same retinal location. Receptive field centres of on-centre cells are smaller than those of the off-centre cells.

The observation of Weale (1975) that the apparent size in a bright square is smaller than that of a dark square for small contrast values was not confirmed. On the contrary, the present data indicate that the edges of the polaroid in Weale's experiments might have introduced an artefact.

4.7. References

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Chapter 5: THE FADING TIME CONSTANT IN FOVEAL AND PERIPHERAL PROJECTIONS.

Chapter 5: THE FADING TIME CONSTANT IN FOVEAL AND PERIPHERAL PROJECTIONS.

5.1. Abstract

Fading of percepts has always been characterized by a fading time. It is not at all clear, however, at what time an empty field (i.e. a field in which all visual contours have disappeared for the subject (Yarbus, 1967)) or the level of a residual brightness (Gerrits, 1978) was reached. For the quantitative measurement of the rate of fading at a certain location in the visual field a fading time constant was introduced. A fading time constant is a system parameter that is determined by the rate of decrease of brightness- or darkness-producing activity within the higher centre. The fading time constant was determined by measuring equalization times of the brightness disappears between a disk and an adjacent annulus. This is much easier to indicate than the moment in time at which the perception disappeared after the onset of a stabilized stimulus. It was found in the experiments described that fading time constants in the foveal projection are on average four times smaller than in the peripheral projections.

5.2. Introduction

Our visible surroundings seem to encircle us without bounds and to extend outwards in three dimensions. There appear to be no graduations of clarity. Only when fixating a particular point in space for some time centre versus periphery distinctions are experienced. When stabilizing images much more differences can be observed. It is generally accepted now that temporal or spatial retinal changes of illumination are necessary to preserve visual perception. Stabilizing an image causes its percept to disappear. Independent of the colour or object, the sequence of disappearance of the perception is always the same: firstly the contours, secondly the colour and thirdly the brightness, which remains, however, up to a faint residual level (Gerrits, 1966; 1978).

As was already pointed out in chapter two, a number of mechanisms determine the percepts observed in the sequence of disappearance. One of these mechanisms is the fading with which this chapter is mainly concerned. Fading is used ambiguously in the literature. Sometimes it indicates the decrease of brightness or darkness, but it is also used to indicate that the percept of an object disappears (fades) from view (table 5.Ia).

In this chapter fading is restricted to the gradual decrease of brightness- or darkness-producing activity. In figure 5.1 two situations have been depicted.

a

Author	Year	Fading time (seconds)	Distance from the fovea to nearest stimulus contour (min arc)	Stimulus luminance cd/m^2
Clarke	1962	6.4	1050	$4.1.10^{-5}$
Fiorentini & Ercoles	1965	3.7 (σ=2.6)	375	52
Millodot	1967	25-34	496-570	31
		8-16	3670-3496	31
Yarbus	1967	1-3	any	max. 100
Sparrock	1969	≈ 10 sec	peripherally	threshold
King Smith et al.	1976	4-5	1.5	≈ 8
Gerrits	1978	2-10	135	100
Bolanowski	1982	10-30	Ganzfeld	
Barlow	1982	< 60 sec	Ganzfeld	318.3

b

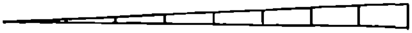
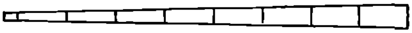
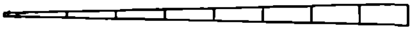
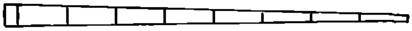
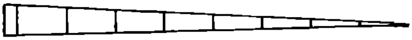
The rate of perceptual fading as a function of the location in the visual field is represented by the width of the band not drawn on scale Left side fovea, right side periphery	Investigation	Method of reduction or elimination of retinal image movement
 Fading never in the foveal area	Troxler (1804)	Fixation
 Small objects never disappear in the foveal area	Clarke (1957)	
 Fading in fovea as well as periphery but foveally slower than peripherally	Clarke & Belcher (1962) Neumeyer & Spillmann (1978)	Fixation
 or  Fading in fovea as well as periphery occurs although most often in the periphery at first	Cibis & Nothdurft (1948) West (1967)	Possibly stab. Stabilized
 In case of satisfying stabilization the foveal area always fades first.	Gerrits et al. 1966,70b,78,84	

Table 5 I a) Fading times measured by different experimenters To provide some reference for the fading times, the distance from the fovea to the nearest contour is indicated as well as the luminance of the stimulus b) Comparison of the rates of perceptual disappearances from various studies

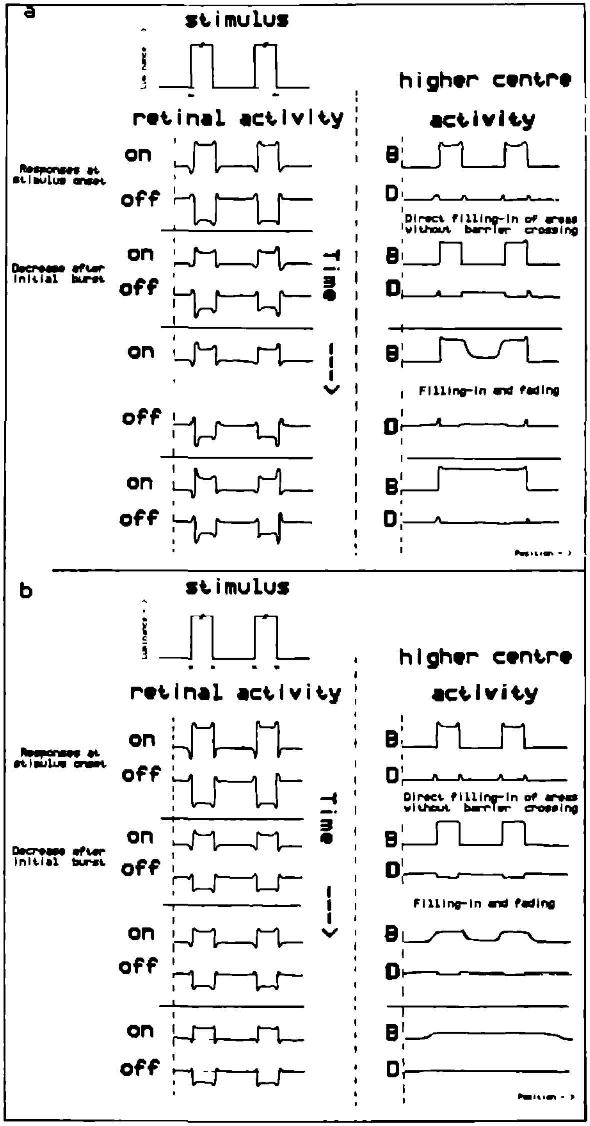


Figure 5 1 Comparison of retinal and higher centre activities The retinal and higher centre activities resulting from the presentation of a stabilized disk on a nonstabilized (a) and a stabilized background (b)

In the upper part a percept of a dark disk on a light background disappears from view because the area is filled-in with the surrounding brightness (Gerrits, 1970b). This filling-in can take place after the darkness-producing activity on the inside of the contour has faded and thus the barrier has become less effective. As the outer contours are not stabilized the brightness in the enclosed area becomes homogeneous and remains constant. This combined effect of fading and filling-in will be called "equalization". So equalization is the perceptual disappearance of gradients in brightness and darkness, while a diffuse overall brightness or darkness may remain. In the following the general term "disappearance" of a percept will be used whenever the contributing mechanisms are not specified. The percept may be the whole as well as a part of the visual scene.

In the lower part of figure 5.1 the outer contour is stabilized as well as the inner one. Now the total percept will fade. Filling-in is still present but it being noticed depends on the difference in brightness between disk and background. So the disk may still be distinguished although its brightness decreases.

The disappearance of a percept can be the result of a combination of the independent mechanisms fading and filling-in. It would be most enlightning if their contributions could be analysed independently. Then three different situations could be distinguished:

a. Only fading: In this case the brightness and/or darkness percept diminishes in strength. The gradient remains visible as long as brightness and darkness are seen.
b. Only filling-in: A homogeneous stimulus is perceived as homogeneous despite the fact that the retina itself is rather inhomogeneous.
c. Both fading and filling-in: This occurs in practice. The two mechanisms cooperate and it will depend on the initial brightness and darkness distributions whether the equalization will be complete before all brightness- or darkness-producing activity has faded.

A way of illustrating the mechanisms is by means of a compartment model, in which the concentration is a measure for the brightness perceived (see figure 5.2). Two independent mechanisms with their own parameters can be distinguished. The fading mechanism is described by the loss, while the filling-in mechanism is described by the flow between the compartments. The parameter of the latter mechanism depends on the barrier at the contour of the stimulus simulated. Depending on the initial concentrations and the flow parameters, the concentrations can be equal before one of the two has reached zero.

In chapter two several investigations (Clarke and Belcher, 1962; Galbraith, 1964; Lehman et al., 1965; Gerrits, 1966,1967; Millodot, 1967) concerning the location of the fading mechanism within the visual system are discussed. The site of its origin has not been found thusfar. One might think that fading is a retinal phenomenon and reflects the decreasing output of the retina after the onset of the stimulus. However, the receptor light adaptation, i.e. the decay of the initial receptor response after an increment of light takes

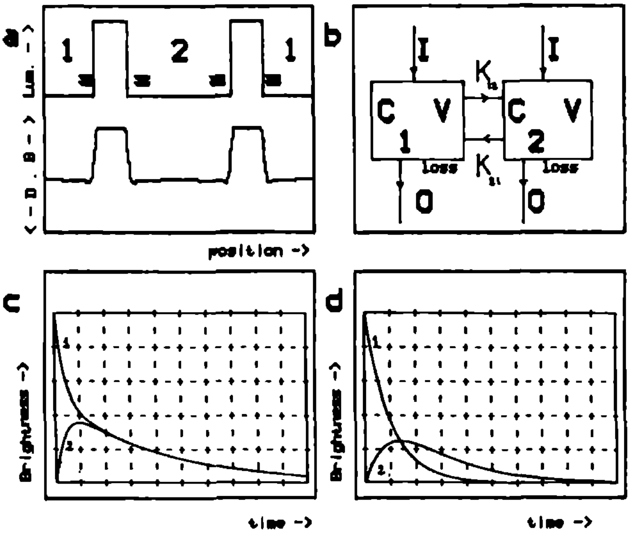


Figure 5 2 An illustration of the fading and filling-in by means of a two compartment model The concentration of compartment 1 represents the brightness in the light annulus The concentration of compartment 2 represents the brightness in the area enclosed by the annulus a) The situation of a stabilized bright annulus represented by the luminance profile of the stimulus and the resulting percept b) A two compartment model representing the fading and filling-in The concentrations in the compartments can be described by

$$\frac{dC_1}{dt} = I_1 + \frac{K_{21}}{V_1} C_2 - \frac{K_{12}}{V_1} C_1 - O_1$$

$$\frac{dC_2}{dt} = I_2 + \frac{K_{12}}{V_2} C_1 - \frac{K_{21}}{V_2} C_2 - O_2$$

c) Simulation for $K_{12} = K_{21} = 5$, $O_1 = O_2 = 1$, $V_1 = V_2 = 20$ and the " onset of the stimulus " I=2000 This simulates the normally perceived disappearance of the percept d) The same as c except for $K_{12} = 1$, $K_{21} = 0$, $V_1 = V_2 = 20$, I=1000 The latter'situation leads to an " impossible " percept about three minutes. This is a much longer time than the decay time of a percept. The fading takes from about two to ten seconds. The rate of change in the bipolar- and ganglion cell's response cannot be related to the time parameters of the fading mechanism either. The output of the retina, i.e. the ganglion cell response, becomes stationary after an initial burst. The fast decay of the burst is not at all compatible with the slow decay of the brightness in stabilized condition.

Apparently the sustained activity is unable to maintain the perception of brightness. The percept fades notwithstanding the sustained retinal signal. When a human optic nerve was constantly stimulated by spike-mimicking electrical pulses, after enucleation of an eye, the elicited bright percept at the onset of the stimulation faded within a few seconds (Nakagawa, 1962). It is therefore obvious that fading does not mirror the decay and cannot be prevented by constant retinal responses. Thus a number of arguments indicate that the fading mechanism is not located in the retina but at a higher level in the visual system.

For a long time there has been some disagreement in the literature about the rate of disappearance of percepts as a function of the stimulus eccentricity in experiments with stabilization or strong fixation (pseudo-stabilization). It has been agreed, however, that in both cases the amplitude of the retinal image movement is too small to preserve the original perception. The degree of image stabilization, necessary to achieve disappearance, depends on the extent and the structure of the stimulus.

In table 5.Ib a survey is given of the various observations of the rate of the perceptual disappearance. At the top it starts with experiments in which disappearances always occur in the peripheral and never in the foveal area. It ends with observations in which the foveal percepts disappear before the peripheral ones.

It is known that perceptive fields increase in diameter with eccentricity (Ransom-Hogg and Spillmann, 1980; Trosclanko, 1982). The observations of perceptual disappearance in the peripheral before the foveal area, could suggest that the brightness- and darkness-producing activity resulting from large receptive field centres fades faster than that of small ones. This also implies that fading is associated with the decrease of activities of one or more perceptive elements signalling brightness or darkness.

From the experiments in which the foveal percepts disappeared before the peripheral ones, the opposite conclusion has to be drawn, i.e. the activities resulting from small receptive field centres fade faster than those from large ones.

The discrepancies encountered between our stabilization results and the literature data obtained from fixation experiments must be due to the influence of remaining eye movements. The effect of these movements is greater the more the stimulus contour approaches the fovea, because the size of the receptive fields is smaller there (Hubel and Wiesel, 1960; Ikeda & Wright, 1972). Small retinal image movements of a local contour can stimulate only the small receptive fields in the fovea. So only from the foveal area brightness and darkness will be signalled. The same movements are too small to shift the stimulus contours sufficiently within the larger peripheral fields to elicit a brightness or darkness response. Thus percepts in the peripheral location may fade (Gerrits et al., 1984) with fixation. Only subjects who are able to maintain strict fixation, i.e. are able to limit their eye movements considerably will experience short fading times for stimuli with edges near the fovea.

Now it can be understood why perfect image stabilization is necessary to observe foveal disappearance before peripheral disappearance. The degree of image stabilization determines the order of the disappearance of the foveal and the peripheral part. An example of this can be found in West (1967, figure 10). He found a different order of disappearances of initially equal percepts. We think that these differences are due to "slipping" of the stabilized retinal image, which has, in principle, the same effect as residual small eye movements. Two specific experiments are relevant in this respect:

a) A narrow, bright stabilized line (e.g. 7 min arc wide, 16 degrees long) disappears firstly in the fovea and thereafter the two halves become shorter subjectively, towards the periphery (figure 5.3; unreported experiments).

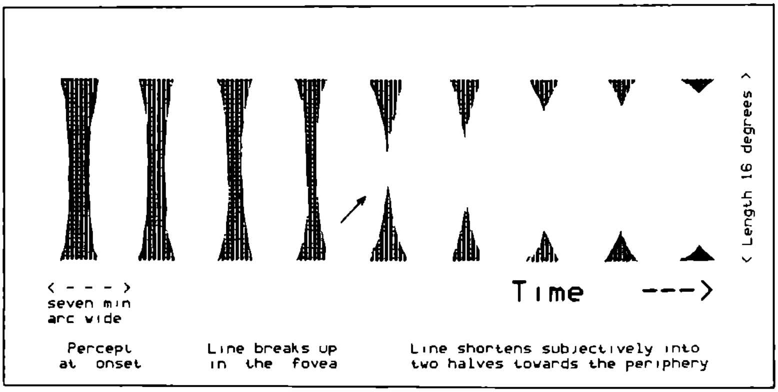


Figure 5 3 A stylized representation of the fading of a narrow line (not drawn on scale) through the foveal area

After the complete disappearance of the percept, the line is seen in deep blackness (darkness) when the stimulus is switched off. This blackness also disappears, firstly in the region that corresponds to the fovea and subsequently in the region that corresponds to the periphery. It should be noted here that in the case of insufficient image stabilization a fading of the "peripheral" part of the line is seen before the "foveal" part. This means that the small retinal "slip" of the line generates activity in the foveal area. Obviously this can compensate for the fading in the foveal but not in the peripheral part, where the activity generated is obviously too small, as will be explained later.

b) A stabilized disk centred at the fovea and surrounded by concentric stabilized annuli shows also a faster fading in the central part of the visual map than in the more peripheral parts (figure 5.4, after Gerrits et al., 1984). When the disk is not centred at the fovea a more complex percept arises. As the foveal area is always the centre of the filling-in (fastest fading) brightness as well as darkness will fill-in depending on the location of the annuli with respect to the fovea. Also in those cases in which square wave gratings were presented, the foveal part faded before the peripheral part (Gerrits, 1978).

Another way of looking at the fading and filling-in mechanisms is possible by considering a model consisting of two filter (weighing) stages that influence a stochastic signal caused by small eye movements. A luminance edge that is displaced over small distances will cause changes giving larger responses the smaller the receptive fields. This may be interpreted as a weighing mechanism of the mean amplitude of the eye movements relative to the local receptive field diameters. So the effectivity of eye movements depends on the retinal location of stimulus contours. For eye movements having a stationary probablility density function of amplitudes as well as velocities, this implies that the effectivity to generate brightness and/or darkness information increases from the periphery to the fovea along with decreasing minimal receptive field centre sizes.

The fading of a brightness- or darkness-producing activity may be interpreted as the second weighing mechanism. It weighs the temporal changes of the brightness- and/or darkness-producing activities resulting from the contour displacements. Activities in the foveal projection fade faster than those in the peripheral projection. So in terms of efficiency one might say that the foveal region is the least efficient in this mechanism. Summarizing it can be said that the location of the first disappearance of a percept depends on the activity generated (weighed by the first mechanism) and the loss of activity (weighed by the second mechanism).

It is clear that the time, it takes for a percept to disappear, table 5.I., depends on the differences in brightness, darkness and eventually colour between the stabilized image and the background. The equalization time of a percept (brightness and darkness difference only) is a function of the luminance contrast and not of the mean luminance. This was confirmed in stabilization experiments, which will not be reported here.

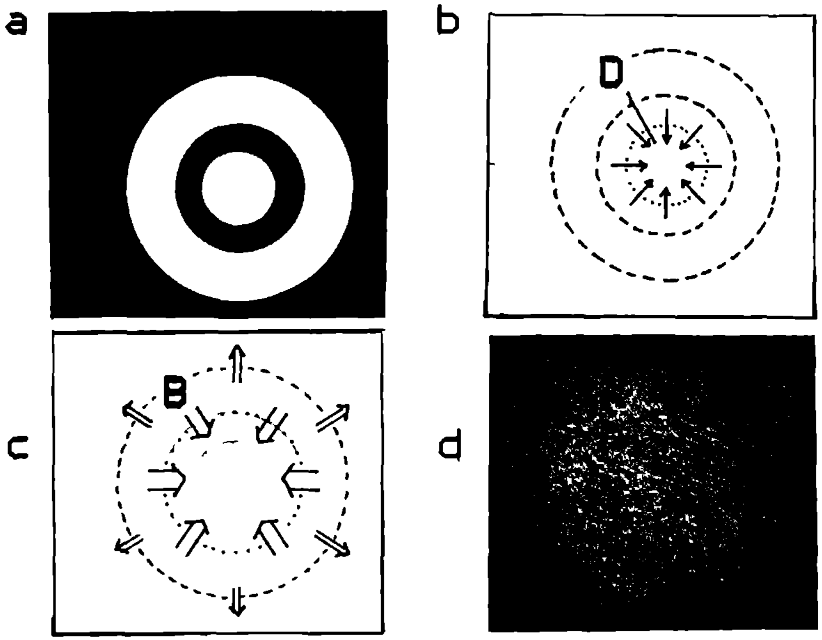


Figure 5 4 A stylized representation of the fading and filling-in of a bright disk surrounded by a dark and a light annulus (after Gerrits et al ,1984) a) The stimulus b) The first barrier (disk <-> dark annulus) has faded sufficiently and darkness fills in c) The second barrier (dark annulus <-> light annulus) has faded sufficiently and brightness fills-in d) The image has almost faded

In the earlier experiments in stabilized condition the fading time was determined and not the fading time constant. The determination of a fading time is inadequate as there is no clear criterion available to indicate when fading has "ended". The system parameter to be determined is the fading time constant. Considering the literature data mentioned thusfar as well as the experiments in our laboratory we conclude that there must be a different fading time constant for various areas in the projection of the visual field. Consequently the fading time of a percept is determined by the location of the contour in the visual field as well as its luminance with respect to a background.

If the fading time constant in the foveal projection would be greater than the constant in the peripheral projection, then the peripheral part should always have disappeared firstly in all experiments (stabilized as well as unstabilized). This is not the case, therefore the following hypothesis is favoured:

"The fading time constant in the central part of the visual map is smaller than in the more peripheral parts."

