

# CORTICAL CONTROL OF EYE MOVEMENTS

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## PREFACE

The absolute threshold and the contrast threshold in vision have been for a long time a topic of study in the Institute. The relevance of such work to practical problems is evident. Knowledge about the performance of the eye under different conditions of illumination is a necessity for the ophthalmologist, the lighting engineer and others.

In previous reports, theoretical analyses have been presented which consider the threshold condition on the one hand as the counting of a number of quanta and on the other hand as the excess of a signal to noise ratio. Crucial parameters in these studies were the visual angle, the exposure time, the luminance of the background and the location on the retina of the test patch. In all these conditions the subject fixated a stationary point. However, the eyes are never motionless. Latour has made an attempt to study in detail the influence of this extra parameter in threshold studies, the movement of the eye.

Two findings relevant to eye movements have been reported in the literature. In the first place it has been reported that stabilization of the image on the retina produces a deterioration of vision. Secondly, however, it has been reported that the threshold is raised during a 'flick', the rapid eye movement made to compensate for a slow drift of the eye. The apparent contradiction between these two phenomena was the starting point of work reported here. Rather than making measurements during involuntary movement, Latour has studied the influence of voluntary movements, using an ingenious measuring and recording technique. It was found that the visual threshold increases during an eye movement and, more intriguing, that this increase

anticipates the eye movement. This indicated the existence of a mechanism which triggers the eye movement, which means in other words that the moment of the start of the eye movement is under cortical control.

In considering the change in threshold in more detail, periodical fluctuations in the sensitivity were observed, and a further facilitation effect was discovered. This in turn was used as a tool to get more insight into the threshold mechanism. Implications are drawn from these new experimental findings about the actual number of quanta for the threshold condition for the dark adapted eye, as well as of the character of the noise in the visual system. Although these hypotheses are based upon a number of assumptions about which one can still argue, the treatment is a fresh approach to a problem which has been under discussion for a long time.

Dynamic vision, in which eye movements, and movements of the stimulus over the retina are involved, is a rather unexplored area. The complexity of the problem and the difficulties met with in experimentation in this area have apparently prevented us from gaining much information about these matters, in particular with regard to situations in which eye movements are involved. This area, however, is very important for an understanding of the visual task of drivers and pilots. The work presented here is on the one hand a termination – for Latour obtained his Ph. D. with it – but is on the other hand a start towards a fresh attack of this problem.

It is to be hoped that Latour will make many further contributions to our understanding of the mechanisms of vision.

PIETER L. WALRAVEN

## CONTENTS

I. INTRODUCTION. . . . .	1
II. EXPERIMENTAL ARRANGEMENT . . . . .	5
III. THE FACILITATION EXPERIMENT . . . . .	14
a. Facilitation experiment . . . . .	14
b. The light adapted experiment . . . . .	32
c. Dark adapted negative flashes . . . . .	34
d. Time dependence . . . . .	35
IV. THE DIP EXPERIMENT . . . . .	37
a. Introduction and mathematical considerations . . . . .	37
b. Experimental results . . . . .	42
c. The influence of the size of the flash . . . . .	57
d. The position of the flash . . . . .	58
e. The colour of the flash . . . . .	60
f. The origine of the eye movements . . . . .	61
g. The angle of the eye movements. . . . .	63
V. TIMING OF EVENTS. . . . .	66
a. The data reduction . . . . .	68
1. <i>The averager</i> . . . . .	68
2. <i>The process of correlation</i> . . . . .	69
3. <i>Autocorrelation of histograms</i> . . . . .	70

b. The data . . . . .	73
<i>Subject 1</i> . . . . .	73
<i>Subject 2</i> . . . . .	77
<i>Subject 3</i> . . . . .	77
<i>Subject 4</i> . . . . .	79
<i>Subject 5</i> . . . . .	80
<i>Subject 6</i> . . . . .	80
VI. DISCUSSION . . . . .	82
VII. SUMMARY . . . . .	88
VIII. REFERENCES . . . . .	91

## INTRODUCTION

The eye is by far the most complicated sense organ, and, as far as the amount of information transmitted is concerned, the most important. Many researchers, driven by their scientific curiosity, have spent their lives gathering data and proposing mathematical models of the visual system. Today we benefit from all that has been done but are still awed by how little we actually know, and how many questions remain unanswered. This applies also for the fairly restricted fields of the absolute and differential visual thresholds, which are studied in this thesis.

As a background for the studies in this thesis a short review of the relevant literature will be given. The eye is stimulated when light quanta fall upon the retina. Due to reflections and absorptions by other media in the eye only a few percent of the number of quanta entering the eye are effectively absorbed by the visual pigments contained in the 120 million photosensitive receptor cells, the rods and the cones. In these receptors the light energy is converted to electrical activity by means of a chemical reaction. This information passes through the layer of bipolar cells, which can be described as a complicated coincidence system (1). The information emitted by the bipolar cells passes through the inner plexiform layer on its way to the ganglion cells of the retina. At the level of the inner plexiform layer, which consists of a network of connections among amacrine, bipolar, and ganglion cells, the corticofugal pathways interact for the first time with the incoming information (2, 5). The resulting pulses have the all or none character which is typical of the transmission of data in the

nervous system. The strength of the stimulation is reflected in the number of pulses pro unit of time, and not in the size of these pulses. Using microelectrodes for the detection of nervous activity in the frogs retina it was found (3, 4, 5) that there are ganglion cells of different types, if we classify them according to their response to different light neglecting influences of color, size or strength of the stimulus. One type will fire if a light is switched on and another type inhibits its firing rate for this stimulus. Other cells respond only to changes in illumination level.

The axons of the ganglion cells, roughly one million for each eye, constitute the optic nerve which runs from the eye to the first relay station in the brain, the lateral geniculate body. Before reaching the lateral geniculate body the optic nerve is divided in two parts at the chiasm, such that corresponding halves of the visual field of each eye are mapped upon one of the geniculate bodies. Here the information is recoded again and transmitted to the visual cortex. Experiments by Kuffler and Woolsey (6, 7) have shown that there exists some kind of mapping at all relay stations. This means that adjacent receptors in the retina stimulate neighbouring areas in higher centers. After the mapping upon the visual cortex the information is processed further in the visual cortex with its rich interconnections, and it is very plausible to assume that here the physical stimulus enters the subject's consciousness. Thus, before a critical signal at threshold strength is perceived it passes several relay stations, each with its inherent noise and threshold conditions, and when measuring visual thresholds this noise and the various thresholds have to be taken into consideration. The extent of this consideration depends upon the kind of experiment and the kind of discriminative task asked from the subject. Hubel and Wiesel (8, 9) have found that the information on its way to the cortex is enriched by classified grouping, which is probably caused by the specific structure of the interconnections at the various relay stations. At a lower layer in the visual cortex one can find cells which react to a line with a certain location in the visual field and a certain orientation. At higher layer cells can be found that react to a certain class of stimuli all with the same angle of their border, regardless of their position in the visual field. The cells in the visual cortex were found to be particularly sensitive to objects moving in the visual field, which may have to do with Man's capacity to survive. As a military application it is well known that motion reveals the best camouflaged soldier. In experimental arrangements in which the image is stabilized on the

retina by means of an optical feedback the importance of motion is emphasized, as vision deteriorates rapidly under such circumstances (10, 11). If the stabilization of the system is removed for an instant, vision is normal again. Thus eye movements which cause the contours in our visual field to shift over the retina seem to be a necessity for normal vision.

When eye movements are measured with a high degree of resolution it is found that the eye is never completely motionless (12). Even during fixation the eye drifts several tens of minutes of an arc away from the fixation point, after which a so-called 'flick' may occur, a rapid movement over about the same angle with a centering tendency to compensate for the slow drift. The bandwidth of these eye movements extends up to two hundred cps, which demonstrates the high muscle power to mass ratio of the eye. The reason for these spontaneous motions-noise-may lie in the retina's desire to shift the borders in the visual field over neighbouring cells in order to discriminate them better. On the other hand, it was found by Ditchburn and Fender (13) that the visual threshold was raised during flicks. This was demonstrated by finding that the subjects could not perceive flashes of short duration which were generated by the flicks. This rise in threshold might serve to suppress images on the moving retina, which could otherwise give rise to perception of an unsteady, jerky world. But this was disproved, as the rise in threshold is not high enough to shut off the retina completely.

The starting point of this thesis was the paradox between these two findings; the deterioration of vision when the image is stabilized, which leads one to believe that eye movements are necessary for perception; and on the other hand the dip in visual threshold during such an eye movement.

An experimental set up was built with which eye movements resulted from the change in position of a fixation light. When the subject was about to shift his gaze from one position to the other a short flash was presented and the chance of perception measured. This experiment differs in at least one respect from the experiment by Ditchburn and Fender, in that these eye movements are intended whereas the flicks were not.

The change in visual threshold as a function of time with respect to the onset of the movement of the eye will be described in chapter IV.

One of the most remarkable results is (14) that the dip in the visual threshold anticipates the eye movement by several tens of milliseconds,

which suggests that the rise of threshold triggers the eye movement, or, put differently, that the blind mind allows the eye to move. This implies that we are not completely free to choose the moment at which we want to start an eye movement. This effect might be reflected in the frequency distribution of the reaction times, if we assume that presentation of the stimulus marks the onset of some cortical or subcortical activity. Or, in case of optokinetic nystagmus, the moments at which the eye makes the saccadic jump back may be generated by subcortical clocklike activity which also times the visual threshold, while no resetting is needed in this case. Periodicities in reaction times have been found by various experimenters (15, 16, 17). It is of importance to notice that those who found periodicities invariably used response methods which could be initiated rapidly. As soon as the subject has to push a button the effect may disappear, due to variations in nerve conduction time.

A description of the frequency distributions in a reaction time experiment is given in chapter V; this forms a part of the original dip experiment, since the reaction time of the eye to a change in position of the fixation light is also measured. In some instances the electroencephalogram of the subject was measured during the reaction time-dip-experiment, in order to look for similarities among the various results. When necessary, an average response computer 'CAT' was used to improve the signal to noise ratio of time locked events, while an off line correlator was used for the detection of events not locked in time.

During the measurements of the dip in visual threshold it was found that structures which were presented at threshold intensity were observed better than could be explained on bases of the chance of perception of the constituents. This led to the facilitation experiment, in which the chance of perception of two simultaneous flashes was measured as a function of the chance of perception of each flash. The results could be described by a mathematical model which also described the dip experiment. As the dip experiment led to an extension of the model, the facilitation experiment will be described first in chapter III, for the sake of clearness. In chapter VI the results are brought together in a general review.

## THE EXPERIMENTAL ARRANGEMENT

The apparatus requirements for the measurement of the visual threshold for flashes of short duration and variable size at the moment at which the eye is about to move, or has just started its movement, were rather specific. In the first place, the eye movements have to be generated by a change in position of the fixation light. The subject was instructed to look at this light, and to react to changes in its position as fast as possible. Secondly, the test flashes must be given in the time interval during which we expect the subject to react to the change in position of the fixation light. Finally, it must be possible to present the flashes on an adjustable background in order to find functional relationships between the threshold function and the level of adaptation.

A functional sketch of the experimental arrangement is given in Fig. 1. An integrating sphere 65 cm in diameter was used to provide for a background of uniform luminosity. An opening 40 cm in diameter was made in this sphere, which gave the subject a circular field of about 60 degrees. The sphere was illuminated by means of a slide projector with stabilized DC supply. By inserting filters in the projector the background could be varied from about  $170 \text{ cd/m}^2$  to zero.

The two fixation lights were projected on the inside of the sphere at the same level as the subject's eyes. The position of each of these lights could be varied in the horizontal plane. To present the lights alternately they were coupled to a bistable element, which was in turn controlled by a random source to prevent anticipation by the subject. The random source consisted of a modulo two shift register, and its output was a

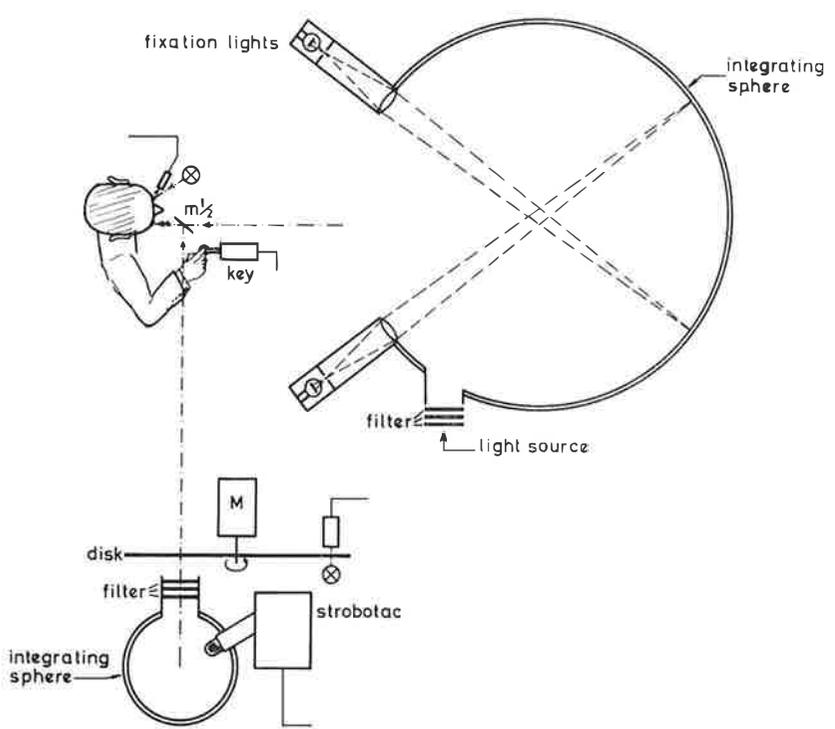


Fig. 1. The experimental arrangement. The subject is seated in front of an integrating sphere with two fixation lights. The flash unit with rotating disk is seen by means of a half silvered mirror.

square wave with a mean on and off period of 1,2 second and a standard deviation of half a second. The fixation lights, Sylvania 1859/R1130B, were switched on and off with this square wave and its conjugated counterpart, the response time of these light bulbs being of the order of one microsecond. The angle between the fixation lights could be varied from 25 degrees to zero. The flash was presented by means of a half silvered mirror in front of the subject's right eye, as indicated in the figure. The flash unit could be moved up or down or sideways to vary the position of the flash with respect to the background and the fixation lights. Usually the flash was presented right between the two fixation lights, about five degrees up to avoid the blind spot. The moment at which the flash was given depended upon the reaction time of the subject. The delay between the change in position of the fixation lights and the moment at which the flash was given was

adjusted to the subject's reaction time by means of a variable oscillator and scaler. During the experiment the delay was varied such that the subject 'passed' several times through the dip.

The flash unit consisted of an integrating sphere, 15 cm in diameter, a strobotac flash tube mounted inside the sphere, and a rotating disk in which four slides were mounted. Filters could be inserted between the rotating disk and the sphere to adjust the intensity of the flash. The position of the rotating disk was sensed by three photodiodes, one for synchronisation, and two for position. Holes were drilled along the edge of the disk in a binary pattern. As soon as the signal for firing was given by the variable delay unit a one was stored in the delayed coincidence circuit. The first synchronization signal from the rotating disk then caused the flash unit-strobotac 1531 A-to fire, and the delayed coincidence circuit was reset. The position of the disk at the moment of the flash, which could be any of the four positions since the time between the flashes was random, was binary coded and stored for further computation.

Such a flash generator is very flexible: one can measure simultaneous responses to different stimuli during one session, and empty slides can be inserted to test the subject's reliability or to correct for false responses. Since the disk rotated at 20 revolutions per second, the maximum extra delay in the delayed coincidence circuit was 12,5 milliseconds. The 0,8 microsecond duration of the flash ensures that no blurring occurs when the flash is presented to the moving eye, as the eye at its highest angular speed can only rotate over less than two seconds of an arc in this time.

The same apparatus was used for the facilitation experiment except that in this case the delay between the change in position of the fixation lights and the flash was adjusted to 500 milliseconds to allow the eye to settle on the next fixation point. It is, of course, not necessary in this experiment to have the subject make eye movements, but for the following reasons we preferred the use of two different fixation points. In the first place this permitted us to make two independent measurements of the facilitation in one session since the visual threshold varies over the retina and consequently the chances of perception of the different stimuli will be different for the two positions. The other reason is that during prolonged fixation on a bright background the Troxler effect interferes with the experiment. At the borders of the field dark and brilliant contours waxed and waned and distracted the subject from his task, which was in this case difficult enough, as he must

distinguish between one or two simultaneous flashes at different places. Moreover it is more natural to make an occasional eye movement. It was necessary to measure the eye movements, in the experiments concerning the visual threshold in the vicinity of an eye movement, in order to be able to relate the onset of the eye movement to the time at which the flash was given. Of the several possible methods, two were used, the electro-oculogram and the photo-electric method. One can measure the electro-oculogram by placing electrodes around the eye (18, 19). Due to a resting potential between the front and back of the eye, movements could be measured as varying voltages. The one advantage of this method was that it was not restricted in bandwidth, as was the case with the photo-electric method due to the low speed of the photodiodes, but there were many disadvantages. The output was low, several microvolts per degree rotation; stabilized DC amplifiers were needed for amplification of the signals; big superimposed DC voltages have to be compensated for; and the human noise, such as the muscle potentials, heart beats, sudden movements of the head which changed the degree of polarization of the electrodes because of a difference in pressure in the connecting leads, transformed such an experiment into a nightmare of compensation, button pushing and adjusting. As we restricted ourselves to horizontal eye movements, it was advantageous to use the photo-electric method, which will be described in some detail. A light bulb with an attached lens was fixed in front of the eye at an angle of about 15 degrees with the horizontal plane. This light bulb illuminated the frontal and slightly nasal portions of the eye. A photodiode of the type Clairex CL 3 was mounted in the same plane with the light bulb, and at an angle of about 15 degrees downward with the horizontal plane; this detected the gross output of reflected light. As the various parts of the eye reflect differently, the output of the photodiode was a function of the vertical and horizontal position of the eye. If one restricted oneself to horizontal eye movements, this function can be made by a few adjustments to be quite simple if not linear, which was surprising. The linearity of the output was within a few percent for angles up to 25 degrees. To avoid having the light interfere with the experiment, an infrared filter was placed in front of it, using a wavelength band to which the photodiode was maximally sensitive. Both the photodiode and the light bulb were mounted on a headband, so that head movements could be made without dramatic changes in the output of the system. It is clear that all the light in the subject's vicinity needed

to be DC supplied, lest hum contaminated the signal from the photodiode.

The rise and fall time of the photodiode is a function of the illumination, and some precautions had to be taken to ensure that the level of illumination was not too low, as this will decrease the bandwidth of the system. The output was compared with the electroculogram at a standard setting and it was found that the rise and fall time of the photodiodes – of the order of 5 milliseconds to 50 milliseconds at this level – were not limiting factors. The output of the photodiode was about 4 Volt per degree, and it was readily amplified with a normal DC amplifier. The sensitivity one can reach after adjustments and some precautions was of the order of several minutes. The limiting factors were the heart beats which are introduced either through the headband or by a true movement of the eye in and out of the orbit. (20) Since the experiments described always involved angles of at least 6 degrees these artifacts were negligible. It must be noted that movements of only one eye were measured; it was therefore necessary to determine if both eyes start and stop simultaneously, because the eye to which the stimulus was applied is not the one whose movement was recorded. This was a precaution to avoid illuminating the eye which was being tested with infrared light which also contained a little red light for ease of adjustment. Very fast but insensitive photodiodes (OAP12) were used to check if the eyes move and stop simultaneously. This proved to be true within the experimental error of 1 millisecond. For a smooth running experiment with a high data processing capacity it was not only necessary to have measurements of the eye movements but, more importantly, to have a device which detected the onset of the movement since this was the point we were interested in. The onset of an eye movement produced a sudden change in DC potential which could be detected in various ways. One can trigger at a certain level or one may differentiate the output of the photodiode and have this differentiated signal trigger a pulse source if it surpassed a certain level. Both of these methods had some disadvantages which had to be dealt with in the design. For the subject's comfort his head position was not fixed during the lengthy experiments and it was entirely possible that the position of the head varied a little as time went on. If a pure DC trigger were used, such a head movement would cause great deviation in the moment at which the output of the photodiode passed through a certain level. On the other hand the differentiating method had the disadvantage that the capacitors in the circuit remembered eye blinks

in between movements too well and this would create an intolerable uncertainty. Two devices were build for the detection of the onset of the eye movements, both utilizing the principle of differentiation. The analog device consisted of a differentiating circuit in which the condenser was kept uncharged till 100 milliseconds after the change in position in fixation lights. After this time the clamp was removed and the first change in the signal of the photodiode that surpassed an adjustable level caused a one-shot to fire. This pulse served to indicate the onset of the eye movement while also putting a clamp on the condensers in the circuit. The delay between the onset of the eye movement and the pulse from the one-shot was about 12 milliseconds, with an uncertainty of 2 milliseconds, as is shown in Fig. 2. It was clear that this device profits from the experimental fact that the slope of the onset of the eye movement is almost constant.

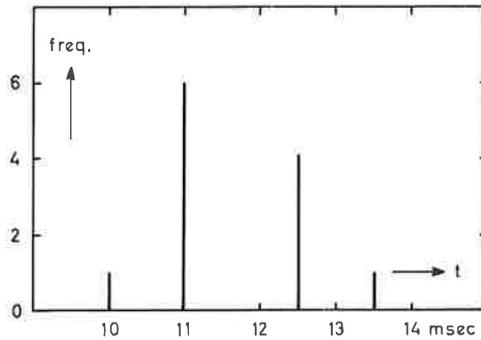


Fig. 2. The frequency distribution of the analog pattern recognizer.

