OBSERVATIONS WITH STABILIZED RETINAL IMAGES AND THEIR NEURAL CORRELATES

A THEORY ON THE PERCEPTION OF CONSTANT BRIGHTNESS

H. J. M. GERRITS

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PROMOTOR: PROF.DR. A.J.H. VENDRIK

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PROEFSCHRIFT

TER VERKRIJGING VAN DE GRAAD VAN DOCTOR IN
DE WISKUNDE EN NATUURWETENSCHAPPEN AAN
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OP GEZAG VAN DE RECTOR MAGNIFICUS
DR.A.J.H. VENDRIK, HOOGLERAAR IN DE FACULTEITEN
DER GENEESKUNDE EN DER WISKUNDE EN NATUUR-
WETENSCHAPPEN, VOLGENS BESLUIT VAN DE
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"BRONDER-OFFSET" ROTTERDAM

Voor de tot standkoming van dit proefschrift heb jij, beste de Haan, ongetwijfeld de grootste bijdrage geleverd. Als proefpersoon heb je aan alle, soms zeer onprettige, experimenten deelgenomen. Als discussie-partner heb je belangrijke bijdragen geleverd voor de interpretatie van de waargenomen verschijnselen. Vele onderdelen van de nog steeds gebruikte apparatuur zijn de vruchten van je inventieve geest. Hiervoor dankbaar, verheug ik me erop dat je me zelfs bij de openbare verdediging van ons werk terzijde wilt staan. Bert, ik hoop dat de vriendschap en waardering voor elkaar, gegroeid in jaren van samen experimenteren, niet door je vertrek van dit laboratorium verloren zullen gaan.

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Aan "Mossi"
Aan Janny, Marleentje en Hansje

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CHAPTER I

INTRODUCTION

§ 1. THE BENEFIT OF STABILIZATION EXPERIMENTS

In order to obtain a proper insight into the functions of the visual system it is necessary to integrate the information obtained from various disciplines. This means that we have to read the articles of workers exploring different fields and also speak their language. Obviously, it is impossible for one man, because of his limited time, understanding and memorizing capacities, to get a clear picture up to the detail of the results obtained up to the present from the extensive and very diversified studies on the visual system. Nevertheless it is fruitful to correlate the main results obtained in the different fields.

Of the various lines along which the research on the visual system is conducted we have considered electrophysiology, psychophysics and morphology. Moreover, we may learn a lot from the influence of pharmaca and those clinical reports which describe the effects of defects in the visual system. We will deal with the last mentioned source later on in this thesis. Let us compare first a few relevant features of two methods used to derive a number of data from the visual system of animal and man.

The electrophysiological approach:

1. An animal having been anaesthetized, paralyzed, operated, the experimenter can collect as much data as possible by means of micro- or macro-electrodes. This acute experiment will entail the death of the animal.
2. It is possible to anaesthetize and paralyze the animal temporarily, to operate

it and allow it to recover after implantation of electrodes. This is a chronic experiment; the animal moves around freely and may live on for years. The experimenter may use the animal over and over again by connecting the electrodes to his stimulators and recorders. However, in this way he is not able to explore other parts of the brain on the same subject, and if he wishes to carry out various explorations, has to start again the time-consuming procedure of implantation and recovery on other animals.

3. In man (patients with tumor, epileptics and so on) these "experiments" are applied likewise. They are not meant to be experiments but to supply indicators for the brainsurgeon permitting him to see which part of the brain functions normally and which part does not and has to be removed by excision. These operations, although performed on sick men, have nevertheless supplied important information concerning the functioning of the brain, and hence also about the visual system.
4. A group of recordings known as electroencephalogram, electroretinogram, electrooculogram has to be mentioned under the heading electrophysiology. These recordings may be made on man and animal alike without causing permanent damage and, unlike the methods described above, reveal integrated activity from large groups of cells.

The psychophysical approach:

1. A freely moving animal can be trained, by means of rewards and punishments, to make a correct choice out of several alternatives. This behaviour enables the experimenter to test the animal's visual capacities. The duration of the training necessary to obtain statistically significant results depends on the animal chosen, as well as on the difficulty of the problem it has to solve. However, the animal supplies only yes-or-no answers (correct or non-correct choices) in every single experiment, and cannot give a description of its perception.
2. Man can respond in the same way as the animal and often better, but in addition is able to describe what he perceives, and he so enables the experimenter to extract more information out of his experiments. One experiment on man has been performed paralyzing the eye-muscles of one of the eyes, and some experiments during which, in one way or another, the visual objects presented did not move with respect to the retina of the subject.

Summarizing the above points it is easy to see that the counterpart of the acute animal experiment are the experiments mentioned under point 2 of the psychophysical approach, in which the effects of the eye movements are eliminated. By performing this type of experiments we profit from the possibility of directly correlating the observations in man with the large amount of information procured by acute animal experiments.

Moreover, elimination of the eye movements offers the advantage of discarding the variable uncontrollable displacements of the stimulus over the retina, which often complicate the psychophysical experiments.

The subject may eliminate part of his eye movements voluntarily by trying to keep his eyes as motionless as possible. This is called fixation. It is easy to demonstrate to the subject his own residual eye movements. Total paralysis of the eye-muscles or complete abolishment of the movement of visual objects with respect to the retina obtained with other methods has been called stabilization.

§ 2. METHODS OF OBTAINING STABILIZATION

The methods available to eliminate eye movements with respect to the object are:

a. Curarization of the subject.
   The eye-muscles are paralyzed with a sligther dose than the muscles needed for respiration. Artificial respiration has to be at hand in order to prevent the experiment from becoming lethal. Curarization is not suitable for frequent experiments.

b. The eye-muscles can be fixed by means of pincets or may be paralyzed by a series of injections with a suitable drug behind the eyeball. This procedure has actually been followed (Kornmüller, 1931). The risk of internal bleedings makes this method unsuitable for frequent experiments.

c. The subject may use a perspex or glass contact lens, which fits accurately his cornea and part of his sclera. A small high-powered lens and the object are attached to this contact lens. In this way the object is expected to make the same movements as the eye (Pritchard, 1961a).

d. The said contact lens may be used with a small mirror fastened to it, instead of a lens and object. This mirror is part of an ingeneous optical system which projects the object invariably upon the same area of the retina, independently of the movements of the eye and mirror (Ditchburn and Ginsborg, 1952; Clowes and Ditchburn, 1959).

e. Instead of a full-fitting contact lens a suction cap, which only touches the eye along a small rim, may be used for cancelling the image movements over the retina. On top of this cap the object or a mirror may be attached (Iarbus, 1957a).

Another way to eliminate the influence of eye movements is the creation of an experimental situation in which nowhere changes in brightness can be observed (milkglass-spheres, halved table-tennis balls). Although, as far as the fading of brightness and color is concerned, the results obtained from these experiments are the same as those described when using other techniques, their usefulness is too limited (Hochberg et al., 1951; Galbraith, 1964).

Hence, a choice had to be made from these methods. The curarization and muscle injections were discarded as being too dangerous.

As is known, an ideally stabilized image, e.g. the entoptic image of the retinal capillaries and fovea, disappears completely and can be recalled only by changing the illumination in one way or another.

According to the literature, the suction cap brings about a complete and permanent disappearance of the images in a few seconds, whereas the contact lens causes the objects to disappear only temporarily and to regenerate afterwards.

For this reason we have chosen the obviously better method of Iarbus, i.e. the suction cap, be it in a modified version, for our experiments.

Byford (1962) demonstrated that the contact lens did not follow faithfully the excursions of the eye for eye movements in excess of 1 degree. Barlow (1963) compared the methods of contact lens and suction cap and concluded that the suction cap provides better stabilization (less slippage) than the contact lens.

Prior to a description of our experiments and observations and before reporting the conclusions we arrived at by comparing our results with the existing electrophysiological data, we have to emphasize the qualitative issue of our work. The difficulty of obtaining complete and adequate descriptions of the subjective changes in the visual perception which, often very rapidly, take place in the stabilized condition, made it necessary to carry out several hundreds of experiments on each of the two subjects highly trained in this work. Part of this thesis has already been published earlier (Gerrits et al., 1963, 1966).

§ 3. OUR OWN METHOD OF OBTAINING STABILIZATION

In all our experiments, except those described in Chapter II, § 2, we have been using the standard cap shown in figure 1.

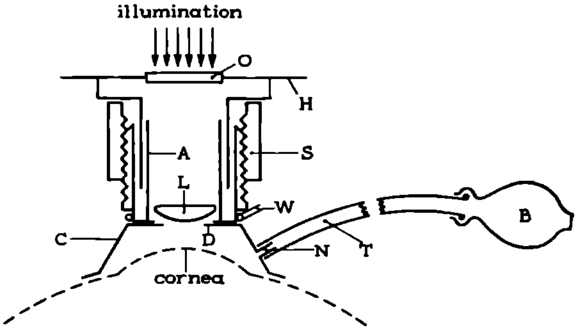

Fig. 1. The standard cap sucked on the eye (not drawn to scale). The object holder H with the object O can be exchanged during the experiment. Weight of the cap 2.2 g, weight of object holder + object 0.8 g. Material used: dural.

A non-reflecting black tube

B	bulb	N	connector
C	dural cone	O	object
D	diaphragm	S	screw
H	object holder	T	flexible tube
L	lens + 50 D	W	warm water connectors

This cap, which is a modified version of the one described earlier (Gerrits et al., 1966), has been redesigned especially to prevent internally reflected light from reaching the eye. A negative pressure (40-50 mm H_2O), generated by means of the rubber bulb B, sucks the cap on the eyeball. A considerable increase of this underpressure will cause ischaemia. Hence, if during the experiment we intend to raise the underpressure up to the ischaemic pressure level, we use an injection syringe instead of the bulb B. The experimenter can easily exchange the object O together with objectholder H during the experiment without taking off the cap.