It is known that by reducing the retinal image movements any centrally fixated light disk will decrease in brightness after its onset, provided the movements of the contours are small with respect to the local receptive fields. The brightness or darkness elicited at any point within the visual field is determined by the locally generated activities as well as the activities generated at the contours (Ronchi and Mori, 1959; Mori and Ronchi, 1960; Jung, 1967, 1972, 1973; von Békésy, 1968; Gerrits and Vendrik, 1970a; Ratliff, 1971). From this notion it follows that the activity generated at the border of a centrally fixated disk determines the level that remains after the stimulus onset. Due to the filling-in mechanism the rapid loss of brightness- and darkness-producing activity within the central area will be compensated for by the activity filled-in from the border elements which fade much more slowly and receive additional input generated by the small contour displacements. For a centrally fixated homogeneous disk this implies that the decrease of its brightness will be determined by the fading time constant of the area in the visual map where the contour of the disk is located as well as by the residual retinal image movement. When an adjacent annulus surrounding the disk is switched on at an interval time of τ seconds after the onset of the disk, it has to be expected that the annulus will look brighter than the disk. This is caused by the fact that the brightness of the disk has decreased already because of fading during the τ seconds interval. For a small annulus it is to be expected that the fading time constant may be assumed to be approximately constant over the annulus width and equal to the fading time constant of a perceptive field at the inside border of the disk. So by varying the interval between the onset of the disk and the annulus a varying brightness difference between the disk and the annulus may be introduced. As said before it is known from experiments in stabilized condition that the equalization of brightness differences takes longer for greater differences. This property was used in the experiments described in this chapter of which the principle aim is the quantitative determination of the difference between the fading time constant in the foveal and the peripheral map. The implications for the qualitative model of the brightness and darkness processing as proposed by Gerrits (1970b) will be considered.

5.3. Method

The stimulus was a light disk on a dark background generated by a programmable video generator connected to a Philips LDN 5006 Video Monitor. The luminance of the disk was 63 cd/m^{2}and the background had a luminance of 6.3 cd/m^2, producing a contrast of 82%. A small adjacent annulus (30 min arc wide) was presented with the same luminance as the disk after an interval of τ seconds after the onset of the disk. Then the time T was measured from the onset of the annulus until equalization of the difference between the annulus and the disk was reached.

By varying the interval time (τ) and measuring the equalization time (T), the fading time constant at a certain eccentricity in the visual map can be determined. Various disk diameters (4 up to 20 degrees) were used resulting in the determination of the fading time constants at various eccentricities. For a stabilized homogeneous disk centered at the fovea the decrease of its brightness is determined by the area with the largest time constant. As its contour is situated at a certain eccentricity and the fading time constant increases with eccentricity it is obvious that the decrease of the brightness is determined by the fading time constant of the perceptive element located at the contour of the disk.

Two thoroughly trained (LvE, HG) as well as two naive subjects (AB, ND) participated in the experiments. Experiments were done in stabilized as well as in non-stabilized conditions, the latter to investigate the influence of residual eye movements in the case of fixation. The method to obtain a stabilized image has been described in detail before (Gerrits and Vendrik, 1970a). A small heated aluminium suction cap (weighing about three grams) was attached to the eyeball by a small underpressure ($-4.10^3 < p < -2.7.10^3$ Pa). The object to be stabilized was observed through a lens (50 D, diameter 7 mm) and an artificial pupil of 2 mm diameter. The object was formed by the image at the end of an image transmitting optic fibre (Gerrits and Vendrik, 1972). The stimulus on the video monitor was projected onto the other (distal) end of the fibre. The eyeball was anaesthetized with novesine. The other eye was closed and covered with a black patch. The subject's position was always supine. The subject started to bring the image in focus and tried to find the most comfortable and satisfactory position of his head and his eyes. He changed his line of sight until no on- and off-borders (caused by small shifts of the cap over the eye) were generated anymore and the image easily faded after light onset. Small shifts of the cap with respect to the eyeball cause destabilization. They occur when a subject moves his eyes too much. The imaqe destabilizes as soon as the object holder touches the subject's nose or eyebrow or if the small rubber tubes (supplying warm water and underpressure) exert a pulling force on the cap. Just by looking at the relative position of the on- and off-borders a trained observer is able to correct a wrong direction of his gaze within a few minutes and to maintain this most satisfactory position.

In the fixation condition (pseudo-stabilization) subjects were seated at a distance of 57 cm from the screen of the videomonitor. The head was supported by a chin- and headrest. The observation was monocular and an artificial pupil of 2 mm diameter was used to limit any effects of pupil variations. A fixation spot of 5 x 5 min arc was used. Subjects started to fixate before they triggered the onset of the disk. Differences in the ability to maintain fixation were manifest. Naive subjects can improve their fixation ability (Winterson and Collewijn, 1976). Eye movements can be suppressed even down to the microsaccades (Steinman et al., 1967, 1973). The well-trained subjects even managed to obtain complete fading of the disk for the larger interval times. But only the stabilization condition overcomes the inability of any subject to "stop" his eye movements completely (see above).

The measurement started when the subject triggered a generator to present the light disk at t = 0. The adjacent annulus was switched on τ seconds after that. Then a difference between the brightness of the annulus and the disk was observed, although there was no physical difference in luminance. As soon as the observed brightness difference had disappeared the subject pushed a button. The timelap between the onset of the annulus and the disappearance of the brightness difference, i.e. the equalization time, was registered. Note that in the stabilized condition the stringent fixation task was absent. The parameters which have been varied in these experiments were: the interval time (τ) and the diameter of the disk.

5.4. Results

In table 5.IIa the results are given of a stabilization experiment in which the subject succeeded to have a very satisfactory stabilization all over the experimental session. The average equalization time is found to be longer for the more foveally located percept. For an annulus of 70 min arc wide the results are given in table 5.IIb. Subjects clearly did not manage to keep up satisfactory stabilization during the entire experimental session. For all three of them the maximally attained equalization time was found for the smallest stimulus, i.e. a stimulus having its contours closest to the foveal area. In table 5.IIc finally the overall averages of 12 stabilization experiments of subject LvE are given. Except for two measurements it is generally found that the equalization time increases with the interval time between the onset of the disk and annulus of equal luminance. In the discussion the variations of the overall mean of the equalization times as a function of retinal eccentricity will be analysed. For subjects ND and LvE the results of the experiments in which the disk was fixated (non-stabilized condition) before the annulus of equal luminance was switched on are given in table 5.III. In the case of an eccentricity of 2 degrees the same results were found in an additional experiment for subjects AB and HG. It can be seen that for an interval time of more than 2 seconds and an eccentricity of more than 2 degrees always a decrease of the equalization time is found as eccentricity is increased.

a Measured equalization times in stabilized condition.

Retinal eccentricity (E) (degrees)	Interval time (τ) (seconds)	Number of obser-vations (n)	Equalization time (T) (seconds) maximum m	mean μ	st.dev. σ
2	4	16	4.7	3.4	1.
8	4	20	4.8	2.7	0.7
2	8	15	5.5	4.5	0.5
8	8	20	4.5	3.7	0.4

b Comparison of equalization times.

		Subject											
		AB				LvE				HG			
			T (seconds				T (seconds				T (seconds)		
E	τ	n	m	μ	σ	n	m	μ	σ	n	m	μ	σ
2	4	20	5.0	3.0	0.7	30	4.9	2.1	0.8	20	2.0	1.4	0.3
4	4	20	3.5	2.4	0.6	31	3.8	2.3	0.8	20	2.1	1.5	0.3
2	8	20	5.6	4.4	0.8	30	6.1	4.4	1.0	20	4.1	2.8	0.7
4	8	20	4.1	3.0	0.4	20	4.9	3.6	0.7	20	3.3	2.5	0.4

c Comparison of equalization times at different eccentricities

E (degrees	0.5		1		1.5		2		2.5	
τ (seconds)	μ	σ	μ	σ	μ	σ	μ	σ	μ	σ
1	0.9	0.1	1.1	0.1	1.3	0.3	2.1	1.1	1.1	-
2	0.9	0.1	1.7	0.3	1.3	0.1	1.5	0.5	1.0	0.1
4	1.3	0.3	2.0	0.3	1.9	0.3	1.9	0.3	1.7	0.3
8	2.1	0.4	3.4	0.4	2.8	0.2	2.8	1.0	2.8	0.3

E (degrees	3		4		6		8		9	
τ (seconds)	μ	σ	μ	σ	μ	σ	μ	σ	μ	σ
1	1.0	0.2	-	-	0.8	0.2	1.0	0.1	-	-
2	1.2	0.2	-	-	1.3	0.7	1.2	0.2	1.3	0.2
4	1.8	0.4	2.3	0.8	1.8	0.6	2.4	0.7	3.0	0.5
8	3.0	0.5	3.6	0.7	3.0	0.6	3.2	0.8	3.4	1.0

Table 5 II Equalization times determined under stabilized image conditions a) Measured equalization times for subject LvE when an annulus of 60 min arc was used b) Comparison of equalization times when an annulus of 70 min arc was used c) Comparison of equalization times at different eccentricities when the annulus was 30 min arc wide

Subject	E (degrees)	1			2			3.5			5.5			10		
	τ (seconds)	T(seconds)			T(seconds)			T(seconds)			T(seconds)			T(seconds)		
		n	μ	σ	n	μ	σ	n	μ	σ	n	μ	σ	n	μ	σ
N.D.	1	10	1.4	0.1	10	1.2	0.1	6	1.7	1.2	-	-	-	-	-	-
	2	10	2.0	0.5	17	1.9	0.5	6	1.4	0.2	-	-	-	12	1.1	0.2
	4	10	2.6	0.7	16	2.6	0.5	6	2.0	0.5	6	1.8	0.2	12	1.6	0.3
	8	10	5.9	0.6	40	4.7	0.9	6	3.0	0.4	6	2.9	0.9	12	2.2	0.3
	16	-	-	-	36	6.3	1.2	6	4.8	0.5	7	3.5	0.5	12	3.2	0.4
	32	-	-	-	11	6.3	0.8	-	-	-	6	5.2	0.5	12	4.5	0.6
L.v.E.	1	10	1.3	0.2	25	1.0	0.1	6	1.6	0.4	-	-	-	-	-	-
	2	10	1.7	0.2	31	1.4	0.2	6	1.4	0.3	-	-	-	15	1.2	0.3
	4	10	2.5	0.4	31	2.1	0.3	6	2.0	0.5	6	1.7	0.5	15	1.4	0.4
	8	10	4.4	0.4	55	4.0	0.8	6	3.6	0.4	6	1.9	0.8	15	1.9	0.5
	16	-	-	-	36	6.0	1.0	6	5.3	0.8	6	3.1	1.1	15	2.7	0.7
	32	-	-	-	11	7.0	1.3	-	-	-	6	4.5	1.2	15	4.0	0.8

Table 5 III Equalization times determined under fixation condition

5.5. Calculation of the fading time constant

In order to reach quantitative results for the local fading time constant these measurements of the equalization time are evaluated by means of a formal model. The model is intended to be a phenomenological framework for the observed dynamical perceptions rather than an adequate neurological description. Although the quantitative determination of the difference between the fading time constant in the foveal and peripheral projection is the only object of this investigation, the mechanism of filling-in has to be incorporated too.

To the perceptual phenomena during the disappearance of the percept of a light disk the following contributions can be discerned:

a. Brightness-producing activity that results from the stimulus onset. The amount of brightness-producing activity determines the perceived brightness.

b. The activation of brightness elements by neighbouring elements under the restriction that the neighbouring elements do have a higher level of activation and that the corresponding elements in the antagonistic system (darkness) are not activated sufficiently any longer. This is the filling-in process, which is controlled by so-called barriers (see Gerrits, 1970b, 1979, and chapter two of this thesis).

c. The activation of neighbouring elements caused by movement of the contours of the image over the retina in the case of imperfect stabilization. The effectivity of a contour displacement as determined by the local receptive field size has to be included in this effect.

d. The adaptation level of the system to the stimulus.
e. The fading mechanism: the loss of brightness- or darkness-producing activity.

Due to the contributing mechanisms, the preservation of a homogeneous brightness perception of a uniform stimulus depends on:

a. the eye movements which displace the contours of the image across the receptive fields. (This results in an inflow of brightness-producing activity from the contours of the stimulus).
b. the filling-in mechanism distributing the brightness-producing activity over the area bounded by the contours.
c. the fading causing loss of the brightness-producing activity.

A schematic representation of these three concepts is given in figure 5.5. As soon as the brightness of the percept of an enclosed area remains constant, an equilibrium is reached between the increase of brightness-producing activity due to filling-in and caused by continuous eye movements and the decrease of brightness-producing activity as a consequence of fading. The fading time constant of the decrease of activity per unit of time is not directly measurable. It has to be estimated from the decrease of brightness or darkness as a function of time. This function can be determined by comparing the actual brightness or darkness of the area investigated with the brightness or darkness of an adjacent area. The way this was achieved here implied that a certain brightness generated at $t = 0$ was compared to an adjacent reference brightness that appeared after a time lap of τ seconds. The time it took for both areas to become indistinguishable in brightness was called the equalization time (T). The level to which the brightness or darkness can decrease depends for the largest part on the amount of eye movement and the receptive field size at the location of the contour. For a small part the residual brightness is determined by the retinal illumination as it influences the fluctuations in the sustained activity of the ganglion cells.

The application of the first order model requires the following simplifications:

a. The process is thought to start with an activity level which is "equal" to the brightness-producing activity at stimulus onset.
b. The inflow is taken to be constant and equal to the average of the varying amount of activity generated by eye movement. In the situation of retinal image movements due to "normal" eye movements the inflow of activity is very difficult to describe as its instantaneous value varies continuously. It is obvious , however, that a mean inflow into the centre of the percept of a homogeneous stimulus results as the contours are moved over distances large enough to change the illumination within the receptive fields at the location of the stimulus edge (see figure 5.5).
c. There is no adaptation influence in the short time of stimulus presentation.
d. The fading time constant is a system parameter that determines the loss of activity. It only depends on the location within the visual field.

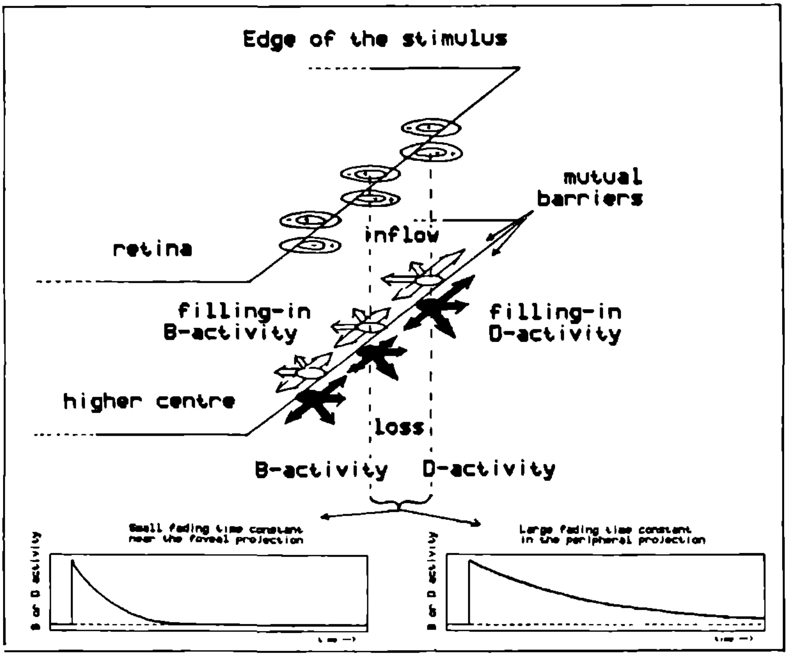


Figure 5 5 A schematic representation of the equilibrium between " inflow " of brightness-producing activity at the higher centre level, the " spreading out " of the activity due to filling-in and the loss of the activity due to fading

In figure 5.6a the model is given for the direct brightness pathway at a certain location. The output of the system, the actual brightness-producing activity , is caused by the input activity coming from retinal and other cells projecting onto a perceptive element and of the activity, that results from the activation of neighbouring elements. Fading is the mechanism whereby perceptive elements lose their activity. If we represent the inflow of activity as an electric current and the actual amount of activity as a potential an electric analogon of the system is readily found (figure 5.6b). The fact that the system does not show instantaneous fading is incorporated in the capacitor that enables the activity to remain for a limited period.

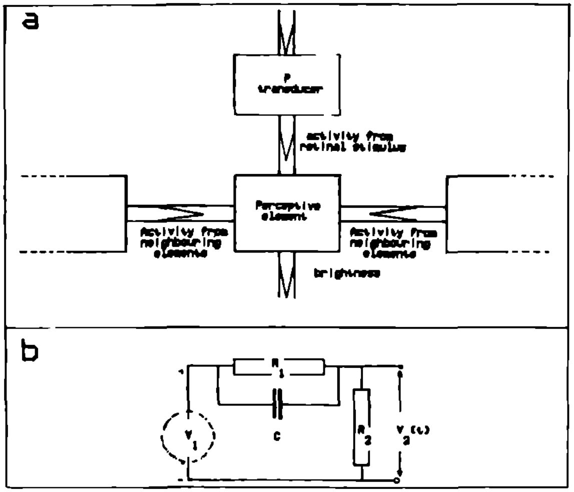


Figure 5 6 a) A schematic representation of a model describing the brightness generation by one perceptive element b) An electric analogon of the system element represented in a The following equations are valid

$$-V_1(t) + V_c(t) + V_2(t) = 0$$

$$i_1(t) * R_1 = V_c(t)$$

$$i_2(t) = C\frac{dV_c(t)}{dt}$$

$$(i_1(t) + i_2(t)) * R_2 = V_2(t)$$

Now substitute $(R_1 * R_2 * C)/(R_1 + R_2) = \Theta$ and $R_2/(R_1 + R_2) = \beta$ this gives

$$V_2(t) + \Theta\frac{dV_2(t)}{dt} = \Theta V_1(t) + \beta\frac{dV_1(t)}{dt}$$

The time constant $\Theta = R_1R_2C/R_1+R_2)$ represents the dynamics caused by fading, while V_1 has to be interpreted as the result of all parallel inputs (direct as well as neighbouring).

Elaborating the corresponding equations results in the following differential equation relating brightness and luminance:

$$B(t) + \Theta\frac{dB(t)}{dt} = \Theta\frac{dL(t)}{dt} + \beta L(t) \quad .... \qquad (5.1)$$

where β : a measure for the faint brightness remaining and a measure for the retinal image movement.
Θ : the local fading time constant.
$L(t)$: the luminance of the stimulus.
$B(t)$: the perceived brightness.
The dimensionality constants are chosen to be equal one in this equation.

Starting with a system at rest, i.e. no brightness activities present, and studying only the case of a positive step function of the luminance , the resulting brightness is described by

$$B(t) = (1-\beta)L_o e^{-t/\Theta} + \beta L_o \ , \ t \geq 0 \qquad (5.2)$$

for a luminance step-function

$$L(t) = 0 \ , \ t < 0$$
$$L(t) = L_o, \ t \geq 0$$

This is the situation in which a disk, which is presented at $t = 0$, starts fading. Because of stabilization $\beta = \beta_o$. Thus the brightness of the disk (B_D) is described by:

$$B_D(t) = (1-\beta_o)L_o e^{-t/\Theta} + \beta_o L_o$$

β_o is the value that accounts for the residual brightness.

Now the fading time constant will be calculated from formerly described results, which were obtained from the experiment in which at first a light disk was presented. The brightness of this disk (B_D) starts fading immediately after the onset. After an interval of τ seconds an adjacent annulus (A) surrounding the disk is presented. Annulus and disk have the same luminance. Due to the fact that the brightness of the disk has faded already during τ seconds the annulus will be perceived to be brighter than the disk.

The disk can still be considered to be perfectly stabilized. Consequently the value of β in the function of the brightness of the disk will remain β_o.

For the annulus the fading starts at t= and so its brightness can be described by:

$$B_A(t) = (1-\beta_o)L_o e^{-(t-\tau)/\Theta} + \beta_o L_o$$

The difference $B_A(t) - B_D(t)$ $(t>\tau)$ is positive during the equalization time (T). As τ increases , T increases also. At the moment $t = \tau + T$ the brightness difference has become perceptually zero.

Up to $t=\tau$ the rate at which the brightness diminished was only determined by the fading process. At $t=\tau$ there appears, however, a brightness in the visual field that is higher than the brightness of the disk. Consequently there appears to be an equalization process active. And so the rate of the decrease of brightness will be determined by fading as well as filling-in. It was seen in earlier stabilization experiments that the time needed for the equalization of a brightness difference is determined by the contrast in the stimulus and not by the mean luminance. Therefore it was concluded that the interval time T needed for the disappearance of the brightness difference between annulus and disk is a measure for the difference itself. This implies that the interval time T is determined by $\Delta B(\tau)$ in one way or another.