The other device was a digital circuit. The output of the photodiode was fed into an analog to digital converter. Of the many possible ways to realise an analog to digital conversion, the up/down counter type was chosen because of its simplicity and the restricted bandwidth of our data. The principle was the following. We used an 8 bit counter which could count up till 11111111, or down till 00000000, and in which a weighted network was built which generated an analog signal proportional to the binary value of the counter. (21) This analog signal is compared with the incoming signal in a comparator. Every 1 or 2 milliseconds the counter was started and it counted up or down in such a way as to minimize the difference between the two signals. After a certain number of counts the analog output passed through the

level of the incoming signal and the comparator changed polarity, causing the counter to stop. The value at which the counter was stopped was linearly related to the incoming signal. If, for instance, a constant voltage was fed into the analog to digital converter it would step up and down one in value after an initial compensation. Incorporated in the analog to digital converter was a device which recognized the onset of the eye movement. This pattern recognizer was designed in a simple way. If the number of counts in four successive conversions was between adjustable limits, and if they all had the same polarity, up or down, then and only then this device produced a pulse on its output. Essentially this device reacts on the slope of the signal, while the level of the signal was of no importance. The pulse from this pattern recognizer arrived 16 to 20 milliseconds after the onset of an eye movement with an uncertainty of 2 milliseconds. That it was a constant relation indeed, and that the moment at which the pulse was generated does not depend on the DC level of the signal is shown in Fig. 3. This photograph was made by having the pulse of the pattern recognizer trigger an oscilloscope, while the output of the photodiode was displayed on it. A last precaution was taken to prevent

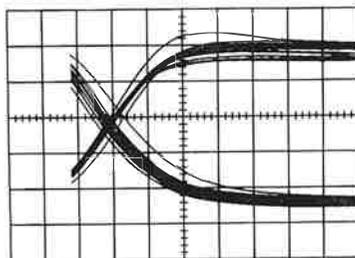


Fig. 3. The eye movement displayed on an oscilloscope which is triggered by the digital pattern recognizer. Horizontal scale is 20 milliseconds per division.

pulses originating in eye blinks or similar disturbances from interfering with the experiment. This was done by time strobing. Only when we expected a pulse from the device – the reaction times lie within certain limits – was it permitted to generate one. A block diagram of the experimental arrangement is given in Fig. 4. The subject was seated in front of the sphere, his photo-oculogram was measured and the pulse generated by his eye movement served to stop the reaction time counter and to start or stop the counter which measured the time



the information into a form suitable for further computation. After the experiment the punched tape was processed and the results of the experiment were presented in the form of a histogram which gave the number of stimuli seen and the number missed in an interval of time with respect to the onset of the eye movement.

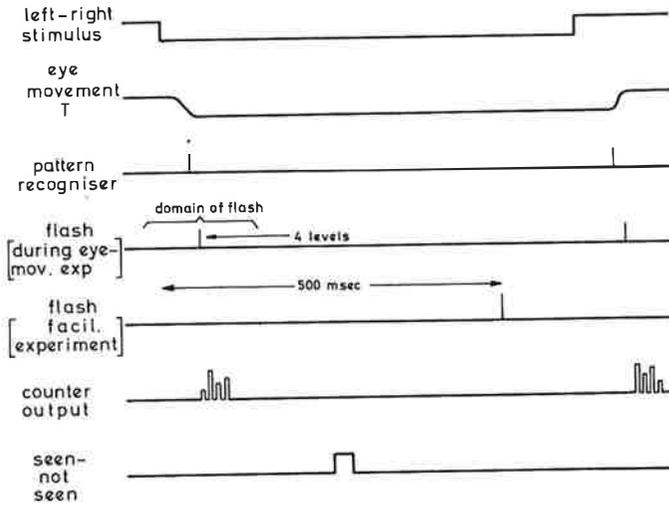


Fig. 5. The time diagram of the experiment. The channels are self explanatory.

A time diagram of the events is given in Fig. 5. The first channel recorded the change in fixation lights, which started the whole sequence. In the second channel the eye movement was recorded. In the third channel the output of the pattern recognizer was given, and in the fourth the flash, which was printed in four pulse-height coded levels, as there were four possible flashes. The fifth channel displayed the time between the onset of the eye movement and the flash in a pulse-height code and in the sixth channel the response of the subject was given. A set of 24 counters was used for the facilitation experiment. There were four different stimuli, two fixation positions and three possible responses. The subject's room was shielded and darkened. When the subject's EEG was measured it was taken from the occipital cortex and recorded on tape, from which it could be processed further with a correlator, while a CAT computer was used on line to average the responses (23, 23).

## THE FACILITATION EXPERIMENT

### A. FACILITATION EXPERIMENT

It is found when observing flashes several degrees in diameter at near threshold intensities that these flashes are either seen completely or missed altogether (24, 25).

This effect cannot be explained by models utilizing coincidence mechanisms, as the chance for stimulation due to coincidences over the total area of the flash is negligible.

A possible explanation of the effect can be based on the assumption that if at any place of the retina the number of quanta is sufficient for perception this stimulation will decrease the threshold of neighbouring elements who in turn facilitate their neighbours.

It is also necessary to assume for flashes of short duration that subliminal stimuli are stored by means of a local effect, which is not relayed to higher centers. But once a neighbouring element has fired this will a posteriori facilitate the stimulus to a transmittable signal.

The term facilitation indicates the mechanism outlined above and deals with the problems concerning flashes with appreciable diameters. It was found in the experiments about the visual threshold in relation to the onset of an eyemovement which will be described in Chapter 4 that stimuli of a complicated structure were perceived better than could be calculated on basis of the parts out of which the structure existed. If, for instance, two points, with a diameter of 7' several degrees apart were presented, each with a chance of detection of 30% the chance for detecting both flashes was found to be 20%, while one should expect a chance of 9%.

This experiment shows that the facilitation mechanism has a longer reach than neighbouring elements, and that facilitation may occur over several degrees, while the cells in between are silent.

The data given above were found for the moving eye, or the eye that was about to move, and it was a matter of interest whether the resting eye also showed this effect.

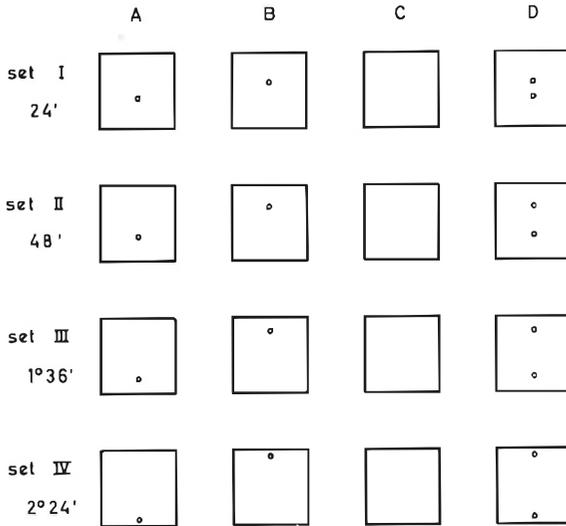


Fig. 6. The four sets of stimuli for the facilitation experiment. The holes were tested with a microscope.

The following experiment was set up. Use was made of four stimuli, which were presented in a random sequence. The four sets of stimuli are given in Fig. 6. The stimuli consisted of aluminum rectangles with holes drilled in them. The holes were measured with a microscope and it was found that they were equal within one percent. The angle under which the holes in column 4 were seen in the experiment was respectively: 24'; 48'; 1° 36'; 2° 24'.

The intensity of the flash and the background were matched in such a way that the chances of perception of stimuli *a* or *b* - a flash with a diameter of 7' - was between 10% and 90%.

The experimentally found chance of perception of both flashes  $P_{am}$  was compared with the calculated chance on basis of:

$$P_{cal} = P_a P_b$$

The experiment was done first under dark adapted conditions. Four subjects ran each many sessions consisting of several hundreds of measurements. It was found that the experimental results for stimuli 2, 3 and 4 (see Fig. 6) were equal, and these results are represented together in Fig. 7.

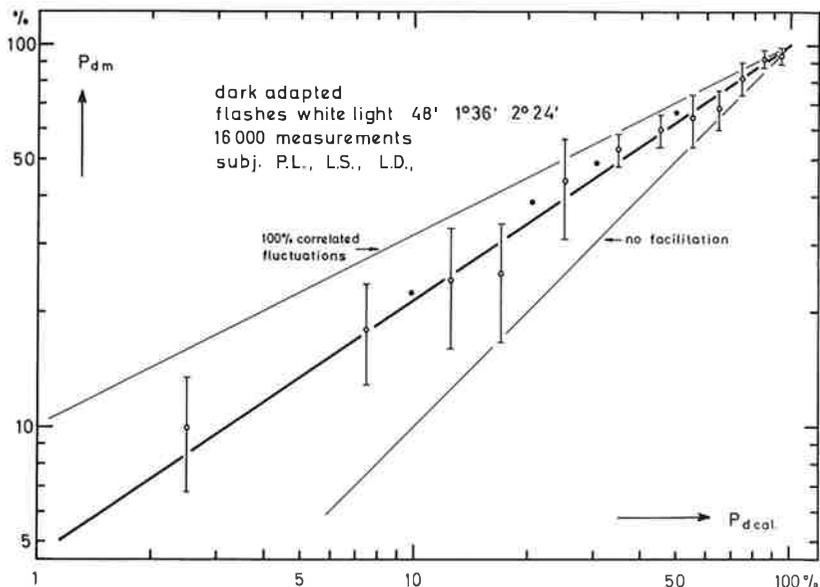


Fig. 7. The experimental result of the facilitation experiment. The solid dots were found by van den Brink in a similar experiment (24). The heavy curve is the simplest approximation used in equation 2, chapter III.

The effect is considerable as can be seen and all points differ from the linear curve which would be valid if no facilitation was present. In a different set up v. d. Brink measured the chance of perception of a flash with a diameter of several degrees as a function of the chance of perception of this flash and a smaller one, presented in the center of the greater flash, with a chance of detection of 30% (24). His experimental points are indicated by the solid dots, and it is clear that his results are equal to the effect of isolated flashes, if we take the small summation effect of his stimuli in account. The facilitation does not

depend on the distance between the stimuli outside the area of summation up to angles of at least  $2^{\circ} 24'$ .

To explain the effect one can look in many directions. Suppose for instance that the sensitivity of the retina fluctuates, and that the chance of perception depends both on the strength of the stimulation and the moment on which the stimulus is presented. If the local correlation in fluctuation is high one can expect that the chance of perception of both flashes, each with a chance of perception of  $P_a$  and  $P_b$  respectively, is equal to or less than the smaller of the two chances, depending on the correlation factor. One finds that the chance of perception of both stimuli  $a$  and  $b$  is equal to  $P_a$ , if  $P_a$  equals  $P_b$  and the correlation equals one, and this curve is drawn in Fig. 7.

All experimental points lie between the two lines given by  $P_{dcor} = P_a$  and  $P_{dcal} = P_a^2$ .

This could mean that there is a reasonable strong correlation between the spots tested in the experiment, which is independent of the distance up to several degrees.

The easiest way to disprove this hypothesis is by grouping the data in three groups.

The first group consists of those experiments in which  $P_a$  and  $P_b$  were about equal. In the second group the ratio of  $P_a$  and  $P_b$  was between 1,5 and 2,5, and the third group finally consisted of those experiments in which the ratio of  $P_a$  and  $P_b$  was higher than 2,5.

$P_a$  and  $P_b$  were about equal in most experiments, and in order to get enough members of group three it was necessary to put a 50% transmission filter in the lower flash channel.

If the effect is now caused by fluctuations of the retina the chance of perception of both flashes has to go down when the ratio of  $P_a$  and  $P_b$  increases, while  $P_a \cdot P_b$  is kept constant.

On the other hand, if the high value of  $P_{dm}$  is caused by a real retinal or cortical facilitation mechanism anything can happen to the value of  $P_{dm}$  when the ratio of  $P_a$  and  $P_b$  is varied, as we have not specified any mechanisms yet.

In Fig. 8 it is shown that the curves of  $P_{dm}$  versus  $P_a \cdot P_b$  do not differ for the three groups and it is therefore impossible to explain the facilitation in terms of a correlated fluctuating retina.

If the sensitivity of the retina varies slowly versus time such that during one session it has traversed its course several times one also finds values for  $P_{dm}$  which turn out to be too high. But this effect can

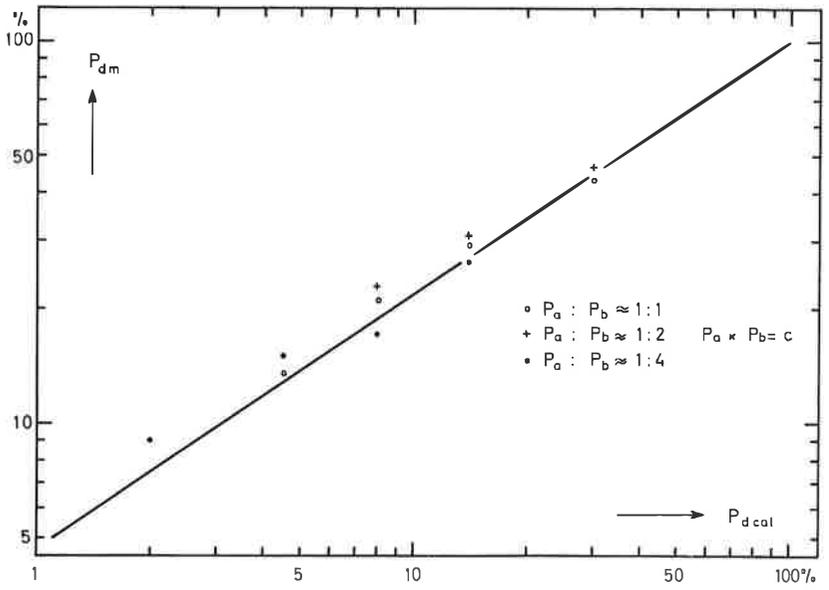


Fig. 8. This figure shows the independence of the facilitation of the ratio of  $P_a$  and  $P_b$  for  $P_a.P_b = \text{constant}$ .

	$P_a$	$P_b$	$P_{dm}$	$\tilde{P}_a^2$	$\tilde{P}_b^2$	$\tilde{P}_a.\tilde{P}_b$
1- 20	20	40	23	25	4	-10
21- 40	55	57	23	900	361	570
41- 60	28	64	14	9	676	78
61- 80	0	62	0	625	600	-600
81-100	28	22	0	9	256	-48
101-120	0	14	0	625	676	600
121-140	10	0	10	225	1444	570
141-160	7	25	0	324	169	234
161-180	21	16	20	36	484	132
181-200	25	16	44	0	484	0
201-220	16	37	22	81	1	9
221-240	55	50	0	900	144	360
241-260	46	40	40	441	4	42
261-280	40	55	28	225	289	255
281-300	22	75	36	9	1369	259
	25%	38%	19%	474	6961	2451

be compensated for if we take this into account and increase the value of  $P_{\text{dcal}}$  accordingly.

To look for these effects the data were grouped into sets consisting of 20 successive stimuli. The values of  $P_a$  and  $P_b$  were calculated for each set the result of which is given in the table on page 18.

The first column gives the  $P_a$  for the successive series of stimuli. The second and third column give the  $P_b$  and  $P_{\text{am}}$ . In columns four and five the standard deviations of  $P_a$  and  $P_b$  are calculated, and in column six the covariance of  $P_a$  and  $P_b$  is given.

In order to find the correlation between  $P_a$  and  $P_b$  as a function of time the following formula were used.

The correlation is given by:

$$\varrho(P_a, P_b) = \frac{\overline{(P_a - \bar{P}_a)(P_b - \bar{P}_b)}}{\sigma(P_a) \sigma(P_b)}$$

while

$$\overline{(P_a - \bar{P}_a)(P_b - \bar{P}_b)} = \overline{P_a P_b} - \bar{P}_a \bar{P}_b$$

Substituting the values of the table one finds:

$$\varrho(P_a, P_b) = \frac{0.0163}{0.167 \times 0.216} = 0.45.$$

The correlation of  $P_a$  and  $P_b$  is considerable and it is therefore clear that the whole retina or perhaps the subjects criteria varies slowly with time. Due to this correlated fluctuation the value for  $P_{\text{dcal}}$  turns out to be too low, and if we want to compensate for this effect we must use the following formula:

$$P_{\text{dcal}} = \overline{P_a P_b} = \bar{P}_a \bar{P}_b + \varrho(P_a, P_b) \sigma(P_a) \sigma(P_b).$$

The last term gives the correction. Applying this formula to our data it is found that the correction is of the order of 1,5% which is too small to take into account on basis of the standard deviations of the measurements. The reason that this correction is rather small is that the excursions of  $P_a$  and  $P_b$  are restricted. They do vary together, but only over a small range.

Finally one can test to what extent successive responses of the subject are independent. Thus given that certain flash is perceived, how influences this fact the chance of perception for the next flash.

It was found that the correlation between successive measurements

was negligible, an effect observed earlier by Pirenne using random stimuli. Pirenne (26) also found the slowly varying sensitivity of the retina, in agreement with our findings.

Now that we have established that the facilitation cannot be explained by correlations of any kind it is important to know whether the facilitation originates in the retina, or in the relaystations in the brain, or even in the visual cortex.

A fairly safe way to discriminate between a peripheral effect and a cortical effect is by using binocular flashes. The upper flash is given in the left eye and the lower flash in the right eye. This was easily done with the help of some polaroid filters which were placed in front of the observers eye's and in the upper and lower channel.

The result of the experiment is given in Fig. 9. Within the standard deviation one can say that the calculated and measured chances for a double flash  $P_{dcal}$  and  $P_{dmi}$  are equal. The conclusion is now that the facilitation is a retinal effect, caused by a shift in threshold which enables (stored) sub liminal stimuli to get through to the brain once a supraliminal stimulation has occurred.

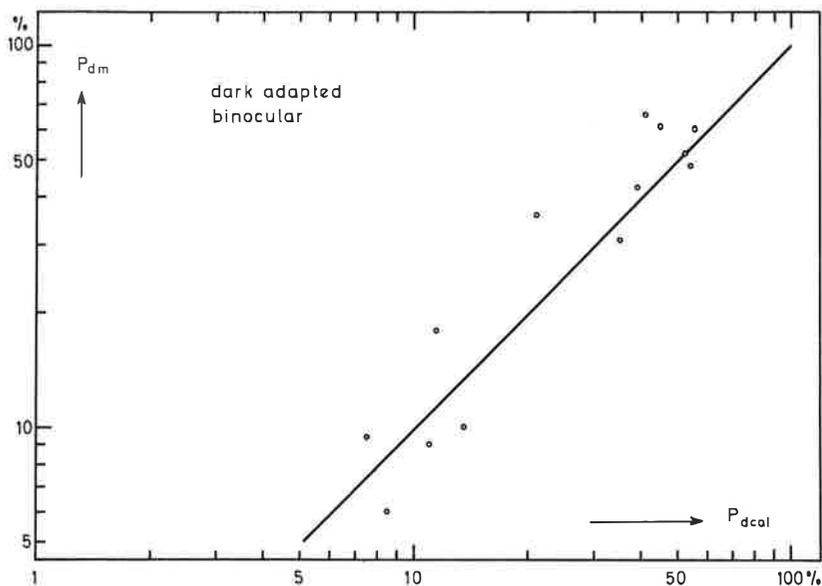


Fig. 9. This figure shows that binocular flashes have no facilitation effect. The curve drawn is the expected curve.

The facilitation does not affect the chances for perception of at least one flash. It shifts the amount of single flashes partly to the double flashes. This is illustrated in Fig. 10 and Fig. 11 respectively for the monocular and the binocular case. These chances coincide with the chance one calculates from:

$P_s = 1 - (1 - P_a)(1 - P_b)$  in which  $P_s$  is the chance of perception of at least one flash.

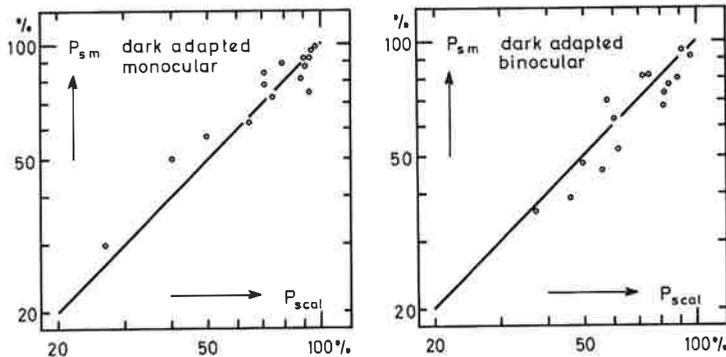


Fig. 10 and 11. The chance for perception of at least one flash, calculated  $P_{scal}$  and measured  $P_{sm}$ . It is seen that these chances are not influenced by the facilitation mechanism which is activated by monocular flashes.

Another important question arises now. If the facilitation proves to be a retinal effect, to what extent then do the two receptor systems, the rods and the cones, influence one another less than interrod or intercone influences.

This question can be answered using stimuli specific to each system. The upper flash used in this experiment was made red with acetate filters, to stimulate the cones and the lower flash was green to stimulate the rods.

Now the measurements were repeated with the results given in Fig. 12. It is surprising that here the facilitation is even slightly better than in the other experiments, it proves beyond doubt that this facilitation is a gross retinal effect, which affects rods and their relay stations as well as the cones and their mutual relay stations. The slight increase in facilitation can be explained if we think of the additional clue in this experiment, the two different colours. This colour difference can

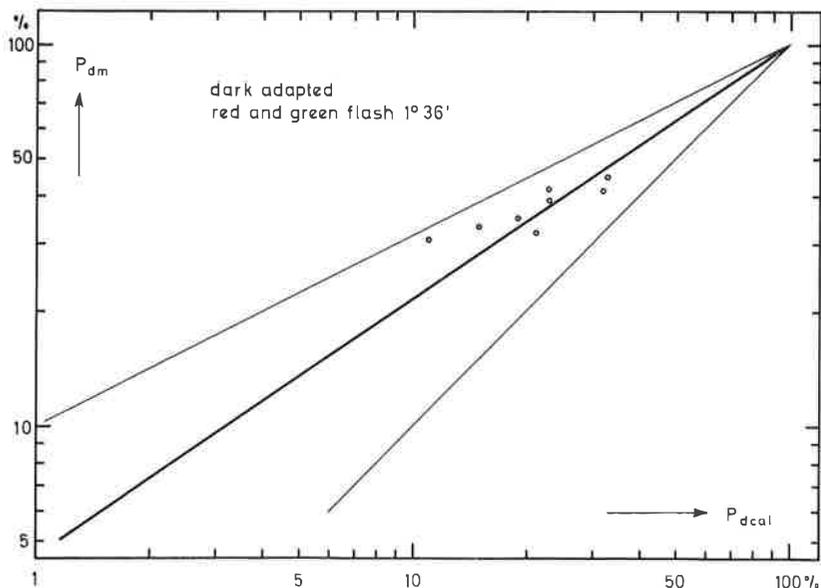


Fig. 12. The facilitation of red and green flashes.

influence the decisions of the subject and he will have less effort to distinguish two flashes from one.