Before starting the experiments the pupil of the subject's eye is dilated and the accommodation of his lens is almost abolished by a mydriatic. The eye is subsequently anaesthetized by a few drops of novesine. The other eye is covered with a black cloth. When the cap and the object have been placed on the eye the subject brings the object into focus by adjusting the distance between object O and lens L by means of the perspex screw S. The system is kept at about body temperature by running warm water through a tube W wound around the cone C, thus preventing condensation of water on the lens. In order to eliminate as many sources of slippage as possible, the axis of the eye is held in vertical position. Therefore all the experiments are carried out with the subject supine.

It proved to be very difficult to screen that part of the sclera not covered by the cap without introducing slippage. The best results were obtained with a very thin black rubber film with a hole in it, and loosely placed over the cap. Having asked the utmost concentration of the subject in order that he might minimize his eye movements, we studied for every type of experiment the influence of light entering the eye via the sclera on the subject's perception. We found this to influence the results in a quantitative way only. The field of vision is limited to 20 degrees in this modified cap, but for comparison purposes a cap with a 60 degrees field has been made.

As is well known the optical axis of the eye does not transverse the fovea. Moreover, we made allowances for the possibility that the position of the suction cap on different subjects would not always be the same. We are able, however, to locate the point of the object which projects to the fovea of the subject after sucking the cap on his eye. For that purpose the light for the illumination of the object is switched on and at the same time a small spot of light is moved over the part of the sclera not covered by the cap. The subject then perceives two images: the object projection and an entoptic image of his retinal veins and fovea. It is easy to train a subject to recognize his fovea in this entoptic image as the place without veins and looking like a collection of small cells (Ehrich, 1958). So he himself can give us the information we want. In difficult cases it may be necessary to tap the cap slightly in order that the perception will not vanish because of stabilization. It was found that the optic axis of the eye practically coincided with the optical axis of the cap (see also figure 17), if the cap had been placed normally on the eye. The rationale of several precautions to be taken in order to obtain satisfactory stabilization is discussed in Chapter III.

All subjects were dark-adapted or nearly so at the beginning of the experiments. All stimuli were of photopic brightness. The light sources used were Ferranti flash tubes CL 63 (green, λ_{max} 520 nm, bandwidth 70 nm), and CL 66 (white), running on stabilized power packs.

These tubes can produce very short light flashes as well as constant illumination. Large areas are obtained by illuminating opal glass by white fluorescent tubes. Monochromatic stimuli are made by means of interference filters with a bandwidth of 11 nm. Moreover, a series of glass filters are available. For those experiments in which the wavelength used did not interfere with the results, we always used the green flash tube. A rough calculation of the brightness that reaches the retina when using this tube resulted in a range of up to 1500 trolands.

The dark room in which the experiments are carried out has been equipped with microphones in order to record on tape the instructions and questions of the experimenter as well as the descriptive response of the subject.

§ 4. RELATION WITH PREVIOUS WORK ON STABILIZED IMAGES

In the following only those experimental results will be cited which bear connection with our own observations.

As already mentioned, an ideally stabilized image, e.g. that of the retinal capillaries, will fade from vision and never reappear. Some experimenters used this type of stabilized images (Campbell and Rosen, 1961; Cornsweet and Dwelly, 1962).

The designer of the suction cap, Iarbus (1957b), claims a total disappearance of his objects and the perception of an "empty field" in 3 seconds.

However, Barlow (1963, 1964) investigating the suction cap, reports an ultimate perception of a very low contrast version of the original image. This perception persists without fluctuations.

Using the suction cap it is our experience that the image disappears completely and does not fluctuate. At higher levels of illumination, however, a faint residual brightness stays in vision.

Most users of contact lenses report only temporary disappearances which, in our opinion, may be caused for a great deal by slippage of the contact lens. On the other hand there are clear indications for a central origin of the more or less periodic fluctuations as evidenced by Fiorentini and Ercoles (1963, 1965) and Lehmann et al. (1965). Furthermore the time of visibility of the object may depend on the image locus on the retina (Ercoles and Fiorentini, 1962).

If the object consists of line patterns, e.g. circles, triangles, crosses, another curious effect is observed in the first seconds of the stabilization.

These figures fade away in fragments which mostly come back again several times. It looks as if the figure has been built up of units which act separately. This fragmentation, which reflects some of the figure analysing operations of the central part of the visual system, has stirred the imagination of many psychologists. It seems that curved lines and meaningful diagrams are longer visible than jagged lines and meaningless figures. These effects have been observed by Pritchard et al. (1960), Pritchard (1961b), Eagle and Klein (1962), Evans and Piggins (1963), Evans (1965) and by ourselves.

The difference between our own observations of this fragmentation and those of the other experimenters is that we observe it only in the first seconds of stabilization and never afterwards. We are convinced that periodic observation of fragmentation, that is during longer observation times, is due to incomplete stabilization. Some tentative evidence for this is given in Chapter VI, § 2.

Surveying the results published by all experimenters we may conclude that there exist different systems for brightness, color and form perception. We arrived at the same conclusion from our own experiments in which always the contour disappeared prior to the color and the color prior to the brightness. Only Beeler et al. (1964) using Ishihara test plates as objects report that the contours of the circles composing the pattern remain visible after the color has disappeared. This can also be explained through incomplete stabilization.

In the opinion of Iarbus (1957b) two distinct processes can be distinguished: the first being fast (taking less than 3 seconds), in which "all visible differences in the test field vanished", the second slow (taking tens of seconds), being detected via after-images. The rapid process is related to the on- and off-effects, the slower process to adaptational changes.

The influence of a periodic change of the illumination level of the stabilized image has also been investigated by different experimenters.

Ditchburn and Fender (1955) report a flicker frequency of 20 c/s to be most effective in eliminating the fading of the stabilized image. They describe a strange great discrepancy between the subjective brightness perceived and the objective brightness of the stabilized image at high interruption rates.

Fiorentini and Ercoles (1960), however, found a flicker frequency of 1 c/s to prevent their stabilized object from disappearing and that higher and lower frequencies were less effective for this purpose.

Also a movement of the image over the retina may bring the image partly or completely back into vision.

Ditchburn et al. (1959) investigated the visibility of a line that had faded earlier by stabilization, as a function of the amplitude of displacement with the frequency of this artificial tremor as a parameter.

They report that in the frequency range of 4 to 20 c/s an amplitude of imposed tremor between 0.3 and 0.5 min.arc is the most effective for regenerating the image.

Iarbus (1959) performed an experiment in which an alcohol solution, colored black by addition of a dye, flew through a capillary sucked on the eye. Evaporation of the fluid caused its meniscus to move in the capillary. These slow boundary displacements permitted him to observe on- and off-comets.

Ditchburn and Fender (1955) found an immediate regeneration of the image on tapping their stabilization apparatus. This tapping may introduce high frequency vibrations of small amplitude.

When Barlow (1963) touched his suction cap he observed a bright line at one side and an intense black line at the other side of his image, while the intervening area did not change its appearance.

We were able to confirm the observations of Barlow and Iarbus in our own experiments (Gerrits et al., 1966).

As may be seen from the outcomes reported above some discrepancies in the observations may well be due to the different methods used to obtain a stabilized image. Moreover, it appears that a systematic investigation of the influence of the eye movements in one and in more directions has not been carried out as yet. Practically nobody has shown the correlation between the observations and the known electrophysiological data from animal experiments. This work is meant to be an attempt to fill up this deficiency.

CHAPTER II

EXPERIMENTS

In these experimental sections we have tried to describe the subject's observations as completely as possible. This completeness inevitably implies that many response details are given which may obscure the more important results. Therefore, the main results obtained from the experiments described will be summarized at the end of each section.

§1. THE TOTALLY STABILIZED IMAGE

The meaning of a few descriptive terms is given first:

Eigengrau is the perception obtained after at least 20 minutes of dark adaptation; it has a non-zero perceptual brightness.

Intense black is the perception of a brightness far less than that of Eigengrau.

An example of the objects presented to the subject in the standard cap is shown in the figures 2A to D. Suppose object 2A is chosen and illuminated with green light (λ_{max} = 525 nm) of moderate intensity. At switching on the light the subject perceives a green ring surrounding a black disk. In one or two seconds the

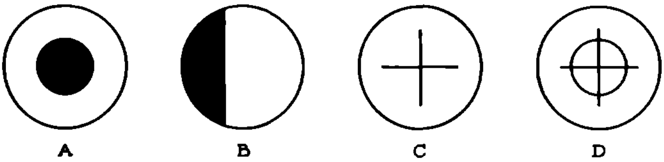

Fig. 2. Some of the objects used. Diameter of object is 20°.

contours blur, then the central disk and the field outside the ring become slightly brighter and green and at the same time the ring becomes less bright and less green. Subsequently the whole picture turns colorless and finally also the brightness fades. Soon the subject notices that the whole field of vision is dark. After a few minutes, however, he observes that the field has darkened still more. Thus in spite of the constant light input in his eye he is not able to perceive the object.

Independently of the color of the object chosen, the sequence of disappearance of the perception stages is always the same: first the contours secondly the color, thirdly the brightness.

At the moment of switching off the stimulus, the subject perceives a very bright after-image of the ring in the complementary color; in casu a purple ring is seen. Often also a colored "after-image" of the black disk and the adjacent black just outside the ring is observed. These parts are then seen in a vivid green (see figure 3). The after-images also show fluctuations. They often alternate with black, their brightness and color diminishing in each period. The purple ring and the green center and halo may fluctuate at totally different frequencies. The brightness of these after-images depends on the duration of the stabilization, the brightness of the stimulus and the remaining background illumination after the stimulus has been switched off, but is much greater than that observed without stabilization.