In figure 5.7a we have schematically drawn the decrease of the brightness of the disk starting at t=0. For a number of interval times τ the onset and the brightness of the annulus have been indicated.

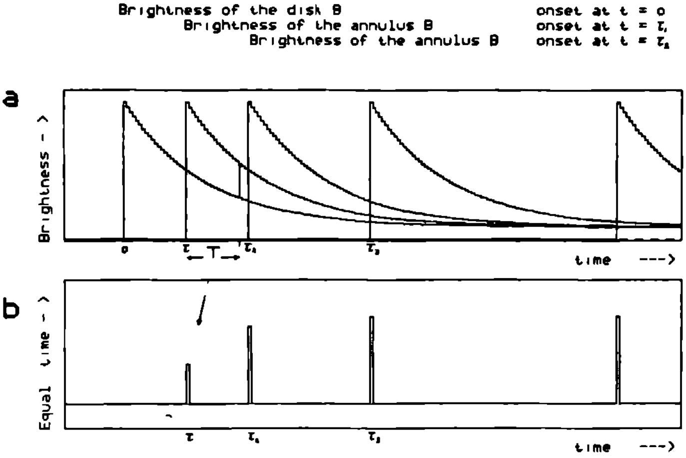


Figure 5 7 a) An illustration of the decrease of the brightness of a disk (B) and annulus (B) according to the hypothetical function $B(t)=10+100 * \exp(-t/2\ 5)$ The onset of the annulus is indicated at τ = 2 4 8 and 16 seconds The disk and annulus are supposed to be seen equal as soon as $(B_a - B_a) < 23\%$ This results in the equalization times T_1, T_2 T_3
b) A display of the equalization times T as a function of the interval times τ according to the criterion $(B_a - B_a) < 23\%$

In figure 5.7b the equalization time as a function of τ has been plotted according to the brightness difference at which equalization is observed (figure 5.7a). It is clear that this curve will be different when the fading time constant has a different value. This implies that for a foveally or peripherally determined sequence of equalization times a different function between T and τ will be found. For the "foveal" as well as the "peripheral" case an increase of the interval time will no longer result in an increase of the equalization time T as soon as an equilibrium is reached for the disk, i.e. when the brightness of the disk has reached the level B_o (figure 5.7b). In the illustration of figure 5.7b it was supposed that the inflow of activity by movement of the boundary was only small and equal for the "foveal" as well as for the "peripheral" situation.

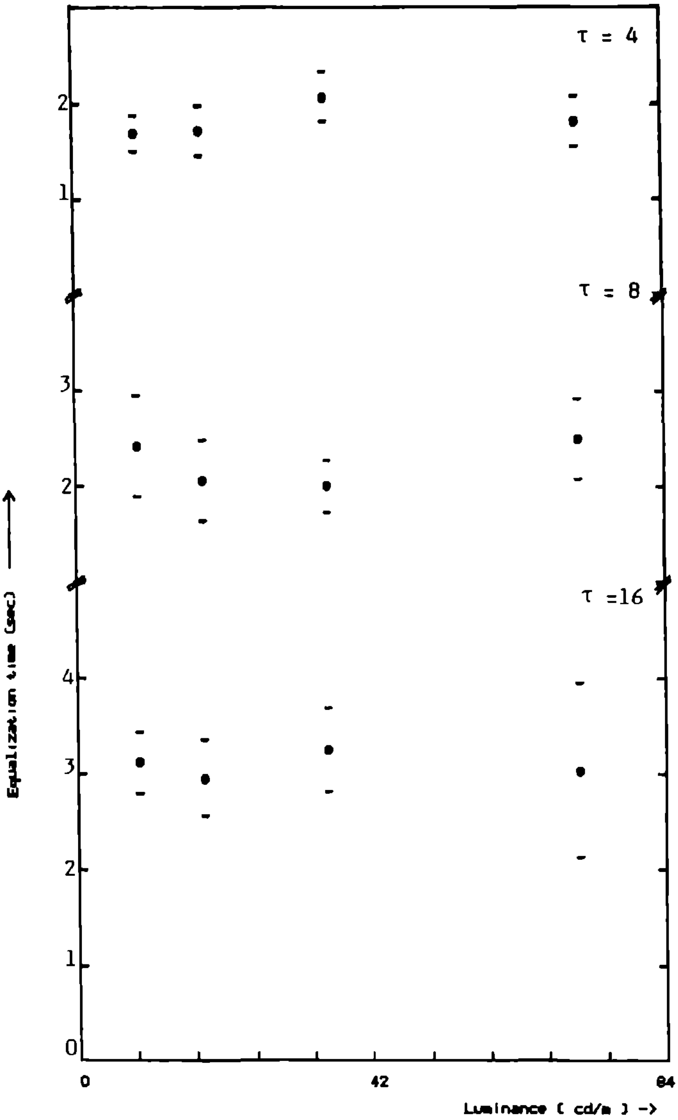


Figure 5 8 A representative measurement of equalization times in a stabilized condition when the luminance of the disk and the annulus were varied Subject HG Disk diameter 4 degrees annulus width 30 min arc

For now the model will be recapitulated as follows: A small time constant of fading in the foveal projection will lead to an increase of the brightness difference between disk and annulus as the interval time τ is increased. This implies that the equalization time increases also. A time constant in the peripheral part that is greater will cause a less pronounced increase of the brightness difference for an increasing interval time τ. So for the peripheral part the equalization time will also show a slighter increase.

There are a number of ways in which the equalization time can depend on the brightness of the disk and the surrounding annulus at time τ. An example was given in figure 5.7a, but a number of different mechanisms which are a priori equally possible will have to be considered. The starting point is the "new" situation at $t=\tau$. The first relation considered is that the equalization time is determined by the absolute brightness difference. However, additional experiments have indicated that the equalization time was not influenced by a variation of the luminance and consequently neither by the absolute brightness (B_o). A representative measurement of the luminance variation is given in figure 5.8 for subject HG.

The second possibility is that the equalization time is determined by a relative difference. This brightness difference may be relative with respect to

a) the brightness of the disk
b) the brightness of the annulus, or
c) the summed brightness of the disk and the annulus.

For these three situations it will be shown how the equalization time (T) varies with the interval time τ (for details see appendix 5.8):

a. If T varies with the relative brightness with respect ot the brightness of the disk, T is related to according to:

$$T_1(\tau) = \frac{\alpha(1 - e^{-\tau/O})}{u + e^{-\tau/O}} \quad , \quad \text{where } u = \frac{\beta}{1-\beta} \text{ and}$$

α some proportionality constant

or

b. If T varies with the relative brightness with respect to the brightness of the annulus this leads to the function:

$$T_2(\tau) = \alpha(1 - \beta)\,(1 - e^{-\tau/\theta})$$

or

c. If T varies with the brightness contrast defined as

$$C_B = \frac{B_{max} - B_{min}}{B_{max} + B_{min}}$$

where B_{max} will be the brightness of the reference annulus and B_{min} the brightness of the disk at $t = \tau$, then the function is

$$T_3(\tau) = \frac{\alpha(1 - e^{-\tau/\Theta})}{v + e^{-\tau/\Theta}} \quad , \text{ where } \quad v = \frac{1 + \beta}{1 - \beta}$$

Note, that apart from a constant determined by the residual brightness the functions $T_1(\tau)$ and $T_3(\tau)$ are the same. A special case is formed when no residual brightness is present. It is supposed here that the residual brightness (during perfect stabilization) is negligible with respect to the brightness level B_o. As an illustration of the importance of the parameter choice $\beta = 0$ is selected, giving $u = 0$ and $v = 1$. Now the functions are described as:

$$T_1(\tau) = (e^{+\tau/\Theta} - 1)$$

$$T_2(\tau) = (1 + e^{-\tau/\Theta})$$

$$T_3(\tau) = \frac{(1 - e^{-\tau/\Theta})}{(1 + e^{-\tau/\Theta})}$$

They are illustrated in figure 5.9 in the same way as the experimental data consisting of combinations of $T(\tau)$ and τ. The first proposition cannot be held for $\beta = 0$ because $T_1(\tau)$ has no asymptotic value.

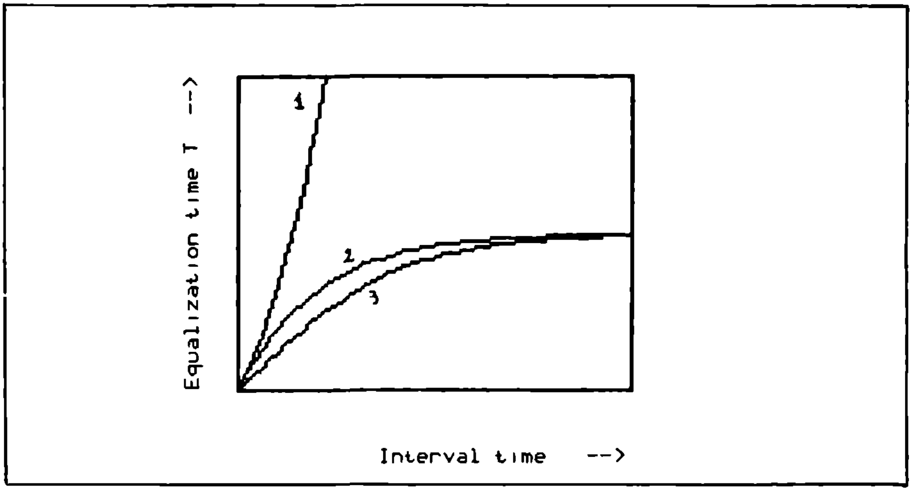


Figure 5 9 The equalization time T as a function of the interval time for three different functions (see text for explanation)

The three possible functions will now be fitted to the data from the fixation experiments. This implies that maximally three parameters have to be adjusted: α, β and Θ. The fit was done with at least squares fit

$$T(\tau) = f(\tau;\alpha,\beta,\Theta) + e$$

of the specified functions to the data values $\tau, T(\tau)$ by means of stepwise Gauss-Newton iterations on the parameters α, β and 0. Within each iteration parameters are selected for modification in a stepwise manner (method of steepest descend). The new parameter value selected at a given step is the one which, differentially at least, makes the greatest reduction in the error sum of squares.

$$y = \frac{p_1(1 - e^{-xp_2})}{1 + p_3 e^{-xp_2}} \quad .$$

This function matches:

$$T_1(\tau) = \frac{\alpha(1-\beta)\ (1-e^{-\tau/\Theta})}{+\ (1-\beta)e^{-\tau/\Theta}} \qquad \text{when } p_1 = \frac{\alpha(1-\beta)}{\beta}$$

$$p_2 = \frac{1}{0}$$

$$p_3 = \frac{1-\beta}{\beta}$$

$$T_2(\tau) = \alpha(1-\beta)(1 - e^{-\tau/\Theta}) \qquad \text{when } p_1 = \alpha(1-\beta)$$

$$p_2 = \frac{1}{\Theta}$$

$$p_3 = 0$$

$$T_3(\tau) = \frac{\alpha(1-\beta)(1 - e^{-\tau/\Theta})}{(1+\beta) + (1-\beta)e^{-\tau/0}} \qquad \text{when } p_1 = \frac{\alpha(1-\beta)}{1+\beta}$$

$$p_2 = \frac{1}{\Theta}$$

$$p_3 = \frac{1-\beta}{1+\beta}$$

The result was that $T_2(\tau)$ produced the smallest error e in describing the data, although α and β could not be determined separately. The fit of the functions $T_1(\tau)$ and $T_3(\tau)$ always tended to a value of 1 for β, a value that has to be rejected on the basis of the fact that this represents the absence of fading. From now on only the function $T_2(\tau)$ will be considered. Without any constraint on the value of the product $\alpha(1-\beta)$ different asymptotic values for the equalization times result. The function $T_2(\tau)$ is basically a function with only two parameters. Therefore a fit function with only two parameters was taken.

$$y = p_1(1 - e^{-xp_2}) \quad , \quad \text{where } p_1 = \alpha(1-\beta),$$
$$p_2 = \frac{1}{\theta}$$

The resulting values of the fading time constant for this fit are given in table 5.IVa.

E (degrees)	1	2	3.5	5.5	10
a	The fading time constant (seconds) estimated from $y = p_1(1 - e^{-xp_2})$				
AB	7.9	12.2			
ND	9.8	6.1	7.5	12.4	11.6
LvE	5.0	8.7	8.6	14.1	11.8
HG	-	18.5	-	-	-
b	The fading time constant (seconds) estimated from $y = p_1(1 - e^{-xp_2})$, with p_1 fixed.				
ND	5.2	6.0	11.5	18.0	22.8
normalized	1	1.2	2.2	3.5	4.4
LvE	7.2	8.5	10.0	25.4	30.2
normalized	1	1.2	1.4	3.5	4.2

Table 5 IV Estimated fading time constants

Under the assumption that the level p_1 is independent of the eccentricity a second fit was made while p_1 was set to a fixed value. Considering the fact that the asymptotic value should be the same for all eccentricities, the fit may be repeated for a fixed value of $\alpha(1 - \beta)$. The asymptotic level was most accurately determined for an eccentricity of 2 degrees out of the fovea.

For a fixed value of p_1 only θ can be determined.
The results are given in table 5.IVb and figure 5.10 the data from the fixation experiments of subjects ND and LvE are given along with the fitted curve. In table 5.IVb also the normalized values of the fading time constant with respect to an eccentricity of 1 degree in the visual field are given as resulting from the estimated values. It appears that fading time constants are in the range from about 5 seconds in the fovea to about 25 seconds in the periphery at a stimulus luminance of 63 cd/m^2.

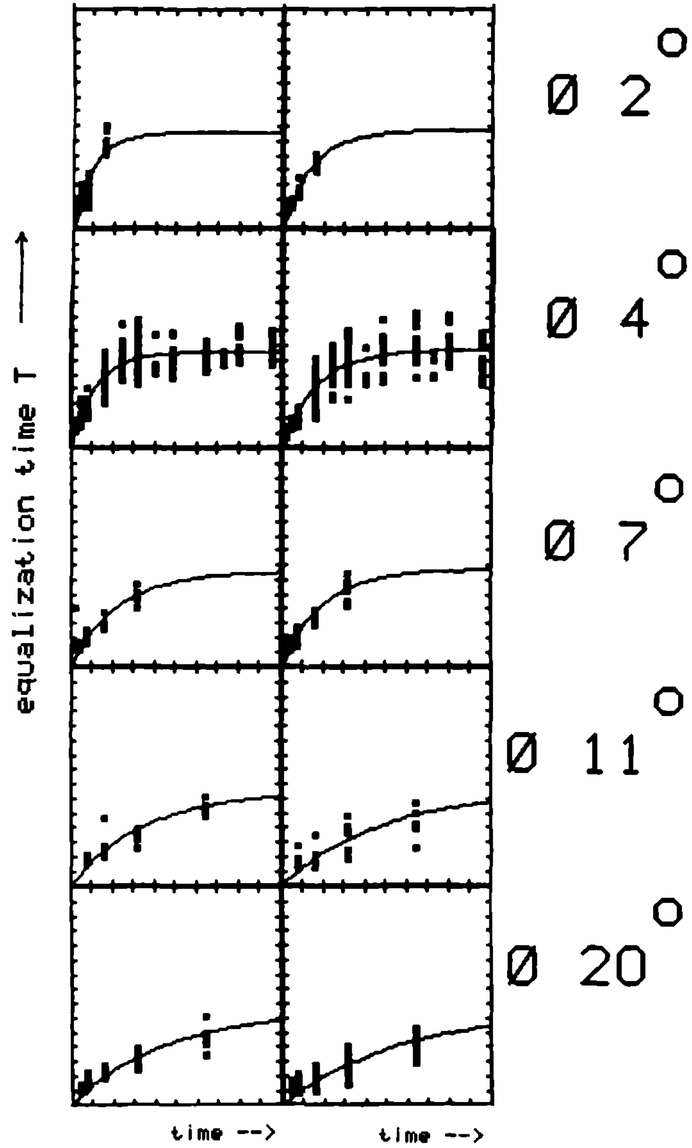


Figure 5 10 Measured equalization times T as a function of the interval time τ The measurements were performed with a disk of 2, 4, 7, 11 and 20 degrees in diameter Left column data from subject ND and right column from subject LvE

5.6. Discussion

Fading time constants were determined by using a first order model to describe the brightness as a function of time and relating the equalization time to the brightness difference that results after the brightness of a disk has faded before an adjacent annulus of the same luminance and surrounding the disk is switched on. The fading time constants had values from 5 seconds (1 degree) up to 25 seconds (10 degrees of eccentricity).

It is impossible to compare these results with experimental data in which the fading time was determined. A fading time is the time it takes for a percept to fade to an undetermined level. Another difficulty is that due to the influence of retinal image movements fading of a peripheral stimulus may be observed before the fading of a foveally presented stimulus. This effect is generally known as Troxler's effect (Troxler, 1804). This effect is often interpreted as the consequence of a faster fading mechanism in peripheral areas of the visual field compared to foveal areas. This is an incorrect conclusion. In our fixation experiments as well as experiments in stabilized condition it was found that equalization times can be longer for foveally presented stimuli than for peripheral stimuli. This indicates that retinal image movement in our fixation experiments as well as e.g. in some stabilization experiments of West (1967) was satisfactorily reduced. The inability to attain an overall mean of decreasing equalization times as a function of eccentricity from several stabilization experiments is probably due to the fact that foveal stabilization requires the greatest efforts from the subject (Gerrits, 1978). Another effect occurs when providing the subject with a "wide" stimulus. Then the suction cap has to be equipped with a 100 D lens. This implies, however, an increase of retinal stimulus displacement with respect to the 50 D lens for a slip of the suction cap of a particular amplitude. So one must not compare measurements from experiments with different lenses in the suction cap when the influence of residual retinal image displacements are the important factor determining the experimental outcome.

These arguments may account for the fact that from the overall mean of the results of the stabilization experiments the fading time of foveal percepts did not proceed significantly faster than for peripheral percepts. As can be seen from table 5.II subjects succeeded in a number of stabilization experiments to achieve sufficient image stabilization to allow the brightness of a small disk to fade considerably more than the brightness of a large disk. Again we want to stress here the fact that the fading time constant is indeed smallest within the foveal projection, the fading of a foveal percept could never have occurred faster than that of a peripheral percept. This is the case irrespective of the residual retinal image movements. The wellknown increase of receptive as well as of perceptive field sizes with eccentricity would not allow this to happen, with or without retinal image movement.

5.7. Conclusion

In this chapter the fading time constant was determined at various locations in the visual map. Fading time constants have values from 5 seconds at an eccentricity of 1 degree in the visual map up to 25 seconds at an eccentricity of 10 degrees.

Thusfar experimenters have only determined the fading time. As no unique criterion exists to indicate when a percept has faded it is inadequate to determine the fading time. By our method of measuring the equalization time (T) of a certain brightness difference as a result of fading during τ seconds the fading time constant would be determined. To determine a fading time constant the final point of disappearance does not have to be used.

5.8. References

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5.9. Appendix

The model describes the brightness of the disk as follows:

$$B_D(t) = (1-\beta)\, B_o\, e^{-t/\Theta} + \beta B_o$$

The brightness difference between the brightness of the annulus and the brightness of the disk at the moment in time $t=\tau$ is decribed as:

$$\begin{aligned}\Delta B(\tau) &= B_o - B_D(\tau) = \\ &= B_o - (1-\beta)\, B_o\, e^{-\tau/\Theta} - \beta B_o \\ &= B_o - \beta B_o - (1-\beta)\, B_o\, e^{-\tau/\Theta} = \\ &= (1-\beta)\, B_o - (1-\beta)\, B_o\, e^{-\tau/\Theta} = \\ &= (1-\beta)\, B_o\, (1 - e^{-\tau/\Theta})\end{aligned}$$

In figure 5.11 the difference $\Delta B(\tau)$ is indicated.