### Conclusions

So far it is clear that the following conclusions can be drawn about the mechanism of facilitation:

1. It is most likely a retinal effect, which affects both rods and cones equally.
2. Outside the area of summation the distance between the two flashes is of minor importance.
3. The chance of perception of at least one flash is not influenced.
4. The effect of a fluctuating retina is negligible.
5. The facilitation is independent of the ratio of  $P_a$  and  $P_b$  as long as  $P_a P_b = \text{constant}$ .

We shall now put forward a simple model which can account for the effects observed and which is – of course – in good agreement with the conclusions given above.

It is closely related to the model used in detection theory.

In the retina we assume noise to exist. In case no stimuli are presented this is the noise of the system, which can be of retinal or cortical origine. When stimuli are presented on a background, the background will be transduced into an increase of the noise, which consists now of two components, one of retinal origine, the other of extra retinal or physical origine. This noise has a density distribution which gives the distribution of the amplitude for a certain experimental condition. As we never see anything in complete darkness the threshold of the visual system is that high that the probability of a false alarm is very low indeed. This is illustrated in Fig. 13.

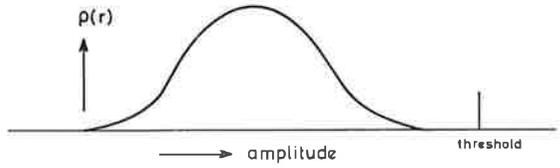


Fig. 13. The density distribution of the noise and its threshold.

The density function  $\varrho(r)$  does not have to have any particular form yet, so we do not assume this distribution to be Gaussian, the only assumption is that  $\int_{-\infty}^{+\infty} \varrho(r) dr = 1$ .

If now a signal of certain strength is presented, this signal is superimposed over the noise with the effect that the whole density function is shifted to the right over a distance linearly related to the stimulus.

The chance of detection then is given by  $P_d(s) = \int_{th-s}^{\infty} \varrho(r) dr$  as is illustrated in Fig. 14.

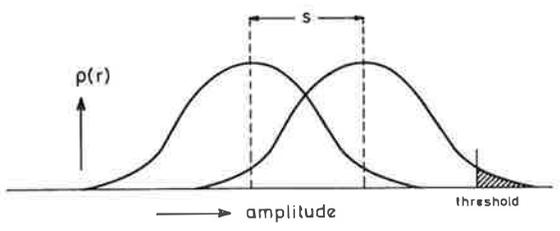


Fig. 14. The density distribution is shifted to the right by a stimulus  $s$ . The area to the right of the threshold gives the chance of perception.

At first sight this formula may appear to be doubtful. Unlike in practical physical systems there is no guarantee whatsoever that the retinal effect caused by a visual stimulus is linearly related to the strength of this stimulus. But this is by no means necessary, as long as the retinal effect increases with increasing intensity of the stimulus, which will certainly be true for threshold phenomena. If the retinal analogon to the physical stimulus is not linear the noise density distribution will be weighted with this same unlinear function, using stimuli of various strength or, as will be shown in a later chapter, by taking profit of a variable threshold.

Thus at the moment it is safe to assume that the density function will be shifted over a distance linearly related to the physical strength of the stimulus.

Now it is possible to construct a frequency of seeing curve which gives the chance of detection as a function of the strength of the stimulus.

This FOS curve is described by: 
$$P_d(s) = \int_{th-s}^{\infty} \varrho(r) dr.$$

We make the following assumption. If at any experiment the stimulus strength plus noise has a value equal to or greater than the threshold value, this stimulus will be perceived and, the perception of this stimulus has the effect on the detection system that the threshold value is decreased with a certain amount, which is independent of the strength of the signal perceived. We may say as an equivalent description that the density distribution is shifted to the right over a constant distance  $k$ . This shifted density distribution will then serve to detect subthreshold or near threshold signals which passed undetected before. It is also necessary to explain the effects observed to assume that these subthreshold stimuli have been stored in the retina at the right location. If they are facilitated, they will be perceived on the right place, else the effect will fade away.

The state of facilitation persists for a limited time, experimentally it was found to be the order of about 100 milliseconds, as will be shown later.

Thus if two stimuli are presented within this interval of time and one of these is detected this will increase the chance of detection of the other stimulus considerably, while the sequence of the two stimuli is of minor importance.

Incorporating the assumptions given above in the formula one finds a facilitated frequency of seeing curve (FFOS) given by:

$$P_{af}(s) = P_a(s + k) = \int_{th-s-k}^{\infty} \varrho(r) dr$$

Now we apply these formula. The two spots of the retina where the flashes  $a$  and  $b$  with intensity,  $S_a$  and  $S_b$  are applied are indicated by  $R$  in Fig. 15. The chances of perception in case only  $a$  or  $b$  are presented are given by  $P_a$  and  $P_b$ , and  $P_a = \int_{th-s_a}^{\infty} \varrho(r) dr$  and  $P_b = \int_{th-s_b}^{\infty} \varrho(r) dr$ .

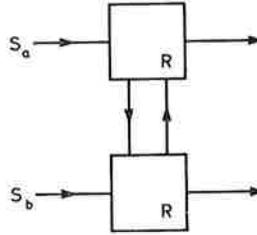


Fig. 15. Interaction in the retina. When either unit has an output the threshold of the other unit is decreased.

If both flashes  $a$  and  $b$  are given the chance for no perception is:

$$P_o = (1 - P_a) (1 - P_b)$$

The chances for perception of exactly one of the two flashes is easily found to be:

$$P_1 = P_a \overline{P_{bf}} + P_b \overline{P_{af}} \text{ in which } \overline{P} = 1 - P$$

Thus the chance of perception of both flashes is equal to:

$$P_2 = P_a P_{bf} + P_b P_{af} - P_a P_b$$

This can be written also as:

$$P_2 = P_a P_{b+k} + P_b P_{a+k} - P_a P_b$$

It was found experimentally that the results of  $P_2$  do not depend on the ratio of  $P_a$  and  $P_b$  as long as the product of  $P_a$  and  $P_b$  remains constant. We substitute  $x$  for both  $a$  and  $b$  and find:

$$P_2(x, x) = 2 P_x P_{x+k} - P_x^2$$

As  $P_2(x, x)$  is a function of  $P_x$  we finally find the following difference equation:

$$2 P_x P_{x+k} - P_x^2 = \Psi(P_x) \tag{1}$$

The  $\Psi(P_x)$  is found experimentally. The most simple curve which fits the experimental points nicely is given by:

$$\Psi(P_x) = P_x^\alpha \quad (2)$$

in which  $\alpha = 4/3$ . This is the solid curve in Fig. 7, 8, 12.

Enriching equation 1) with this information and dividing by  $P_x$  we finally find:

$$P_{x+k} = \frac{1}{2} P_x + \frac{1}{2} P_x^{\alpha-1} \quad (3)$$

It is regretful that no simple solution of equation 3) exists. This is however probably no fundamental equation as formula 2) could be approximated in many ways, perhaps with formula more suited for the solution of 3).

Using Booles recessive method (27) it is quite simple to find the numerical values of  $P_{x+ik}$  for any  $i$  if  $P_x$  is chosen arbitrarily and  $k = 1$ . The curve given in Fig. 16 is found in this way. From this curve the density distribution of the noise can be calculated. This density distribution is given in Fig. 17.

Now that a FOS curve and a FFOS curve are constructed that fits our data time has come to reflect over the method.

In the assumptions of the detection theory used in this chapter it is impossible to assign uniquely the noise and signal. It could as well be that the retina has a fixed threshold, and that the incoming signal has a noise due to quantum effects. In fact the curve given in Fig. 16 resembles the very much the curve one computes for the chance arrival of at least several quanta as a function of the intensity. And all could then be explained by assuming a quanta model, in agreement with the findings of Bouman and v. d. Velden (28, 29).

But there is evidence that this is not the actual mechanism. Anticipating the data of the experiment for the light adapted eye which will be given in B, it must be remarked that the experimental results, of this experiment are identical to the dark adapted experiment. The results are the same in case the flashes are superimposed on a background of 170 cd/m<sup>2</sup>. It is impossible that the same energy distribution describes the flash, and the noise must therefore be of retinal or retinal plus transformed physical background origine. It is surprising that about the same density distribution holds for the retina, both for the light adapted case and the dark adapted case.

Later experiments with the moving eye do however confirm this fact to some extent. A more detailed discussion will be given in the following chapter. It was found experimentally that the facilitation mecha-

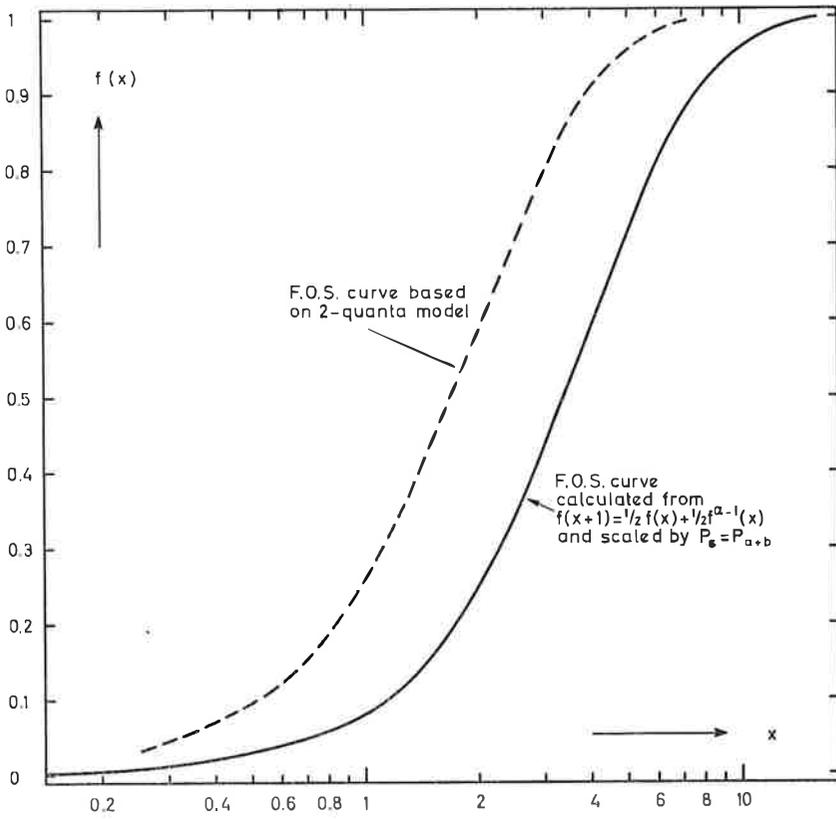


Fig. 16. The frequency of seeing curve based on the facilitation model.

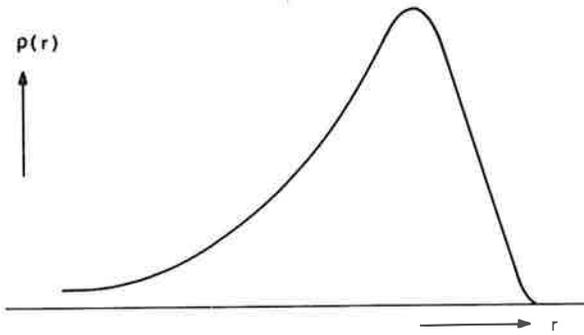


Fig. 17. The density distribution of the noise calculated in the facilitation model.

nism is active over distances of several degrees. Due to convergent and divergent branches in the transmission this may be precisely the projection of a certain retinal area on a ganglion cell. Before proceeding to the facilitation within the area of summation it must be remarked that the FOS and FFOS curve are in good agreement with the conclusions given on page 22.

#### Facilitation within the area of summation

When two flashes are presented within an area of certain size their energies are added, and the chance of perception is much higher than if they were outside this area. This size of this area is between 10 minutes of an arc and 1 degree according to the various experimenters. There are discrepancies between the different sources, and Hallett (30) suggested that these discrepancies could be accounted for by specific structures in the retinas which divided mankind into at least two groups, one with an area of summation of about 10 minutes of an arc, and one with such an area of considerable greater size.

It was found in our experiments concerning the facilitation that the measurements of two stimuli 24 minutes apart differed markedly from those 48 minutes or more apart. It was assumed then that these stimuli were close enough together to put the mechanism of summation into effect. With another set of stimuli the effects of a 12 minutes distance was tested also, and here it was found that the facilitation was less than the 24 minutes experiment. This was doubtless due to the problem of the subject to see the two spots apart.

As a fair compromise it was therefore decided that stimuli 24 minutes apart represented the effects of both facilitation and summation without too much problems concerning the classification.

The clearest indication of the presence of the effect of summation (31) is that the chance of perception of at least one of two flashes is much higher than is found according to the formula:

$$P_s = 1 - (1 - P_a)(1 - P_b)$$

This is illustrated in Fig. 18.

The chance of perception of both flashes is given in Fig. 19.

The records were tested for a slow and fast correlation of the retina and as expected the results could not account for the effect of facilitation as was the case outside the area of summation.

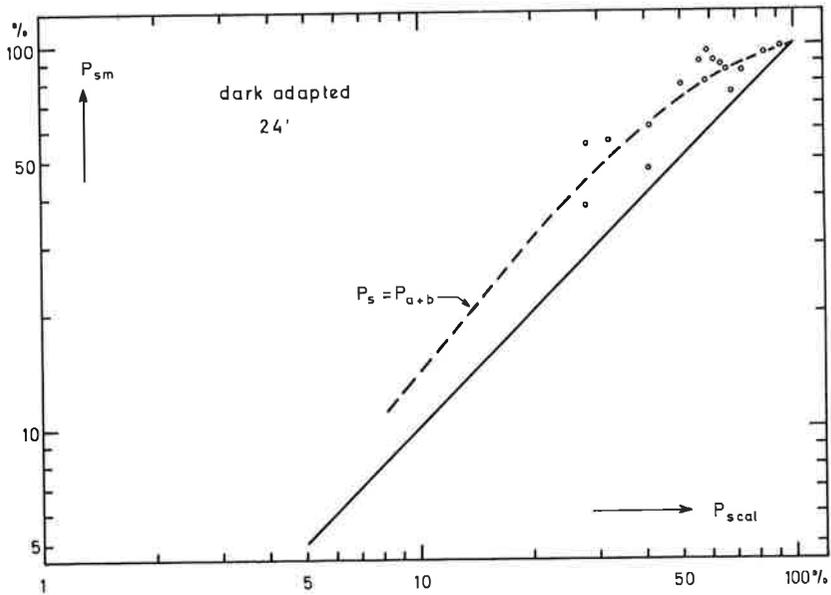


Fig. 18. The chance of perception of at least one flash is much higher than calculated inside the area of summation. The solid curve is valid outside the area of summation. The other curve was used as the best approximation and it served to scale the FOS curve.

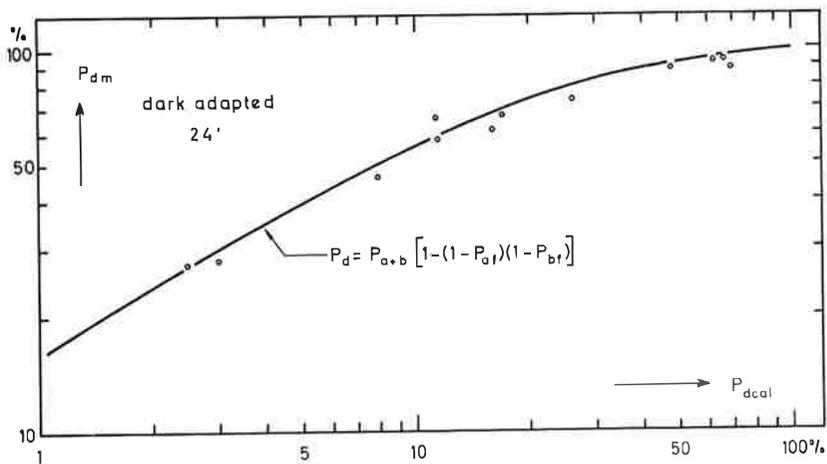


Fig. 19. Facilitation inside the area of summation. The curve drawn is calculated in equation 5, chapter III.

Referring to the conclusions given before it can be stated now that the conclusions 1, 4 and 5 still hold.

We shall now apply our formula to stimuli within the area of summation. See Fig. 20.

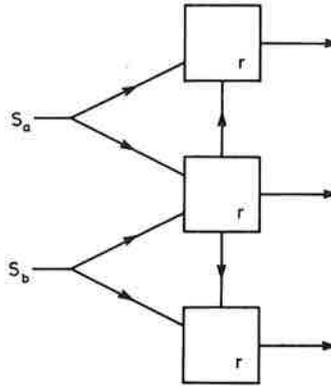


Fig. 20. Retinal representation with interaction inside the area of summation, based on the facilitation model.

Again the retina is represented by an  $R$  in the figure. There are two flashes with strength  $S_a$  and  $S_b$  and chances of perception if they are given by themselves of  $P_a$  and  $P_b$  respectively. In the central retinal black box above, the summated flashes  $S_a$  and  $S_b$  are detected by a mechanism in which the FOS curve is applied to the sum of the intensification of the two flashes. If this mechanism produces an output this will serve to facilitate both other retinal black boxes according to the FOS curve.

We now make the assumption that if either one of these boxes produces a signal two flashes are perceived. This reflects to some extent the findings of the subject. When two stimuli are presented it occurs quite often that three dots are perceived, one lying about right between the other two.

It is hard to give a description of all possible perceptual findings, but the one given above is very frequently occurring. Another quite often occurring subjective impression is that of two flashes bright and brilliant, without any structure between them.

This could be caused in case the two stimuli did not need the facilitation to be seen.

The third group with a fair frequency of occurrence is that in which it is perceived that one of the flashes is elongated to one side with structures as fantastic as in a nightmare. This could be caused in case the sum facilitates and just one of the other stimuli manages to get through to the brain, and it may well be that specific structures in the retina are enhanced.

If we apply our hypothesis to the formula we find:

Chance of facilitation-which is equal to the chance of seeing at least one point:

$$P_f = P_1 = P_{a+b} \quad (4)$$

The chance for at least another point: is equal to:

$$1 - (1 - P_{af}) (1 - P_{bf}).$$

And finally the chance of perception of two flashes:

$$P_2 = P_{a+b} \{1 - (1 - P_{af}) (1 - P_{bf})\} \quad (5)$$

The formula 4) enables us to assign an unique  $x$  to the solution of the difference equation. It is clear that if  $f(x)$  is a solution of the difference equation,  $f(x + y)$  is also a solution, for arbitrary  $y$ . We now choose the solution of  $f(x)$  such that if the FOS curve is used for the estimation of the chance of perception of two flashes within the area of summation, in which case the energies are added, the proper curve is found for the chance of perception. This curve is given in Fig. 18, and it was selected from a family of curves for different values of  $y$  as the best approximation. The FOS curve which is found in this way describes both the facilitation mechanism, in which case an increase of chance of perception is given by an increase of energy of one unit, and the experimental summation curve, in which case the energies are added and the corresponding value of the FOS curve gives the chance of perception within the area of summation.

This unique solution is given in Fig. 16. It is seen that this FOS curve and the one computed for the 2 quanta model run parallel, while the actual mechanism is quite different and the number of quanta for a 60% chance is equal to 4.

The experimental points and the curve based on equation 5) are given in Fig. 19. The fit is completely, and this justifies also the approach given above.

The facilitation experiment was done also under light adapted conditions. The background consisted of an integrating sphere with a luminance of  $170 \text{ cd/m}^2$ . The stimuli were presented by means of a half silvered mirror as is indicated in Fig. 1. This arrangement is very convenient, as the subject has no clues whatsoever about the location or size of the stimuli, a necessary condition for the prevention of false alarms.

For the stimuli the same set as in the dark adapted case was used, and they were presented at the same place,  $7^\circ$  peripherally.

The results of the experiment are presented in Fig. 21. Each point consists of about 300 stimulus presentations, from which the various chances were calculated.

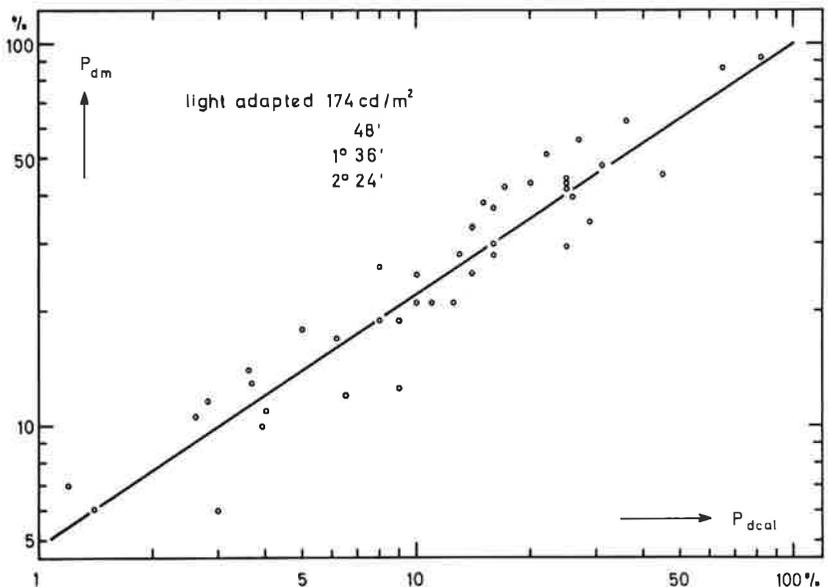


Fig. 21. The facilitation for the light adapted eye. The curve drawn is from the experiment in darkness. The dots give the data of five subjects.

The curve drawn in Fig. 21 is the curve from the dark adapted experiment, based on the formula  $f(x + 1) = \frac{1}{2} f(x) + \frac{1}{2} f(x)^{\alpha-1}$ .

It is clear that this curve also fits the data for the light adapted case and this is the reason that the noise of the model should originate in

the retina, as the stimuli are now way out of the statistical fluctuations of a few quanta. It is surprising that the fit is so well in Fig. 21, as the noise is now generated in a light adapted retina. The conclusion one can draw from this is that the physical background is transformed to a retinal activity with about the same density distribution, while the original noise in the dark retina is probably much less. This is in agreement with the de Vries-Rose law which states that the differential threshold intensity is proportional to the square root of the background intensity. As both the background and the stimulus have to pass through the same mechanisms, it is likely that the same law will hold after the transformation. In the light adapted case no experimental differences were found for stimuli of, 48', 1° 36' and 2° 24'.