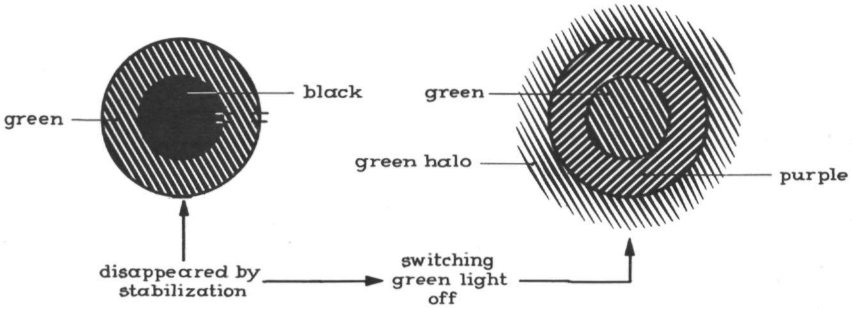

Fig. 3. The "after-image" of the stabilized object.

The lower the illumination level used, the less purple is observed at light off. If no or almost no purple is observed, the ring is seen in intense black.

Generally speaking it may be said that also a shortening of the duration of the illumination results in less black and less purple in the image at light off.

Decreasing this duration results first in a disappearance of the purple, and subsequently also the blackness of the after-image diminishes continuously. But a strong after-image at light off is still perceived when the duration is so short that the effect of the stabilization during light on is only just perceptible. Of course at very short durations the perception at light off is the same as in the stabilized condition.

Another peculiar effect is observed when using, for example, object 2D. At light on a green field is perceived with a black cross and circle on it. Subsequently these black lines and the outside contour of the object fade, but during the first few seconds fragments of the circle and of the cross reappear as units, i.e. a horizontal line or a vertical line, or the complete circle alone and so on. During these partial temporary regenerations the color and brightness fade gradually just as without lines. At light off these formerly black lines reappear in green against a purple field, and moreover, often fluctuate in separate units, just like they did formerly after light on. This fluctuation effect has been observed earlier (Pritchard et al., 1960; Pritchard, 1961; Eagle and Klein, 1962; Evans, 1963, 1965).

At higher illumination levels of the object there remains a very faint brightness after the fading of contours and color. This remaining brightness is far less than the brightness of the original image but higher than that of Eigengrau.

Summarizing: The perception of a stabilized image vanishes within one minute. If the image is composed of line patterns these disappear and reappear temporarily in fragments during the first seconds of the stabilization.

The contours always disappear first, subsequently the color and finally the brightness. At high illumination levels a faint brightness may remain visible. At light off strong after-images are perceived in intense black or in the complementary color.

§ 2. STABILIZED IMAGE ON A MOVING BACKGROUND

a. Homogeneous background

Instead of stabilizing the whole field of the observer we may present him a stabilized image against a normal non-stabilized background. Another type of cap, shown in figure 4, has been made for that purpose. With this cap a

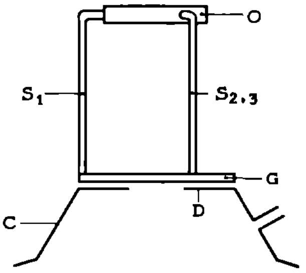

Fig. 4. Cap used to obtain a stabilized image surrounded by a non-stabilized background. Weight 0.5 g.

C dural cone
D diaphragm
G transparent plate
O object
S_1, S_2, S_3 rods

stabilized image of object O is obtained, but the background, seen through the diaphragm D adjacent to O, is not stabilized. This background is so large that, in spite of the eye movements, the object O is always surrounded by it. The diameter of the diaphragm is small (0.3 mm) and ensures a sufficiently sharp image of the object on the retina (in a second model there is a lens instead of the diaphragm). If object O is a homogeneous black disk and for instance a green background illumination is switched on, the subject perceives the black disk on a green background. In a few seconds, however, the black disk has completely disappeared and adopted the brightness and color of the background. Upon switching off the background illumination, the subject will perceive a green disk on a normally dark or slightly purple background. The contour of this green disk is not as sharp as that of the original black disk; it seems to be slightly larger and blurred, like all after-images. This now green disk slowly fades by losing first its color and then its brightness. However, the subject does not perceive a large spread of this disk as in the former experiments (see also figure 5A).

Whereas in the above described experiment the disk is perceived immediately after switching off the light, this was not always found to be the case at higher illumination levels. Mostly then a dark or purple, homogeneous, after-image of the background, or one with the disk in a very faint colorless light in it is seen.

The after-image of the background often disappears subsequently to a few fluctuations, the after-image of the disk becoming much brighter and green, and then, after having disappeared and come back again (often many times) with lower brightness and less green, the after-image at last disappears completely. Screening the sclera with the black rubber film causes the disk to stay in vision at light off (or to return earlier) in green, and at the same time the frequency of the fluctuations diminishes. If the subject turns his head or eye to the black field adjacent to the green surround after filling-in has taken place, he always immediately observes the green filled disk contrasting with the black field. The difference is under these circumstances that the subject's retina receives diffuse green light that has penetrated his sclera. If the stabilized part is only a little smaller than the non-stabilized background, it is more difficult to obtain a homogeneous field. Often then a slightly darker grey patch can be seen in the center of the disk.

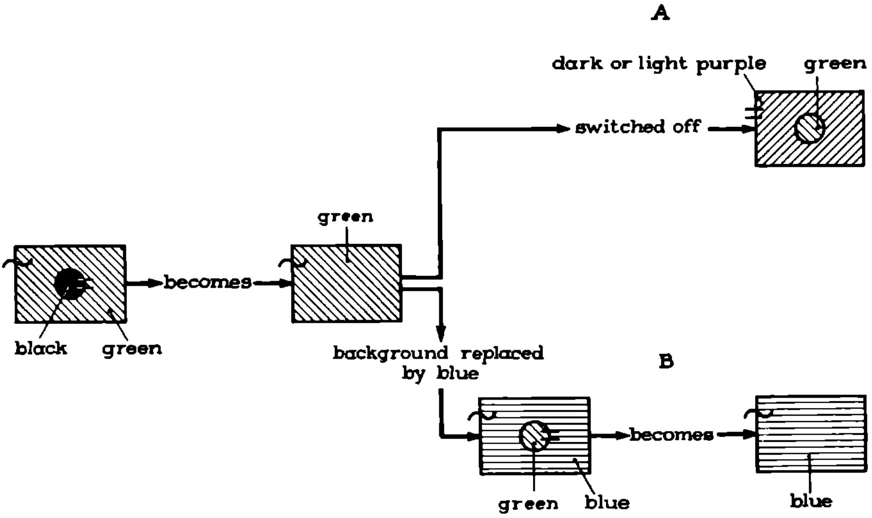

Fig. 5 A and B. Perception of a black stabilized object surrounded by a non-stabilized green background when this background is switched off (A) or is replaced by a blue one (B).
~ contour of the non-stabilized field = contour of the stabilized field.

b. Changing the background color

Now we do not switch off the green background after the filling-in has taken place, but replace it by another, for instance a blue one. The subject then observes a green disk on the new blue background. In a few seconds, however, the green color of the disk is changed into blue of the same hue and brightness as the blue background. Again the black stabilized object seems non-existent (see figure 5B).

c. Effect of a non-homogeneous background

Even when the background is not homogeneous, but e.g. partly red and partly yellow (see figure 6) a filling-in of the stabilized object with the color and brightness of the background adjacent to it is brought about. The subject perceives one half of the object becoming red, the other half yellow, the transition of red to yellow being gradual.

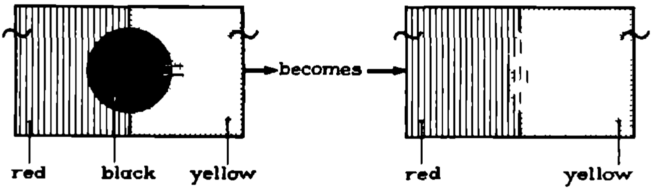

Fig. 6. Perception of a stabilized object on a non-stabilized non-homogeneous background.

The effects described above take place independently of the background color chosen and of the form of the stabilized object. It is always the stabilized part of the field that disappears and is filled in with the same color and brightness as the non-stabilized field adjacent to it. The part filled in is not switched off together with the background and so its perception fades very slowly.

This will be discussed in more detail on page 72 of this thesis.

Summarizing: The stabilized image surrounded by a non-stabilized field loses its form, color and brightness. It is filled in, however, with the color and brightness of the adjacent non-stabilized field. When switching off the surrounding field, the brightness and color of the part filled in fade away slowly.

§ 3. MOVEMENT OF A STABILIZED IMAGE

With the knowledge gained, i.e. that elimination of all relative movements results in a complete loss of perception, the next logical question is whether all the movements carried out by the eye are really necessary for continuous brightness perception.

As is well known there are 6 extra-ocular muscles which determine the position of the eye. Roughly speaking we may say that one pair of them are the executors of a small rotation of the eyeball around its visual axis. The other two pairs which enable the subject to direct his gaze to any point in space, work along two axes which are almost perpendicular to each other. So what we have to do next is to investigate whether a movement in one direction is sufficient to bring the image back to perception.

Let us first give a few definitions concerning the terminology used:

The on-border or on-trail is that part of the retinal image which is newly illuminated as a result of the movement.

On-activity is the neural activity causing the subject to perceive the on-border or on-trail.