The relative brightness can be defined with respect to the brightness of the disk or the annulus. With respect to the disk we get:

$$\begin{aligned}\frac{\Delta B(\tau)}{B_D(\tau)} &= \frac{(1-\beta)\, B_o\, (1 - e^{-\tau/\Theta})}{(1-\beta)\, B_o\, e^{-\tau/\Theta} + \beta B_o} = \\ &= \frac{1 - e^{-\tau/\Theta}}{e^{-\tau/\Theta} + \frac{\beta}{1-\beta}} \\ &= \frac{1 - e^{-\tau/\Theta}}{u + e^{-\tau/\Theta}} \qquad \text{with } u = \frac{\beta}{1-\beta}\end{aligned}$$

With respect to the brightness of the annulus we get

$$\frac{\Delta B(\tau)}{B_o} = \frac{(1-\beta)B_o(1 - e^{-\tau/\Theta})}{B_o} = (1-\beta)(1 - e^{-\tau/\Theta})$$

The relative brightness difference with respect to the sum of the brightness of the annulus and the disk is the brightness contrast:

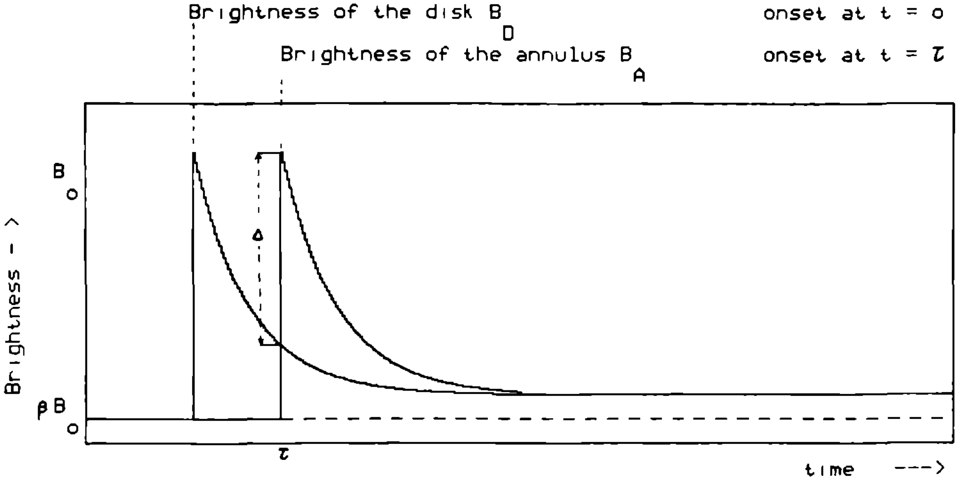


Figure 5 11 An illustration of the decrease of the brightness of a disk (B_D) and annulus (B_A) according to the hypothetical function $B(t)=10+100* \exp(-t/2\ 5)$ The onset of the annulus is indicated at $\tau = 4$ seconds The disk and annulus are supposed to be seen equal as soon as $(B_A-B_D)< 23\%$ This results in the equalization time T The difference ΔB at $t=\tau$ is indicated in the figure

$C_B = \dfrac{B_{max} - B_{min}}{B_{max} + B_{min}}$, where B_{max} stands for the brightness of the annulus and B_{min} stands for the brightness of the disk. By substitution we get:

$$\frac{\Delta B(\tau)}{B_D(\tau) + B_o} = \frac{(1 - \beta)B_o(1 - e^{-\tau/\Theta})}{(1 - \beta)B_o e^{-\tau/\Theta} + \beta B_o + B_o} = \frac{(1 - \beta)(1 - e^{-\tau/\Theta})}{(1 - \beta)\, e^{-\tau/\Theta} + (1 + \beta)}$$

$$= \frac{1 - e^{-\tau/\Theta}}{e^{-\tau/\Theta} + \frac{(1+\beta)}{(1-\beta)}}$$

$$= \frac{1 - e^{-\tau/\Theta}}{v + e^{-\tau/\Theta}} \quad \text{with } v = \frac{1+\beta}{1-\beta}$$

For perfect stabilization β is nearly zero which implies that u is almost zero while v tends to be equal one. For this situation the curves were calculated and given before in figure 5.9. It can easily be shown that the equalization time T is a transcendental function of Θ which in a first approximation can be expressed as linearly related to the relative brightness defined before. Then we have:

$$T_1(\tau) = \frac{\alpha(1 - e^{-\tau/\Theta})}{\frac{\beta}{1-\beta} + e^{-\tau/\Theta}} \quad ,$$

$$T_2(\tau) = \alpha(1 - \beta)(1 - e^{-\tau/\Theta}) \quad ,$$

$$T_3(\tau) = \frac{\alpha(1 - e^{-\tau/\Theta})}{\frac{1+\beta}{1-\beta} + e^{-\tau/\Theta}} \quad , \text{ where } \alpha \text{ is a dimensionality constant.}$$

The program that optimally fits the parameters of these functions to the measured τ , combinations, optimizes the fit on the basis of the minimalization of the sum of the squares of the difference between the measured and the calculated value. The minimalization is acquired by varying the parameters guided by the behaviour of the partial derivatives with respect to the parameters (steepest decent method). The fit procedure turned out to be sensitive to the start values when the range was too wide (The calculated results should stay within certain limits). To indicate a range of expected parameter values that was as narrow as possible, the minimum and maximum values in the data were used to determine the limiting values of the functions.

For instance, for T_1 this gave:

$$T_1 : \tau = 0 \quad T_1 = 0$$

$$\tau \to \infty \quad T_1 = \frac{\alpha(1 - \beta)}{\beta}$$

Substitution of

$$p_1 = \frac{\alpha(1 - \beta)}{\beta} \quad , \quad p_2 = \frac{1}{\Theta} \quad \text{and} \quad p_3 = \frac{1 - \beta}{\beta}$$

leads to the following equations:

$$T_1(\tau) = \frac{p_1(1 - e^{-\tau p_2})}{1 + p_3 e^{-\tau p_2}}$$

$$\frac{\partial T_1(\tau)}{\partial p_1} = \frac{1 - e^{-\tau p_2}}{1 + p_3\, e^{-\tau p_2}} = \frac{T_1}{p_1} \rightarrow T_1 = p_1 \frac{\partial T_1}{\partial p_1}$$

$$\frac{\partial T_1(\tau)}{\partial p_2} = \frac{p_1\, \tau\, e^{-\tau p_2}\, (1 + p_3)}{(1 + p_3\, e^{-\tau p_2})^2}$$

$$\frac{\partial T_1(\tau)}{\partial p_3} = \frac{-\, p_1\, e^{-\tau p_2}\, (1 - e^{-\tau p_2})}{(1 + p_3\, e^{-\tau p_2})^2}$$

For T_2 and T_3 similar expressions are found and it turns out that T_1 and T_3 even have the same form although with a different meaning of the parameters.

The ranges for the parameters p_1, p_2 and p_3 were chosen to be

$$0 < p_1 < 10$$

$$10^{-20} < p_2 < 10$$

$$0 < p_3 < 9$$

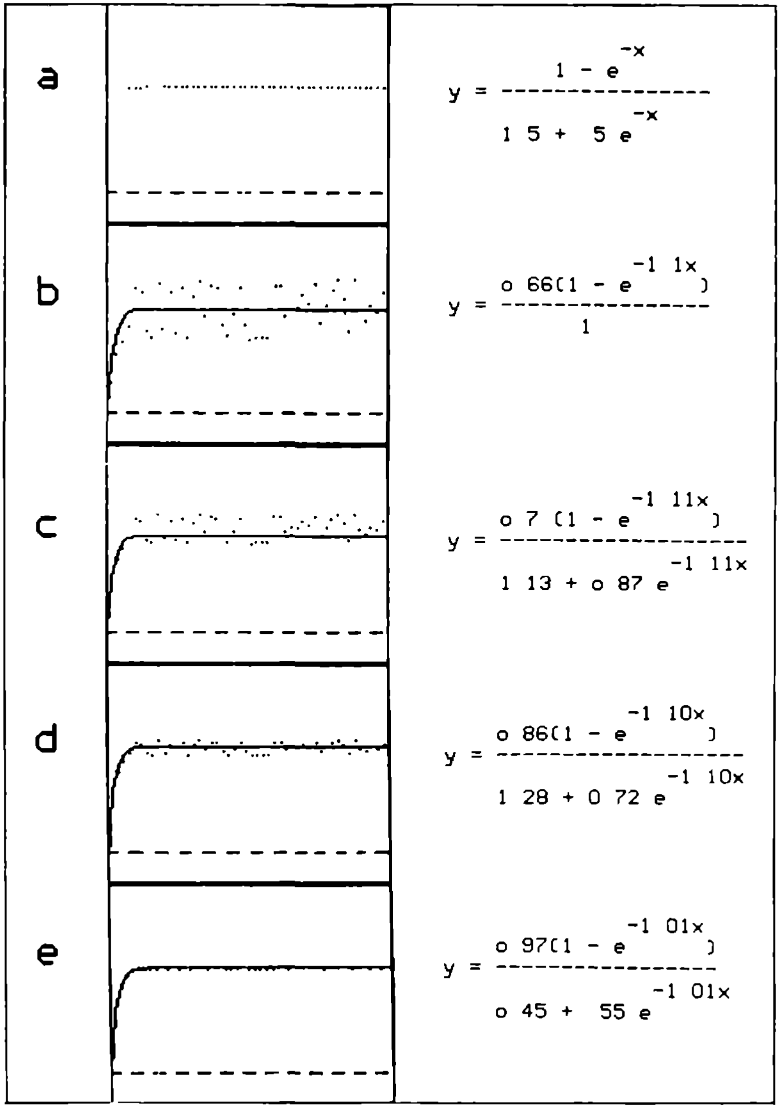
So in fact there are only two situations:

a) for T_1 and T_2 three parameters have to be estimated
b) for T_2 only two parameters have to be estimated.
In both cases Θ can be determined uniquely.

To investigate how the "noise" in the data influences the estimated parameter values data were generated by calculating the function values. This is shown in figure 5.12 for the function

$$y = \frac{q_1(1 - e^{-xq_2})}{1 + q_3 + (1 - q_3)e^{-xq_2}} \quad \text{with } q_1 = 1,\ q_2 = 1 \text{ and } q_3 = 0.5$$

Then uniformly distributed noise was added to the function values. Noise ranges of ± 0.2, ± 0.1, ± 0.05 and ± 0.01 were used. From these data the parameters q_1, q_2 and q_3 were determined by fitting. The dots indicate the data function values plus noise. The curve represents the estimated function. At the right the analytical description is given for the parameter values estimated.
After a number of tests, the fit procedure was started for the data of the fixation experiments, which gave the results shown in table 5.IV.



$$y = \frac{1 - e^{-x}}{1\ 5 + \ 5\ e^{-x}}$$

$$y = \frac{0\ 66(1 - e^{-1\ 1x})}{1}$$

$$y = \frac{0\ 7\ (1 - e^{-1\ 11x})}{1\ 13 + 0\ 87\ e^{-1\ 11x}}$$

$$y = \frac{0\ 86(1 - e^{-1\ 10x})}{1\ 28 + 0\ 72\ e^{-1\ 10x}}$$

$$y = \frac{0\ 97(1 - e^{-1\ 01x})}{0\ 45 + \ 55\ e^{-1\ 01x}}$$

Figure 5 12 The results of the parameter fit to the separate function (a) and with additive noise in the range of + 0 2 (b), + 0 1 (c), + 0 05 (d) and + 0 01 (e)

Chapter 6: A SIMULATION MODEL OF THE BRIGHTNESS/DARKNESS SYSTEM.

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6.1. Introduction

There is no way to obtain direct information regarding the physical systems which subserve visual sensations. The only way to describe visual perceptual mechanisms is by translation of the inside hypothetical representation as 'viewed' by the 'output' of the brain measured either as electrical activity or as mechanical responses.

By means of this output information it is possible to construct some physical reality that leads to the same or a very close visual phenomenon as was revealed by the original experiment. However, it is difficult if not impossible for a human observer to describe with sufficient reliability his sensations quantitatively as a function of time (Eijkman, 1959). Often it is impossible to compare the experienced effect in some experimental condition with the effect one sees in another situation. This is , for instance, the case in stabilization experiments. The percepts that one 'sees' by viewing a stimulus in a stabilized condition cannot very well be compared directly with a series of percepts generated artificially which are viewed under normal conditions. The best comparison that can be made is to look repeatedly and very accurately in a stabilized condition at the different percepts and give a verbal report as the experimental output (Gerrits, 1979). This leads to an 'artists' view which can be inspected under normal viewing while the verbal report may help to identify the specific percepts. Nevertheless a simulation model containing known facts and hypothetical addins may serve to gain a better understanding of the necessity or sufficiency of some hypothetical constructs. Therefore we decided to develop a simulation model. Obviously a 'real time' simulation would resemble the perceptual changes the most. With the available computer and video facilities such a high speed was not attainable, however. So a slow motion version of the perceptual changes was obtained which was sufficiently precise to analyse 'perceptual' phenomena that take place when the visual information is transferred along the visual pathways within the brightness/darkness system. Despite the fact that the model is incomplete and a number of aspects are lacking in our approach while others are approximated too coarsly, it appears to be a general framework that allows us to check in a consistent way qualitative predictions that parallelled the many observations in stabilized condition. This simulation model broadens the insight into the mechanisms underlying the interactions between brightness- and darkness-producing activity in order to control the filling-in mechanism, in the process that is responsible for the contour fading and the time course difference between foveal and peripheral fading. In figure 6.1 it is diagrammed how the model is used in an interactive way. By varying stepwise various parameters their influence may be studied in search of 'percepts' which resemble real percepts more and more.

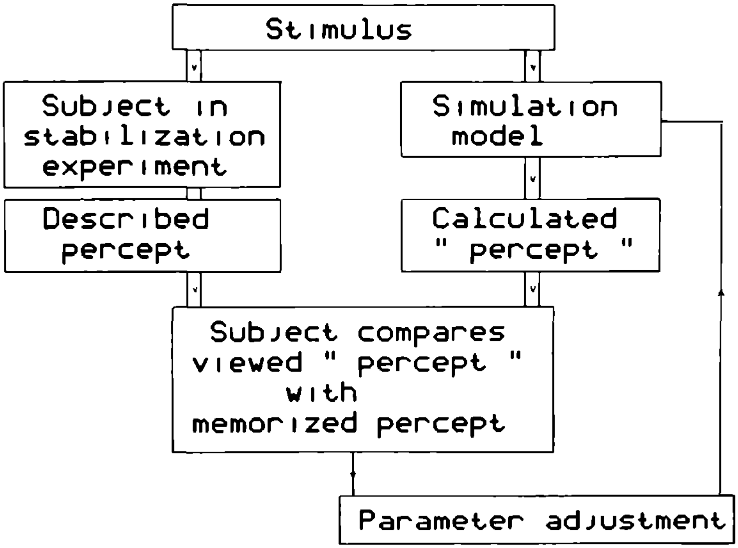

Figure 6 1 The interactive use of the simulation model

6.2. Method

The different stages in the brightness/darkness system were specified by formulating a number of calculation rules. To keep the model as transparant as possible, separate calculations were made for every functional stage in the system, resulting in a chain of subroutines. The software was written in Fortran IV plus. Partly new specific programs were developed and partly a general matrix manipulation program package with general mathematical functions (MAThematical FUNcations, Bruijns) was used. The calculations were performed on a Digital Equipment PDP 11/45 minicomputer and the images, representing the percepts, were sequentially stored on tape. Display was done by data transfer from the tape to a Ramtek 3300 Display system with a Barco Colour Video Monitor. Here the pixel values were converted to luminance values by means of a look up table which determined the grey scale. A pixel value of zero was chosen to be the middle of the scale as brightness (more luminance) as well as darkness (less luminance) had to be represented. A cine like representation was obtained by recording the 'percepts' on videotape and playing them back at a different speed.

The implementation of the characteristics of the brightness/darkness system in the software simulation model was performed in the following way.

Obviously a number of approximations had to be made using a discrete approach of the brightness/darkness system. In a temporal sense the real system is analogous, in a spatial sense it is a sampling system. The real spatial sampling system is much better than we can reach with our simulation model forcing us to use a spatially coarse approximation. It was not considered an impedement for the dynamics we wanted to study, however.

At first the receptive fields of the ganglion cells had to be modelled by their characteristics: centre and surround. The detailed description of the rest of the retinal network such as the receptor connections was not modelled. It is known from electrophysiology that proceeding to the more central areas a repeated remapping occurs. It was assumed that structurally the brightness system can be described by two kinds of cells: on-centre cells: signalling only increases of luminance and off-centre cells: signalling only decreases of luminance. In that sense the brightness/darkness system transmits only the excitatory changes in the "visual world" from the eye to the brain. In the first stage of the model the response of a cell is determined by the "visual" scene at the input and is calculated according to its receptive field property. In this way the stimulus (a luminance distribution) as an input generates a "field" of cell activities after convolution with the specific cell receptive fields. Note that we are considering the situation that eye movements are absent simulating the stabilized image condition.

It is known, that there are a number of cells functionally related to a specific location. Each cell has its own field of view (small or large) from where stimulus information contributes to the cell activities.

The visual stimulus is modelled by a 2 dimensional matrix containing the 'luminance' values. It is the first stage in figure 6.2. The receptive field matrix contains the receptive field characteristics in a sampled way. When the calculation of the convolution is performed it is assumed that 'outside' the stimulus an area of zero luminance exists. In a first approach the receptive fields for the brightness- and the darkness-system were chosen opposite in sign but equal in size. However, a number of data are available that indicate that on-centre receptive fields are on the average smaller in a certain location than off-centre receptive fields (see chapter two). Larger receptive fields are considered to be "looking" at a larger part of the world than smaller receptive fields. In the higher centre, where activity contributions of smaller and larger receptive fields will have to be combined, the matrix of the smallest fields will determine the resolution. To achieve this a large receptive field will activate a number of small elements. In the model this was implemented as a separate option.

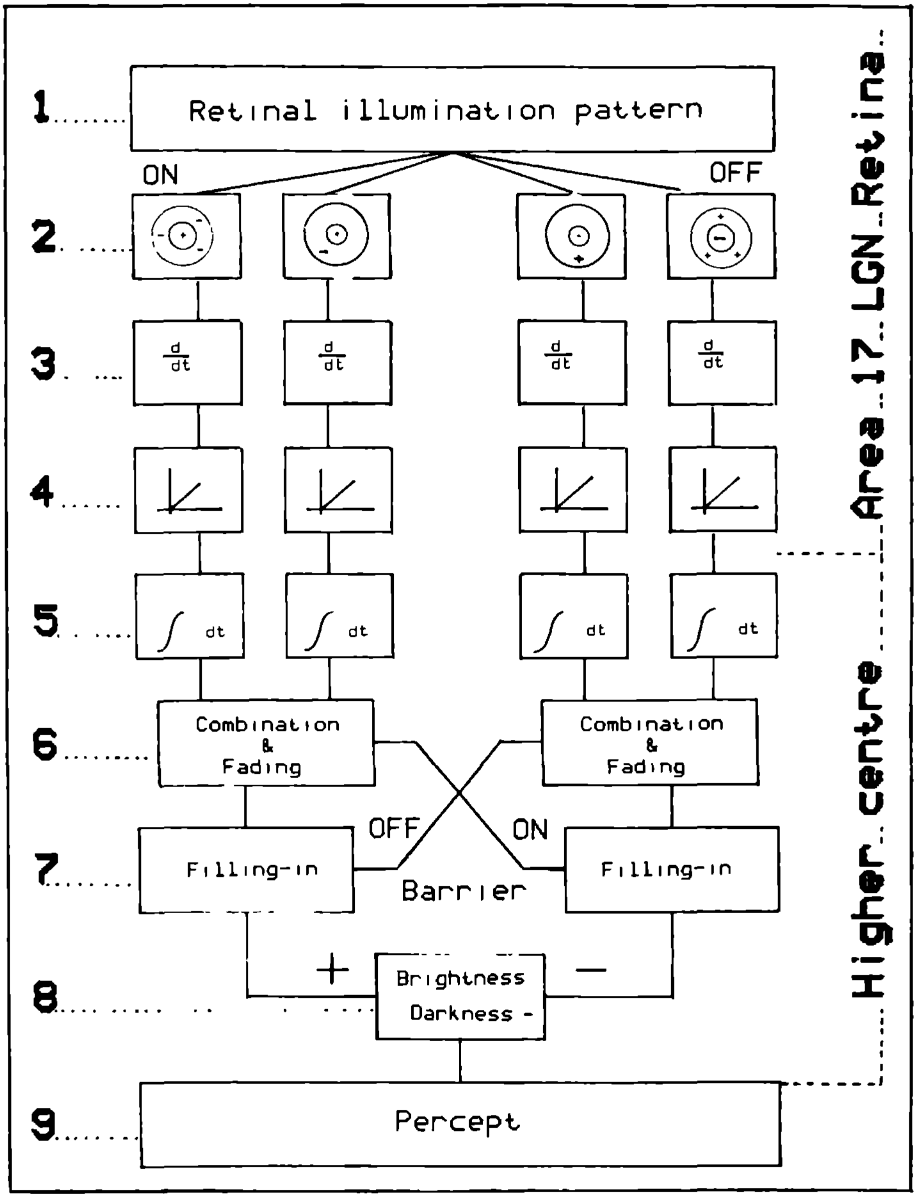

Figure 6 2 A schematic diagram of the simulation model To illustrate the existence of smaller and larger receptive field centres two on- and off-channels are drawn

The output of the second stage in figure 6.2 results in two matrices: one containing the convolution of the stimulus with the on-centre receptive field and a second with the result of the stimulus convoluted with an off-centre receptive field. The choice of receptive field parameters was determined by values known from the literature. As we used the model of Rodieck (1965) to describe a receptive field with the difference between two Gaussian functions, four parameters were needed. To describe the strength of the receptive field the ratio gain-centre/gain-surround (g_c/g_s) must be specified. To describe the width the ratio of the "standard deviations " sigma centre and sigma surround must be given. The values used were in the order of 3 for g_c/g_s and about 0.3 for σ_c/σ_s according to Hines (1976), Moors (1978), Wilson (1978) and Ransom-Hogg and Spillman (1980).