The facilitation is more for the 24' than for the cases mentioned above but not quite as big as for the dark adapted eye. This is illustrated in Fig. 22. The two curves drawn are the facilitation curves based on  $f(x + 1) = \frac{1}{2} f(x) + \frac{1}{2} f(x)^{a-1}$  for the two cases outside and inside the area of summation, and the experimental points lie between the two curves.

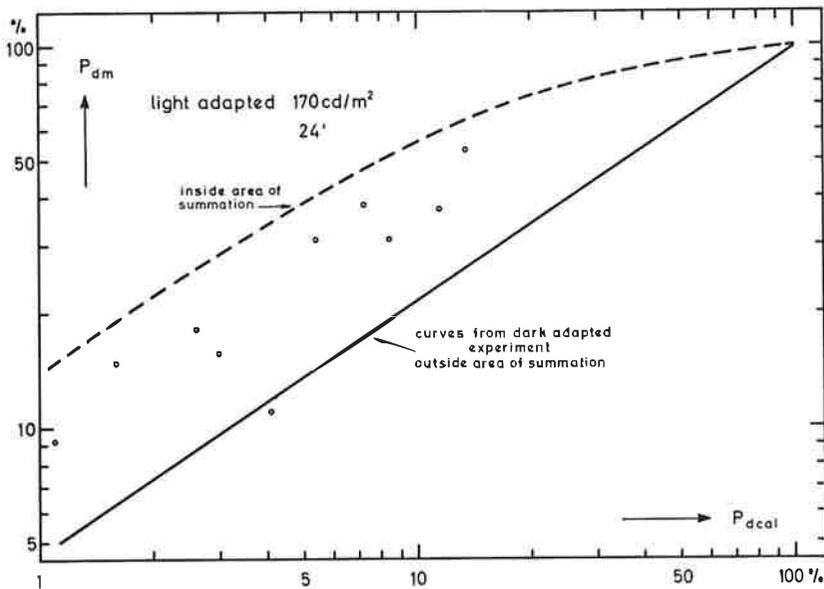


Fig. 22. Facilitation inside the area of summation for the light adapted eye. See text.

There are at least two reasons for this effect. In the first place it is well known that the area of summation decreases as the level of adaptation increases (32). It is possible therefore that at this distance of 24' no complete summation occurs.

Moreover the task for the subject to classify the various stimuli in the light adapted case is more difficult than in the dark adapted case and he will thus miss some stimuli. The network like structures as mentioned in A are not present, probably due to the general background. But within the experimental limitations the agreement is reasonable. Finally it must be remarked that the same procedures as for the dark adapted case were followed with the same results leading to the same conclusions.

### C. DARK ADAPTED NEGATIVE FLASHES

Another amazing effect concerning the mechanism of facilitation is found using negative flashes.

The experiment was done in the following arrangement.

The subject fixated a dim red fixation light which was presented monocularly. The negative flashes were presented ipsilateral 5° peripheral in the following way. Two „pinlites” with a distance of 4° were switched on for 3 seconds. After 1½ second either one or both or neither of the pinlites was switched off for 30-40 msec. The sequence of the stimuli was generated with a modulo 2 shift register, with a period of 31.

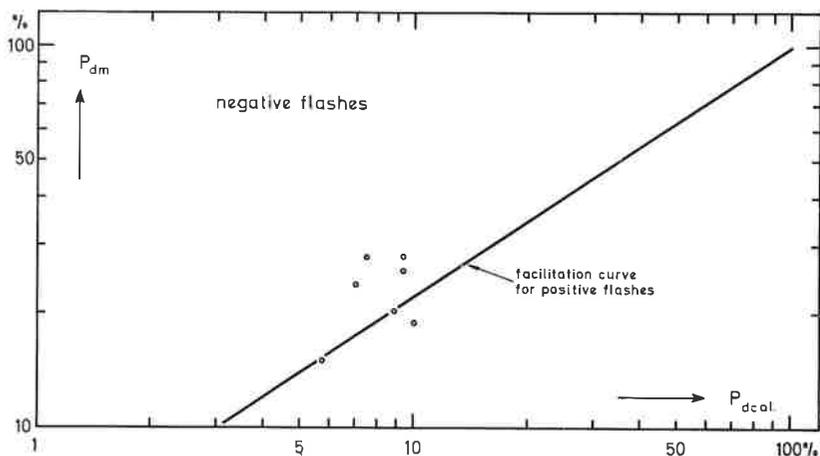


Fig. 23. Facilitation of negative flashes outside area of summation.

The pinlites were switched off for 3 seconds, after the 3 seconds of light thus each measurement costed 6 seconds.

The subject reported if he had seen no, one or two negative flashes and these data were used. The results of the experiment are presented in Fig. 23.

It is surprising indeed that negative flashes facilitate one another also. It demonstrates that at the level where the decisions are made positive flashes are as significant as negative flashes. It is probably pure coincidence that the experimental points lie close to the curve for the positive flashes, the most important thing that matters is that the facilitation occurs and that the origin of the mechanism with its noise must lie in the visual system.

#### D. TIME DEPENDENCE OF THE FACILITATION.

A final question about the mechanism of facilitation that will be answered here to some extent concerns the timing of the flashes. So far all experiments were done with simultaneous flashes, and it is of interest to know how long subliminal flashes can be stored in the retina.

The experiment under C was modified in such a way that two positive flashes with a duration of 20 milliseconds and different timing could be given. The intensity of the flashes was such, that the chance of detection of flash A was about  $2\frac{1}{2}$  times the chance of detection of flash B. Now the time dependence of the facilitation was measured as a function of the delay between the two flashes and the order of sequence.

The following formula was used as a measure of the degree of facilitation:

$$\beta = \frac{P_{am} - P_{acal}}{P_{af} - P_{acal}}$$

In this formula  $P_{am}$  is the measured chance of perception of both flashes,  $P_{acal}$  the calculated chance of perception of both flashes on basis of:  $P_{acal} = P_a P_b$  and  $P_{af}$  the calculated chance of detection of both flashes from the facilitation model.

Thus if the timing is such that the facilitation is complete,  $\beta$  is equal to 1.

Absence of facilitation is indicated by  $\beta = 0$ .

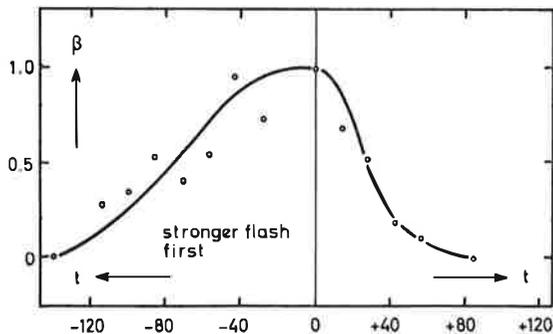


Fig. 24. Time dependence of the facilitation effect.

In Fig. 24 the value of  $\beta$  as a function of the delay and the order of sequence is given. For the negative times the stronger flash is preceding the weaker one. As is seen in the figure the effect is asymmetrical. It is indicated clearly that a stronger subliminal flash is stored longer than the weaker flash, as one would expect.

A very interesting fact which corroborates the model is that the subject is unable to tell which flash was presented first, even if the flashes are 40 milliseconds apart. As soon as the proper sequence can be given, the facilitation mechanism is no longer present, and  $\beta = 0$ .

## VISUAL THRESHOLD DURING EYEMOVEMENTS, THE 'DIP' EXPERIMENT

### A. INTRODUCTION AND MATHEMATICAL CONSIDERATIONS

The 'dip' experiment concerns the variations in visual sensitivity due to eyemovements.

The apparatus and experimental method for this experiment is described in Chapter II. The four different stimuli were mounted in a rotating disk, and they were selected randomly. One of the four stimuli was usually blank to check for and, if necessary, compensate for false alarms. The subject responded by means of a pushbutton. The time between the presentation of the stimulus and the onset of the eye movement was recorded also during the experiment. Thus for each stimulus the chance of perception as a function of time in relation to the onset of the eye movement could be plotted. A typical curve is given in Fig. 25.

The goal of the experiment is not, of course, to measure only the various chances as a function of time, but to give a description of the sensitivity of the eye versus time.

This is an often occurring problem in psychophysical experiments in which a continuous curve has to be computed on basis of a limited number of alternative answers. By making several plausible assumptions and leaning heavily on methods in use by the detection theory, developed first for radar applications and extended to psychophysical problems by Swets and Tanner, this problem can be solved (33, 34).

In general and particularly in the light of the findings of Chapter III

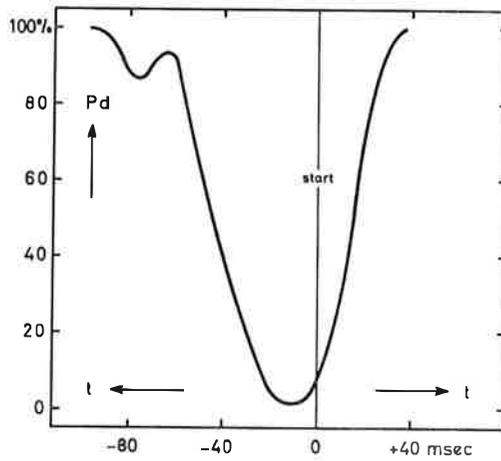


Fig. 25. The chance of detection  $P_d$  as a function of time from the onset of an eye movement.

it is natural to assume a stochastic activity in the visual system, which is not related to external conditions for the dark adapted case (56). In case a background is provided for, the statistical fluctuations of this background will be transduced by the eye into statistical fluctuations in the nervous activity, which activity adds with the autonomous activity. This activity finds its origin in the fluctuations in the firing rates of the various nerve cells and receptor cells in the retina and possibly its relay-stations when the eye is dark adapted, and in the transformed statistical fluctuations of the background if a background is provided for. This noise  $R(t)$  has a density function  $\varrho(r)$  in which  $r$  is a variable directly related to the strength of the stimulus, an assumption justified for small signals or small differential signals. All measurements will be weighted with the same non linear function if the mechanism is not linear. The input signal itself will also have its fluctuations in energy due to quantum effects. For the moment however we think these fluctuations negligible in comparison to the noise of the visual system. Thus if a stimulus is presented on a background, fluctuations in the background intensity will after their transformation be considered as noise of the system. The threshold of the eye is thought to be described by a sensitivity function  $A(t)$  which varies with time if the eye is going to move, and superimposed on this, the noise function  $R(t)$ .

As stated before this noise function itself is not related to the changes in the threshold function  $A(t)$ . It is a pure 'white' noise – the bandwidth is of course restricted by the nerve elements – and its density function satisfies the relation:

$$\int_{-\infty}^{+\infty} \rho(r) dr = 1$$

In case a stimulus with strength  $s$  – in neural excitation units or related to this, in physical intensity units – is presented at  $t = t_1$  this will lead to a perception if:

$$s + R(t_1) \geq A(t_1) \quad (1)$$

Thus the chance of perception of a stimulus with intensity  $s$  is given by:

$$P(s, t) = \int_{A(t)-s}^{\infty} \rho(r) dr \quad (2)$$

This is illustrated in Fig. 26.

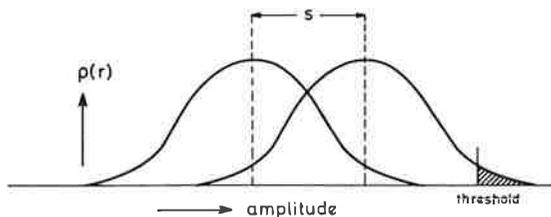


Fig. 26. The density distribution  $\rho(r)$  is shifted to the right by a stimulus  $s$ . The area to the right of the threshold gives the chance of perception.

The chance for a false alarm is given by:

$$P(o, t) = \int_{A(t)}^{\infty} \rho(r) dr$$

This chance is negligible – less than 2% – as is found by using one black stimulus. The variables that are measured in the experiment are the  $P$  and the  $s$ , and  $A(t)$  and  $\rho(r)$  are the functions we want to know.

We proceed in the following way, we compute the derivate of  $P(s, t)$  versus  $s$  and versus  $t$  and find, provided  $A(t)$  is a differentiable function:

$$\frac{\delta P(s,t)}{\delta s} = \varrho[A(t) - s] \quad (3)$$

$$\frac{\delta P(s,t)}{\delta t} = -A'(t) \varrho[A(t) - s] \quad (4)$$

Eliminating  $\varrho[A(t) - s]$  we find:

$$A'(t) = -\frac{\delta P/\delta t}{\delta P/\delta s} \quad (5)$$

and finally:

$$A(t) = -\int \frac{\delta P/\delta t}{\delta P/\delta s} dt \quad (6)$$

Thus even without knowing  $\varrho(r)$  it is possible to find  $A(t)$ . Once  $A(t)$  is found the  $\varrho(r)$  can be calculated from equations 3) or 4). As long as the  $\delta P/\delta t$  and  $\delta P/\delta s$  are well defined the problem is solved. This stands to reason. Only in the regions in which  $P(s,t)$  varies with  $s$  and  $t$  we may expect to yield some information about  $A(t)$  and  $\varrho(r)$ , and it is therefore necessary to adjust the intensities in the experiment in such a way that the maximum of information is obtained.

How one should perform the experiments is now easily seen. In one session one should measure  $P(s,t)$  for various slightly different values of  $s$  with a proper adjustment of the background, such that the  $P(s,t)$  starts below 100% for the lowest  $s$ , and  $P(s,t)$  never gets to zero for the strongest  $s$ . This implies usually that three to four different stimuli must be used, with a difference of 10 to 20 percent in intensity. A typical result of an experiment with two different stimuli is given in Fig. 27.

The stimulus was a flash with a duration of .6  $\mu sec$  and a diameter of  $4^\circ$ , presented  $7^\circ$  peripherally. The background luminance was 2,7  $cd/m^2$ .

The fixation lights were 14 degrees apart, and the flash was given  $4^\circ$  higher than the fixation lights, to prevent interaction with either the fovea or the blind spot. The difference  $\Delta s$  in luminance between the two stimuli was 10%,  $\Delta s = 0,1 s$  and they were presented monocularly. These data may be used nicely although the  $P(s,t)$  is 100% for the stronger of the two stimuli some 50 msec before the start of the eyemovement.

The calculation of  $A(t)$  and  $\varrho(r)$  from equation 6) and 3) respectively is a time consuming matter. The statistical fluctuations in  $P(s,t)$  also cause the  $A(t)$  curve to be quite irregular.

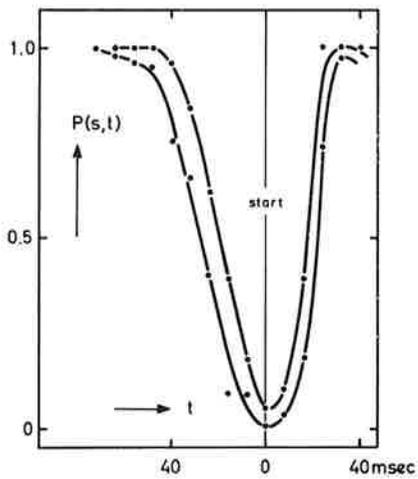


Fig. 27. Two detection curves with a difference in stimulus strength of 11%.

The best way to find  $A(t)$  and  $\varrho(r)$  is graphically. Smooth curves representing  $P(s,t)$  are drawn in order to do this. Then a staircase like function is drawn between the two  $P(s,t)$  curves as is illustrated in Fig. 28.

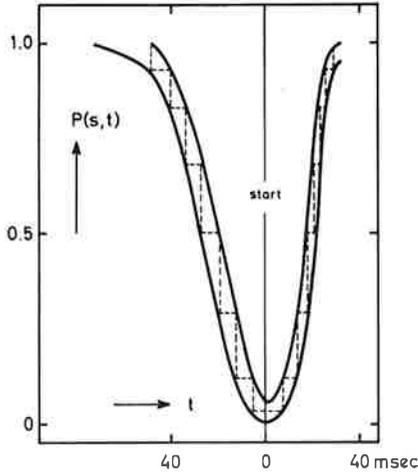


Fig. 28. A staircase is drawn between the detection curves. The retinal sensitivity  $A(t)$  and the density distribution  $\varrho(r)$  with the exact location of the threshold can be found from this staircase.

Both  $A(t)$  and  $\rho(r)$  can be found directly from this staircase. Each vertical bar represents  $\delta P/\delta s$  and each horizontal bar gives the length of time that is needed for  $A(t)$  to increase  $\Delta s$ . Thus plotting the successive  $\delta P/\delta s$  parts one obtains the density distribution of the noise, and  $A(t)$  can be plotted by using the length of the horizontal bar for a  $\Delta s$  increase. The results of this procedure are given in Fig. 29.

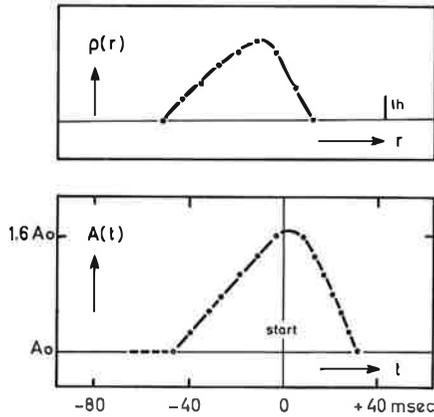


Fig. 29. The density distribution  $\rho(r)$  with its threshold  $th$  and the sensitivity function  $A(t)$  as constructed from Fig. 28.

It is possible also to find  $A(t_0)$  for the resting eye because both  $s$  and  $\Delta s$  are known. This is indicated in the figure, as  $A(t_0)$  is given by the location of the threshold. It is interesting to notice that  $A(t)$  is not very close to the  $\rho(r)$  density distribution, and that this density distribution is skew, and resembles – as it should – the noise density distribution found in the facilitation experiment.

Further remarks and conclusions about the results will be given later in this chapter. This introduction served only to introduce the method of presentation of the experimental data.

## B. THE EXPERIMENTAL RESULTS

§ 1. In the dip experiment many parameters have to be considered, with the goal to give a functional relationship between the parameters and the threshold function.

The following parameters were considered:

The chance of perception versus time.

The position, intensity, size and colour of the flash.

Binocular or monocular presentation of the flash.

The intensity of the background.

The angle of the eye movement.

The origin of the eye movement.

In each session the chance of perception versus time was measured with respect to the onset of the eye movements for four different flash intensities. The flash was presented monocularly on a fixed background, and during the experiment the position, size and colour of the flash was usually not varied. One flash was a blank one, and the other three flashes had differences in intensities between 5 and 10 percent depending upon the experimental conditions, such that the chance of perception varied between 100% and 0%, and two of the  $P_{det}$  curves could be used to calculate the sensitivity. The angle of the eye movement was fixed on 15 degrees in these experiments. The influence of the angle on the suppression mechanism will be considered later in this chapter in a somewhat different arrangement.

It was found that the suppression mechanism of both eyes was the same by presenting the test flash monocularly to either of the eyes, which shows that the mechanism has an identical influence on both eyes.

The origin of the eye movement is determined by whether the eye movement was intended or not. The eye movements generated by a change in position of the fixation lights are clearly intended eye movements.

In order to check if some generalities found for the intended eye movements were valid also for eye movements of different origin an optokinetic drum was installed which served to generate the optokinetic nystagmus during which the threshold was measured. The results of this experiment are presented at the end of this chapter.

A final remark about the position of the flash of which it was said that it was held constant. By this is meant that the flash unit was not moved but it implies of course that the flash is presented  $7\frac{1}{2}$  degrees to the left when the eye fixates the right fixation light, and  $7\frac{1}{2}$  degree to the right in case the other fixation light is on. It was found that the experimental results of the two positions were the same – the difference in retinal sensitivity was nihil for our subjects – and the data of the two different fixation positions were added and treated together. It was checked regularly if this operation was permitted and to our satisfaction this was found to be the case.

§ 2. The first series of experiments concerns the chance of perception of a flash with a diameter of 7 minutes of arc at various background levels. For the sake of clearness we shall once more perform the mathematical manipulations given in A and derive an estimate of the error. In Fig. 30<sup>a</sup> the  $P(s,t)$  curves for subject A.B. are given. The subject was dark adapted and the difference in intensity of the two stimuli was given by  $\Delta S = 0.12 S$ .

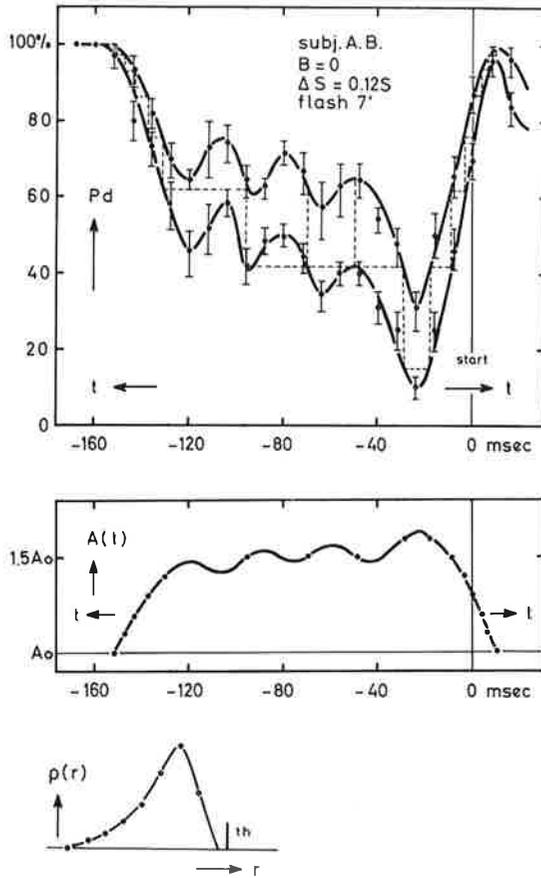


Fig. 30. Two detection curves with the associated staircase function, from which

$A(t)$  and  $\rho(r)$  are constructed.

The oscillations in sensitivity are significant and are therefore added to the  $A(t)$  function with the correct amplitude, as can be estimated from the height of the vertical step. The four experimental points prior to the start were used in the calculation of Fig. 31.

The rapid oscillations are way out of the uncertainty of the experimental points as can be seen in the graph. The smooth curves are drawn already, and between the smooth curves a staircase is drawn, which gives an estimate of  $\delta P/\delta t$  and  $\delta P/\delta s$ .

The  $A(t)$  curve from Fig. 30<sup>b</sup> is constructed from this staircase function. The vertical steps coincide with the steps in sensitivity.

The noise density distribution  $\varrho(r)$  can be constructed by plotting the successive heights of the vertical steps, which is done in Fig. 30<sup>c</sup>. As it is known that  $\Delta s = 0.12s$ , the location of the static threshold must be between 8 and 9 steps from the first point in the  $\varrho(r)$  curve. This location is also given in Fig. 30<sup>e</sup>.