The off-border or off-trail is that part of the retinal image from which the illumination is extinguished because of the movement.

Off-activity is the neural activity causing the subject to perceive the off-border or off-trail.

The spreading of black does not explicitly mean that the areas in which the spreading takes place are necessarily perceived as black. It is also possible that a previously existing brightness is decreased by the invading darkness. In some cases this may indeed be perceived as black.

a. Movement in one direction

The easiest manner to cause a movement of a stabilized image is tapping with a pencil against the cap. Using the standard cap and one of the objects shown in figure 2, an impression of what the subject perceives is seen in figure 7.

When the stabilized image (green light, object 2A) has disappeared, tapping the cap will cause the perception of beautiful on- and off-borders. The use of this green light will make the on-border visible as bright green, the off-border as intense black, sometimes combined with a purple glow. This intense black is much more homogeneous and much darker than Eigengrau. The area between the moving borders seems to brighten partly or totally if the movement is large enough.

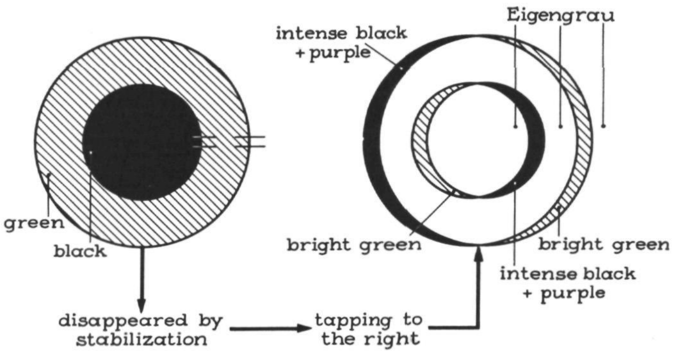

Fig. 7. Perception of on- and off-borders by slightly moving an object in one direction after the perception has disappeared by stabilization.

A better method of obtaining adjustable movements in one direction (see figure 8) has been found. A perspex rod R consisting of three parts (opaque-translucent-opaque) can be moved in a channel K by means of a specially designed volume-pump P. When the pump pushes the liquid in the closed circuit

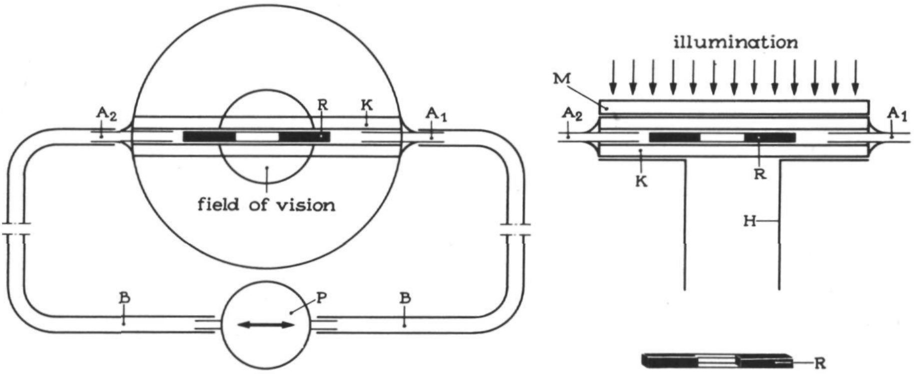

Fig. 8. System used to obtain movement in one direction only of a stabilized object. Weight of object holder + object 2.1 g.

A_1, A_2 channel connectors
B flexible tubes
H object holder
K perspex channel
M opaline plate
P volume pump
R perspex rod

to the right or to the left, the rod R, fitting accurately in the channel K, moves with the liquid. The object holder together with this system is contained in the standard cap which is placed on the eyeball, and the subject is asked to bring the rod into focus by adjusting the screw S (figure 1). The green light is switched on while the rod is not yet moving. The subject perceives the rod and the contours of the channel K on the green field. In a few seconds the whole picture disappears and becomes dark. Now the pump is started in order to move the rod (see figure 9).

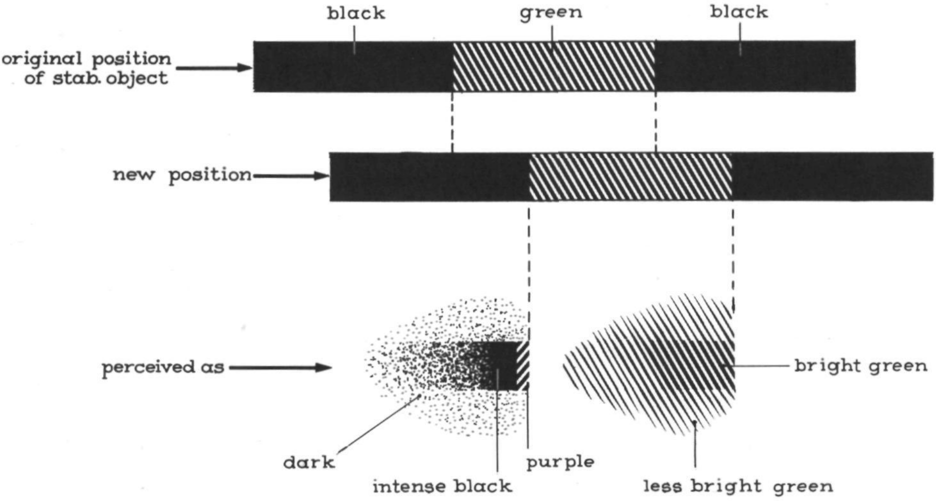

Fig. 9. The perception of on- and off-trails by the movement in only one direction of a formerly stabilized object.

Let us first describe the momentary perceptions when the rod is being displaced at a medium speed.

When the rod moves to the right an on-trail at the right-hand side and an off-trail at the left-hand side are clearly discernable. The on-trail has a sharp boundary at the moving right-hand edge of the translucent part of the rod. On this edge the brightness is greatest and the color is green. With increasing distance from the edge to the left, the brightness and color gradually fade and finally even a colorless area can be seen. The brightness and color spread outside the track of the rod, but the brightness outside the track is considerably less than the brightness of the track itself.

The right-hand boundary of the off-trail, on the other hand, although being sharp too, is intense black with a purple front; to the left, the blackness and the purple fade, the purple disappearing first. Moreover, a spreading of blackness outside the track of the rod can be seen. This is less black than the part following the purple, but darker than the peripheral Eigengrau. If there is any spreading of the purple at all it is certainly far less than that of the blackness. When the movement is stopped, the sharp right-hand boundaries blur and also now a spreading to the right is started, but at the same time the trail shortens. This shortening is due to the fact that the activity locally generated diminishes continuously. The ends of the trail, which had been activated first and thereby have also lost their activity first, seem therefore to retract to the right.

With slower movements of the object the subject perceives a narrowing of the green on-trail and also of the purple and the intense black off-trail. Besides, the spreading outside the track diminishes considerably.

With a large, fast, stepwise movement of the rod the on- and off-trails lengthen. The spread of the green and of the brightness outside the track is very vast, reaching far into the periphery. In the same way the blackness spread covers a larger area now.

The spreading capacity as well as the time constant of local adaptation (lapse of time necessary for its disappearance) seems, however, to be smaller for the off-activity than for the on-activity. Although under these circumstances the purple is found over the whole length of the off-trail, its spread outside the track is still negligible.

The image locus on the retina and the duration of its stabilization before the movement is started have also an influence on the brightness, blackness and color of the on- and the off-trail, and also on their spreading (compare page 39).

The complementary color in the off-trail at low speeds, then present only in the very first part of it, can only be seen by experienced observers.

When the pump is moving the rod continuously to and fro, the subject observes the on- and off-trails alternately on the left-hand and on the right-hand side. The frequency of the movement can be varied from 0 to 30 c/s, this being the major range of normal eye movements. The amplitude can also be varied over a wide range. However, it is not possible, by any adjustment of the movement's frequency or amplitude, to restore the original situation, i.e. that which existed before stabilization, when the rod was seen to be homogeneously illuminated. The activity spread outside the track in the direction perpendicular to the stabilized contour spoils the regeneration of the original image of the rod.

We will now direct our attention to the purple in the off-trail. One might think that the arrival of intense black following the purple is due to a longer latency time of black as compared with that of purple. This is not so: the very first part of the off-trail consists of two components: a purple, having brightness and color (the complementary color of green), and a blackness (the complement of brightness). The brightness component of the purple prevails over the brightness-suppressing black component, so that a saturated purple is seen. The decrement of the purple is obviously greater than that of the black, causing the gradual change-over from purple to black. That this argumentation is bound to be correct is shown by experiments in which the illumination levels used are so low that the purple is no longer seen. In that case the whole off-trail is intensely black.

Summarizing: The movement of an image in one direction causes the subject to perceive a bright on-trail and a black off-trail, which are the correlates of the on-, respectively the off-activity generated locally by the boundary displacement. Furthermore the subject observes a spreading of these activities far outside the area where they originate. It is in no way possible to restore the perception of the original image by unilateral displacements.

b. Multidirectional movements

b.1. Random movements of a bright object

Since unidirectional movement proved to be insufficient to regenerate the complete stabilized image, we had to set up an artificial image tremor in all directions. The first system designed by us for this purpose is shown in figure 10.

Here the four inlets are connected to the same pump as the one used in the experiment described above. The action of the pump causes irregular movements of the black annulus R, resulting chiefly in eccentric rotations, provided the annulus lies approximately in a horizontal plane. If not, the movement will principally be undirectional, as a consequence of gravity.