The next stage performs the time differentiation over the whole matrix for on- as well as off-"activity". From electrophysiological data (see chapter two), it is known that only the changes in the stimulus are transmitted to the more central areas (higher centres). Therefore the results of the convolution are stored and compared with the actual convolution output. Obviously a stationary stimulus causes only at its onset information that has to be transmitted, such as is the case in stabilized condition. It implies that when eye movements are present a continuous flow of 'new' stimuli is given with only small changes with respect to the preceding stimulus.

For brightness as well as darkness only the increase in activity is transmitted. It is generally assumed that no information for the brightness/darkness system is available in the decrease of the ganglion cell activity (see chapter two). This is realized in the fourth stage of the simulation model which controls the passing through of only positive changes.

Summarizing we can say that the whole process of transformation and transmission of visual information up to the higher centre is simulated by the first four stages.

In the fifth stage the new incoming information is added to the activities that may be still present from the preceding stimulus. Although the model has different stages for fading and filling-in, it is thought that the higher centre shows fading and filling-in, at the same level. The activities that exist at a certain location decrease at the course of time according to the fading time constant. The amount of brightness- or darkness-producing activity of an element within the "higher centre" matrix is represented by its actual value. Fading may be considered as a decrease of this value as time proceeds. In the model it is performed by multiplying the activity distributions with a factor (a) between zero and one. This implies that the activity at moment t can be described as

$$I(t) = I(k\ .\ T) = I_k = I_0\ a^k\ ,\ k = 1,2,........K$$

where I_0 is the initial value resulting from the input, I(t) is an exponential function of t while T represents the "time"-interval between two calculations of the fading. Obviously this "time"-interval may be chosen arbitrarily as absolute time is not relevant but only the ratio of this T and the time it takes the filling-in to proceed. In chapter five we discussed the existence of a fading time constant as the brightness- or darkness-producing activity was described to fade with time in an exponential way. It is assumed that brightness- and darkness-producing activities fade equally fast. In a first approximation the fading factor is the same at every location. A next step will be the implementation of a fading time constant that depends on the location in the visual field.

In the seventh stage the ideas about filling-in were implemented. It incorporates the barrier theory of Gerrits (1979), who states that the activity in the brightness-system controls the distribution of the activity in the darkness-system and vice versa. In this model this was implemented in the following way. For every element in the "brightness" distribution it was checked whether it had a neighbouring element carrying at least one percent more activity. If this was the case and moreover the corresponding element in the "darkness" system showed an activity not exceeding a criterion value, then the "brightness" element is able to receive spread activity from its neighbours. The same inspection was done vice versa for elements in the "darkness" distribution to see whether they could receive spread activity from their neighbours. A barrier is thus formed by an antagonistic neighbouring element preventing the spread of activity between so-called synergistic (Jung, 1973) elements. For all elements that satisfy these restrictions the new value (old value plus contribution of neighbouring elements) is calculated. According to the superposition theorem for voltages and currents in linear networks a parameter that determines the decrement of the filled-in activity is incorporated. When activity is "allowed" to pass a barrier the decrement is influenced by the value of the antagonistic mechanism that provides the barrier. The decrement was also adjusted for the distance between the selected element and the actual source elements.

After the determination of all new values for the whole matrix, they are substituted. The filling-in can be accelerated by repeating calculations a number of times before a new "percept" is generated. As long as conditions are fulfilled, the filling-in proceeds until all elements have been filled-in that were classified as elements that could receive extra input.

The eighth stage is used to combine activities. Stage nine represents the transformation of the pixel values to a luminance distribution which results by observation in a real percept.

As mentioned before, the activities are calculated in steps. The discretization of the time course opens up the possibility of getting insight into the development of a "percept". There are two time periods: τ and T. One, τ , determining the interval times at which the filling-in is calculated. The other, T ($T \geq \tau$) determining the interval between"percepts". Because of this separation it is possible to simulate different speeds for the mechanisms fading and filling-in. A timing diagram is given in figure 6.3.

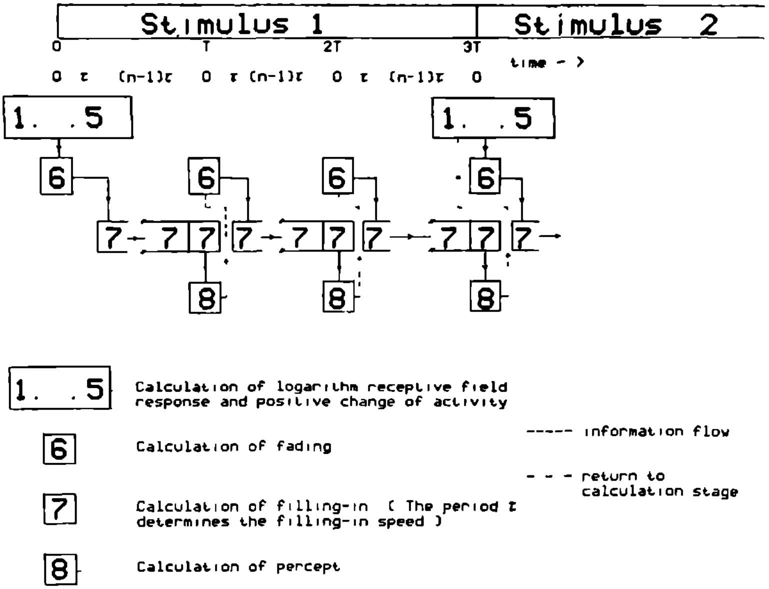

Figure 6.3 Timing diagram of a simulation. The filling is calculated every period τ. A percept is calculated every period T (T > τ). Stimuli can only change at nT

6.3. Simulations

1. The onset of a bright annulus.

In this first example the two dimensional distributions of the activities within the eight stages are displayed in a pseudo three dimensional way (figure 6.4). The initial state is supposed to be zero in all stages before a "bright annulus" is switched on. In the first row the activity pattern representing the "bright annulus" is given. In the second row the receptive field, which has the same size for every element in this simulation, is drawn. It is a digitized form of a Gaussian function and parameters were chosen in order to have a clear positive centre part and a clear negative surround part for an on-centre cell. The size of the receptive field has been exaggerated to show the centre and surround parts. It should be small compared to

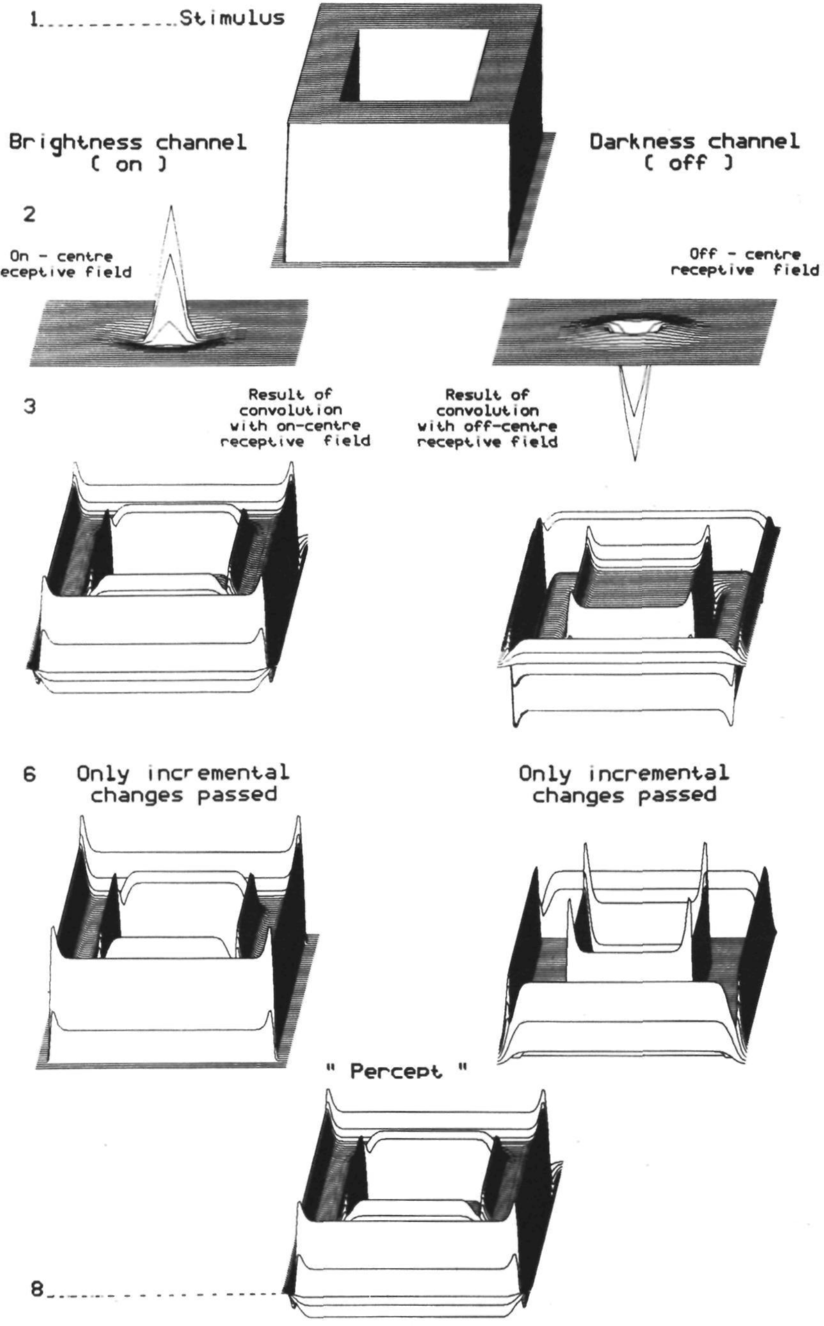

Figure 6.4 A graphical representation in a pseudo three dimensional way of the activity distributions at the various levels within the simulation model.

stimulus dimensions. In the third row the convolution output is given. It represents the output of the second stage. In the left column the activity within the "brightness channel" is given, while the right column represents the activity in the "darkness channel". In the fourth row the matrices are displayed after the rectification process. Only one size of receptive field was used in this simulation. As fading and filling-in did not have much influence yet it suffices to display only the matrix of stage seven because it is almost equal to that of the fifth and sixth stage. In the last row the final "percept" is drawn. Note the Mach bands along the borders of the annulus. As said before this is a representation of the onset of a bright annulus. Immediately after this onset the filling-in will equalize the area enclosed by the annulus (the inner area). Remember that there is no barrier of "brightness"-producing activity to halt the filling-in of "darkness"-producing activity. As filling-in proceeds almost instantaneously the "percept" of the onset cannot be observed in real perception.

2. The fading of the "stabilized" bright annulus.

For clarity only a cross-section of the two dimensional distributions will be displayed in the following drawings. In figure 6.5 again the situation of the onset of the bright stimulus (figure 6.4) is given, indicated by A. In the remaining part of the figure the "percepts" are drawn that resulted as time lapsed and the stimulus remained constant. At the point indicated by B the equalization of the annulus as well as that of the inner and outer area is completed. This represents the normal percept observed some time after the onset of a bright annulus in stabilized condition. As the stabilized condition is simulated the fading proceeds and the strength of the "percept" is seen to decrease. Due to the fact that the input remains constant and as a consequence no changes occur that can be transmitted to the higher centre, this decrement is not compensated for. By the fading also the strength of the barrier is decreased and the brightness-producing activity starts to fill-in the inner and outer area. This is indicated by C in figure 6.5. As fading and filling-in proceed together the "percept" becomes weaker and more blurred.

3. The offset of a faded "stabilized" bright annulus.

When the simulation of the fading of the "stabilized" bright annulus is continued the values in all higher centre stages (6,7 and 8) will reach zero and remain at that level. "Switching off" the bright annulus will cause the appearance of a"negative percept" of the bright annulus. This is indicated in figure 6.5 by D. Again its duration is too short for subjects to observe this offset. Instead a filled-in version is seen. The generation of the "brightness" in the inner area is caused by the decrease of the inhibitory rebound of the on-centre cells situated with their centres along the inside border of the inner area. Part of the surround of their receptive fields was illuminated previously by the annulus. Likewise the brightness increase in the outer area is achieved. So in the "brightness channel" an increase in activity is signalled within the inner and outer areas.

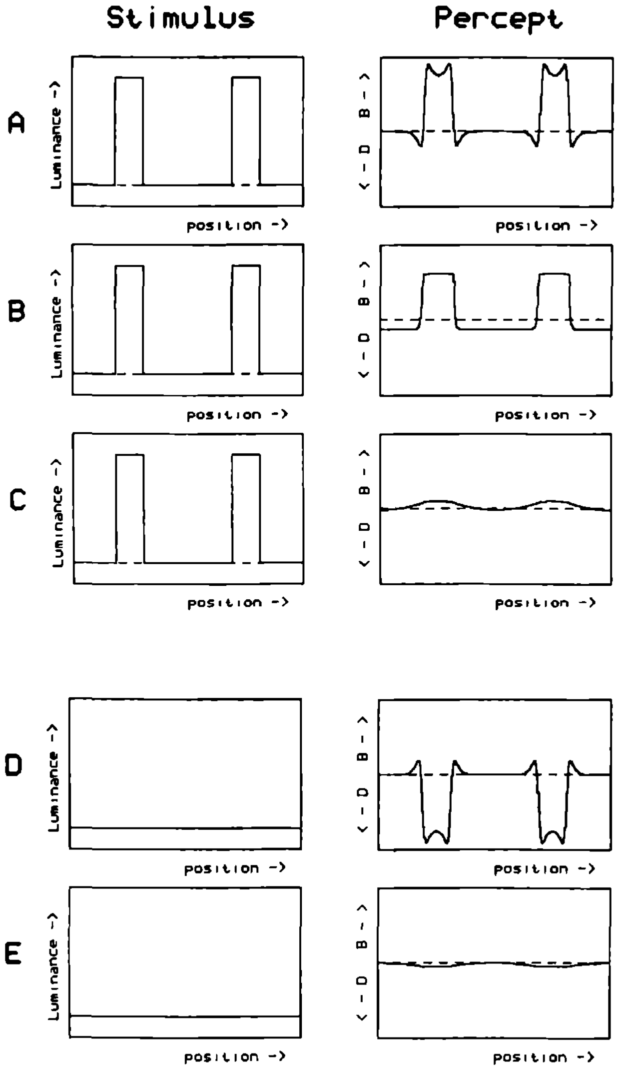

Figure 6 5 An illustration of a simultation with the computer model Three " moments in time " of the disappearance of the percept after stimulus onset are given and two after stimulus offset In the left column the stimuli and in the rigth column the corresponding percepts are given

The annulus offset induces a strong increase in the corresponding locations within the "darkness channel". Due to the fact that the filling-in does not encounter a barrier within the inner and outer area these areas will be equalized as well as the annulus itself. As "time" lapses the fading will decrease all barriers and the darkness of the annulus will fill-in the inner as well as the outer area (E in figure 6.5). In the simulations of the "percepts" after the onset as well as after the offset of a stabilized annulus it is seen that filling-in of an area proceeds very fast when barriers are absent. The spreading out of brightness- or darkness-producing activity into an area over a barrier takes much more time. It is thought that the observation of decremental spread of activity or a fast homogenization of enclosed areas are both phenomena resulting from the same mechanism: filling-in. The difference between these percepts are due to the presence of slowly fading barriers and the complete absence of barriers.

The existence of a barrier is also responsible for the difference between the perception of a black area and that of a retinal scotoma of the same size (Gerrits, 1969). At first sight one is tempted to compare these two situations expecting the same percept. As a retinal scotoma represents an area where receptors and transmitting neurons are lacking, this may be represented by a multiplication of the convolution output of stimulus and receptive field matrix with a matrix with information that determines the area of the scotoma. This will imply that from the associated area no brightness or darkness will be signalled to the corresponding higher centre areas. Thus no barrier information will be present in the higher centre projection of the scotoma. It will be clear then that filling-in may proceed immediately and a real scotoma will thus not become visible.

6.4. Discussion

In general it can be said that the simulation model has satisfied the expectations with respect to the generation of "percepts", that looked like the observations done in stabilization experiments. The fact that the qualitative model of brightness and darkness perception had to be formulated in calculation rules has broadened the insight into the various mechanisms, but has also led to notable problems. As fading and filling-in were represented at a separate level in the simulation model their separate contributions could be analyzed. For each receptive field size a different fading time constant was used. The activity distributions were combined at the level of filling-in. This implies that filling-in was controlled by barriers that contained activity distributions of small as well as large receptive field sizes. As soon as filling-in had been calculated it was impossible to return from this activity pattern to the separate activity pattern of each receptive field size at the fading level.

Due to the non-linear barrier effect it makes a difference whether filling-in is calculated from the combined activity resulting from small and large receptive fields or filling-in is calculated for each receptive field separately.

Even more important is the fact that it seems useless for the system to have different receptive field characteristics when the filling-in causes an overall distribution of brightness- and darkness-producing activity based on the barriers caused by the combined response resulting from the various receptive field sizes. One can perfect the model by adding parallel channels with different receptive field sizes whilst the cells with smaller centres dominate the cells with larger centres. For the time being it remains an open question whether or not filling-in and fading occur at the same level in the visual system.

Another point to be discussed about the model is the actual state of the control of the activity level within the higher centre stages. In the higher centre the reduction of activity is achieved by fading, not by an active reduction as a result of compensating for the activity in the antagonistic system. In other words "brightness" and "darkness" do not influence their mutual activity distributions.

Finally it should be noted that the calculated "percepts" refer only to the stabilized image condition. Therefore the effects of fading and filling-in could be analysed carefully without the intervention of effects due to retinal image movements. The investigation as to how the visual system is capable of maintaining the perception of homogeneously illuminated areas demands, however, an extension of the "static" simulation model to a "dynamic" one. The software already offers the possibility to have more stimuli in a sequence and to shift a stimulus to another position.

6.5. References

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SUMMARY

The initial object of this investigation was the continuation of the experimental work of Stassen (1980). The object of the latter was the precise measurement of natural eye movements and the determination of the part, that drifts and saccades play in the preservation of a remaining visual perception. The investigation of natural eye movements came from experiments of Gerrits (1967) with stabilized images. A stabilized image is a retinal pattern of illumination, which is presented in such a way (image stabilization) that it remains fixed on the retina despite eye movements. The percept of a stabilized stimulus fades except for a very faint residual brightness. By extending the stabilization set-up with an optic fibre it became possible to move the image in an accurate and controlled way across the retina. It appeared, however, impossible to regenerate the original percept of a previously faded image to its full extent by movements of a "physiological" amplitude (Gerrits, 1970, 1974; Stassen, 1980).

At this stage the investigation described in this thesis was started. It was tried to get more insight into the factors, that determine the quality of a percept when a stimulus is inspected. Therefore subjects were asked to direct their gaze at a small spot of light, that moved about in the stimulus display. By moving this spot according to a specific pattern and instructing the subject to give an indication as soon as the quality of the percept deteriorated, information was gathered about the mutual differences between the functions of drifts and saccades. This led to the confirmation and extension of the hypothesis, which implies the following. Whenever there are a sufficient number of differences of luminance within a stimulus (texture) in the direct vicinity of the fovea, drifts are sufficient to preserve the foveal percept. Meanwhile the percept will fade, however, within more peripheral areas. This is a consequence of the fact that the drift movement is insufficient to excite the visual system at those locations (Troxler, 1804). As soon as a saccade is made the stimulus is replaced with respect to the retina over a relatively large distance. This can be interpreted as a new stimulus presentation. The above mentioned hypothesis is described in the appendix of this thesis (Gerrits et al., 1984).

Returning to the starting-point it can be said, that at that moment still too much knowledge about the information processing of light and dark was lacking. Therefore an investigation of some basic concepts of the visual information processing was started.