The standard deviations in the original  $P(s,t)$  curves are calculated from the experiment and are given by:

Delay  $x_i$ :  $N_1$  stimuli seen,  $N_2$  stimuli missed

$$\text{Chance of perception: } P = \frac{N_1}{N_1 + N_2}$$

$$\text{Standard deviation in } P: \sigma_P = \sqrt{\frac{P(1-P)}{N_1 + N_2}}$$

The standard deviation of  $p$  varied between 5% and 15% absolute accuracy in practical all experiments such that on the average:

$$P = \bar{P} \pm 0.1$$

In Fig. 30 it can be seen that the oscillations in sensitivity which are clear in the  $P(s,t)$  curves have a smaller amplitude in the  $A(t)$  curve. This is due to two effects. In the first place the vertical step at the level of the oscillation is quite big, which means that small differences in stimulus strength yields large differences in  $P(s,t)$  and conversely that the variations in  $A(t)$  are smaller than those in  $P(s,t)$ . Secondly the choice in  $\Delta s$  influences the precision with which one can draw the staircase function. A compromise is necessary here as too small differences in intensity necessitates a much preciser measurement of the two individual  $P(s,t)$  curves, as will be shown in the following analysis.

We now shall calculate an estimate of the precision in the number of steps of the staircase under the assumption that the staircase is constructed between two straight lines with only slightly different angles in which each of the lines is given by four experimental points, such as the last part of the  $P(s,t)$  curve in Fig. 30.

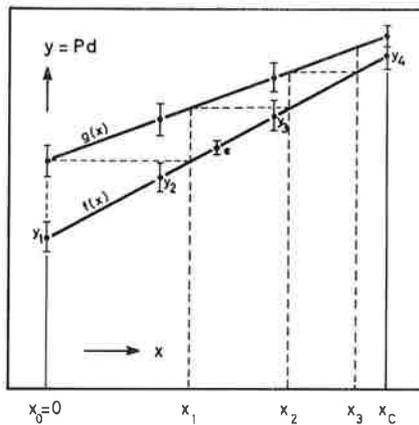


Fig. 31. The calculation of the standard deviation in the number of steps of the staircase for the steep part of Fig. 30.

Thus given two curves  $f(x) = ax + b$  and  $g(x) = cx + d$ .

$$\text{We have: } x_{n+1} = \frac{c}{a} x_n + \frac{d-b}{a}$$

$$\text{Thus: } x_n = \frac{d-b}{a} \cdot \frac{(c/a)^n - 1}{c/a - 1}$$

The value  $x_c$  is approximated best for a certain  $n_c$  for which we can write:

$$n_c = \frac{\log \left[ \frac{c-a}{d-b} \cdot x_c + 1 \right]}{\log \left[ \frac{c-a}{a} + 1 \right]} \approx \frac{ax_c}{d-b}$$

This formula holds also for  $c = a$ .

Now we draw the lines  $f(x) = ax + b$  and  $g(x) = cx + d$  according the following prescription:

If the four points  $y_1, y_2, y_3, y_4$  of  $f(x)$  are given we have for  $a$ :

$$\begin{aligned} a &= \frac{1}{10} \left[ y_2 - y_1 + y_3 - y_1 + y_4 - y_1 + y_3 - y_2 + y_4 - y_2 + y_4 - y_3 \right] = \\ &= \frac{3y_4 + y_3 - y_2 - 3y_1}{10}. \end{aligned}$$

Here the influence of the points  $y_i$  on  $a$  are weighted according their distance. The weight increases linearly with their horizontal distance. Assuming that all experimental points have the same standard deviations  $\sigma$  we find for  $a$ :

$$a = \frac{3 y_4 + y_3 - y_2 - 3 y_1}{10} \pm \frac{\sqrt{20}}{10} \sigma.$$

To find  $b$  we first calculate the point  $e$  given by

$$e = \frac{y_1 + y_2 + y_3 + y_4}{4} \pm \frac{\sigma}{2}$$

From the values of  $a$  and  $e$  we can find  $b$  as:

$$b = e - \frac{3}{2} a \pm \frac{\sqrt{70}}{10} \sigma$$

For  $f(x)$  we now have the following points:

$$\begin{aligned} y_1 &= 0,1 \pm 0,05 \\ y_2 &= 0,27 \pm 0,05 \\ y_3 &= 0,46 \pm 0,05 \\ y_4 &= 0,70 \pm 0,05 \end{aligned}$$

Thus  $a = 0,2 \pm 0,02$

and  $b = 0,08 \pm 0,04$

And for  $g(x)$ :

$$\begin{aligned} y_1 &= 0,31 \pm 0,05 \\ y_2 &= 0,5 \pm 0,05 \\ y_3 &= 0,65 \pm 0,05 \\ y_4 &= 0,88 \pm 0,05 \end{aligned}$$

$c = 0,18 \pm 0,02$

$d = 0,31 \pm 0,04$

For  $n$  we now find:

$$n = \frac{3 a}{d - b} \pm \frac{3 a}{d - b} \cdot \sqrt{\frac{\sigma_a^2}{a^2} + \frac{\sigma_{d-b}^2}{(d - b)^2}} = 3 \pm 0,8.$$

This is in good agreement with  $n = 3$  found graphical in Fig. 31.

From this calculation we can draw the conclusion that the error in the number of steps is maximal about 30%. It will be much less usually

because the number of steps can be calculated for the decreasing part of  $P(s,t)$  and for the increasing part.

This estimate does not imply that the oscillations are insignificant. It was remarked already that the oscillations are significant in the  $P(s,t)$  curve, and therefore they are significant here also. Only the level of the calculated  $A(t)$  on which these oscillations occur may be one step wrong.

From the formula of  $n$  it is seen that the estimate of  $n$  is better for greater values of  $d - b$ . This is the reason that  $P(s,t)$  curves were measured for such different intensities that the curves were not too close together.

§ 3. The first series of experiments concerns the chance of perception of a flash with a diameter of 7 minutes at various background levels. As remarked in A the results will be given in the form of  $A(t)$  in which  $A(t)$  gives the threshold function of the eye, with respect to the onset of the eye movement and a  $\rho(r)$  which describes the density function of the noise of the detection model.

The following background intensities were used.

7,8	cd/m <sup>2</sup>
1,6	cd/m <sup>2</sup>
0,08	cd/m <sup>2</sup>
0,007	cd/m <sup>2</sup>

In Fig. 32 and Fig. 33 the  $A(t)$  for two subjects is given for the different background intensities.

The horizontal axis is the time axis with reference to the onset of the eye movement. The vertical axis gives the threshold level in intensity units normalized to the same chance of perception level. Thus if  $A(t)$  is equal to 1,4  $A_0$  this means that the intensity of the flash has to be increased with a factor 1,4 in order to get the same chance of perception as for the static condition.

The variations in the threshold level are rather restricted as can be seen in the figure, and it is not possible to speak of a retinal shut off. It can be stated taking all curves together that the rise in threshold or at least the influence of the eye movement on the threshold starts about 100 msec before the onset of the eye movement.

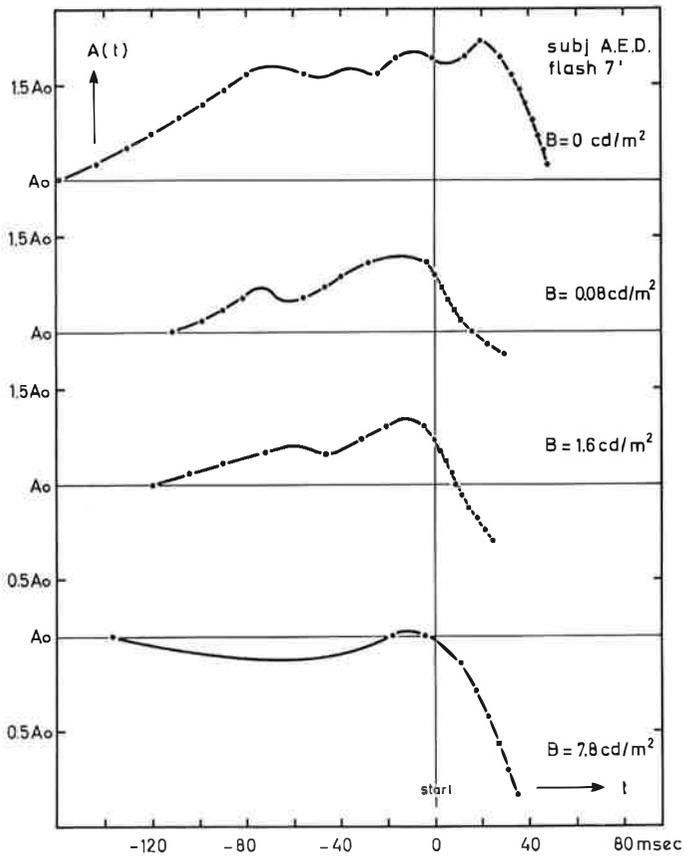


Fig. 32. The dip in sensitivity for a flash with a diameter of 7' as a function of the adapting background for subject A.E.D.

The rise in threshold is maximal for the dark adapted eye, and it is here that a periodic oscillation occurs. These oscillations in sensitivity were found for all subjects for the 7 minutes flash in the dark adapted eye. The period of the oscillations is 28 to 37 msec for the different subjects. The regular oscillations disappear and when the background is presented and irregular bumps occur.

This suggests that the sensitivity of the retina oscillates in the dark adapted eye, and that the onset of the eye movement locks these oscillations to external events, through which one can measure the oscillations. It is also possible that during the oscillations the sensitivity is constant, and that the noise of the system performs almost

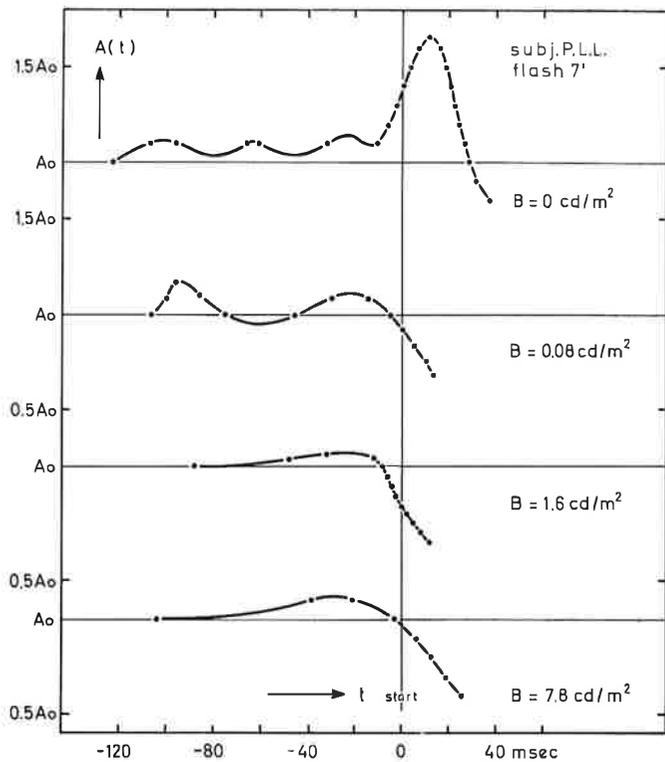


Fig. 33. The dip in sensitivity for a flash with a diameter of 7' as a function of the adapting background for subject P.L.L.

periodic oscillations. This means that successive samples are dependent. As the amplitude of these oscillations is only small with respect to the  $\varrho(\tau)$  function this could very well be the case. This matter will be dealt with in more detail in chapter VI.

The two sets of curves have two general tendencies. The first is the moment on which the  $A(t)$  reverses its time course. In the dark adapted case this moment occurs 18 to 24 msec after the onset of the eye movement, while the light adapted eye reverses its sensitivity at about minus 8 msec with respect to the onset of the eye movement.

The second tendency concerns the rise in threshold. For increasing background intensities this rise becomes less, while the reversed part during which the sensitivity increases is about constant. Particularly

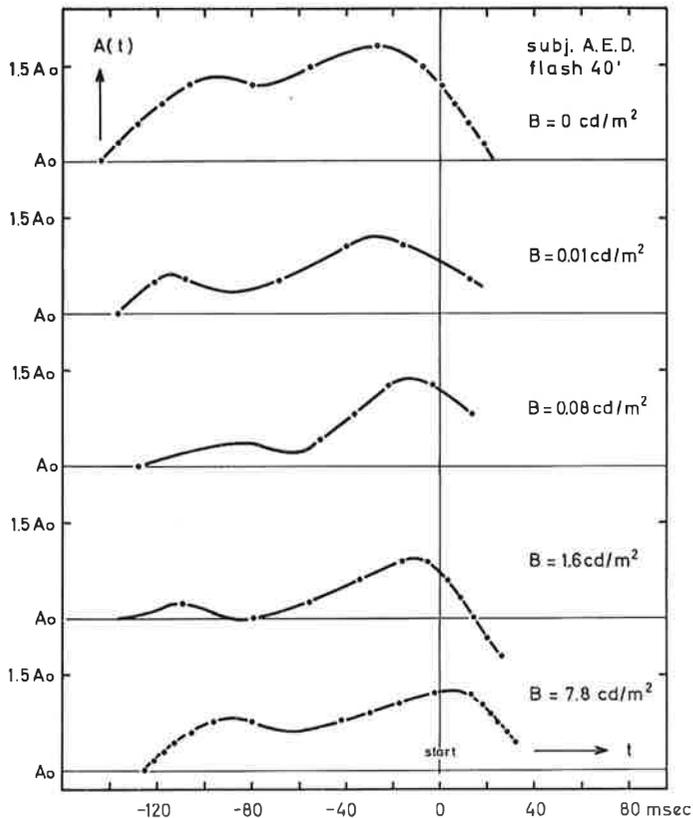


Fig. 34. The dip in sensitivity for a flash with a diameter of  $40'$  as a function of the adapting background for subject A.E.D.

the fourth curve in Fig. 33 shows that there is no dip at all, but a peak in sensitivity. It must be borne in mind when looking at positive times that the eye has already started its movement, and that the flash is presented to a different part of the retina, which might influence the chance of perception. To compensate for this effect the sensitivity of the retina at the various spots was measured, and it was found that in this rather restricted area the sensitivity varied to little to be of importance.

This result was more or less expected as the reversed part of  $A(t)$  starts at different moments for the different backgrounds, with the eye movement onset as a reference. Particularly this applies in cases in which the decrease of  $A(t)$  starts before the onset of the eye movement.

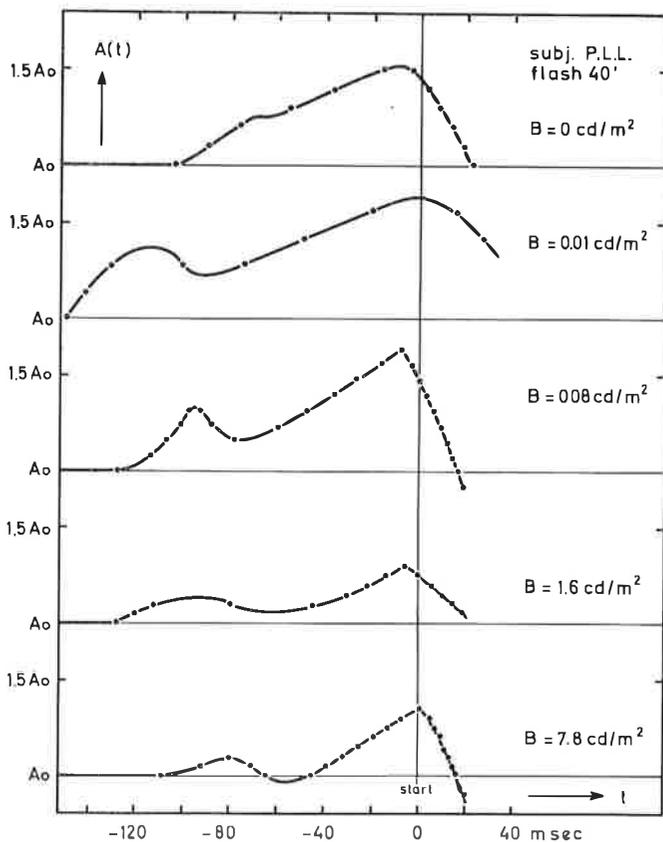


Fig. 35. The dip in sensitivity for a flash with a diameter of 40' as a function of the adapting background for subject P.L.L.

With the same set of background intensities the experiment was done with flashes with a diameter of 40 minutes. The angle of the eye movements was again 15 degrees.

The results of this experiment are given in Fig. 34 and 35.

There are several differences with the set of curves for the 7' flash. In the first place it is seen that the regular oscillations have disappeared for the dark adapted case. This indicates that the autonomic oscillatory retinal noise extends over a limited area, and if a flash greater than this area is presented the various units will cancel one another. It must be remarked when reflecting over this effect that even during fixation the eye has its tremor of several minutes of arc, while the size

of the fixation lights is 10 minutes. Due to differences in position of the eye when the flash is presented the effect of the local oscillations will be smoothed and it is therefore very likely that oscillations found in the  $A(t)$  for the 7 minutes stimuli are already to some extent integrated, and that the real amplitude of the oscillations is much greater than is found in the experiment.

From these data it is difficult to give a measure of the extent of the local oscillations, but it could be any value lower than say 20 minutes. The increase of the threshold function is somewhat higher for the 40 minutes stimulus, and later experiments confirm that the rise in threshold one finds increases with increasing flash diameter. In C this effect will be considered.

So far the density distribution of the noise has not been considered. In Fig. 36 and Fig. 37 the  $\varrho(r)$  is given for the experiments described in par. 2 and 3. The  $\varrho(r)$  distributions were standardized in this sense that the width of the distribution was made equal for all experiments. From this scaling the position of the threshold for all experiments could be compared, and the relative position is given in the figure. Now it is possible to link the various parameters together.

In Fig. 38 the flash energy as a function of the background for the same chance of perception is given.

It is clear that the range of the backgrounds extends to intensities in which the de Vries-Rose (35) law does not apply any more, in agreement with similar experiments by v. d. Brink (36).

The curve presented in Fig. 38 is in agreement with the curve found by other experimentors (36). The  $\Delta B$  threshold value is indicated in the figure, and the relative energy of the flash for the dark adapted eye. Now that the strength of the threshold energy for the flashes is known as a function of the background and the position of the threshold with respect to the density distribution  $\varrho(r)$  as a function of the background it is possible to give the width of the noise density distributions as a function of the threshold. This is done in Fig. 39.

It is clear from this figure that the noise in the system increases linearly with the square root of the background, and that it can be described as the transformed fluctuations in the background. This applies even up to the intensities for which the de Vries-Rose law is no longer valid. The retinal noise level for the dark adapted eye can be calculated also and this value is in good agreement with other experimental findings as established by the just visible  $\Delta B$  method (36). In Fig. 36 and Fig. 37 it can be seen that the threshold is optimal for

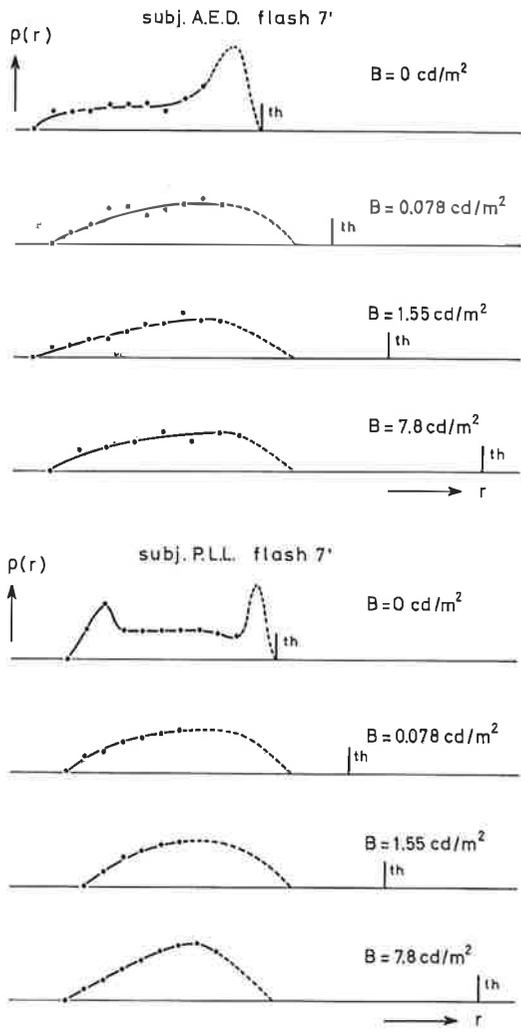


Fig. 36. The noise density distribution  $\rho(r)$  and its threshold  $th$  as a function of the background for a flash of 7 minutes of arc.

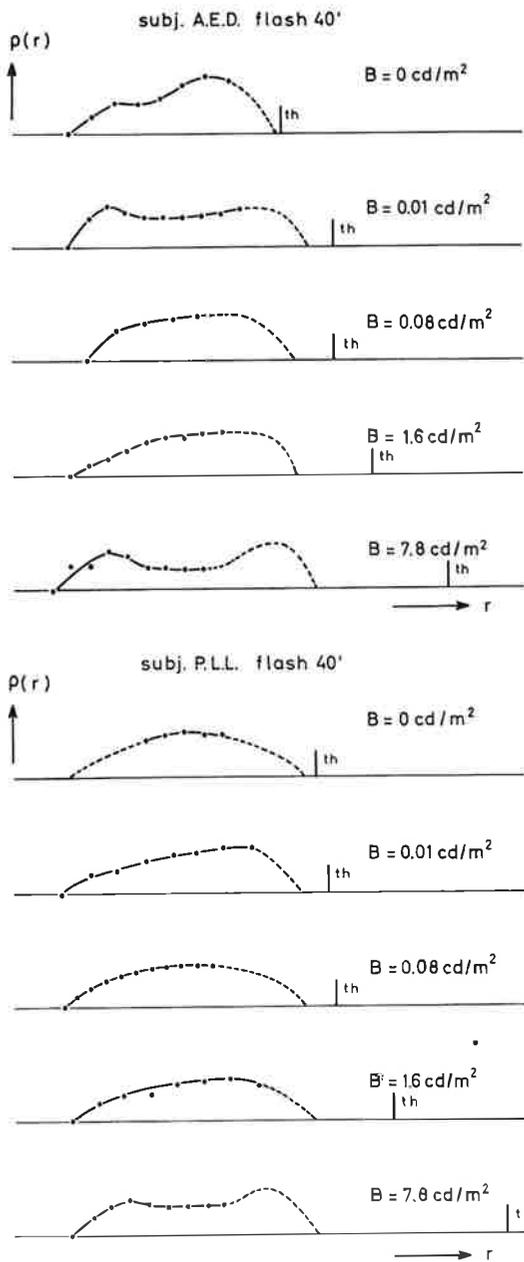


Fig. 37. The noise density distribution  $\rho(r)$  and its threshold  $th$  as a function of the background for a flash of 40 minutes of arc.