The subject perceives the illuminated round hole O which has been placed on his eyeball in the usual way by means of the standard cap and illuminated with green light. When the annulus is at rest, the perception of the object vanishes. Then the pump is started. After a few movements of the annulus the

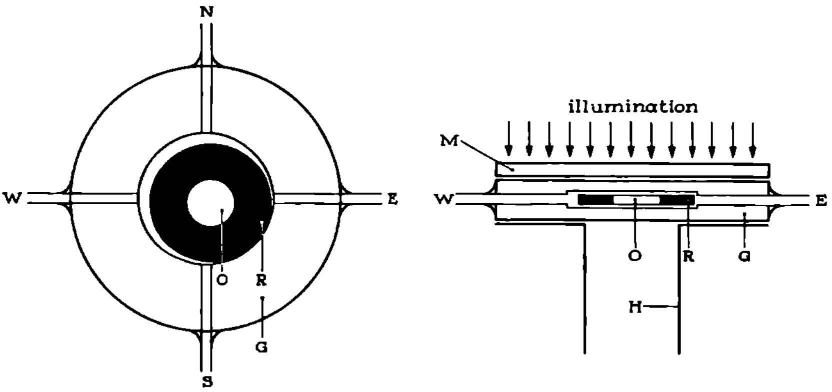

Fig. 10. System used to obtain random movements in all directions of a formerly stabilized object. Weight of object holder + object 2.7 g. N, E, S, W 4 inlets.

R black annulus
O hole H object holder
M opaline plate G perspex leader

subject perceives a homogeneous, bright and green colored image of the hole O, even though the maximum movement of the hole is no more than a quarter of its diameter. In so far as the subject is able to remember, the perception of the hole O after its reappearance is the same as it was initially when the light was switched on.

This effect is produced when the annulus moves irregularly, performing about one revolution per second. Slower movement frequencies result in the observation of on- and off-borders, with some spatial spreading. Much higher frequencies (about 10 sec^{-1}) are also ineffective for filling in the hole, and will cause the perception to disappear in the same way as it does in the case of an immobile stabilized image. In our opinion this is due to the fact that the time available is too short for the newly activated on-borders to spread their excitation sufficiently to the inside of the contour (see page 38). The excitation available is then insufficient to permit it to spread to the center of the field and to eliminate the local adaptation.

It might be emphasized that it thus appears possible to cause the subject to perceive the hole as being homogeneous and colored by choosing the correct range of frequencies and of movement amplitude of the contour alone.

This result is important, as will be explained in the theoretical part, which is to follow.

The disadvantage of this device is that its rotation is very irregular. The best we could do was to estimate the mean time necessary for the performance of one rotation, and moreover it was found impossible to keep the rotation frequency constant. In view of these disadvantages and because we wished to arrive at a better confirmation of the outcome, we were continuously in search of a light-weight device that should enable us to obtain an adjustable stable movement of the object in all directions.

Summarizing: The movement in all directions solely of the contour of an object the perception of which has vanished by stabilization is sufficient to cause the object to be filled in and perceived homogeneously.

b.2. The electric synchronous motor

We were very happy to receive the help from the N.V. Philips' Gloeilampenfabrieken, Eindhoven.* In the physical laboratory of this firm a very small electric synchronous motor has been developed, the components of which were placed at our disposal. The details of this motor will be published by Bollée. Using these components we built a rotating object on top of an object holder in the manner shown in figure 11.

The coil and iron core of this motor have been fastened between two transparent plexiglass plates P_1 and P_2. Two small jewels serve as bearings for the object's axis. A ferroxcube ring, magnetized to form 16 equally spaced north and south poles, fits tightly around a transparent plexiglass object. A generator feeding a sinusoidal waveform to this system will cause the ferroxcube ring and the object to turn in the center of the coil and of the iron core with a rotation frequency of 1/8 of the frequency supplied. This motor is attached to an object holder by means of a steel spring.

In figure 12 the three types of object used up to the present are shown. These are called: motor objects. The field of vision is equal to the inside diameter of the ferroxcube ring.

The motor objects A and B are complementary: in A a bright object rotates in a dark field, in B a dark object rotates in a bright field. As can be seen in figure 12 the center of the bright and that of the dark field are eccentric with

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* We are very obliged to the N.V. Philips' Gloeilampenfabrieken, Eindhoven, who put to our disposal the components of a very small electric synchronous motor, developed in their physical laboratory, and to Ir. B. Bollée, who demonstrated this motor to us and has given valuable advice concerning its use for our experiments.

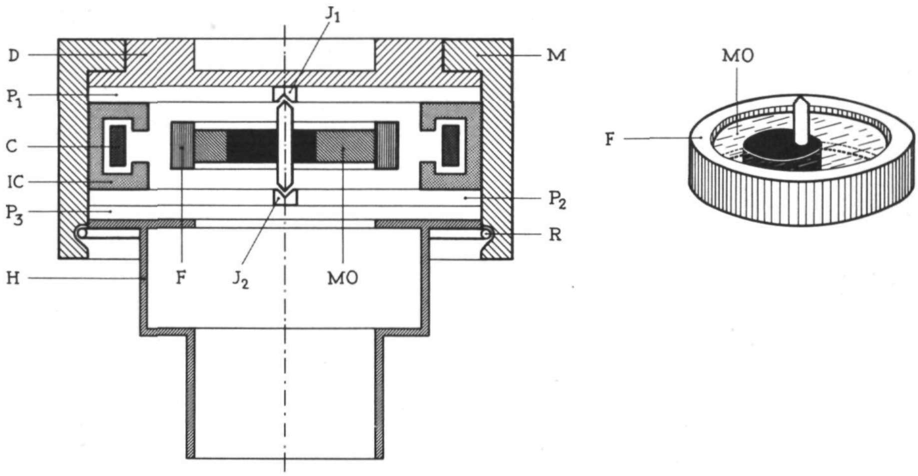

Fig. 11. The electric synchronous motor.

C	coil		
D	diffusing plate	MO	motor object
F	ferroxcube ring	O	(modified) object holder
IC	iron core	P_1 P_2	plexiglass plates
J_1 J_2	bearing jewels	P_3	secondary object
M	black plastic motor housing	R	metal ring

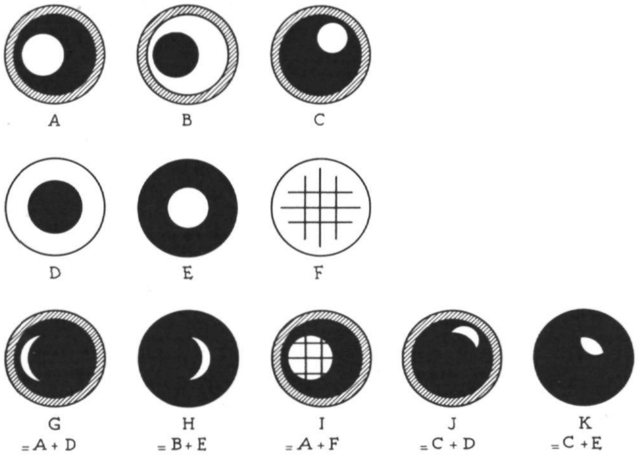

Fig. 12. A, B, C, motor objects
D, E, F secondary objects
G, H, I, J, K combinations

respect to the motor. The transparent plexiglass plate P_3 may be replaced by any other plate, like those shown in figure 12 D, E, F. These plates will be called secondary objects. The combination motor objects and secondary objects allows us to compose many combinations of moving and stabilized objects (figure 12 G to K).

The range of rotation speeds we are interested in varies from 0 up to a few revolutions per second. At these low speeds this motor turns very irregularly and thus cannot be used, but at higher speeds its functioning is very stable. However, from the mechanical point of view a rotation speed as low as possible was recommended. We therefore decided to let the motor object rotate at a speed of about 50 revolutions per second and use a stroboscopic illumination of about the same frequency. This is well above the flicker fusion frequency of the eye for the intensities of the light used.

In a series of exploratory experiments we actually found no differences in the perception when using higher frequencies.

Another difficulty arose when we found that this motor has to be started at a low speed; i.e. a driving generator frequency of ≤ 16 c/s, and hence a revolution speed of this 8-pole motor of ≤ 2 c/s. From this frequency the speed of the motor object could be raised up to a driving generator frequency of 400 c/s. All stable waveform generators known to us use decade switches in their frequency range setting. These generators are not useful because by switching them the motor is immediately stopped. So we had to use an old beat frequency oscillator. The range of this generator is about 10 c/s to 20 kc/s, continuously variable, but the inconstancy was really unacceptable. Consequently, we switched the motor over to a very stable generator, the Servomex L.F.51 MK II supplying 400 c/s. This matching is effected at the moment at which the frequency, the amplitude and the phase of both generators are equalized by manual adjustment, which equalization can be estimated viewing the screen of a 502 Tektronix oscilloscope.

Although the motor was now driven by a stable source, we needed a second stable generator for the stroboscopic illumination.

For this we chose the Nagard 5002 double pulse generator. If the frequencies of these two generators are exactly equal, the subject will perceive the object at rest, provided the width of the pulse supplied by the Nagard generator, i.e. the duration of the lightflash, is equal to or shorter than 1 ms. This is equivalent to 18 degrees of rotation during vision. A longer duration results in the perception of movement of the object during the flash, even when the frequencies of both generators are exactly equal. In our experiments we set the pulse width at 0.7 ms. Of course the two generators are not absolutely stable, but a skilled experimenter can easily correct this shortcoming by watching the phase shift of the two driving waveforms (sinus and pulse) on the screen of the cathode ray tube (CTR) and by adjusting the variable pulse delay of the Nagard double pulse generator.