This investigation has resulted in a further specification of the relation between receptive fields, perceptive fields, perceptive elements and perceptive pixels. A receptive field is an area of the visual field in which stimuli determine the response of a specific cell within the visual system. Within a receptive field a central part, the centre, and an antagonistic surrounding part, the surround, can be indicated. A perceptive field is a concept, that was introduced by Jung and Spillmann (1970) as the psychophysical analogon of a receptive field. It too has a centre and a surround. The concept of a perceptive

element was defined by Gerrits (1978) as an element within the higher centre. The higher centre is a hypothetical area in the higher stages of the visual system. The activation of a perceptive element leads to the perception of a small area in perceptual space in brightness or darkness. Such an area was defined in chapter two as a perceptive pixel. Chapter two consists of a review of the electrophysiological and anatomical data to be used in the other chapters. It is not meant to be a complete and detailed description of all materials, which contribute to the perception of brightness and darkness, but rather as a delimitation of the mutual interactions. Only those concepts, that form a basis for the hypotheses about insensitivity percepts (chapter three), size illusions (chapter four), fading time constants (chapter five) and the simulation model (chapter six) are described in detail.

In chapter three experiments are described in which part of the retina has been made insensitive by means of a very intense illumination with a photoflash. At first the well-known afterimage appears. The use of a flash prevents the image from smearing across the retina due to eye movements. An afterimage is defined to be the fluctuating brightness percept remaining for some time in complete darkness after the extinction of the generating stimulus. The percepts, that can be seen after the disappearance of the afterimage against a homogeneous background, were mentioned before by Carpenter (1972). They resemble effects observed in stabilized condition (Gerrits, 1977). These percepts are defined as insensitivity percepts. In the third chapter results are given from experiments in which insensitivity percepts were inspected against modulated backgrounds. It appeared that the rate of change of the background luminance has to be sufficiently fast with respect to the fading time of the percept generated. Besides it turned out that test stimuli must have a short duration to avoid adaptation to their mean luminance.

To explain the origin of insensitivity percepts a hypothesis was formed, that considers the sensitivity of the exposed and un-exposed parts of a cell's receptive field. Only those cells, that are located along the contour have to be considered. It was found that cells with an insensitive centre and an insensitive part of the surround, respond abnormally when illuminated diffusely. Cells that normally signal light-on now signal light-off and vice versa.

Also on the basis of the behaviour of cells located at the contour of a square, an explanation can be given of the so-called classical size illusion. This illusion implies that a light square on a dark background is seen larger than a dark square on a light background (see chapter four, figure 4.1). From the results of a number of preliminary experiments Gerrits concluded, that the size of objects is determined by the off-centre cells. From the data presented in the fourth chapter it follows that that conclusion cannot be correct. The brightness as well as the darkness system have to be involved in the explanation of the change of apparent size as a function of contrast between square and background. The changes measure about eight min arc. This value is in agreement with the range of receptive field diameters found electrophysiologically in monkies and determined psychophysically in man. In order to explain a new size effect described by Weale (1975) a thin black or white line was placed along the edge of the square. When modulating the contrast it was found that a strong movement illusion appeared. This brings about the perception of an alternatingly expanding or shrinking square. Also for these effects a satisfactory explanation on the basis of the receptive field concept can be given.

Until now it has not been considered how or what aspect of a receptive field is perceived. Due to the many parallel channels it is impossible to indicate a specific receptive field from which a certain small patch of brightness or darkness originates. By precise consideration of the properties of receptive and perceptive fields it was found that these fields may be connected by means of the perceptive elements and in chapter two defined perceptive pixels. A change of the luminance is signalled during normal vision by a number of receptive fields and leads to the activation of a number of perceptive elements. Their activity results in the perception of a number of bright or dark perceptive pixels and in this way one or more "activated" perceptive fields are formed. Only in very special stabilization experiments it is possible to perceive separate perceptive pixels (Gerrits, 1978). The rate at which the activity of perceptive elements decreases was determined in the experiments described in chapter five by the estimation of a fading time constant. It was done by describing the fading mechanism as a first order model. The parameters were determined by optimally fitting the model to the data. The fading time constant of perceptive elements within the foveal projection turned out to be smaller (about 5 seconds) than that of those located within the peripheral projections (about 25 seconds). This result was previously described in a qualitative way by Gerrits (1978). It is important to note that based on the Troxler effect (1804) often an opposite conclusion is drawn.

In order to demonstrate the perceptual appearances encountered in stabilization experiments a simulation model was built that used the up to now known functional relations between components of the brightness and darkness information processing system. With this computer model video-"percepts" can be generated corresponding to a stabilized stimulus presented as a matrix of numbers. A sequence of calculated "percepts" may be played back like a "movie". This enables specific properties present or just lacking to be compared to percepts described during stabilization. Several subjects, participating in the stabilization experiments, can simultaneously inspect the display under normal viewing conditions.

SAMENVATTING

Het oorspronkelijke doel van dit onderzoek was het voortzetten van het experimentele werk van Stassen (1980). Dit beoogde de nauwkeurige meting van natuurlijke oogbewegingen en de bepaling van de rol, die drifts en saccades spelen in het waarborgen van een blijvende visuele perceptie. Dit onderzoek van natuurlijke oogbewegingen kwam voort uit experimenten van Gerrits (1967) met gestabiliseerde beelden. Een gestabiliseerd beeld is een retinaal belichtingspatroon, dat op een dusdanige manier wordt aangeboden (stabilisatie), dat het zich niet over de retina verplaatst ondanks oogbewegingen. Het percept van een gestabiliseerde stimulus verdwijnt (fading) op een zeer geringe residuele helderheid na. Door middel van een uitbreiding van de stabilisatiemethode met een optische beeldgeleider werd het mogelijk het beeld een zeer nauwkeurige gestuurde beweging over het netvlies te laten maken. Het bleek echter niet geheel mogelijk het oorspronkelijke percept van een eerder weggezakte stimulus door middel van bewegingen met een "fysiologische". amplitude terug te krijgen (Gerrits, 1970, 1974; Stassen, 1980).

Bij deze stand van zaken werd het in dit proefschrift beschreven onderzoek aangevangen. Teneinde meer inzicht te krijgen in de faktoren, die tijdens het inspecteren van een stimulus de kwaliteit van het percept bepalen werd proefpersonen gevraagd een fixatiespotje te volgen, dat zich over de stimulus verplaatste. Door dit spotje volgens een specifiek patroon te laten bewegen en de proefpersoon te laten aangeven wanneer het percept slechter werd, werd inzicht verkregen in de onderlinge verschillen tussen de functies van drifts en saccades. Het heeft geleid tot een bevestiging en uitbreiding van de hypothese, die zegt dat wanneer er voldoende luminantieverschillen (textuur) in een stimulus aanwezig zijn in de directe omgeving van het centrale punt van het blikveld (de fovea), drifts voldoende zijn om het foveale percept in stand te houden. Tegelijkertijd zal het percept echter in gebieden, die verder van het centrum van het blikveld verwijderd zijn wegzakken omdat daar niet voldoende beweging aanwezig is om het visuele systeem daar ter plaatse voldoende te blijven aktiveren (Troxler effect, 1804). Wanneer er echter op tijd een saccade gemaakt wordt, wordt de stimulus ten opzichte van de retina verplaatst over een relatief grote afstand. Dit kan als een nieuwe stimulusaanbieding worden beschouwd. Bovenstaande hypothese staat beschreven in de appendix van dit proefschrift.

Terugkerend naar het uitgangspunt, kan gesteld worden, dat er toen nog onvoldoende informatie aanwezig was over de verwerking van helderheid en donkerte in het visuele systeem. Daarom werd een nader onderzoek van enige basiskoncepten in de visuele informatieverwerking opgezet.

Het onderzoek heeft geleid tot een nadere precisering van de relatie tussen receptieve velden, perceptieve velden, perceptieve elementen en perceptieve pixels. Een receptief veld is de lokatie in het visuele veld, waarbinnen stimuli de responsie van een bepaalde cel in het visuele systeem bepalen. Binnen een receptief veld kan een centraal deel, het "centre", en een omgeving de "surround" worden aangegeven. Een perceptief veld is een koncept, dat werd ingevoerd door Jung en Spillmann (1970) als het psychophysisch analogon van een receptief veld. Het heeft eveneens een "centre"en "surround". Het begrip perceptief element werd door Gerrits (1978) gedefinieerd als een element in het "higher centre". Het "higher centre" is een hypothetisch gebied hogerop in het visuele systeem. De aktiviteit van een perceptief element heeft als gevolg dat een klein gebied in de perceptuele ruimte als helder of donker wordt gezien. Een dergelijk gebied werd in hoofdstuk twee gedefinieerd door het begrip perceptief pixel. Hoofdstuk twee wordt gevormd door een overzicht van de electrophysiologische en anatomische data, die in andere hoofdstukken gebruikt wordt. Het is niet zozeer bedoeld als een volledige en gedetailleerde beschrijving van alle bouwstenen, die bijdragen tot het helder en donker zien, maar eerder een afbakening van de onderlinge samenhang. Slechts die koncepten, die een basis vormen voor de hypotheses ten aanzien van ongevoeligheidspercepten (hoofdstuk drie), grootte-illusies (hoofdstuk vier), fading tijdkonstantes (hoofdstuk vijf) en het simulatiemodel (hoofdstuk zes) worden uitvoerig beschreven.

In hoofdstuk drie worden experimenten beschreven waarin een gedeelte van de retina ongevoelig is gemaakt door middel van een zeer intense belichting met een fotoflitser. Allereerst ontstaat er dan het welbekende nabeeld. Door het gebruik van een erg korte aanbieding kan worden voorkomen, dat de belichting wordt uitgesmeerd over de retina als een gevolg van oogbewegingen. Een nabeeld is hier gedefinieerd als het fluktuerende helderheidspercept, dat in het donker enige tijd zichtbaar blijft ondanks het feit dat de veroorzakende stimulus al is uitgegaan. De percepten, die na het verdwijnen van het nabeeld gezien worden ten opzichte van een diffuse achtergrond werden eerder door Carpenter (1972) beschreven. Ze lijken op effecten zoals werden waargenomen in gestabiliseerde toestand (Gerrits, 1977). Deze percepten worden gedefinieerd als ongevoeligheidspercepten. In hoofdstuk drie worden resultaten beschreven van experimenten waarin ongevoeligheidspercepten werden bekeken ten opzichte van gemoduleerde achtergronden. Gebleken is dat de snelheid waarmee de luminantie van de achtergrond wordt veranderd, voldoende snel moet zijn in verhouding tot de fadingtijd van het percept, dat wordt gegenereerd. Bovendien bleek, dat teststimuli van korte duur moeten worden gebruikt om adaptatie aan de gemiddelde luminantie in de teststimulus te voorkomen. Ter verklaring van het ontstaan van ongevoeligheidspercepten werd een hypothese opgesteld, die de onderlinge gevoeligheid beschouwt van de door de intense lichtstimulus belichte en niet-belichte delen van receptieve velden. Slechts de cellen, die met deze velden verbonden zijn en die tevens langs de kontour zijn gelegen behoeven te worden beschouwd. Gebleken is dat cellen, die een ongevoelig geworden "centre" gebied en ongevoelig deel van de surround hebben, abnormaal reageren by diffuse belichting. Cellen, die normaal licht-aan signaleren, signaleren nu licht-uit en omgekeerd.

Op basis van het gedrag van cellen waarvan eveneens het receptieve veld gelegen is langs de rand van een vlak, blijkt ook een verklaring gegeven te kunnen worden van de zogenaamde klassieke grootte-illusie. Deze illusie houdt in dat een helder vlak op een donkere achtergrond groter wordt gezien, dan een donker vlak op een lichte achtergrond (zie hoofdstuk vier, figuur 4.1). Uit de resultaten van een aantal voorafgegane experimenten werd door Gerrits gekonkludeerd, dat de grootte van voorwerpen werd bepaald door "off-centre" cellen. Uit de in hoofdstuk vier gepresenteerde data blijkt echter dat dit niet juist kan zijn. Zowel het helderheids- als het donkertesysteem blijken betrokken te moeten worden in de verklaring van de gemeten grootte-effekten als functie van het kontrast tussen vlak en achtergrond. De grootte van de effekten ligt in de orde van acht boogminuten. Deze waarde komt goed overeen met de variaties in receptieve veldgrootte, die elektrofysiologisch voor de aap en psychofysisch voor de mens werden gevonden. Ter verklaring van een door Weale (1975) beschreven effekt werd over de rand van het vlak, dat als stimulus werd aangeboden, een dun zwart of wit lijntje geplaatst. Bij modulatie van het kontrast wordt gevonden, dat er een sterke bewegings-illusie van het lijntje ontstaat. Bovendien blijkt het vlak hierdoor groter of kleiner te worden gezien. Ook voor deze effekten blijkt een bevredigende verklaring op basis van het receptieve veld koncept gegeven te kunnen worden.

Tot nu toe is er nog niet gesproken over wat er van een receptief veld wordt gezien. Vanwege de vele parallelle kanalen kan er niet een enkel receptief veld worden aangewezen, dat tot een bepaald lichtvlekje aanleiding geeft. Uit de nauwkeurige inventarisatie van de eigenschappen van receptieve en perceptieve velden is echter komen vast te staan, dat deze gekoppeld kunnen worden door middel van de door Gerrits (1978) gedefinieerde perceptieve elementen en de hier in hoofdstuk twee ingevoerde perceptieve pixels. Een verandering in helderheid of donkerte wordt tijdens normaal zien door een aantal receptieve velden gesignaleerd en leidt tot de aktivatie van een aantal perceptieve elementen. Deze aktiviteit leidt tot het zien "oplichten" van een aantal perceptieve pixels in helder of donker, op die manier een of meerdere geaktiveerde perceptieve velden vormend. Slechts in zeer speciale stabilisatie-experimenten is het mogelijk om afzonderlijke perceptieve pixels waar te nemen (Gerrits, 1978). De snelheid waarmee de aktiviteit van perceptieve elementen afneemt werd bepaald in hoofdstuk vijf door het schatten van een tijdkonstante. Dit werd gedaan door de fading met behulp van een eenvoudig eerste orde model te beschrijven. De parameters werden bepaald door het model optimaal aan de data aan te passen. Gevonden werd dat de fading-tijdkonstante van perceptieve elementen, die corresponderen met het centrum van het blikveld kleiner (ongeveer 5 seconden) is dan van elementen, die corresponderen met meer perifere lokaties (ongeveer 25 seconden). Dit resultaat werd al eerder door Gerrits (1978) op een kwalitatieve manier beschreven. Het is belangrijk op te merken, dat op grond van het Troxler effect (1804) vaak een tegengestelde konklusie wordt getrokken.

Om een indruk te kunnen geven van percepten, die optreden ten gevolge van retinale beeldstabilisatie werd een simulatiemodel opgesteld, dat gebruik maakt van de tot nu toe bekende funktionele relaties tussen elementen in het systeem voor helder- en donker-informatieverwerking. Met dit computermodel kunnen video-"percepten" worden gegenereerd behorend bij een aangeboden "gestabiliseerde" stimulus in de vorm van een getallenmatrix. Een reeks van gegenereerde percepten kan als een "film" worden weergegeven. Dit maakt het mogelijk specifieke aanwezige of juist niet aanwezige "percept"-eigenschappen te vergelijken terwijl meerdere proefpersonen, die aan stabilisatie-experimenten deelnamen, het weergavescherm kunnen beschouwen in een situatie waarin normaal wordt waargenomen.

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Appendix. THE ROLE OF DRIFTS AND SACCADES FOR THE PRESERVATION OF BRIGHTNESS PERCEPTION

Abstract
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   References

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THE ROLE OF DRIFTS AND SACCADES FOR THE PRESERVATION OF BRIGHTNESS PERCEPTION

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Abstract.

A number of subjects observed squares of various sizes (15' x 15' up to 240'). They were instructed to keep their direction of gaze within the square . Their eye movements, being so restricted, were recorded, analyzed and separated into drift and saccadic components. These components were simulated and used to move a uniformly bright square in a stabilization set-up to investigate their contributions for generating or preserving the percept of brightness. The influence of the retinal eccentricity of the stimulus contours was also investigated.

When increasingly larger squares were observed, only the subject's mean saccade amplitudes increased, whereas drifts did not. Drift movements are effective in preserving vision only when stimulus contours are located in or near the foveal area. For larger stimuli saccades are needed as well. Intersubject differences and perceptual differences resulting from normal and simulated eye movements were also analyzed.

It is discussed how the small amplitude drifts and the larger amplitude saccades cooperate to preserve vision. The correlation of receptive (perceptive) field diameters and fading time constant, both increasing towards the periphery, are relevant for the understanding of the behavior of drifts and saccades in response to larger stimuli.

Introduction.

Attempts made to prevent the image of a stimulus from shifting over the retina, i.e. , to stabilize the image, have led to controversial conclusions. Some experimenters found that the stabilized images fade away in a faint residual brightness (Barlow, 1963; Ditchburn & Pritchard, 1956; Gerrits, 1978; Gerrits, de Haan, & Vendrik, 1966; Yarbus, 1967), whereas others reported that the images come back in a few seconds or observed recurrent reappearances of lines or parts of lines (Evans & Piggins, 1963; Gerrits, 1979; Riggs, Ratliff, Cornsweet, & Cornsweet, 1953). Complete and permanent disappearances have also been described (Campbell & Robson, 1961).

One reason for these discrepancies is the lack of a method that ensures adequate stabilization of the image, i.e. a method in which the remaining destabilization is so small that it cannot be observed at all in any place of the visual field (Barlow, 1969).

Stabilization techniques were developed by researchers interested in the significance of physiological eye movements (Ditchburn & Ginsborg, 1953; Riggs et al., (1953) or those who wanted to study attention (Yarbus, 1967), p.171). Ditchburn (1973) described the different methods used nowadays to obtain a stabilized image. All workers in this field agree that a percept disappears or, at least deteriorates severely when the image is stabilized. This means that we only continue to see thanks to the continuous displacements of the image across the retina, resulting from eye and/or head movements. One way to investigate the importance of the various components of the natural eye movements is to destabilize a stabilized image with these components. In order to evaluate the reports on destabilization it should be kept in mind that the effects of destabilization depend critically on the location of the boundaries of the image on the retina.

Krauskopf (1957) and Ditchburn, Fender, and Mayne (1959) were the first experimenters to destabilize images. They investigated the effect of sinusoidal movements of a dark or bright line projected onto the fovea. Although eye movement components below 10 Hz seemed most important, the relative effectiveness of slow drifts and rapid jerks did not become clear. Ditchburn et al. (1959) stated that the drift movements, imitated by these oscillations, are by themselves inadequate to maintain the percept. Yarbus (1959) investigated the effect of unidirectional movement and described strong bright (on-effects) and dark (off-effects) comets evoked by this displacement. Riggs and Tulunay (1959) varied the amount of stabilization to allow for different image displacements across the retina. They presented a bipartite field inside an annulus and instructed the subject to fixate in the middle. They found that the fraction of time during which an image was seen (visibility time) increased with the contrast between stimulus and background if the degree of stabilization was held constant.

Campbell and Robson (1961), Barlow (1963) and Sharpe (1972) all found a decreasing effectiveness of regular, small amplitude, movements. That this "fatigue" was not observed by Krauskopf (1957) and Ditchburn et al. (1959) may be due to non-intended destabilization effects and the short observation times. Recent reports on the visibility time during which a moving line in the fovea is seen were published by Ditchburn and Drysdale (1977a, 1977b) and King-Smith and Riggs (1978). These experiments showed that saccades of 4.5' provided fairly good vision if they occurred more frequently than one per second. Even drifts and tremor appeared to be sufficient to maintain tolerably good vision of high contrast targets with sharp boundaries.

Tulunay-Keesey and Bennis (1979) investigated the effect of motion on the contrast sinsitivity. These authors used spatial sinusoidal gratings as stimuli and one of their conclusions was that sensitivity can be lowered, primarily during long periods of fixation and image disappearance. Most of the reports mentioned before concern the visibility of lines or blood vessels(Drysdale, 1975). Nobody has raised the question of how the visual system manages to preserve the perception of the brightness or the darkness of larger stimuli. To investigate this question we provided our stabilization set-up with an optic fiber bundle (Gerrits & Vendrik, 1974 and fig. 26.1 in this chapter) enabling us to destabilize a square of 4 by 4 degrees with different movement modes. Using sinusoidal or triangular movements (amplitude: 0-120' peak-to-peak; frequency: 0.5-3.0 Hz), a reasonable percept of the square was generated only for the large, non-physiological amplitudes of movement. It was, however, often observed that these movements caused habituation, especially for the smaller movement amplitudes. In contrast, imitated drift and saccadic signals generated from Gaussian and binary noise signals did not cause habituation effects. Moreover, the amplitudes of the noise signals needed to evoke the perception of a nearly homogeneous bright square were much smaller than those needed when sinusoidal or triangular signals were used. However, it proved impossible to generate exactly the same percept of the square as that observed during normal vision. Our conclusion was that in order to preserve the perception of uniform brightness, the movement of the square ought to be: (a) irregular, in order to prevent habituation; (b) continuous, in order to prevent fading. Only drifts possess these characteristics and therefore they seemed important to preserve perception in the foveal and parafoveal area. The discontinuous character of the saccadic movement seemed less suited for this purpose. The same conclusion about the importance of drifts was reached by Yarbus (1967).