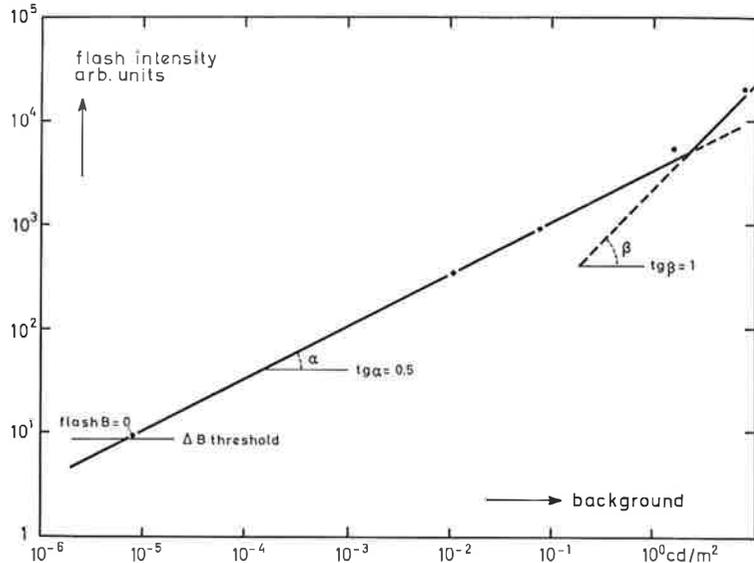


Fig. 38. The flash energy as a function of the adapting background for a fixed chance of perception.

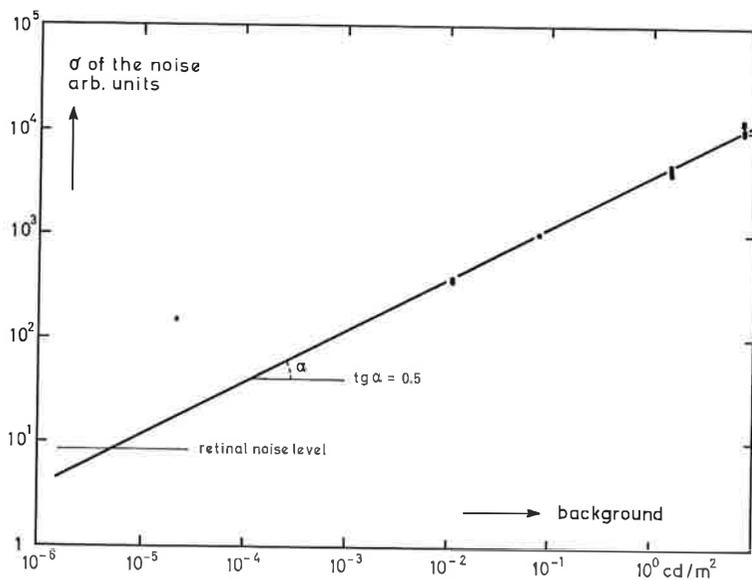


Fig. 39. The width of the noise density distribution as a function of the adapting background.

low background intensities, such that a small signal has a reasonable chance of perception, while the chance of a false alarm is negligible. The retina gives up her economy for higher background intensities, and the thresholds runs away from the density distribution. This effect just causes the transition from the de Vries-Rose law to the Weber-Fechner law.

It is possible to construct frequency of seeing curves as a function of the background and target size from the density distribution and the threshold value. In case the threshold lies close to the density distribution the steepness of the fos curve is mainly determined by the particular shape of the density distribution.

The thresholds is further from the density distribution for higher background intensities and here the steepness is determined chiefly by the distance of the threshold to the density distribution.

This is the only generality we want to consider at this moment. The FOS curve becomes steeper as the background intensity increases.

The variations between the different  $\varrho(r)$ 's are such that it is premature to attach theoretical significance to the steepness of various FOS curves.

### C. THE INFLUENCE OF THE SIZE OF THE FLASH

It was remarked already in section B that the rise in threshold for the 40' stimulus was greater than the rise for the 7' stimulus.

This is a general feature, that increasing the size of the flash lead to an increase of the steepness and depth of the dip.

This result is in agreement with our expectations, which we can formulate in the following manner.

A flash of a size greater than an area of summation can be divided into several subflashes each of the size of an independent area of summation. This independent area of summation has a size of at least an area of summation, but it is probably much larger. The independence indicates that the different areas do not summate their stimulations. If at one of these subareas the flash intensity is such that it will lead to a perception, the other areas will decrease their threshold due to the effect of facilitation, and the total flash will be seen. If we assume that the sensitivity of the retina is constant in the area over which the flash is presented and if the chance of perception in a sub-area is given by  $p$ , the chance for perception of the greater flash is found to be  $P(t) = 1 - (1 - p(t))^k$  if the greater area consists of  $k$  subareas.

It can be seen from this formula that small changes in  $p(t)$  will cause great changes in  $P(t)$ . The exact calculation of the effect requires knowledge about both the FOS curve for very small chances of perception and the number of independent areas. As both these quantities are unknown in this experiment, as it is impossible to gather data at such low chances of perception without contamination due to false responses, and while the independent area was introduced without any experimental justification, it is clear that the results of this experiment are hard to interpret quantitatively, and this experiment was therefore discontinued. Thus we shall satisfy ourselves by presenting only the two  $A(t)$  curves for a flash of two degrees in diameter and a flash of 40 minutes. See Fig. 40.

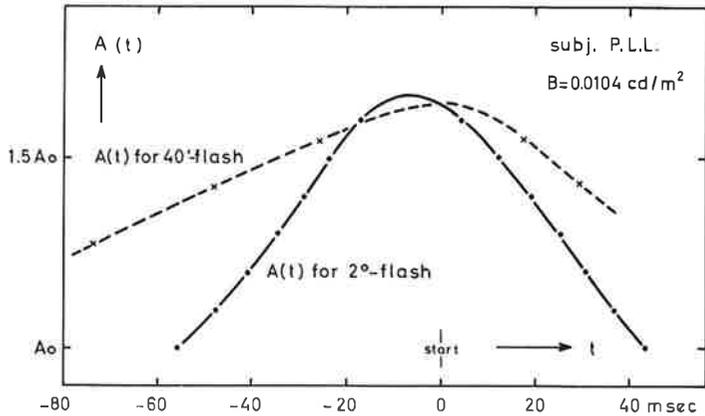


Fig. 40. The dip in retinal sensitivity  $A(t)$  for two flashes of different size.

#### D. THE POSITION OF THE FLASH

By presenting the flash at a position outside the center of the two fixationlights the threshold function of the retina can be measured as a function of the location on the retina.

The flash unit was moved for this purpose such that the flash was given at an angle of 5 degrees with the left fixation light and 10 degrees with the right fixation light as indicated in Fig. 41.

The position was reversed after the experiment and the experiment was repeated. The main reason for this experiment was to find whether the sensitivity of the retina varies synchronously over the retina, or that the sensitivity could be described as some kind of a travelling

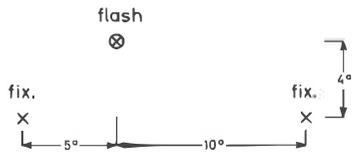


Fig. 41. The flash unit is shifted to the left over  $2.5^\circ$ .

wave over the retina such that adjacent parts were influenced successively.

It was found in C that the steepest change of perception curves were found with flashes of appreciable diameter and as the main question here concerns the maximum of the dip, this experiment was done with flashes with a diameter of 50 minutes.

The results of two experiments is given in the figures 42 and 43.

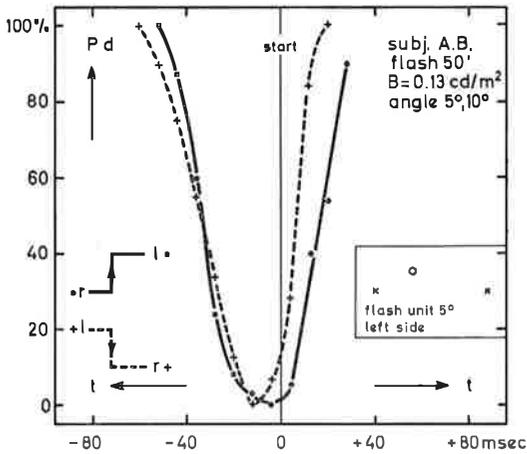


Fig. 42. The detection curves for two different positions of the flash.

It can be seen from this figure that within the error of the experiment the maxima coincides for spots on the retina five degrees apart.

From the preceding experiments it was already understood that the thresholds for locations  $7\frac{1}{2}$  degrees to the left and to the right occurred simultaneously and this makes it very plausible that the sensitivity of the retina varies synchronously over the whole retina or, put differently that the threshold mechanism does not depend on the retinal location. Once more this suggests the cortical character of this phenomenon. It

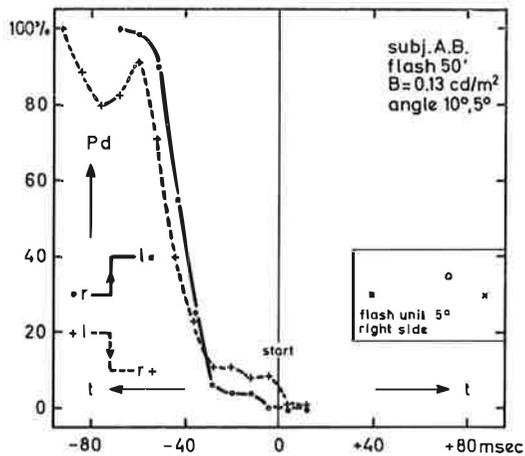


Fig. 43. The detection curves for two different positions of the flash.

is not a retinal wave which spreads over the retina, but a relaystation in which the transmission is reduced.

#### E. THE COLOUR OF THE FLASH

The next question concerns the possible colour dependence of the threshold mechanism.

This dependence is measured by using colored flashes with matched intensities as in the facilitation experiment. The stimuli used were flashes with a diameter of 40 minutes and two different colors, red for the cones, and green for the rods. The results of this experiment are given in Figs. 44 and 45.

Here the chance of perception is given as a function of time.

As the red and the green stimuli were measured during the same session it was not possible to insert enough slides to measure the chances of perception for stimuli varying in intensity.

The results however have such a remarkable likeness, that this experiment is sufficient to show that both the rods and the cones are governed by the same threshold mechanism, which affects both systems simultaneously. In a way this is also a verification of the experiment concerning the position of the flash that the rise in threshold occurs at the same moment for both systems.

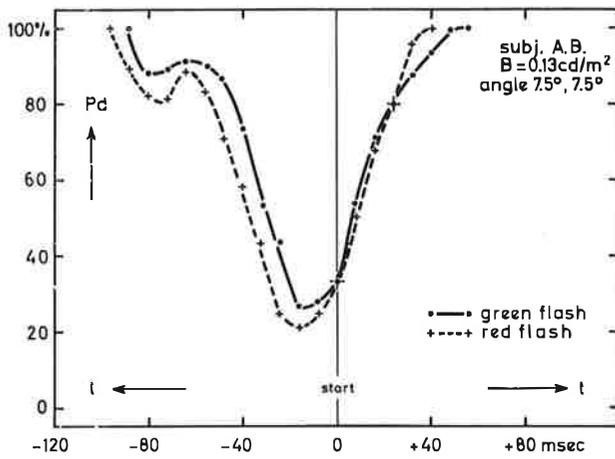


Fig. 44. The detection curves for two different colours of the flash.

#### F. THE ORIGIN OF THE EYE MOVEMENTS

The conclusion one can draw from the experiments in B, C, D and E are that the retinas of both eyes vary in sensitivity when an eye movement has to be made. Colour, size, position, and monocular or binocular presentation of the flashes does not affect the result. The influence of the background is not great either, because a rise in background intensity of the order of  $10^6$  does not yield spectacular

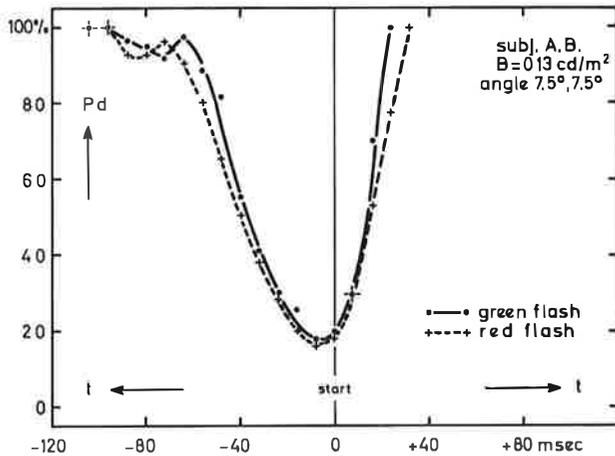


Fig. 45. The detection curves for two different colours of the flash.

differences in the measured chance of perception. The eye movements considered so far were intended eye movements, as they were the response of the subject to a change of position of the fixation lights. The question arises if this suppression mechanism found for the intended eye movements will be activated also by eye movements of different origin.

The suppression was found first by Ditchburn and Fender for the flicks (13) of which man is not even aware. As our apparatus was not suited for the measurement of eye movements to this degree of resolution another method was sought to generate eye movements of unintended character.

A solution was found by replacing the two fixation lights by an optokinetic drum.

The subject was instructed to neglect the drum, but in spite of his efforts his eyes start to follow the drum, followed by a quick swing of the eye in the reversed direction. The amplitude of the eye movements depends on the experimental conditions, such as the width and intensity of the spacing of the bars on the drum, and in our experiment the movement was of the order of several degrees.

The origin of the optokinetic nystagmus is of great importance, to decide the location of the threshold mechanism, but this origin is still partly unknown. The slow phase is elicited by the medial and Bechterev's nuclei of the 8th nerve (Weale 39).

The pathway of the rapid phase is unknown. The suggestion that the proprioceptors of the eye muscles initiate the action was disproved by Klein (40), who demonstrated that even after local anesthesia the optokinetic nystagmus does not change.

In animals it was found that after section of the brain at the level of the oculomotor nucleus the nystagmus is still present (41).

In our experiment the rapid phase of the optokinetic nystagmus was considered as the synchronizing effect. The question was if there was a difference in threshold which was correlated in time with the rapid phase.

The drum was presented binocularly, and the flash as usual monocularly random in time.

The recorder was run at high speed to get better time resolution, and the chance of detection as a function of the onset of the rapid phase was measured. As the amplitude and position of the optokinetic nystagmus varied during the experiment possible variations in retinal sensitivity were of minor importance. The subjects task is extremely

difficult in this experiment, as he has to fixate, is brought into nystagmus, and has to respond to flashes at a more or less unknown location. The flash unit makes an audible sound to his advantage which helps him to decide if he saw the flash at a specific instant of time. The energy of the test flash had to be chosen four to ten times higher in order to see the flashes than in the experiment with the two fixation lights, while also a blank was used to check for false alarms. The result of the experiment is given in Fig. 46.

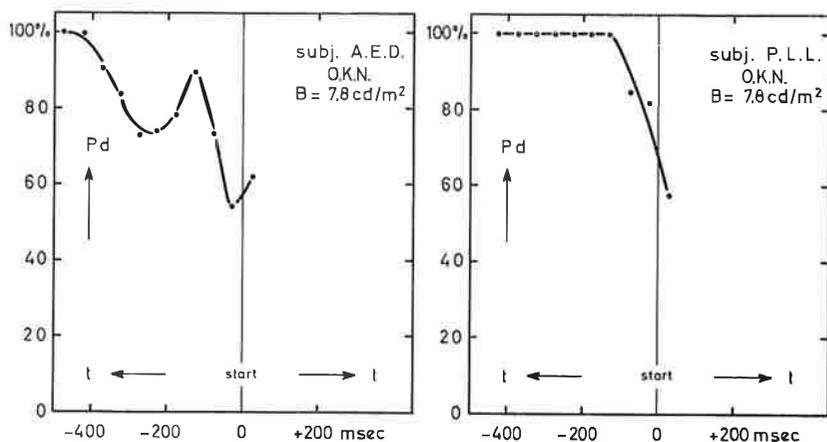


Fig. 46. The detection curve for the case that the eye movements are induced by an optokinetic drum. See text.

The figure shows that the suppression mechanism is activated also by the rapid phase of the optokinetic nystagmus and this finding places the mechanism really deep in the head.

The results given above are too sketchy to attach significant meaning to the degree of the suppression, but for such measurements the fixation method is advantageous, while this experiment mainly served to indicate the presence of the dip.

Thus it is found for the suppression so far that eye movements independent of their origin activate the mechanism.

#### G. THE ANGLE OF THE EYE MOVEMENT

The last parameter we need to consider is the angle of the eye movement. To measure the dependence of the angle on the suppression

mechanism by an unbiased method it is necessary to generate changes in position of the fixation lights of different angles and to measure if for a certain starting position the chance of detection is influenced by the angle of the eyemovement. The apparatus was a little modified for this purpose.

A third fixation light was projected right in the center between the two fixation lights and under the flash unit. The three fixation lights were governed by a digital circuit in such a way that only one of the three lights was on and the sequence in which the lights were switched was determined by a random source. To avoid a possible interaction of the central fixation light with the flash due to facilitation, the flash unit was raised till the flash was seen 10 degrees up.

The subject was instructed to follow the changes in position, and to press the button if he saw the flash.

The data from this experiment were separated in six groups, four of which were used. They were for the following movements.

L → R  
R → L  
L → C  
R → C

As stated earlier the first two groups and the last two groups could be taken together, as the direction of the eye movement is of no importance.

Two different flash intensities were used and a blank. The results of the experiment are given in figure 47 for two angles, 6° and 12° resp. 10° and 20°.

Finally the first parameter that influences the mechanism has been found. The suppression mechanism is about proportional to the angle of the eye movement, as can be seen in Fig. 47. The slope of the  $A(t)$  function is about equal for the different angles and it is therefore possible to describe the findings above in the following way; the threshold as described by  $A(t)$  increases linearly with time till the maximum has been reached. The greater the eye movement, the earlier  $A(t)$  will start to increase. As the moment on which the maximum is obtained does not depend on the angle, the dip in vision will increase with the angle of the eye movement.

This sheds a remarkable light over the findings of Ditchburn and Fender (13) as these experimenters noticed the dip for eye movements of several minutes of arc. A possible explanation can be given using

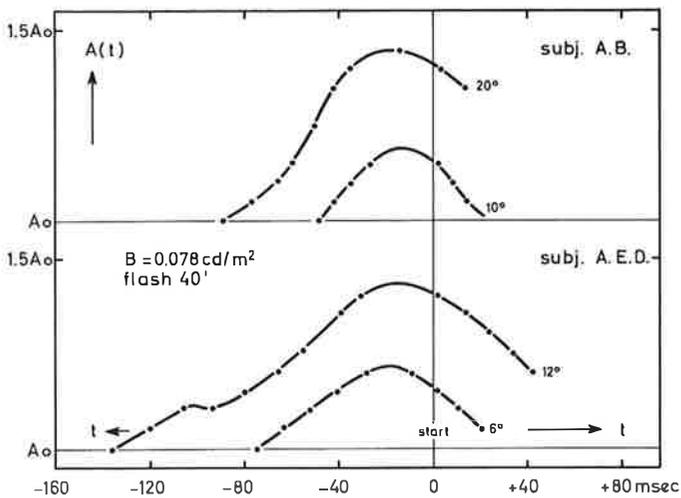


Fig. 47. The dependence of the suppression mechanism upon the angle of the eye movement for two subjects.

the speed of the eye movement rather than the angle. The relation between the maximal speed of an eye movement of certain angle as a function of that angle is given in Fig. 48. It is shown in this figure that even for the smallest angles the speed of the eye has a lower limit. Thus even very small eye movements can give an appreciable dip if the mechanism is proportional to the speed of the eye movement. As the relationship between speed and angle of the eye movements is about linear, this result would still be compatible with our findings.

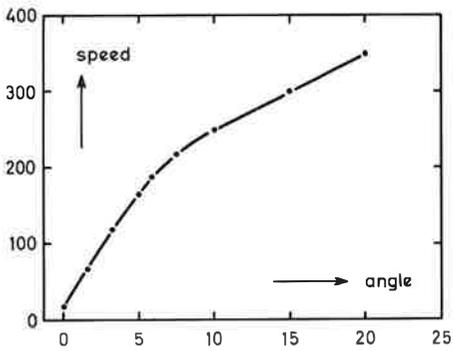


Fig. 48. The maximal angular speed of the eye as a function of the angle  
See text.

## THE TIMING OF EVENTS

Time plays an important role in the human data processor. It was shown in the preceding chapter that in threshold experiments the time at which a stimulus is presented relative to the 'internal timing of the subject' determines partly its detectability.

For suprathreshold signals we can ask the subject to initiate a specific action depending on the signal. In such a task the reaction time of the subject is measurable, and the results have led to many proposals concerning the timing of the human operator.

Stroud (42, 43) has postulated that reaction times and other more general human actions are divided into units with a length between 50 msec and 200 msec. This purely hypothetical suggestion has been tested by many experimenters (15, 16, 17, 44, 45, 46) and it was found that reaction times in tasks of various difficulty have the tendency to cluster around certain equally spaced values, which means that reaction times in first order approximation can be written as:  $T = t_1 + kt_2$  in which  $t_1$  is the time for the neural conduction, and  $t_2$  the cycle time of the internal processor, and  $k$  an integer.

In the microdecisions one can reflect about the threshold mechanisms at the onset of an eye movement. It was found that the threshold for a flash with a diameter of 7 minutes of arc varies sinusoidally with time over several tens of milliseconds for the dark adapted subject.

Such effects can be found only if there is a reference in the time base which in this case was the onset of the eye movement. It is very likely that the sensitivity of independent spots on the retina varies more or less sinusoidally also when the eye does not move and the eye move-

ments have a synchronizing effect on these fluctuations, or conversely that the fluctuations determine at which moment the eye will start its movement. Our first concern is the macrotiming, evidence for which can be found by measuring reaction times of the eye to visual stimuli.