Both generators set at 50 c/s caused a subjective disappearance of the object for several minutes in spite of the residual phase shifts due to the experimenter's reaction time. If the Nagard generator is set at 51 c/s, the object is expected to rotate at a speed of one revolution per second. The experimenter can check this by counting the number of pulses that shift along the sinuses of the motor driving generator in a given time, as well as with the help of the subject, who will be invited to count off loudly the rotations he perceives. This verbal report may be averaged from the tape record afterwards. A sketch of the whole set up is given in figure 13.

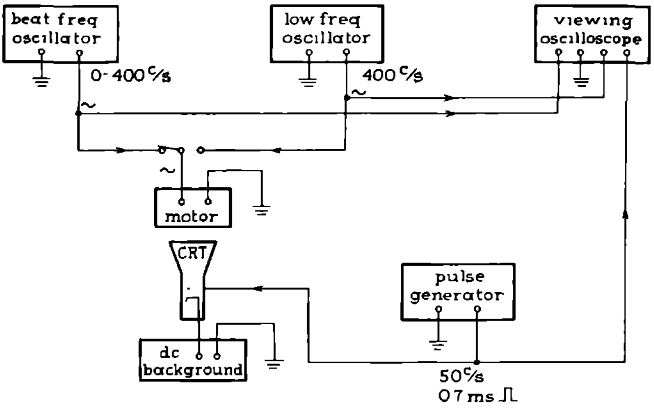

Fig. 13. Diagram of connections of motor driving generator and stroboscopic light driving generator.

In order to eliminate the manual control of the Nagard generator's pulse delay an apparatus is being developed, by means of which, starting from a high frequency and using a series of dividers, the motor as well as the light source shall be driven. By selecting the number by which the high frequency is divided in order to attain the driving frequency of the light source, a very constant difference frequency, i.e. rotation speed (be it one which is not continuously variable), can be obtained.

We will now describe what the subject perceives when the said motor is being used.

b. 3. Regular eccentric movements of a bright object

The object holder together with the motor and an object, shown in figure 12A, is placed in a standard cap and green light is used. The center of the bright part of the object has been placed outside the visual axis; for the area situated in the center, the illumination is always constant, but on the other hand the projection of the eccentric part of the field turns over the retina. For the receptors lying in this part of the retina, the light is periodically switched on and off.

We start with the object standing still, thus rotation frequency zero. At light on the subject quite normally perceives the bright green disk. Since it is stabilized, the contours fade, the green color and brightness tend to spread outside the disk, but at the same time the whole picture loses its green color and brightness and finally no more than a dark field is left.

We now set the rotation frequency at a low value, e.g. 0.2 c/s. The subject immediately sees a very narrow bright green on-sickle and a very narrow purple-black off-sickle, quite like those shown in figure 7, but now rotating. At this very low rotation frequency no or a negligible spreading of green and black outside the sickles can be perceived. The subject describes the center of the field as having the same darkness (Eigengrau) as everywhere in the periphery.

It should be emphasized that he immediately perceives the form by means of the purple-black and the green border, but that the disk is not homogeneous. The subject states: "The off-border is situated outside the disk, and does not form part of it, but the on-border, on the contrary, is situated inside the disk". The sickles are not seen as broadening with progressing time, which means that the activity, or at any rate the perception of it, has faded during the displacement.

By increasing the rotation frequency up to about 0.8 c/s the whole picture is changed. In figure 14 the momentary perception is shown. The on-border, which seems to be a little broadened now, is still seen as standing in bright green against the background. This background, however, is no longer identical with Eigengrau. From the bright green on-border green light spreads to the inside and the outside of the disk. The brightness and the color of the on-

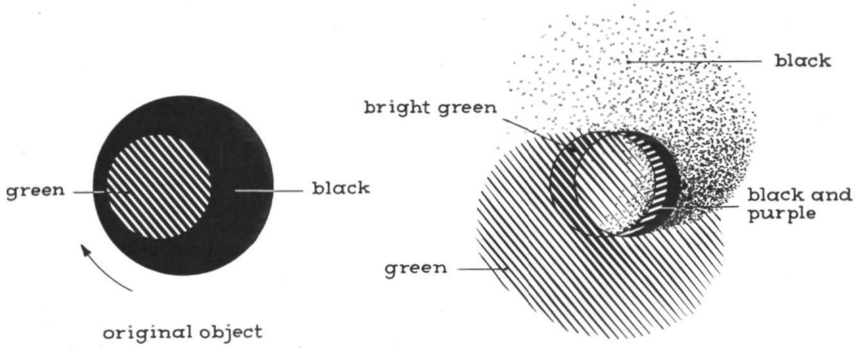

Fig. 14. The momentary perception of the bright disk of fig. 12 A, rotating eccentrically at a frequency of about 0.8 c/s.

activity spread remain far below those of the on-border. The off-border, perceived as black and purple, and which moreover seems a little broader than the one generated at 0.2 c/s, has a darkening influence outside the areas where the light has been switched off. The darkness of this spread black is far less pronounced than the off-border itself. Consequently, inside the disk, bordered by the on and off, a gradual decline of color and brightness at one side and of darkness at the other side is perceived. This darkness is estimated (very difficultly!) to be slightly darker than the Eigengrau in the far peripheral parts.

By increasing the frequency still more principally the same effects as those described above are produced, but now much more pronouncedly.

At about 2 c/s (the frequency depending a little on the level of illumination used) the disk and even the parts in the center of it, which never undergo any change in illumination, are perceived as being homogeneous. Probably there is a subjective reduction of the brightness and, certainly, of the blackness of the on-, respectively the off-border.

The field outside the disk is not completely dark, but the brightness and the color seen to spread there at lower rotation frequencies are enormously reduced now. It is easy, however, to recognize the cause of this residual brightness outside the disk: in fact it is on-activity, generated by the momentary on-border, spreading to the outside and not cancelled by the spread and the rest activity of the off-border. The source of the off-activity (the off-border) is always situated diametrically against this slightly lighter patch of outside spread on-activity and is seen there as a slightly darker patch. Both these activities rotate together with the disk.

Consequently, the delayed presence of the off-border at the place which borders the source of on-activity results in a disturbance of the darkness of the surround we expected to observe if the non-stabilized condition would be restored.

A further increase of the frequency rapidly spoils the perception of the homogeneity of the disk. In most cases 4 c/s is sufficient to break up the image obtained at 2 c/s into a grey-green diffuse field, which slowly loses most or all of its brightness, and often only a very dim flickering field without any color or contour is left. We think that in this case the time allowed to the on-border to spread its activity is too short; in fact the off-activity cancels the on-activity before it can spread to neighbouring areas.

Summarizing: A small light-weight motor, mounted on top of an object holder has enabled us to obtain a very constant rotational movement of the contour of an object. This could be attained by placing the object eccentrically with respect to the motor axis. The preliminary results obtained in the experiment described in § 3.b.1. have been confirmed: the movement of the contour alone in all directions is sufficient to bring the whole inside field back into vision. The optimum rotation frequency for reaching this goal is about 2 c/s.

b.4. Analysis of results

We will now analyse the process which leads to the filling-in of the disk and the darkening of the periphery. In figure 15 three positions of the disk are shown; the disk is supposed to rotate clockwise. Although in reality the activities spread in all directions, we shall consider only spreading in two directions, this in order to simplify matters; for the rest, this simplification detracts nothing from the validity of the argumentation.

The center of the disk at 3 consecutive moments is represented by M_1, M_2, M_3, and the center of rotation by R. In a short interval the part between the contour lines D_1 and D_2 is darkened and seen as the off-border, while during the same time the part between B_1 and B_2 is brightened and seen as the on-border. If we stop the movement, the on-activity generated (X) will spread decreasingly to the inside of the disk (direction x_1) and to the outside (direction x_2). In the same way the off-activity generated (Y) will spread decreasingly to the inside of the disk (y_1) and its outside (y_2). However, if the movement of the disk is continuous (i.e. towards the contour line B_3-D_3) and sufficiently

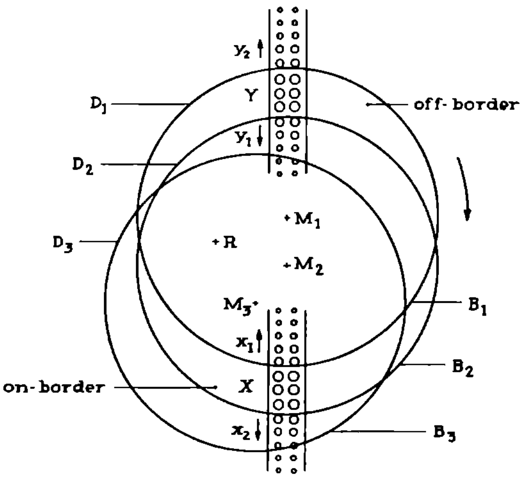

Fig. 15. Spread of the on- and off-activity to the inside and outside of the disk.

fast, the on-activity generated earlier (X) may still spread to the inside of the disk (direction x_1), but the new on-activity generated between B_2 and B_3 (the new on-border) overtakes the activity spread in the direction x_2, i.e. to the outside. Consequently, if the disk rotates so fast that the velocity of the contour (and with it the velocity of the locally generated on-activity) equals the velocity of the spreading on-activity, we would not expect any spreading of on-activity outside the disk. On the other hand, the on-activity is able to continue spreading to the inside of the disk until it is switched off. Movement of the disk causes contour line D_2 to shift to D_3. The new off-activity now generated overtakes the off-activity spread in the direction y_1 (to the inside) and does not interfere with the activity spread to the outside (y_2). For the same reason that holds for the on-activity, we would expect no spread of off-activity to the inside of the disk at a certain rotation frequency.