In order to investigate the role of drifts and saccades in normal vision for the preservation of brightness and darkness perception in different retinal locations, we recorded and analyzed the eye movements made when larger stimuli were presented. Then we destabilized the image with the components of the recorded as well as artificially generated eye movements. The chapter starts, however, with the description of an experiment showing that the fading time constant, determining the time required for a local brightness- or darkness-activity to diminish a certain fraction, depends on the retinal eccentricity. This is essential for understanding how drifts and saccades preserve the continuous perception of brightness and darkness.

1. HOW DOES THE FADING TIME DEPEND ON THE RETINAL LOCATION OF A STIMULUS CONTOUR?

Method.

Our method to stabilize images on the retina has been described previously (Gerrits & Vendrik, 1970a): A suction cap is used (Fig. 26.1a) which adheres to the eye of the supine subject by a small underpressure (max. 30 mm Hg = 4.10^3 Pa). The cap is heated to match the temperature of the subject's eye and to avoid condensation on the lens, which would obscure vision. The eye of the subject is anaesthetized with novesine. The non-moving, photographic negative in the object holder is observed through a 50 diopter lens and an artificial pupil of 2 mm diameter. The field of vision is 20 degrees. Experiments to demonstrate that the foveal part of a line fades faster than the more peripheral parts (Gerrits, 1978), are very difficult because they demand an extremely high degree of stabilization. The stimulus used here consisted of the disc and annulus shown in Fig. 26.2a. This stimulus, if fixated in the center of the disc, is much easier to stabilize because it presents no

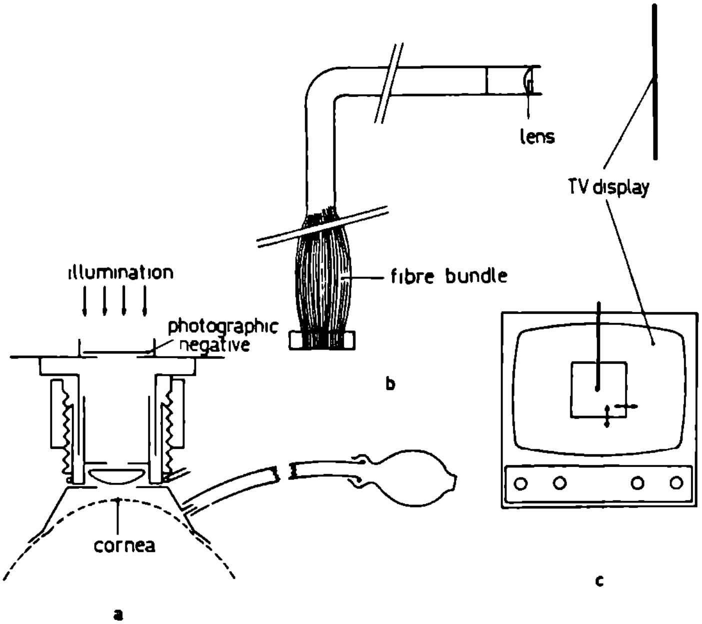


FIG. 26.1. The suction cap, optic fiber bundle and TV display used in the stabilization set-up (a) The subject focuses the stationary stimulus, a photographic negative, by adjusting the distance between object holder and lens (b) The proximal end of the optic fiber bundle replaces the photographic negative when moving stimuli are to be presented. (c) The stimulus on the TV display A bright square can be moved horizontally and vertically by artificial eye movements The stationary disc is only observed when the stabilization is imperfect due to slippage of the suction cap

contours in the fovea. In this first experiment the subject is asked to give an accurate description of the perception of the stimulus after light-on.

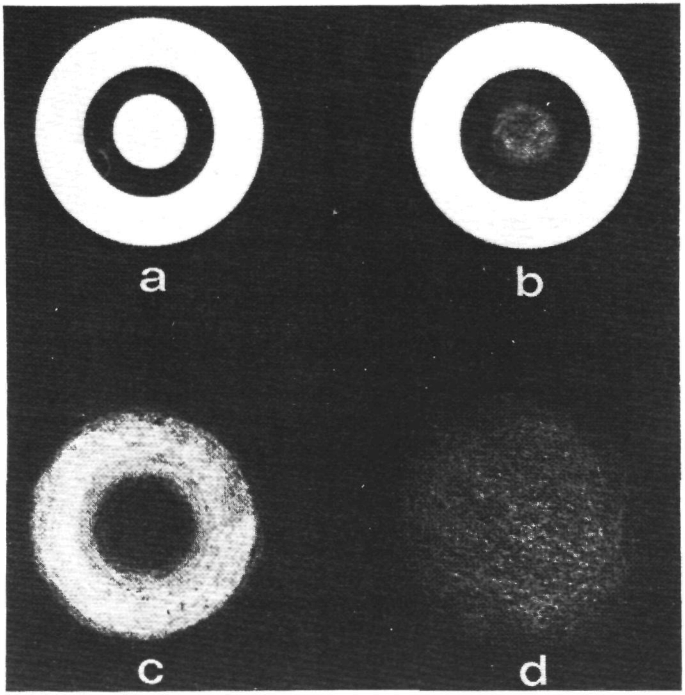


FIG. 26.2. Activities closer to the fovea fade faster than activities further in the periphery. When an activity has disappeared it is filled in with the adjacent activity. (a) The stimulus consists of a bright disc (diameter 7°), surrounded by an equally bright annulus (inner diameter 12°, outer diameter 20°). Fixation is in the center of the bright disc. (b) The bright disc is the first to disappear and that area is filled in with the adjacent darkness-activity, resulting in a bright annulus around a uniform dark disc. (c) This darkness-activity disappears next. The homogeneous dark disc (see above) is filled in with brightness-activity from the bright annulus. (d) As soon as the dark homogeneous disc has disappeared completely a large homogeneous disc of diminishing brightness is observed which also finally disappears.

Results.

The results can be seen in the drawings made according to the subject's observations (fig. 26.2b,c,d). The central parts situated closer to the fovea fade first and these faded areas are filled-in with the darkness (fig. 26.2c) or brightness (Fig. 26.2d) of the neigboring remaining part of the image. This property of the visual system is, in our opinion, important to understand the effects of the natural eye movements. The findings of West (1967) that the more peripheral parts disappear first may be attributed to imperfect stabilization. Small residual movements prevent fading in the fovea, but not in the periphery (Clarke, 1957; Clarke & Belcher, 1962; Neumeyer & Spillmann, 1977; Troxler, 1804).

2. WHAT IS THE DISTRIBUTION OF NORMAL EYE MOVEMENTS FOR SQUARES OF DIFFERENT SIZES ?

Method.

In order to measure the eye movements of the subject looking at different stimuli, a modification of the method described by Robinson (1963) was adopted and built by Stassen (1980). In this set-up a small search coil, attached to the eye, moves in two perpendicularly oriented alternating electromagnetic fields driven at 30 kHz and 20 kHz for the horizontal and vertical direction, respectively. By selectively amplifying and measuring the voltages induced in the search coil by means of two lock-in amplifiers (Princeton Applied Research, model 128 S), eye movements can be accurately recorded. This search coil, designed by Collewijn, Mark and Jansen (1975), embedded in a silicone rubber annulus, was sucked onto the sclera, the eye with the search coil was anaesthetized with novesine, the other eye was closed.

The frequency response of the system was flat from 0 Hz up to 220 Hz(-3dB) and the peak-to-peak value of the noise amounted tot 18' in the 300' measuring range. As we wanted to record only the eye movements of the subject, not his head movements which also introduce voltages in the search coil, the subject's head was clamped in a suction pillow. It was found that errors due to head movements were reduced to about 3' maximally.

The eye-movement signals were recorded on tape by means of a 12-bit pulse code modulation system (Kaiser, Munich), enabling five channels to be recorded simultaneously at a rate of 500 samples per second for each channel. The peak-to-peak noise level in the replayed signals measured about 20'. A digital computer (PDP 11/45) was used to analyze the recorded eye movements. The saccadic and intersaccadic components (drift and tremor) of the eye movements as well as the blink-associated eye movements were separated. Thereafter, the characteristics of the saccades, drifts, and tremor were calculated by determining the mean value and standard deviation of the amplitude- frequency-, and velocity-distributions as well as the durations of the drifts (i.e., the intersaccadic intervals). A drift vector and a saccade vector were calculated from the horizontal and vertical drift and saccadic components. For further details concerning the recording and analysis see Stassen (1980).

Four subjects participated in the eye-movement recording experiments. Uniformly bright squares having a luminance of 5,27 or 150 cd/m^{2}and a contrast of 96% were presented on a TV display and the eye movements monitored. Squares ranged in size from 15' by 15' up to 240' by 240'. Subjects were instructed to fixate the surmised center of the square and , subsequently, to move their eyes in such a way around this center that a uniform perception of the square was obtained. Crossing the borders of the square was not allowed.

Results.

Eye movements recorded during 180 sec are shown in Figs. 26.3 and 26.4 for an experienced subject (HS) and an inexperienced subject (JB). In general the eye movements increased in size with increasing dimensions of the square. Subject JB produced larger eye movements than subject HS observing a particular square size.

From the analysis of horizontal and vertical eye movement components it was found that during the observation of small squares two to three saccades in rapid succession were made. The saccades did not show overshoots. The characteristics of the eye movements elicited by the smallest and the largest square can be found in Table 26.1 for three subjects. For all subjects the measured positions of the eye had approximately a bivariate normal distribution. Both the horizontal and vertical standard deviations increased about linearly with the length of the side of the square. The magnitude of the mean saccade vector increased with square size for subjects JB and GP by a factor of 5-6, for HS by a factor of 3. The magnitude of the mean drift vector increased much less if at all (HS). The change of the drift duration with square size was markedly different among the subjects.

The strategies followed by the subjects to produce the greater eye mobility required during the observation of increasingly larger squares were different:

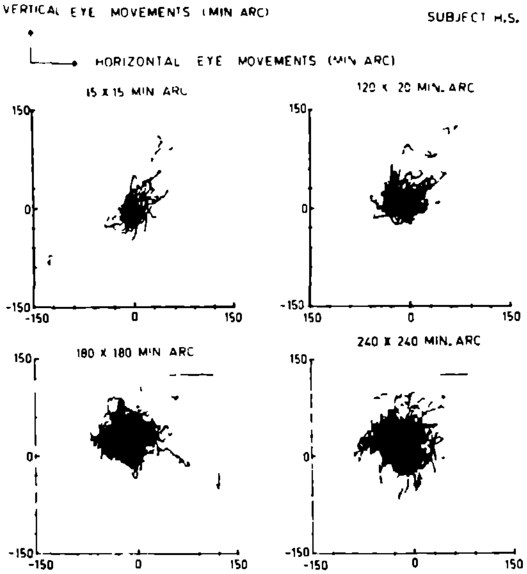
-Subject JB produced larger saccades and drifts, with no systematic influence on the saccade rate;

-Subject HS produced only larger and more frequent saccades without any systematic influence on the drift vector magnitude;

-Subject GP produced mainly larger and more frequent saccades while his drift vector magnitude increased only slightly.

For all three subjects the mean drift vector velocity increased about equally during the observation of larger stimuli.

The following general conclusion can be drawn: A greater mobility of the eye is required to maintain the percept of brightness in larger squares. This greater mobility is mainly brought about by the saccades.



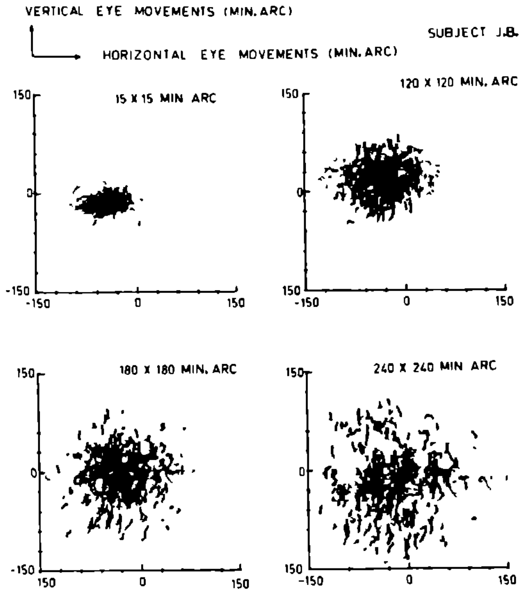


FIG 26 3 and FIG 26 4 Two-dimensional plots of eye movements of subjects HS and JB, recorded during 180 sec, as a function of square size The subject's task was to move his eyes around the surmised center of the square, not outside the square, in such a way that a homogeneous image without brighter on- and darker off-borders was observed (Note that because of DC- shifts the (0,0) position does not necessarily coincide with the center of the observed square)

TABLE 26.1

	Subject HS		Subject GP		Subject JB	
Square size (min arc)	15 × 15	240 × 240	15 × 15	240 × 240	15 × 15	240 × 240
Mean drift duration (seconds)	1.25	0.37	0.80	0.50	0.76	0.75
Mean saccade vector magnitude (min arc)	8.6	25.6	13.7	80.5	18.8	94.5
Mean drift vector magnitude (min arc)	9.2	8.6	5.9	7.2	7.9	13.9
Mean drift vector velocity (min arc/sec)	20.3	38.2	16.4	22.9	16.6	25.3

3. CAN A FADED PERCEPT BE RESTORED BY DESTABILIZATION?

Method.

In the stabilization set-up (Gerrits & Vendrik, 1974) a square was destabilized with either formerly recorded drifts or saccades or a combination of drifts and saccades. So we investigated the effectiveness of the eye movement components for the restoration of brightness and darkness. This was done by replacing the photographic negative (Fig. 26.1a) by the proximal end of a coherent optic fiber bundle directed to a color TV display on which the stimulus was presented (Fig.26.1b). The thickest optic fiber bundle we used contained 160,000 individual fibers, each of 10 micron diameter, equaling 1.8' in the visual field when a 50 diopter lens was used. The diameter of the visual field of this bundle was 13 deg. The stiff protecting mantle of the fiber bundle was removed over a length of 30 cm in order to allow the bundle to follow the subject's eye movements. These eye movements did not affect the position of the image on the subject's retina as long as the suction cap adhered well to his eye (Fig. 26.1a). The optic fiber bundle had, however, a small braking effect and, therefore could cause slippage.

To enable the subject to distinguish between a percept generated by a genuine stimulus movement or by an unwanted slippage of the suction cap, a small black disc at the end of a non-moving stalk was placed in front of the color TV display. This disc functioned as a control spot relative to the moving square (Fig. 26.1c) and enabled the center of the square to be projected onto the fovea before the onset of the movement of the square.

The stimulus was a uniform, bright square of 4 by 4 deg. and its luminance(5 $\mathrm{cd/m^2}$;27$\mathrm{cd/m^2}$) was corrected for the loss of light occurring in the fiber bundle and at the artificial pupil present in the suction cap. After the subject reported the disappearance of the bright square, the experimenter started to move it on the screen. Two trained subjects (HG, HS) participating in these experiments were asked to describe their percepts.

(a) First, the previously recorded eye movements (section 2) were used to move the square over the retina. However, it proved impossible to determine the efficiency of the drifts or the saccades in this way as these eye movements were interrupted by the recorded blinks. These blinks drove the square off the screen of the TV display and thereafter presented the square as a new stimulus at the end of the blink movement. The blinks occurred three to seven times per minute. As their frequency spectrum overlapped with the spectrum of the other eye movement components, they could not be removed by filtering.

(b) Because of this difficulty, an 8-sec section of the eye movement record having no blinks was used in an endless loop. However, the resulting presentation of the square caused strong fluctuations in the generated percepts. These fluctuations correlated with the movement pattern. Moreover, the subjects soon recognized the recurrent sequence of the endless loop.

(c) Obviously, real eye movements could not be used to answer the question whether saccades or drifts or both were needed to preserve vision. Therefore, it was decided to imitate the drifts and saccades, their characteristics being determined from the computer analysis. Artificial drift signals were generated by low-pass filtering (0.1-3 Hz: -6 dB/oct; above 3Hz:-12 dB/oct) and amplifying (15'-240' peak-to-peak) Gaussian noise to match the specific drift properties of each subject. The saccades were imitated by a sequence of jumps with normally distributed amplitudes (0-300' peak-to-peak). Constant saccade frequencies ranging from 1-5 jumps/sec were used. The combination of these artificial signals enabled the experimenter to move the stimulus with various combinations of drifts and saccades. When the subject indicated that the image had disappeared, the experimenter started to destabilize this image by the artificial drifts, artificial saccades, or both. It should be remembered that these signals showed the same amplitude distribution and frequency spectrum as the eye movements recorded when a subject observed the same square in the non-stabilized condition. To distinguish the different perceptual stages, the following scale was adopted:

0-Nothing at all, or only occasionally on- and off-borders while the rest of the stimulus remained as dark as the background.
2-A square with on- and off-borders and a very weak brightness in the center which is just detectable against the background.
4-A square with on- and off-borders and a weak brightness in the center which is clearly brighter than the background.
6-A square with on- and occasionally off-borders and a center brightness which is clearly lower than the on-borders.
8-A homogeneous, bright square with occasionally on-borders near the contours.
10-A homogeneous, bright square without any borders near the contours.

Uneven numbers were used to describe percepts in between the above described classes. Apart from these descriptions a row of drawings had been produced. Drawing 10 represented a homogeneous bright square of 100% brightness. In drawings 8,6,4 and 2 the center brightness was 85, 75, 60 and 30% of the center brightness of drawing 10. Also in these drawings on-borders were indicated.

The subjects were able to judge the quality of the percept during the experiment by comparing the brightness of the midpart of the square with that of the on-borders. Moreover, they refreshed their memory of the adopted scale by consulting the drawings before and after each experiment.

Results.

As a result of the destabilization, the subject observed bright on-borders, dark off-borders(Gerrits & Vendrik, 1970b), and an inhomogeneous brightness in the center of the square. Bright on-borders were only generated at that location of the retina which was newly illuminated as a result of a stimulus movement. Dark off-borders arose where the illumination was switched off. Between these borders darkness and brightness were induced: darkness adjacent to the on-border and brightness adjacent to the off-border. The spreading of this induced brightness and darkness to the center of the square resulted in an inhomogeneous percept. The presence and strength of this brightness- and darkness-activity depended on the movement amplitude, the frequency and the location of the stimulus on the retina.

For both subjects (HG,HS) at least 20 to 30 sec of movement were needed before the midpart of the moving square had acquired its maximal brightness although it still fluctuated in time. Altogether it took 2 to 3 minutes of observation before they could decide on the quality of the percept. This time was needed both to average the fluctuating percept and to discard observations resulting from slippage of the suction cap (see Method).

The outcome is given in Table 26.2. When the square was moved only with the imitated drift signals, subject HG classified the percept with scale number 6 and 7 for the darker (5 cd/m^2) and brighter (27 cd/m^2) square, respectively.

TABLE 26 2

Subject	*Stimulus Luminance* $cd\ m^{-2}$	*Retinal Illumin* td_{eff}	*Percept Qualification (Midpart Brightness in % of On-set)*		
			Drifts Only	*Saccades Only*	*Drifts + Saccades*
HG	5	90	6 (75%)	7 (80%)	7 (80%)
	27	430	7 (80%)	7 (80%)	7-8 (80–85%)
HS	5	70	2-6 (30–75%)	7-8 (80–85%)	7-8 (80–85%)
	27	290	2-6 (30–75%)	7-8 (80–85%)	7-8 (80–85%)

In comparison, the classification by subject HS varied from 2 to 6. For both subjects the quality increased to 9 (90% of the brightness at on-set) if the artificial drift amplitude was increased to five times the level measured during the eye movement recording (not shown in Table 26.2). When the square was moved with artificial saccade signals, the percept for subject HG was largely unchanged, whereas subject HS obtained better and less fluctuating percepts than with drift signals. When the artificial saccade amplitude was increased above the physiologically recorded values, the observed brightness also increased for both subjects. When the saccadic frequency was increased, the quality of the percept increased only slightly for subject HG, but considerably for subject HS in the 1 to 3 Hz range. Also with this type of movement the brightness values, attributed to the percept,fluctuated, mainly as a result of the noisy character of the movements. The combination of artificial drifts and artificial saccades did not improve the percept substantially.

It should be noted that the percept of the square, indicated by scale number 8 and the brightness observed in the midpart of the image (85%), is about equal to that perceived during the recording of the restricted eye movements. Remember that this restriction did not allow the subjects to obtain an optimal percept.

Discussion.

From the fact that even an increase of the amplitudes of the artificial eye movements did not result in a normal percept we realized that in all these experiments the movements were started after the image had completely faded. Could it be that the normal eye movements do not generate but preserve the percept of brightness? A number of additional experiments showed that it made no difference whether the artificial eye movements were started at light-on or after complete fading of the image.