The periodicity in reaction time disappears when the response is pushing a button or taking similar action. This is probably due to the differences in conduction time of the efferent impulses which constitute the response. The eye is much better suited to these experiments, because of its high muscle power to mass ratio and because the length of the pathways to the nuclei of the motor nerves of the eye muscles is much shorter. The fluctuations in conduction time will thus have less effect and the eye can respond rapidly, resulting in better time resolution.

After finding certain periodic behaviour in a subject it is natural to look for other periodic phenomena which may cause or may have a common factor with these periodicities. One such is the periodic alpha wave of the EEG. The influence of the eye on the alpha activity is sufficiently demonstrated by phenomena such as the flicker driven alpha (47, 48, 49) and the influence of closing or opening both eyes on the amount of alpha bursts.

When measuring reaction times it is therefore a good policy to measure the EEG of the occipital cortex also, keeping in mind that the hidden clock in the brain is not necessarily the alpha rhythm but possibly a source much lower in midbrain structures which determines in a complex way both the alpha activity and the reaction times.

The EEG of the subjects discussed in this chapter was measured as a possible indication of the strength and period of the clock-like activity. Also the on line averager 'Cat' was used to average the EEG over a period of several hundreds milliseconds at presentation of the stimulus. This stimulus was the same as in the preceding experiments; it consisted of two alternately burning fixation lights, and all the subject had to do was to shift his gaze toward the fixation light that was switched on.

If reaction times show a periodicity in such an experiment it is necessary to assume that presentation of the stimulus had a synchronizing effect on the clock. However even if the clock is very precise and constant we will fail to find periodicities if the synchronizing effect of the stimulus is not sufficient. This limitation can be eliminated by measuring the time between the autonomic eye movements, for

instance by having the subject fixate an optokinetic drum. Due to reflex activities this will generate optokinetic nystagmus; we can then measure the time intervals between the successive rapid phases. These data can be treated as free running reaction times, and they will probably reveal more about the clock mechanism than the reaction times to various stimuli.

It must be noted that different pathways are involved in normal voluntary eye movements than in optokinetic nystagmus (OKN). When looking at a rotating drum the subject is not even aware of his nystagmus. It is impossible to give a description of the pathways involved, as these are still partly unknown.

But the attention of the subject is a prerequisite for OKN, and as long as the OKN persists his attention is devoted to the experiment, which is a more favourable situation than in the RT experiment in which the attention of the subject fluctuates due to the waiting period between the stimuli. Furthermore it seems that OKN occurs through more reflex pathways than voluntary eye movements, and this more basic control makes it plausible that more basic mechanisms – such as the clock – have greater influence (4, 50). In this chapter the findings concerning the periodicities in the reaction time, the optokinetic nystagmus, and the cortical activity will be given for several subjects but first we shall give an analysis of our data reduction methods.

## A. THE DATA REDUCTION

In processing the data, extensive use was made of two modes of data reduction, the process of averaging and the process of correlation. As both these methods are generally well known and comprehensively discussed in the literature their effect and range of applicability will be indicated briefly here, while a more extensive calculation is given of the process of correlating a histogram of finite length, in order to find an estimate of the significance of the results of the data.

### 1. The Averager

The process of averaging is indicated in those experiments in which the response is coupled in time to a known event and of insufficient amplitude with respect to the noise in which it is embedded to be studied. By repeating the experiment and adding the successive responses with their noise the signal to noise ratio can be increased with

a factor proportional to the square root of the number of times that the experiment has been repeated. This follows from the fact that the response will increase linearly with the number of responses averaged, while the noise in which the response is embedded will increase with the square root of the number of averages due to the statistical independence of the successive responses. In most practical applications this statistical independence is found and the signal to noise ratio can be increased which enables one to measure evoked responses at very low signal levels (23, 51, 52).

In the digital special purpose computer 'ARC' or 'CAT' this averaging is done such that the incoming signal is fed into an analog to digital converter and the digital value is stored in successive addresses, the number of which depends upon the length of the sample one is interested in.

At the next stimulation the digital value of each of the addresses is added to the new value of the analog-digital converter, and stored again at the same location.

This process is repeated till the number M has been reached, after which the averaged evoked response is displayed.

## 2. The process of correlation

The need for an unbiased estimate of an experimentally obtained time function  $f(t)$  is apparent. Particularly if this time function is a subjects EEG which we want to classify (22, 23).

Moreover the need is felt that this classification does not depend on the typical EEG sample that was taken, but that the classification is independent of the sample if the external conditions are not changed.

Thus we assume the time function to be both stationary and ergodic, an assumption that is justified only if indeed the estimate is not a function of the sample taken. Thus, instead of averaging over time, we may average over the ensemble with identical results as a consequence of the conditions stated above.

For the unbiased estimate of  $f(t)$  we now can take the correlation function defined by:

$$R(\tau) = \lim_{T \rightarrow \infty} \frac{1}{T} \int_{-\infty}^{+\infty} f(t) f(t + \tau) dt \quad 1)$$

For practical applications we use the correlogram which is defined as:

$$C_T(\tau) = \frac{1}{T} \int_0^T f(t) f(t + \tau) dt \quad 2)$$

The correlogram defined in 2) is a function of the length of the sample  $T$ , and the question arises if the correlogram is an unbiased estimate of the autocorrelation function.

Thus as  $C_T(\tau)$  is a random variable we would like to know its probability distribution as a function of  $\tau$  and  $T$ .

This problem is not solved yet, but we can calculate the expectation and variance of  $C_T(\tau)$ , under the assumption that  $f(t)$  is stationary and ergodic.

$$\begin{aligned} E[C_T(\tau)] &= E \left[ \frac{1}{T} \int_0^T f(t) f(t + \tau) dt \right] = \frac{1}{T} \int_0^T E \left[ f(t) f(t + \tau) \right] dt = \\ &= E [ f(t) f(t + \tau) ] = R(\tau) \end{aligned}$$

The variance of  $C_T(\tau)$  can be calculated also and it can be shown that the variance approaches zero for  $T \rightarrow \infty$ .

In most practical applications  $T$  is large enough to justify the use of  $C_T(\tau)$  as an estimate of the  $f(t)$ . In the literature (54, 55) this matter has received quite some interest, and particularly the finiteness of the sample has been pursued in detail. The justification of our assumption that  $f(t)$  is stationary and ergodic can be found by repeating the process of correlating and verifying that the result reproduces.

The effect of the correlogram is that it provides the experimenter with the knowledge which periods are present in the time function  $f(t)$ . In particular the period of the  $\alpha$  rhythm can be found even if the overall  $\alpha$ -activity is too small to find it directly in the records.

The result of such an autocorrelation is given in Fig. 49.

### 3. Autocorrelation of histograms

The reaction times of the subject or the time intervals between the rapid phase of the OKN are plotted in a histogram. The goal is, of course, to establish if certain time intervals are preferred which might indicate that the reaction times are generated by a clock-like mechanism. The histogram is autocorrelated for this purpose and the question now arises what standard deviations can be expected in order to give the significance of the result. We reverse the question for this calcu-

lation and calculate the standard deviation for a random process which then can be compared with the experimental results.

Let us assume that we have  $m$  cells along the  $x$  axis and that the chance that an experiment gives a reaction time which increases the number of results by one in cell  $\nu$  is given by  $p_\nu$ , and that  $p_\nu$  is a gaussian distribution, symmetrical around cell  $m/2$ .

We now take  $N$  measurements and if  $N_\nu$  is the number of hits in the  $\nu^{th}$  cell,  $N_\nu = N p_\nu$ .

The chance of  $N_\nu$  hits in the  $\nu^{th}$  cell is given by the binomial formula

$$p(N_\nu) = \binom{N}{N_\nu} p_\nu^{N_\nu} (1 - p_\nu)^{N - N_\nu}$$

We now make another step. We subtract from  $N_\nu$  the expected value of  $\bar{N}_\nu$  and form  $V_\nu$ ;

$$V_\nu = N_\nu - \bar{N}_\nu$$

This  $V_\nu$  function has the properties that the average is equal to zero, which has its advantages for the following calculation.

As an estimate of the presence of periodicities in the histogram we use the formula:

$$R_\mu = \sum_{\nu=1}^m V_\nu V_{\nu+\mu}$$

and we now want to find the expected value for  $R_\mu$  and the standard deviation in  $R_\mu$ :

$$\sigma^2 R_\mu = \overline{R_\mu^2} - \bar{R}_\mu^2 = \overline{R_\mu^2} \quad \text{as} \quad \bar{R}_\mu^2 = 0 \quad \text{for} \quad \mu \neq 0$$

We use the following relations:

$$\begin{aligned} \overline{V_\nu} &= 0 \\ \overline{V_\nu^2} &= \overline{(N_\nu - \bar{N}_\nu)^2} = \overline{N_\nu^2} - \bar{N}_\nu^2 = \bar{N}_\nu (1 - p_\nu) \end{aligned}$$

We now have:

$$\begin{aligned} \sigma^2 R_\mu &= \overline{R_\mu^2} = \sum_{\nu, \varrho} \overline{V_\nu V_{\nu+\mu} V_\varrho V_{\varrho+\mu}} = \\ &= \sum_\nu \overline{V_\nu^2 V_{\nu+\mu}^2} + 2 \sum_\nu \overline{V_\nu V_{\nu+\mu}^2 V_{\nu+2\mu}} + \sum_{\nu, \varrho} \overline{V_\nu V_{\nu+\mu} V_\varrho V_{\varrho+\mu}} \\ &\quad - \sum_\nu \overline{V_\nu^2 V_{\nu+\mu}^2} - 2 \sum_\nu \overline{V_\nu V_{\nu+\mu}^2 V_{\nu+2\mu}} = \\ &= \sum_\nu \overline{V_\nu^2 V_{\nu+\mu}^2} = \sum_\nu \bar{N}_\nu \overline{N_{\nu+\mu}} (1 - p_\nu) (1 - p_{\nu+\mu}) \\ &\approx N^2 \sum_\nu p_\nu p_{\nu+\mu} \end{aligned}$$

In order to simplify the calculation we now assume  $m$  to be even and we shift the  $m$ -cells- symmetrical around zero.

Thus:

$$p_\nu = \sqrt{\alpha/\pi} e^{-\alpha\nu^2} \quad \text{for } \nu = -\frac{m}{2}, \dots, \frac{m}{2}$$

and:

$$\sum_\nu p_\nu \approx \sqrt{\alpha/\pi} \int_{-\infty}^{+\infty} e^{-\alpha\nu^2} d\nu = 1$$

We substitute the value of  $p_\nu$  in the formula of  $\sigma^2 R_\mu$  and find:

$$\begin{aligned} \sigma^2 R_\mu &= \frac{\alpha}{\pi} N^2 \sum_\nu e^{-\alpha\nu^2 - \alpha(\nu + \mu)^2} \\ &\approx \frac{\alpha}{\pi} N^2 e^{-\frac{\alpha\mu^2}{2}} \int_{-\infty}^{+\infty} e^{-\left(\frac{\alpha\mu}{\sqrt{2\alpha}} + \sqrt{2\alpha} \nu\right)^2} d\nu = \frac{N^2 \sqrt{\alpha}}{\sqrt{2\pi}} e^{-\frac{\alpha\mu^2}{2}} \end{aligned}$$

For  $R_0$  we find:

$$R_0 = \sum_\nu \overline{V_\nu^2} = \sum_\nu \overline{N_\nu} (1 - p_\nu) \approx N$$

We are still free in our choice of  $\alpha$  and  $m$  and we now want to choose  $\alpha$  such that:  $Np(m/2) \approx 1$

This gives:  $\alpha \approx 1/m^2$

The number of cells must be chosen such that the relation above is true: thus:  $Np(m/2) \approx 1$

This gives:  $m = 0.65 \sqrt{N}$

With both  $m$  and  $\alpha$  properly chosen we find for  $\sigma R_\mu$ :

$$\sigma R_\mu = 0.77 N^{3/4} e^{-\frac{\mu^2}{1.7N}}$$

The data of the RT experiment are handled as the cells in this calculation with this difference that the  $\overline{N_\nu}$  which is subtracted from  $N_\nu$  is now derived from;

$$\overline{N_\nu} = \frac{1}{5} \sum_{k=\nu-2}^{\nu+2} N_k$$

This smoothing process serves to suppress the high frequency components in the  $\overline{N_\nu}$  function, which is then subtracted from the original

frequency distribution. After this manipulation the  $R_\mu$  is calculated and the position of  $R_o$  and  $\sigma R_\mu$  of a random process with the same number of points and cells is indicated in the figures.

If there are preferred time intervals this will be found in two ways in the  $R_\mu$ . In the first place the  $R_o$  measured will be higher than the  $R_o$  calculated due to greater fluctuations in the occupancy of the cells, and if the timing is periodical we may expect regular apices and valleys in  $R_\mu$  as a function of  $\mu$ . This is shown in Fig. 62 and Fig. 63.

## B. THE DATA

### Subject 1

This subject displayed a very strong alpha rhythm – whether his eyes were open or closed – as is clear from his typical thirty second autocorrelated EEG sample.

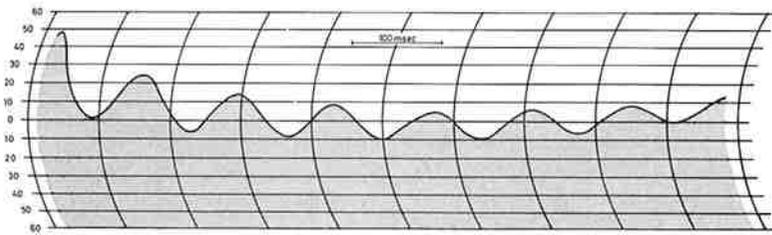


Fig. 49. A typical thirty second autocorrelated sample of the EEG of subject 1. Delay increment was 4 msec. The subject was resting.

During this recording no stimuli were presented.

The periodicity found is  $110 \text{ msec} \pm 2 \text{ msec}$ .

During stimulation with twenty degree block stimuli in fixation this pattern changed completely.

Instead of the many alpha bursts as were usually seen in the subject's recordings there were now two different types of bursts, a slow one with a period of  $73 \text{ msec} \pm 2 \text{ msec}$  and a fast one of  $29 \text{ msec} \pm 0.6 \text{ msec}$ . These latter bursts displayed such a sinusoidal character as is shown in Fig. 50, that the periodicity was easily determined by measuring the length of these bursts on recording paper.

These fast burst occurred only during the stimulation.

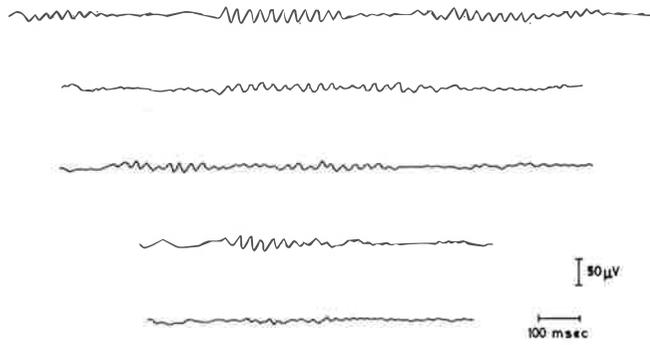


Fig. 50. Direct recordings of subject 1's EEG. The periodic bursts are easily recognised.

In the autocorrelated EEG under stimulation these phenomena are easily recognized. The autocorrelograms of Fig. 51 and 52 show successive recordings with less than a minute between them.

In Fig. 51 no stimuli are presented.

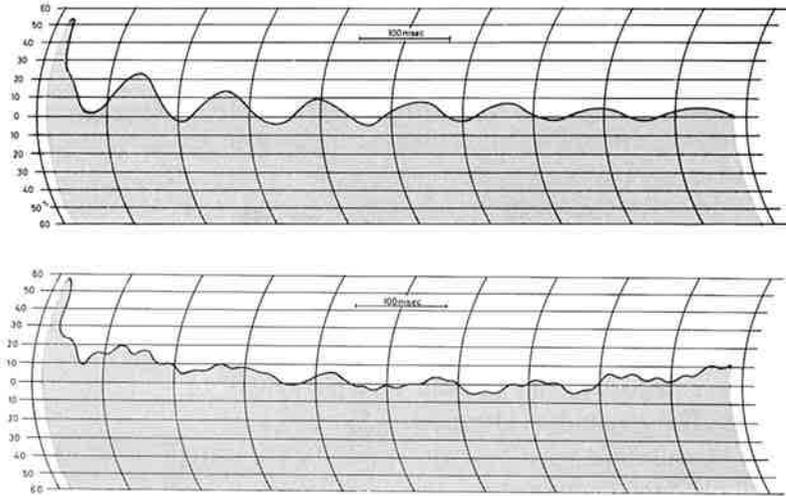


Fig. 51 and Fig. 52. Two successive recordings of subject 1 are autocorrelated. The subject follows the changes in position of the fixation light during the second period.

In an effort to find a common denominator to the periodicities observed we can state that within the precision of the experiment these periods are related as follows:

$$5 \times 29 \text{ msec} = 145 \text{ msec} = 2 \times 73 \text{ msec}$$

$$3/2 \times 73 \text{ msec} = 109 \text{ msec} = 1 \times 110 \text{ msec}$$

Now this procedure is doubtful in confirming the harmonic relation between the various periodicities as the numbers are arbitrarily chosen and are not small enough to restrict to only a few possibilities.

Nevertheless the fact that these numbers can be found in all occasions, together with the fact that they sometimes link two periods to a known third improves the situation somewhat.

It was noted when measuring the reaction times that the distribution of left to right stimuli and right to left stimuli were different, and they were therefore treated separately. After autocorrelating the reaction time histograms two periodicities were found.

For the lr stimuli a periodicity of 14.5 msec and for the rl stimuli a periodicity of 9.7 msec.

These periods are related also as:

$$3 \times 9.7 \text{ msec} = 29.1 \text{ msec} = 2 \times 14.4 \text{ msec.}$$

Here we have the case that two new periodicities are linked through another known periodicity, which is reassuring.

The time between the saccadic jumps to the right were measured in a reading experiment and treated as reaction times, a periodicity of 14.1 msec. was found, a value that does not differ significantly from those in the lr experiment.

In the experiment with the optokinetic drum, which rotated to the left a very definite periodicity of 14.5 msec is apparent, as is shown in Fig. 53.

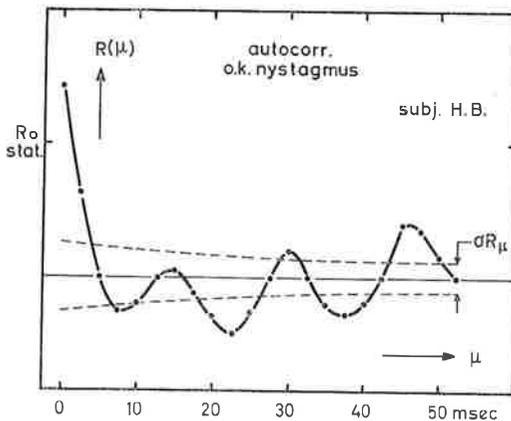


Fig. 53. The intervals between the rapid phase of the optokinetic nystagmus are treated as reaction times, and the histogram is autocorrelated. The  $R_o$  and  $\sigma R_\mu$  indicated in the Fig. are calculated for a gaussian distribution of the data.

See text.

This is the same value of the  $I_r$  stimuli and the reading experiment. With the average response computer ARC 100 EEG samples were averaged with a length of 250 msec, the trigger being synchronized with the  $I_r$  or  $r_l$  stimuli. Many times this failed to show any regularly building average but in a few cases a response was found, a typical one of which is shown in Fig. 54. The histogram of the reaction times of the selfsame experiment is shown also in the same figure.

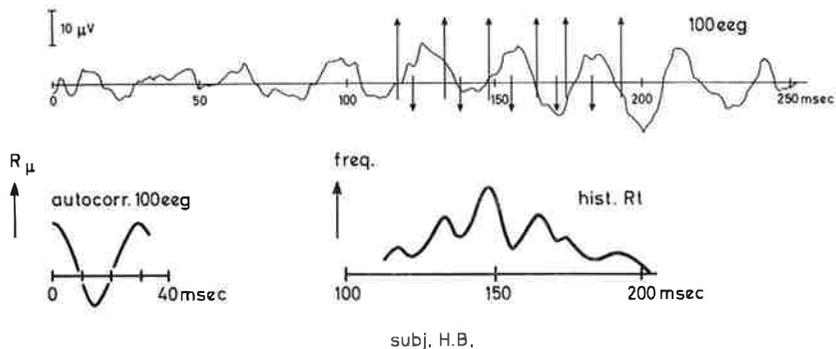


Fig. 54. An averaged EEG and an histogram of the same session. The correspondence is indicated by the arrows.

The relation between the two is evident. The zero crossings of the averaged response coincide with the apices of the peaks in the histogram, while the maximal values of the averaged response are above the valleys.

This is surprising as we should expect some time shift between the two as the evoked response is recorded from the cortex and the histogram is based on data from the effector output. Thus it may be necessary to shift the histogram to the left over a time equal to the conduction time. In any case the periods of the two phenomena are related, as they differ by a factor 2.

All the periodicities mentioned proved to be very stable in this subject. In a period as long as six months the experiments were repeated and the periodicities, found were always the same. The only difference concerned the degree of synchronisation, or the amplitude of the auto-correlated data, which varied from one day to another, while in a few cases no periodicities were found at all.

## Subject 2

This subject has no definite alpha rhythm if any at all, as is shown in Fig. 55. When stimulated, however, there is a clear bump in his autocorrelated EEG with a delay of about 32 msec which shows that there is a fast decaying component in his EEG of about 33 cps. (Fig. 56).

His averaged response never showed a periodical character. Nevertheless periodicities were found in most of his autocorrelated histograms. These periodicities varied from one day to another, were multiple in character, and could not be characterized by simple relations.

One can extract the information from the data of this subject that a strong alpha rhythm is a necessity for clear periodicities in the reaction times, a hypothesis which was confirmed by the other findings.

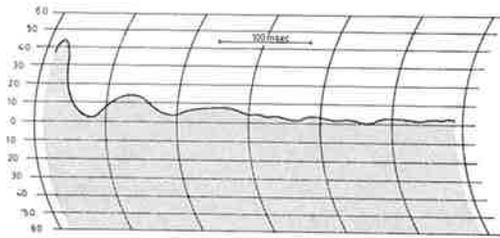


Fig. 55. A typical thirty second autocorrelated sample of the EEG of subject 2. Delay increment 4 msec. The subject was resting.