We have to consider however that we cannot go on moving the contour line in one direction, but that the disk is rotating, so that at a given moment the movement in the direction x_2 - y_1 will be reversed. Although figure 15 helped us to understand why there may be an activity spread in one direction (x_1 and y_2) but not in another direction (x_2 and y_1) at certain rotation frequencies of the disk, this reasoning tells us only part of the story.

Figure 16 shows how the off-activity helps us to perceive the disk clearly contrasted against the background. Here the disk is shown in different consecutive positions characterized by the position of its center (capital letters A to G). Considering the activities generated in different retinal points denoted as a, b, c and d along a line PQ through the center of rotation R, we see that point a is illuminated first, and then consecutively the points b, c and d. The duration of illumination and hence the time available for this locally generated on-activity to spread to the inside of the disk are longest for point a and shortest for point d, as is shown by the figure. Point a is illuminated during the time necessary for moving the disk from point A to point G, point b from point B to point F, etc. Here the fully drawn circles evince that the disk possesses on-activity generating properties for the points a to d, whereas the broken curves denote that it has off-activity generating properties.

It is obvious that for point d, which is illuminated only for a very short moment, there is practically no time left to spread its activity to the inside or the outside. In figure 16 can be seen what happens in certain points inside the disk, e.g. the points a and b. Point a, activated first, will lose part of its activity by local adaptation. Probably the activity spread of b, which is activated later, will compensate this loss. There must be a summation of activities because the center of the disk, though never re-illuminated (or even covered - see later experiments) is filled-in up to the same brightness and color as the rest of the disk. The argumentation concerning the off-activity and its spread is

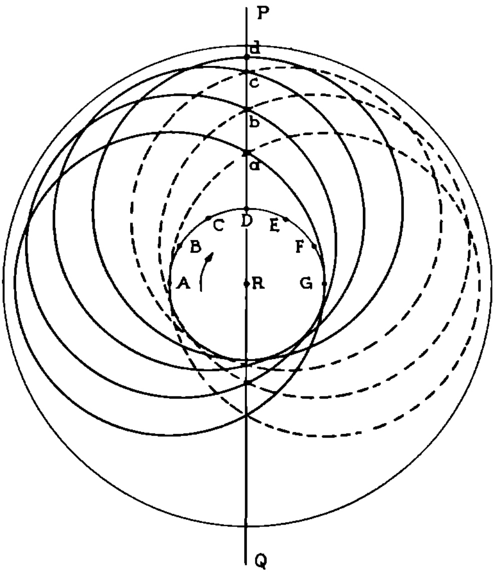

Fig. 16. Consecutive positions of the bright disk of fig. 12 A.

conducted along the same lines and will for this reason not be repeated here. Contrary to the on-activity, the off-activity spreads to the outside, and the points with the maximum off-activity are found just outside the contour of the disk.

In an experiment described earlier a rod was moving in one direction only (see § 3.a., page 26). We there observed the on-activity to spread to the inside and the far outside of the track of the rod. However, in that experiment the off-border in the direction of the movement was missing. We may conclude therefrom, that the off-activity acts like a barrier preventing the on-activity from spreading further or that it cancels this spreading.

Obviously it is necessary to move the contour of a stabilized image in more than one direction in order to bring the original image back to perception.

An additional remark concerning this experiment should be made: The width, the brightness, the darkness and the color of the on- and off-border are not equal in all the points of the retina. We used a large diameter black disk (secondary object, figure 12D) centered in the visual axis, in order to obtain a very narrow sickle to investigate this. We found the on-border to be narrowest and brightest subjectively near the fovea, and broader, less sharp and less bright on the peripheral side. The same holds for the off-sickle and the purple color in it: the sickle seems to broaden, to diffuse and to lose its color in the periphery. These are strong impressions and no more, because it

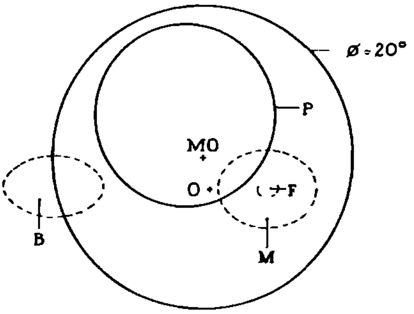

Fig. 17. Position of the field vision ($\emptyset = 20^{\circ}$) projected on the retina of the right eye. (drawn to scale)

B	blind spot (7x3.5°)
F	fovea and rod-free area (54')
M	macula (7x5°)
MO	motor axis
O	visual optic axis
P	momentary position of eccentric object

is difficult to observe sharply and accurately images at this distance outside the fovea (about 13 degrees). At low rotation frequencies these very narrow sickles disappear partly when they are projected on the blind spot (see figure 17, which is drawn to scale). At higher frequencies no irregularities, however, are seen there.

b.5. Combinations with secondary objects

In the experiment described above (§3.b 3., page 34) a bright object (a disk) rotated eccentrically. As can be seen in figure 16, which shows the consecutive positions of this object, a small part of the visual field is constantly illuminated and a large part of it is periodically illuminated and darkened. So it could be argued that we are not justified to conclude from this that the movement of the contour alone is sufficient to cause the whole field to be filled in homogeneously. Qualitatively the same sequence of observations as a function of the rotation frequency is found, however, when a large black disk is screening the central part of the object in the manner shown in figure 12 G. Even then there is a filling-in of the center of the disk at about 2 c/s. The larger the black disk in the middle, the more difficult it is to make it homogeneous, because the rotation frequency is more critical now. This can be correlated with the outcomes of electrophysiological experiments, see page 74.

With the light switched off after filling-in the perception is quite different as compared with the experimental set-up without this secondary object 12D. In the latter case the whole field is dark, but when a black disk is being used this stands out in green against the dark field. This green activity fades slowly. This behaviour, which is similar to that of the disk used in the experiment described in § 2.b., page 21 (stabilized field amid non-stabilized surround) is self-evident.

Another experiment demonstrates that movement in all directions of the contour of a stimulus that has faded by stabilization, does not cause all the lines and irregularities, which are still stabilized, to come back in the center of the stimulus. Each of these lines and irregularities must be moved in order to be seen.

In order to obtain the image of figure 12 I we use the same motor, but now in combination with the secondary object 12 F. We set the subjective rotation frequency at zero and switch the light on. The subject observes a green field with a part of figure 12 F in black lines over it. The stabilization causes these lines and the green field to disappear, and finally nothing is left. Now the green field is rotated at a frequency of 2 c/s. After a small number of rotations the whole field is again perceived homogeneously in green. Not a bit of the black line pattern is seen in this green field, because it is not reactivated by the field-contour movement and evidently has also been filled in with green. However, the eccentric rotation of the disk causes a rotating periodic retraction of the on-border over the outer ends of the lattice (figure 12 F) which have been filled in with green. Retraction of the on-border signalizes that the light is switched off there and that off-activity is thereby generated, which activity is perceived as black. On the contrary the green-filled lattice endings are not switched off (it is not possible to switch off the physically black lines). So these endings stand out in green against the off-border and the rest of the dark field (see figure 18). The off-activity spreading from the off-border in the direction of the lines seems to be insufficient to eliminate these lines.

On switching off the illumination the lattice pattern situated in the disk shows up in green, sometimes fluctuating with darkness.

The brightness and color of the stimulus field are brought back to perception by the movement of the contour of this field, but the stabilized black lines inside this contour will not come back.

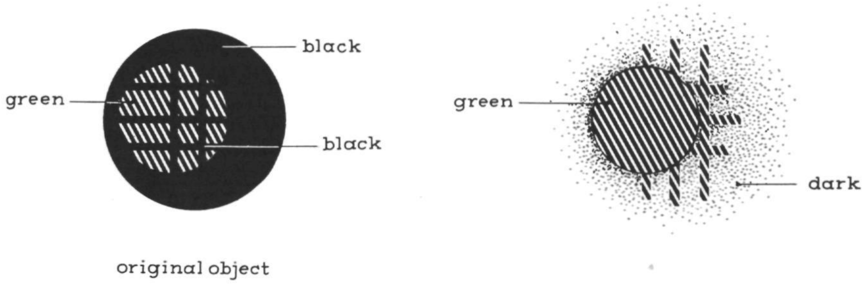

Fig. 18. The absence of perception of stabilized lines in an eccentric rotating object.

Summarizing: In confirmation of the results obtained in § 2.a. and § 3.b.3. it was found that the movement in various directions of no more than the contour of a bright field with a black line pattern, which pattern had faded by stabilization, brought about the perception of a homogeneous bright field. Any irregularity which is then still stabilized in the center of the stimulus does not come back in this way.

b.6. Regular eccentric movements of a dark object

For this experiment the motor with object shown in figure 12B (a black disk over a bright field) is placed on the standard cap. After disappearance of the image through stabilization a low rotation frequency is introduced (0.2 c/s). The subject perceives a very narrow purple-black off-sickle and a very narrow bright green on-sickle. The part in between and the periphery remain unchanged. Here too the form of the object is immediately recognized, but it is not yet homogeneous. The observer now states the off-border to be situated on the disk. Although not being a naive observer he must have arrived at this conclusion on the ground of the direction of rotation (clockwise or anticlockwise) and of the black off-border front of the disk.

At higher frequencies (1 c/s) a little on-activity spreading to the inside of the disk (see figure 19) may still be found, but to the outside the spread is enormous. A slight tap against the cap reveals that the on-activity spreads far outside the original green background in the object. The off-activity, with its maximum on the inside border of the disk, spreads most of its activity to the center of the disk, although also outside the disk some black spread may be found. The picture looks exactly the negative of the one obtained with the bright disk. This could have been foreseen on the ground of the analysis given in § 3.b.4. (page 36).