In normal vision the image deteriorates only if the subject stares at the stimulus by fixating a part of it, i.e., by pseudo-stabilization. By deterioration we mean the occurrence of on-borders and off-borders and/or the occurrence of brightness fluctuations in the square. A preliminary experiment showed that the image of a stationary, non-stabilized square of 4 by 4 deg. did not fade or deteriorate if the subject was allowed to move his fovea at and across the contours, inside and outside the square, instead of only around the surmised center of the square (as in the previous experiment, section 2). Again the subject still limited the amplitudes of his saccades. He did not blink. The results of this experiment suggested that the distance between the fovea and a contour of the square is an important parameter in normal vision. Van Erning, in our group, started to investigate the influence of this distance on the perception.

4. IS THE REQUIRED IMAGE MOVEMENT DETERMINED BY RETINAL ECCENTRICITY OF THE CONTOURS?

Method.

Four experiments were undertaken with LvE and HG serving as subjects. A homogeneous, bright square (4 by 4, 63 cd/m^2) and a fixation spot

(10' by 10', 300 cd/m^2) on a background of 6 cd/m^2 served as stimuli on a TV display. The square and the fixation spot could be moved independently. Each separate movement in the horizontal as well as in the vertical direction was controlled by an electrical signal. These signals were generated such that their combined action positioned either the fixation point at a constant distance from the contours of the stationary square or moved the contour of the square at a constant distance from the stationary fixation spot. An example of subsequent locations of the fixation spot, at a constant but adjustable distance D from the contours of the stationary square, is given in fig. 26.5. The sequence of locations of the fixation spot on the "imaginary square" was chosen by a constantly running special purpose random generator. The sequence of the jumps displacing the square or the fixation spot was different in each trial of an experiment. Within an experiment the distance D was adjusted to 0.5, 1, 1.5 , or 1.75 and the frequency was set at 0.5, 1, 1.5, 2 or 3 jumps per second. The task of the subject was to indicate when he detected any non-uniformity of the bright square. The time duration T between the start of the movement and this moment was considered to reflect the effectiveness of the movement to preserve brightness.

In the first experiment the square jumped around and the subject had to fixate the stationary spot. His eye movements were monitored. In the second experiment the subjects had to follow the jumping fixation spot while the square was stationary. The eye movements were monitored again. From the records it was found that the subjects managed to follow the spot correctly only if the number of jumps did not exceed two per second. In the third experiment the subjects inspected the jumping homogeneous square through the stabilization set-up (Fig. 26.1). The fixation spot, being stabilized, disappeared. Under all three conditions, the bright image deteriorated notwithstanding the movements imposed on it. We therefore decided to use a different sequence of jumps. In the fourth experiment, a certain sequence of jumps lasting maximally 64 sec was presented again and again as an endless loop. The movement could be started each time from the same point in the sequence as well as from any other point. Experiments 1 and 2 were repeated with this "endless movement".

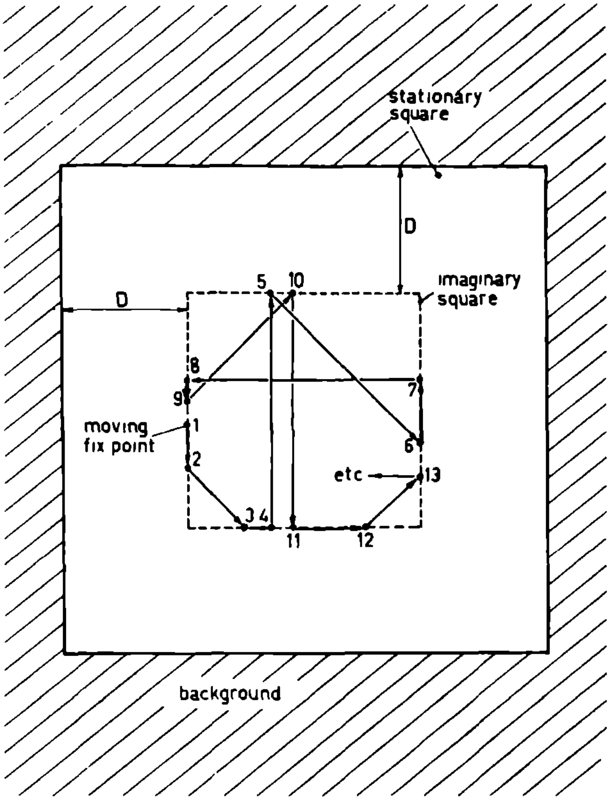


FIG. 26.5. An example of a part of the movement sequence of the fixation spot on a stationary square of 4 by 4 deg The subject had to follow the spot which remained at a fixed distance D from the nearest contour of the square. The reader can carry out the same experiment if he fixates the subsequent numbers in the figures

Results.

During fixation, the image of a jumping square deteriorated after a few seconds, in other cases after tens of seconds, if the fovea remained 0.5 deg or more from the contours. Although the distance D was kept constant, the time duration T fluctuated heavily within one session. When the square was stationary and the spot jumped, the subjects perceived the same deterioration and again T fluctuated heavily. Also in the stabilized condition it was found that T fluctuated.

In all these experiments the bright image deteriorated in spite of the movements imposed on it, sometimes sooner, sometimes later. Besides the question of why the movements of the square did not preserve the homogeneous image with any combination of the distance D and the frequency of jumping, the problem arose as to why the time duration T fluctuated so much. It proved to be due to the different successions of jump amplitudes within each sequence. When the sequence was started at arbitrary points, i.e., datarecorder not triggered, the time duration T fluctuated. However, when the movement was started a number of times from the same point in the sequence, i.e., datarecorder triggered, the duration time T fluctuated much less. When another starting point was chosen by the experimenter, the repeated presentation of the movement resulted in a different, nearly constant time duration T . If at each presentation the sequence of movements was started from the same point, the subjects were able to indicate where they observed changes within the original homogeneous image and what aspect of the percept had changed (brightness, borders). The outcomes proved that the character of the imposed movements caused the perceptual fluctuations. To demonstrate this relation the movement pattern was registered on line on an X-Y- recorder. The percept of the subject was so strongly related to the movements that the experimenter, watching the movement pattern, was able to tell the subject when and at what position within the image the subject had observed a deterioration, as he knew from experience that a number of small saccades followed by a larger one resulted in deterioration. A decrease of the distance D (fovea closer to the stimulus contours) resulted in a longer period of homogeneous perception (compare with the results of section 3).

DISCUSSION OF THE IMPORTANCE OF DRIFTS AND SACCADES.

In the following we discuss the basic ideas about the cooperation of the drifts and saccades in preventing fading of brightness in uniform areas.

Receptive fields and their psychophysical analogs, perceptive fields (Jung & Spillmann, 1970) are small near the fovea (Spillmann, 1971) but become increasingly larger towards the periphery (Kornhuber & Spillmann, 1964). Natural eye movements continuously activate the cells having these receptive fields by changing the amount of illumination. No movement means no change and this results in the gradual disappearance of the percept observed after the on-set of the illumination. A small movement of a contour located at a large retinal receptive field may insufficiently change the illumination within this field. In that case the image fades in spite of the eye movement. Thus, the effective movement amplitude is always closely related to the diameter of the receptive field at the location of the stimulus contour.

As a result it is understandable that it is extremely difficult to stabilize foveal images: Residual eye movements present with most stabilization methods are highly effective in the foveal area which has the smallest receptive fields but not in the periphery where receptive fields are larger.

Even if the eye movements suffice to move the contours of a large square adequately over the local receptive fields preventing fading there, receptive fields that are located in the center of the square receive a constant illumination. This part of the image could be considered as stabilized and should therefore disappear. What happens, however, is that these parts of the image are filled in with the brightness and eventually the color of the surrounding nonfading parts. An example of this behavior, as observed in a stabilization experiment, was shown in Fig. 26.2b,c,d. From this and several other stabilization experiments, it was found that the fading time constant, determining the time required for a local brightness- or darkness-activity to diminish a certain fraction, is much smaller in the fovea than in the periphery. An image in the fovea may fade fast, within a second, while the same image located in the far periphery may need seconds to disappear. Note, that this is not contrary to what is found in Troxler fading and the decrement of the fading time with the eccentricity of the stimulus contour, as observed by Neumeyer and Spillmann (1977). In both cases foveal fading is prevented by the fixational eye movements. Their observations have to be attributed to the decreasing effectiveness of residual eye movements with increasing eccentricity.

The increase of the receptive (and perceptive) field diameter and the increase of the fading time constant towards the periphery play an important role in the effectiveness of our eye movements, the continuous, small amplitude drifts, and the larger amplitude saccades.

Suppose we had only the drift movements to displace the image across the retina and the stimulus, i.e., a square was presented in such a way that its center fell upon the fovea. As the fovea moves around this center in accordance with the drift movements, the contours of the square move with the same amplitude. Whether these amplitudes are adequate to prevent the image from fading depends, of course , on the diameter of the receptive fields at the location of the contours. Large objects will fade, as is easily confirmed by fixating the surmised center of a large square.

In other words, the drifts are capable of preserving the perception of stimuli in and around the fovea but not of stimuli with contours far outside the fovea. What function have saccades in preserving vision of large squares?

Imagine the situation that the fovea is located in point 1 (see Fig. 26.6a) of a large square and drifts around that point. The part of the border denoted A-B is close to the fovea: The drift movement effectively changes the illumination of the receptive fields located there and activates the corresponding brightness-signalling cells (Jung, 1961). The local brightness-activity, mediated by these cells and resulting from the foveal stimulation, fades fairly fast but the continuous drift movements, activating new brightness-signalling cells and re-activating others, makes up for the short fading time. For the cells with larger receptive fields on the opposite side of the square (part C-D of the contour, Fig. 26.6a), the drift movement is insufficient. The corresponding brightness-activity begins to fade immediately after a saccade has ended, but here fading occurs more slowly. For another part of the contour, between E and F (Fig. 26.6a), the fading time of the corresponding brightness-activity lies in between those of the brightness-activities resulting from stimulation of areas A-B and C-D.

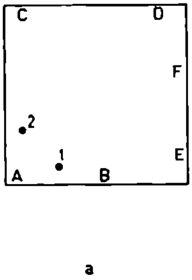
When a saccade is made, from point 1 to point 2 (see Fig. 26.6a), the square is repositioned with respect to the fovea, as shown in Fig. 26.6b, it will be seen that the fovea is now close to an adjacent border and activities are generated there by the drift movements. The slowly fading brightness-activity corresponding to the former border C-D is completely neutralized by darkness-activity (Gerrits & Vendrik, 1970a). This is indicated in the figure by "light-off". Adjacent to the part E-F of the former contour new activity is generated by the newly illuminated part (indicated by "light-on").

Thus, saccades are needed because with drifts alone we would be unable to preserve vision of large stimuli. But can we preserve vision with saccades only? The saccades activate large new parts of the retina by moving the eye. At the same time, however, they bring the fovea close to the borders of the stimulus. The brightness-activity originating from the foveal area will fade rapidly when the image is not moved in between the saccades. The drift is needed to prevent the fading of that part of the image located in and around the fovea. So we need both drifts and saccades for large stimuli.

It is therefore understandable why the amplitudes of the drift did not increase with the size of the square (section 2). All subjects increased their saccade amplitudes considerably, but their drift amplitudes increased only slightly as larger squares were presented. If one of the tasks of the saccades is to bring the fovea close to the contours of the stimulus, the saccade amplitude should indeed increase with square size. Once the fovea is displaced near a contour there is no need for the drift to increase its amplitude as the cells with small receptive fields present around the fovea are effectively activated as a result of the drift movement.

It proved impossible to preserve or to restore the original homogeneous bright percept of the square by moving the square with the artificial eye movements. A further analysis of the artificial and real eye movements to reveal differences, not encountered so far, is in progress.

Finally, we may remark that physically, in the stabilized condition, a moving stimulus is equivalent to a stationary stimulus seen by the moving eye. The experimental results over the last years have strengthened our belief in the equivalence of stimulus movement and eye movement for the perception of brightness and darkness. As for the perception of movement , the two conditions are different because in the latter case no movement of the stimulus is observed.



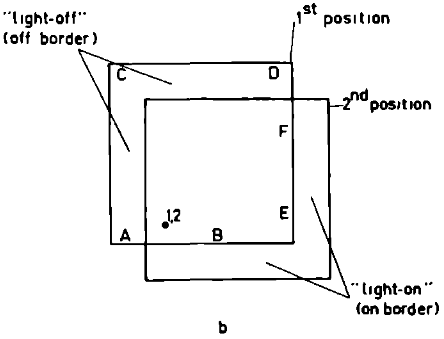


FIG. 26.6a. When the eye drifts around the fixation spot (1), the area A–B is effectively activated, area E–F less and area C–D the least The brightness activities in these peripheral areas fade, but slowly Then the fovea jumps to the new position of the fixation spot (2)

FIG. 26.6b. The image is now displaced from position 1 to position 2 If the brightness-activity in area E–F has faded too far the brightness-activity in the newly illuminated part of the retina ("light-on") is stronger than that in area E–F and an on-border is reported If the brightness-activity in area C–D has faded too far the darkness-activity in this darkened part of the retina ("light-off") is stronger than the residual brightness-activity and an off-border is reported in area C–D

Stevens, Emerson, Gerstein, Kallos, Neufeld, Nichols, & Rosenquist (1976) came to the same conclusion when they described the visual perceptions of three subjects paralyzed with curare.

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Zonder de medewerking van vele anderen was de totstandkoming van dit proefschrift onmogelijk geweest. Ik wil een aantal van hen met name noemen omdat zij in belangrijke mate hebben bijgedragen aan het hier beschreven onderzoek. Daarom:

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en
... Minny, pour ce qu'on ne dit pas.

Curriculum Vitae.

Ik werd op 2 mei 1951 geboren te Oss (N.B.). Daar heb ik mijn HBS-opleiding gevolgd aan het Titus Brandsma Lyceum. Daarna begon de studie elektrotechniek aan de Technische Hogeschool te Eindhoven. Binnenlandse stage-onderwerpen waren de bouw van een hardware pariteitsgenerator, de bepaling van de oppervlaktecconditie van silicum na oxidatie en de ontwikkeling van een software module in een interaktief programmapakket voor signaalanalyse. De buitenlandse stage werd verricht in het Centre d'Etude et de Technologie Appliquées à la Chirurgie te Lyon. Onder leiding van Dr. Ing. C. Fourcade werd gewerkt aan een detektor voor de bundel van His. Het afstudeeronderzoek vond plaats in de vakgroep Medische Fysica en Biofysica van de Katholieke Universiteit te Nijmegen onder leiding van Prof. Dr. A.J.H. Vendrik, Dr. P.I.M. Johannesma en Prof. Dr. Ir. J.E.W. Beneken (THE). Het had betrekking op de mathematische analyse en visuele representatie van geluid. Op 15 maart 1979 werd deze studie afgesloten met het doctoraal examen elektrotechniek.

Vanaf 11 november 1978 tot 1 januari 1984 ben ik werkzaam geweest als wetenschappelijk medewerker op het laboratorium voor Medische Fysica en Biofysica in de werkgroep V17 onder leiding van Prof. Dr. Ir. E.G.J. Eijkman (tot 1 september 1980 Prof. Dr. A.J.H. Vendrik) en Dr. Ir. H.J.M. Gerrits. Het onderzoek in deze werkgroep beoogt door middel van stabilisatie van beelden, psychofysisch verkregen resultaten te combineren met gegevens uit de elektrofysiologie, anatomie en kliniek. Na een aanvankelijk onderzoek van natuurlijke oogbewegingen in hun relatie tot de waarneming van een blijvend helderheidspercept werd de laatste jaren vooral aandacht besteed aan de fundamentele eigenschappen van receptieve velden in relatie tot ongevoeligheidspercepten, de visuele groottewaarneming en fading. Bovendien werd een computermodel ontwikkeld om "gestabiliseerde percepten" te simuleren. Van deze laatste periode zijn de verkregen resultaten in dit proefschrift weergegeven.

Sinds 1 mei 1984 ben ik als wetenschappelijk medewerker verbonden aan het instituut voor Radiodiagnostiek van het Sint Radboudziekenhuis te Nijmegen. Binnen de werkgroep digitale beeldverwerking wordt hier onder leiding van Prof. Dr.J.H.J. Ruys en in samenwerking met Drs. M.A.O. Thijssen onderzoek verricht naar de mogelijkheden om ten aanzien van de diagnostiek beeldverbeteringen te bereiken van zowel beelden uit de computertomografie, digitale substractie angiografie als echoscopie.

STELLINGEN

bij

ON VISUAL PERCEPTS RELATED TO
RECEPTIVE AND PERCEPTIVE FIELD PROPERTIES.

An investigation of insensitivity percepts, size illusions and fading

1. Het is onjuist te veronderstellen, dat de drempel voor het zien van helderheid binnen een nabeeld-gebied, onder alle omstandigheden gelijk is aan de drempel waarbij dit nabeeldgebied zelf te onderscheiden is.

   Rushton, W.A., Nature <u>234</u>, 546-247 (1971)
   Dit proefschrift, hoofdstuk drie.

2. De waarneming, dat het percept van een goed gestabiliseerd gebied snel verdwijnt hoeft niet te betekenen dat de gevoeligheid van het visuele systeem is afgenomen.

   Lennie, P., Hayhoe, M.M., MacLeod, D.I.A.,
   Vision Res. <u>22</u>, 827-833 (1982)

3. Een niet-lineariteit van het helderheids systeem zoals werd verondersteld door Marimont en von Békésy volgt niet noodzakelijkerwijze uit het niet even breed zijn van de lichte en de donkere Mach band.

   Marimont, R.B., J. Opt. Soc. Amer. <u>53</u>,
   400-401 (1963)
   Von Békésy, G., J. Opt. Soc. Amer. <u>58</u>,
   1-8 (1968)
   Dit proefschrift, hoofdstuk vier.

4. Het is waarschijnlijk, dat de schijnbare beweging van een dunne contourlijn langs een vlak bij kontrast-modulatie berust op hetzelfde fenomeen als de door Gregory gepresenteerde "cafe-wall" illusie en de reeds in 1897 door Munsterberg beschreven " verschobenen Schachbrett Figur ".

   Gregory, R.L. presentatie op de Eerste
   "European Conference on Visual Perception"
   (1979)
   Liebmann, S., Psych. Forsch. <u>9</u>, 300-353
   (1927)
   Dit proefschrift, hoofdstuk vier.

5. Voor the veroorzaken van een "motion aftereffect" is geen reele beweging in het visuele veld vereist. Een geschikte keuze van het faseverschil tussen de luminantie-modulatie van aangrenzende vlakken is voldoende.

6. Met de door Ransom-Hogg en Spillmann en Troscianko gehanteerde Hermann grid methode wordt lokaal slechts het centrum van het meest dominante perceptieve veld bepaald.

Ransom-Hogg, A., Spillmann, L., Vision Res. 20, 221-228 (1980)
Troscianko, T., Vision Res. 22, 1363-1369 (1982)

7. Door de ontwikkeling van steeds snellere video- en beeldverwerkingstechnieken zal het mogelijk worden analoog aan de door Aertsen geintroduceerde Intensiteit-Frekwentie-Tijd-Kubus voor auditieve neuronen, voor visuele neuronen, een hyper-kubus te bepalen om een twee-dimensionaal spatio-temporeel receptief veld te karakteriseren.

Aertsen, A.M.H.J., Proefschrift
Katholieke Universiteit Nijmegen (1981)

8. De term " response compressie " of " range compressie " voor de verandering van de responsie van kegeltjes is misleidend omdat het alleen refereert aan de reductie van de range van responsies op een luminantie increment.

9. Het gebruik van een gemiddelde grootte van de oogbeweging in modelbeschrijvingen is in het algemeen slechts toegestaan als aangetoond kan worden dat amplitudes van drifts en saccades een gelijkwaardige betekenis voor de perceptie hebben.

10. Het feit, dat Plateau blind werd en Fechner jarenlang last van zijn ogen had geeft te denken over de algemene geldigheid van de waarnemingen, die door hen gedaan werden.

Plateau, G., Poggend. Ann.d. Physik, 32, 543 (1834)
Fechner, G.Th., Poggend. Ann.d. Physik, 44, 221 en 513 (1838); 50, 427 (1840)

11. Gezien de vele uitvindingen, die de mens doet om zijn arbeid te verlichten, zal het spreekwoord " Arbeid adelt " vermoedelijk een " self destructing prophecy " blijken.

12. Zonder signifikante reductie van de beeldkwaliteit van de röntgen foto's zou vermindering van de stralingsbelasting voor de patient bereikt kunnen worden door toepassing van een versterkingsscherm en het beter afperken van het te bestralen gebied.

Aken, J.v., Proc. 3rd ICMFR

13. Gefixeerd kijken naar de wereld leidt tot een reductie van het zicht op de wereld.

Nijmegen, 23 november 1984 Leon van Erning.