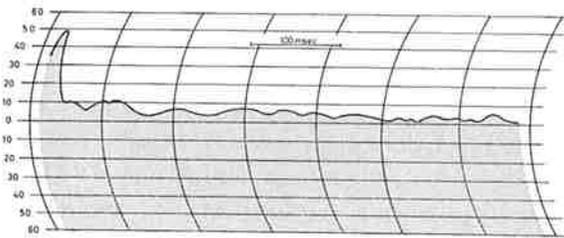


Fig. 56. A typical thirty second autocorrelated sample of the EEG of subject 2. Delay increment 4 msec. The subject follows the changes in position of the fixation light.

## Subject 3

A 30 second autocorrelated sample of the EEG of this subject, eyes fixating one of the fixation lights, is given in Fig. 57. There is a clear period of 87.5 msec.

In the experiment with the block stimuli this subject showed over and over again a 12.5 msec periodicity for the lr stimuli and a 22 msec periodicity for the rl stimuli. This is shown in Fig. 58.

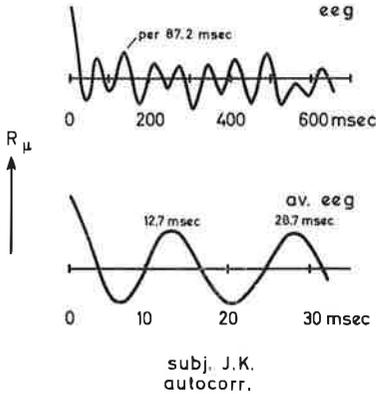


Fig. 57. A typical thirty second auto-correlated sample of the EEG of subject 3 calculated on a digital computer. The subject follows the changes in positions of the fixation light. Also an autocorrelated averaged EEG, triggered by the onset of the eye movement.

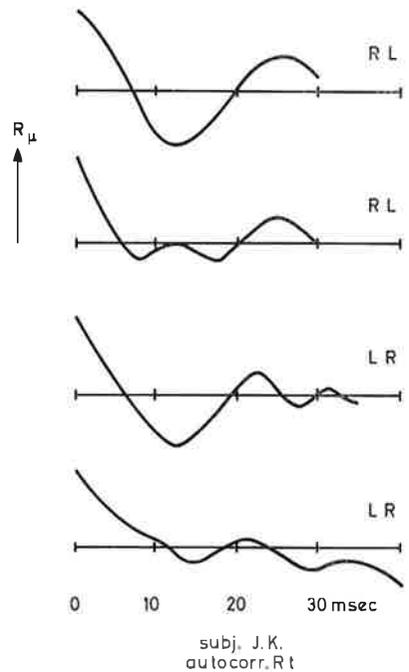


Fig. 58. Periodicities in the reaction times of subject 3. The data were autocorrelated on a digital computer.

With an average 100 EEG samples were averaged and the result was autocorrelated. Here two periods were found, one of 12.7 msec and one of 28.7 msec. The experiments with this subject were repeated monthly over a period of six months and we find for the average of these months:

Average lr periodicity	12.6 msec ± 0.2 msec
Average rl periodicity	21.7 msec ± 0.2 msec

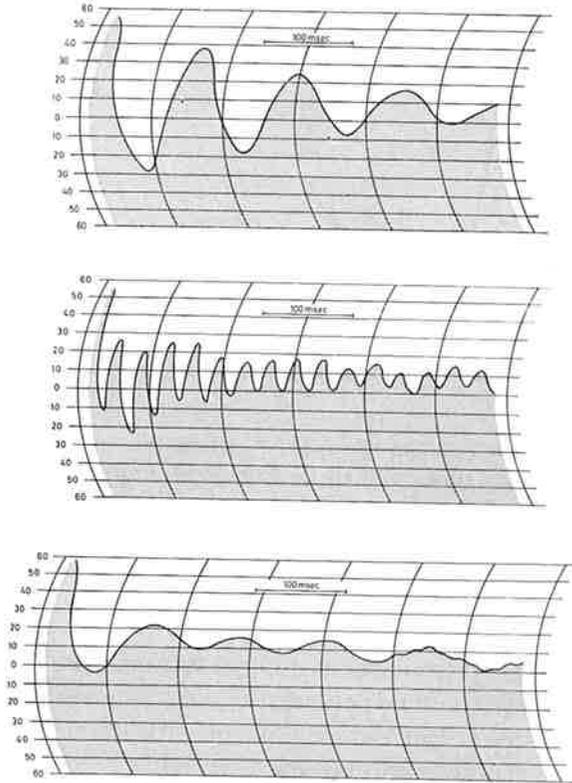
We have the following relation

$$\begin{aligned}
 7 \times 12.6 \text{ msec} &= 88.2 \text{ msec} \\
 4 \times 21.7 \text{ msec} &= 86.8 \text{ msec} \\
 3 \times 28.7 \text{ msec} &= 86.1 \text{ msec}
 \end{aligned}$$

Here the alpha rhythm seems to link the different periodicities.

## Subject 4

A test was made with this subject to see if his EEG changed under stimulation. Three recordings were made in a continuous session. During the first five minutes the subject was resting, then he was stimulated for five minutes, after which he rested for another five minutes. The result of the autocorrelated EEG is given in Fig. 59, 60, 61.



Figs. 59, 60 and 61. A typical second autocorrelated sample of the EEG of subject 4. Delay increment was 4 msec. In Fig. 59 and 61 the subject is resting, in Fig. 60 the changes in position of the fixation lights are followed.

It is clear from the recordings that this subject was a promising one for these experiments and we regret that they had to be discontinued because of the lack of time. It is clear out example that the cortical activity is drastically changed during a task.

## Subject 5

This subject has no appreciable  $\alpha$  rhythm. Consequently no clear periodicities were found in the subject's reaction times. The optokinetic nystagmus however showed a periodicity of about 100 msec thus once again the timing is found best in the experiment with the optokinetic drum (Fig. 62).

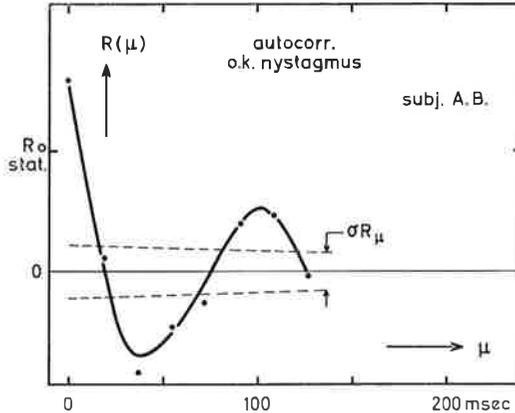


Fig. 62. The intervals between the rapid phase of the optokinetic nystagmus are treated as reaction times, and the histogram is autocorrelated. The  $R_o$  and  $\sigma R_\mu$  indicated in the Fig. are calculated for a gaussian distribution of the data. See text.

## Subject 6

This subject behaved similarly as subject 5. Again the alpha activity was rather restricted, and no periodicities were found in the histograms of the reaction times. But the experiment with the optokinetic drum revealed that a timing is still present (Fig. 63).

### DISCUSSION OF THE RESULTS

It is clear from the data obtained that the optokinetic nystagmus reveals most of the hidden clock, and is the best method to establish time quantization. The laws which govern the mechanism are at this stage not fully understood because many factors tend to influence human behaviour. The subjects 5 and 6 for instance were highly trained subjects, with which most of the experiments in chapter 3 and 4

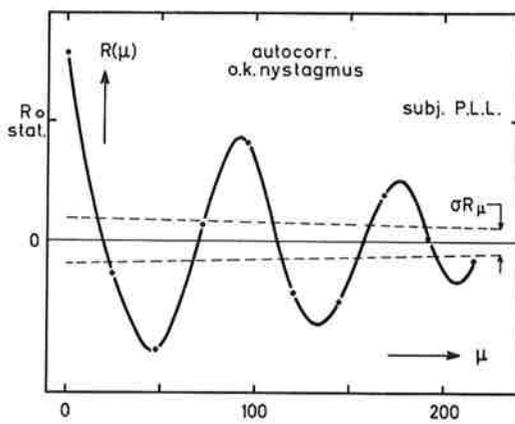


Fig. 63. The intervals between the rapid phase of the optokinetic nystagmus are treated as reaction times, and the histogram is autocorrelated. The  $R_o$  and  $\sigma R_\mu$  indicated in the Fig. are calculated for a gaussian distribution of the data. See text.

were done. Due to this training the reaction time of these subjects was much more constant than in other subjects, while the standard distribution was so small that it is doubtful that these periodicities could be found a priori. The experimental conditions are much more in favour of a positive result for the optokinetic experiment, for the following reasons:

1. The clock does not need to be reset after each action.
2. The pathway is through reflex arcs and includes probably more basic structures in the brain than in case reaction times are measured. The effect of the basic structures will therefore be greater.
3. The spread in the time distributions is larger for the optokinetic experiment which allows one to look for periodicities in a more extended time domain.

## DISCUSSION

Several remarks made in the preceding chapter will be raised once again in an attempt to justify the general line of approach, and, if possible, to signal their interrelationships. In the first place the use of the detection model for the evaluation of the threshold and the FOS curves needs investigation. The question may be asked as to what extent our interpretation of the data is already channeled to a specific model. The answer is reassuring. The use of the detection model puts no constraints whatsoever on the underlying mechanism. In fact, as a first line of approach, any model can be described in terms of the detection model with its density distribution  $\varrho(r)$  and threshold  $th$ . Once both these functions are found it is possible to identify the result with well known theories which concern the actual detection mechanism, such as for instance, the two quanta hypothesis.

In chapter III and in chapter IV however discrepancies with this hypothesis were found which concerned, in effect, the position of the threshold. It was found that there exists a gap between the density distribution  $\varrho(r)$  and the position of the threshold. For higher background luminosities this effect is appreciable, but for low background luminosities the effect is about unmeasurable, because it requires knowledge of the very beginning of the FOS curve. But the data suggest that for each background luminosity there exists a threshold value  $I_0$  such that flashes below this threshold value are never perceived. This is a remarkable difference with theories based on a quanta coincidence mechanism.

It suggests that the retina has an analogous mode of operation rather than one based on the specific interconnections of the receptors.

Furthermore it was found in chapter III that a total energy of about four quanta was needed for a 60% chance of perception for a small flash of short duration. The slope of the FOS curve at the 60% point does not coincide with the slope one calculates for a four quanta coincidence model, which also suggests an analogous mode of operation. Still more evidence for this point of view is supplied by the threshold fluctuations of the dark adapted eye just before the onset of an eye movement, as was illustrated in the Figs. 30, 31, 32, 33.

Such fluctuations could be explained by the coincidence mechanism requiring a fluctuating number of coincidences, but it is more likely that the total energy of the flash, integrated over time – 50 msec – and over space – 20 minutes of arc – is weighed by the retinal sensitivity. In chapter IV it was argued that these fluctuations in sensitivity probably constituted only a fraction of the real fluctuations, due to imperfect fixation by the subject.

It is very plausible to assume that these fluctuations in sensitivity with their almost periodic character are always present, and that they can be measured only because their phase is coupled to the onset of an eye movement. The further our threshold estimate is separated in time from the onset of the eye movement, the worse the synchronisation will be, and it is therefore necessary to look for another kind of experiment which can give us the exact information about the threshold variations. Before describing such an experiment it must be stated that these threshold variations are an essential point in our hypothesis that the threshold function has an analogous mode of operation. A possible way to measure these threshold variations is by presenting the subject double flashes in time, and to measure the chance of perception of both flashes as a function of the time interval between them.

This time interval, of course, needs to be large with respect to the integration time. In this way we may obtain data concerning the bandwidth and amplitude of the retinal variations in sensitivity. Only in case that the fluctuations are that undeterministic that a specific threshold value at time  $t_1$ , does say nothing about the threshold value at time  $t_2$ , while  $t_2 - t_1 > \tau$  the result of the experiment will be negative.

Suppose for instance that the sensitivity varies sinusoidally and that the chance of perception is given by:

$$P_{det} = P_o + a \sin \omega t$$

Using single flashes we find for the average threshold:

$$P_{det} = P_o$$

The chance of perception of both flashes  $T$  units of time apart is given by:

$$P_2(T) = (P_o + a \sin \omega t) (P_o + a \sin \omega (t + T)) = P_o^2 - \frac{a^2}{2} \cos \omega T$$

Thus the effect of such a sinusoidally varying threshold is measurable. In a preliminary experiment the chance of detection of both flashes as a function of the time interval between them was measured, and the result is given in Fig. 64.

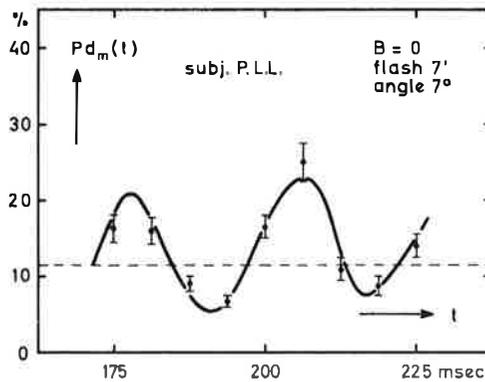


Fig. 64. The chance of perception of two successive flashes as a function of the interval between the flashes. The average value calculated from the chance of perception of one flash is indicated by the broken line.

For this experiment the subject was dark adapted. The diameter of the flash was 7', and the flash was presented 7° peripheral. The duration of the flash was 1.2  $\mu$ sec.

The data in Fig. 64 clearly indicate that this direct measurement of the threshold supports the theory that the threshold fluctuates in an almost periodic way. This result will have to be investigated much further and it will lead consequently to a systematic research of the fluctuating centers in the retina in an attempt to find the areas, frequency spectra, and spacial distributions of these fluctuations. One

can also measure the extent to which a background will change the pattern. Still another aspect of the threshold variations can be found in the slowly varying chance of perception, a phenomenon familiar to all experimenters. With a period between several tens of seconds to several minutes the sensitivity waxes and wanes, and the subject's score goes up and down.

Incorporating these effects in the model of the visual system we now assume that we have no fixed threshold, but a varying threshold with rapid and slow oscillations. In the detection model this assumption puts some constraints on the noise, without affecting the density distribution  $\varrho(r)$ . Furthermore the position of the threshold is such that the chance of a false alarm is very low, which implies more or less that there is a gap between the density distribution and the position of the threshold. If a background is presented, the statistical fluctuations in this background are transformed to statistical fluctuations in the visual system which add to the existing noise. The position of the threshold is changed by this background, such that the total noise has a very low chance to trigger the response and cause a false alarm.

In chapter IV the experimental curve giving the flash energy for a constant chance of perception as a function of the background luminosity is given. This curve can be described by the following equation:

$$th = a_0 + \alpha_1 \sqrt{B} + \alpha_2 B$$

The constant term  $a_0$  gives the energy required for the dark adapted eye. If a background is provided for, the threshold energy increases with the square root of the background luminosity over about six log units. For still higher background luminosities the energy increases linearly with the background.

It is a simple matter to construct an ad hoc model which incorporates this formula.

Suppose for instance that the neural message, coded in spike frequencies, is fed into a scaler which scales with a ratio proportional to its output.

The output frequency of this scaler is now proportional to the square root of the input frequency.

Furthermore it is very natural to assume that such a scaler can be saturated, which means that the scaling ratio has an upper limit.

If this limit is reached, the output frequency will be proportional to the input frequency.

If finally the threshold value is set at a discrete level above the scaling ratio, we have a device which incorporates the formula for the threshold. Whether such a mechanism is really present in the retina can not be answered.

This model only served to imbed a long description of experimental facts into easily understood terms. The fundamental question concerning the existence of the gap between the density distribution  $\varrho(r)$  and the threshold can also be answered on basis of experimental results of other investigators.

If a flash of area  $A$  and duration  $T$  is presented it is known that the flash energy for a constant chance of detection as a function of size and duration can be described by the following laws:

$$\begin{aligned} E &\approx \sqrt{A} && \text{Pipers' law} \\ E &\approx \sqrt{T} && \text{Pierson's law} \end{aligned}$$

When both  $A$  and  $T$  are large with respect to their summation areas, respectively in space and in time, a remarkable deviation from the laws quoted above occurs. For this case the flash energy for a fixed chance of perception can be written as:

$$\begin{aligned} E &\approx A && T > \text{summation time} \\ E &\approx T && A > \text{summation area} \end{aligned}$$

Taking these experimental facts together in one formula which gives a fair approximation for the total flash energy for a fixed chance of perception as a function of area and size we find:

$$E = \alpha \sqrt{AT} + \beta AT$$

In this formula  $\alpha$  and  $\beta$  must be chosen such that when  $A$  or  $T$  is small the first term dominates, while when both  $A$  and  $T$  are large the second term dominates.

As  $E = IAT$  the relation above can be also written as:

$$\begin{aligned} IAT &= \alpha \sqrt{AT} + \beta AT \\ \text{or } (I - \beta)^2 AT &= \alpha^2 \end{aligned} \tag{1}$$

Here we have a relation between area, duration and the intensity of a flash for a fixed chance of perception.

We now turn around and calculate the chance of perception of a flash with area  $A$  and duration  $T$  from its independent samples.

The number of independent samples is proportional to  $AT$  and if the

chance of detection of each of the samples is given by  $p(I)$  – this is a function of  $I$  only – the chance of detection of at least one subflash is given by:

$$P(I) = 1 - (1 - p(I))^{kAT} \approx kATp(I) \quad \text{in which } k \text{ is a constant.}$$

Due to facilitation in time and space this detection will lead to perception of the total flash. Thus, for a fixed chance of perception of the total flash we have the relation:

$$ATp(I) = \text{constant} \quad (2)$$

Eliminating  $A$  and  $T$  from equations 1) and 2) we find for  $p(I)$ :

$$p(I) = D(I - \beta)^2 \quad \text{in which } D \text{ is a constant.}$$

This formula, in which  $p(I)$  is expressed in  $I$ , is in agreement with the existence of a gap with a width equal to  $\beta$  between the density distribution  $\varrho(r)$  and the threshold.

Moreover it indicates that the density distribution increases linearly at its borders, instead of being gaussian. It is very probable that this is caused by the physical constraints of the actual mechanism.

## SUMMARY

It was found by Ditchburn that the visual threshold rises during a so-called flick, an eye movement of several minutes of arc with a centering tendency. This rise in threshold might serve to suppress the images on the moving retina which could otherwise be interpreted as coming from an unsteady world. On the other hand, it was found that vision deteriorates during presentation of a stabilized image when eye movements could have no effect on the retinal position of an image. The starting point of this thesis was the paradox between these two findings.

To gain further insight in the underlying mechanisms the visual threshold was measured in relation to the onset of an eye movement. It was found that a rise in threshold anticipates an eye movement by at least 40 milliseconds, while the threshold is about normal some milliseconds after the onset of the movement. This finding disproves the theory that the rise in threshold serves to suppress the moving images on the retina, and it also shows the cortical origin of the effect. The rise in threshold was found to be independent of the retinal position and the colour of the flash. The threshold was measured with adapting backgrounds ranging from zero till  $170 \text{ cd/m}^2$  but little effect was found of this background variation on the threshold rise.

Both eyes were found to be governed by the same threshold mechanism, which once more shows the cortical origin of the mechanism. The only variable that had great effect on the suppression was the angle of the eye movement, or perhaps the speed of the eye for that particular angle. The rise in threshold being about proportional to the angle of the eye

movement it was found that 100-120 milliseconds before the onset of the eye movement, thus about 60 milliseconds after the change in position of the fixation light, the eye already 'knows' how great the angle will be.

The data of the experiment were processed in a most general way, which led automatically to detection theory, with the following results. Noise is present in the visual system, originating from fluctuations in the receptors and neural elements. If a background is presented, the statistical fluctuations in the background are transformed to statistical fluctuations in the visual system, and it was shown that these fluctuations are proportional to the square root of the background luminosity. Thus for each background the noise in the visual system can be described by a density distribution  $\rho(\nu)$ . Associated with this density distribution is a threshold value  $th$  which has a discrete distance from the density distribution. If a signal of intensity  $I$  is presented, the noise density distribution shifts towards the threshold  $th$  over a distance proportional to  $I$ , and the area of the density distribution cut off by  $th$  is proportional to the chance of perception.

The visual noise is restricted in bandwidth, and for the dark adapted eye it is plausible to assume that it is an almost periodic function of time.

Furthermore it was found that fluctuations 40 minutes of arc apart are not correlated, which implies that the independent fluctuation centers are of the order of 10 minutes of arc.

A similar model was used for the description of the facilitation experiment in which the chance of perception was measured for two flashes of variable temporal or spacial separation.

The facilitation mechanism was found to be independent of the colour of the flashes or their position, while the distance between the flashes had little effect within the range of 48 minutes of arc to  $2^{\circ}24'$ .

Facilitation was shown to be of retinal origin as binocular flashes showed no effect. The level of adaptation of the eye did not affect the mechanism, identical curves being found for the dark adapted eye and for an eye adapted to a background of  $170 \text{ cd/m}^2$ . This made it possible to give a description of the effect regardless of the quanta fluctuations of the stimulus, as these fluctuations are quite different in the two cases mentioned above.

The FOS curve from the detection model could be scaled for two flashes within the area of summation such that it described both the data of the facilitation experiment – in which it was assumed that detection of one of the flashes served to lower the threshold of the

other flash with an equivalent of one unit of energy – and the experimental curve of the chance of perception within the area of summation, in which case the FOS curve is applied to the sum of the energies. From this scaled FOS curve a curve could be calculated which described the facilitation within the area of summation, and which fitted the data extremely well. It was found that negative flashes are also subjected to the facilitation mechanism, and that missing one flash facilitates the missing of the other flash. The chances found in this experiment were about equal to the facilitation of positive flashes outside the area of summation.

The influence of the timing of the flashes on the facilitation mechanism was also measured, and it was found that strong flashes are stored for a longer period than weaker flashes, this period being of the order of 50 milliseconds.

In chapter VI some characteristics of the timing are revealed. Many almost periodic phenomena, such as the fluctuations in retinal sensitivity, the subjects  $\alpha$  rhythm, the frequency distribution of reaction times, and the intervals between the rapid phases of the optokinetic nystagmus are mentioned.

The best periodicities were found in the optokinetic nystagmus. It is very plausible that the influence of the basic rhythms is maximal in this situation, while there is no need for any resetting action.

Finally it was found that the visual threshold varies periodically in time with a period of about 25 milliseconds.

The interrelationship among all these rhythms are far too complex for us to understand their modes of operation, but it is conceivable that these periodicities serve the same goal as the timing of the peripheral apparatus of a digital computer: synchronisation of actions and data transfer.

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