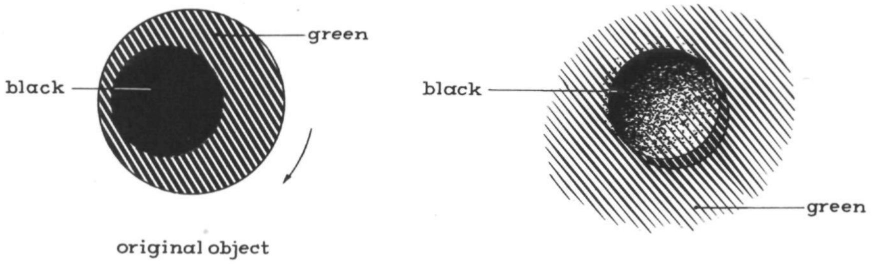

Fig. 19. Momentary perception of a dark object, rotating eccentrically at a frequency of about 1 c/s.

At frequencies around 2 c/s the disk is practically homogeneous; sometimes a faint green glow shining over the black disk is still seen, and that glow must be some spread on-activity that was not suppressed by the off-activity. Taken as a whole, the disk is dark, in fact much darker than the Eigengrau, but not as dark as the intense black which may be seen in the off-activities when very low rotation frequencies are used. The on-activity is spreading decreasingly everywhere outside the black disk, as there is no boundary that restricts its spreading. Also with this rotating object the brightness and darkness of the on-, respectively the off-border seem to diminish at higher rotation frequencies.

Summarizing: The movement in all directions of no more than the contour of a homogeneous black disk which latter disappeared by stabilization, is sufficient to bring the disk back to perception in its original appearance.

b.7. Regular, non-eccentric, movements of a bright object; correctness test of the analysis

We have already found that an important condition for the regeneration of the perception is that we allow the on- and the off-activity to spread in one direction but prevent it from spreading in the opposite direction. If in fact this spreading asymmetry were all we need, the third motor object (figure 12C - a small bright disk over a black field) may do as well. When this motor object turns around, not all the points of the retina lying along radial lines through the axis of rotation are illuminated for an equally long period. As is shown in figure 20A, point R is illuminated for a longer time than point Q, and point S for a longer time than point T. The points P and U are illuminated and then immediately darkened. This means that the points R and S have a longer period available for spreading their activity than the points Q and T.

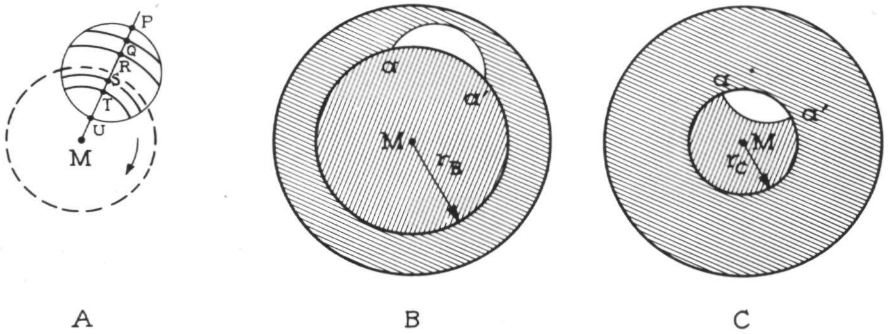

Fig. 20 A, B, C. A: Non-eccentric rotating motor object of Fig. 12 C
The points P to U are not illuminated during an equally long time.
B: Combination of motor object of fig. 12 C and secondary object of fig. 12 D.
C: Combination of motor object of fig. 12 C and secondary object of fig. 12 E.

We availed ourselves of this asymmetry by combining this object with secondary objects, and by so doing we obtained the objects B and C of figure 20. In object B the longest trajectory a-a' is situated closest to the rotation center M; all the points situated farther from the rotation center M receive the light later, and this later light is switched off earlier than the points along a-a'. So we expect more spreading to the inside than to the outside, and hence the inside field will be filled in. The argumentation regarding the spread in object C is exactly the negative of that for object B. Here we expect the light to spread to the outside. The correctness of the above reasoning has been confirmed by the results of the experiments described below:

At low rotation frequencies the disks are seen to spread their on-activity to the outside and to the inside. But at higher frequencies the asymmetry expected is clearly seen. The frequency necessary to get the best results is extremely critical and depends on the illumination level. At higher illumination levels lower frequencies are more efficient. The optimum frequency range is situated somewhere between 2 and 3 c/s.

By the term "best results for object B" is meant: The center part of the field (radius r_B, figure 20 B) homogeneous green, but less bright than the bright object itself; the rest of the field fairly dark. The bright object is not seen as part of the field's center. At light-off this green filled-in center is not switched off but slowly dies away without any spread.

"Best results for object C" supposes: The field inside the center (radius r_C, figure 20 C) slightly dark, except the part of it that is periodically illuminated by the rotating bright object. The field outside this center is bright green, brightest and greenest in the areas bordering the center. The spread develops towards the far peripheral parts. The bright green rotating object is part of the center field, according to the subject's statements.

Although the outcome of the experiments made with this motor object of figure 12C did come up to our expectations, the frequency setting proved to be much more critical than in the experiment described in § 3.b.3.and §3.b.5. In our opinion this is due to the shortness of the contour line a-a'(see figures 20 B and C). Undoubtedly there is also an optimum frequency of rotation at a given illumination level ("optimum" meaning here: the production of the most homogeneous and bright green) for the objects with the longer contour. A small deviation from this optimum frequency may remain unobserved with the longer contours, but have a great influence on the spreading capacities of objects with a shorter contour. It should be emphasized that the constancy of the rotation frequency depends for a great deal on the ability of the experimenter to correct by hand (pulse delay) any change in the frequency difference of the two driving generators. This task, which presents increased difficulties with increased rotation frequencies (2 c/s), will in future be assumed by an electronic device.

Summarizing: The results reported earlier have shown how one of the important conditions to obtain the restoration of the original image, viz. allowing the generated activity to spread in one direction and not in the opposite direction, can be fulfilled. From this analysis we may conclude that a similar asymmetry of the spread can be obtained by rotating a non-eccentric stimulus of a special form. This conclusion has been confirmed by the results.

b. 8. How to imitate the zigzag eye movements

The above described method of stimulating the eye enables us to draw important conclusions about the working of the visual system which corresponds remarkably well with the neurophysiological data (see Chapter V, § 6). Nevertheless, it should be borne in mind that this stimulation is no more than an imperfect imitation of the normal eye movements. As a matter of fact, normally the eye performs a series of small zigzag movements (see Pritchard, 1961b, figure on page 74) in several directions, owing to the continuous fast small contractions of the eye-muscles.

In contrast with the fact that under our experimental condition using the motor the retinal elements are consecutively illuminated and darkened, the normal zigzag eye movements cause many of these elements to be illuminated and also many other elements to be darkened instantly. This may result in a greater activity and an increased perceptual efficiency of the activity spread.

Apart from this probably more effective form of stimulus movement there remains the condition of a movement in more than one direction for closing the contour. So the real eye movements could be imitated better by stepwise movements of the object caused by two independent rod-systems (experiment §3.a., page 25) nearly perpendicular to each other; this however presents very great technological difficulties. But with the electrical synchronous motor this problem can be solved.

If the rotation frequency of the motor and the frequency of the stroboscopic illumination are exactly the same, the object stands still subjectively. The introduction of a continuously increasing positive or negative phase shift between the motor rotation frequency and the stroboscope frequency results in a subjective clockwise or anticlockwise rotation of the disk. But a periodic stepwise shift of this phase angle from 0 to 180 degrees will result in the periodic perception of the disk in two diametrically situated positions. The change in the position of the disk takes place during the dark phase of the stroboscopic illumination (short flashes of 0.7 ms) and hence will not be perceived. As may be seen, this method imitates better the real stepwise eye movements, be it in one direction only.

In order to close the contour a movement in a second direction is necessary. This can easily be obtained by introducing a second periodically stepped phase shift of 90-270 degrees.

In this way the disk will be illuminated for a short while in 4 different positions of its rotation, with a separation between them of 90 degrees. The frequency of the periodic phase shift of 0-180 degrees and that of 90-270 degrees are separately adjustable.

An apparatus working according to this principle of phase shifting is being developed. We expect that with such an experiment the subject will receive the impression of lateral to and fro displacements of the disk along two perpendicular axes.

Preliminary experiments with the phase shift controlled by hand did result in observations resembling those obtained with the moving rod. The time necessary to fill in areas with spread on-activity seems to shorten considerably. The increased speed in obtaining a high level of color and brightness inside the area is evidence that this is indeed a more efficient way of stimulation. On theoretical grounds we arrive at the same conclusion.

§4. ANALYSIS OF THE OFF-EFFECTS OBSERVED

So far nothing has been said about the off-activity seen immediately following the bright green moving object. Figure 21 shows what can be perceived of the off-activity as a function of the rotation frequency when using the object shown in figure 12 J = 20B.

In order to make comparison easier, the round form seen by the subject is represented in the drawing by a straight line; so the end is in reality the start of the next rotation. The frequency scale in this figure is but a very rough indication, since the perception depends on the illumination level. At any rate this representation is a true indication of the sequence of changes as a function of frequency in the case of constant illumination. At very low frequencies an off-activity consisting of a very narrow bright purple region followed by an intense black region can be seen behind the on-activity. Up to about 2 c/s the purple and the black part grow in length, but their brightness and color or blackness diminish along their course. A further increase of the rotation frequency causes the purple to disappear completely, and in that case only a small dark part that follows the on-activity is seen. A still faster rotation abolishes the whole off-activity, and a closed green ring with a brighter part in it is then seen.

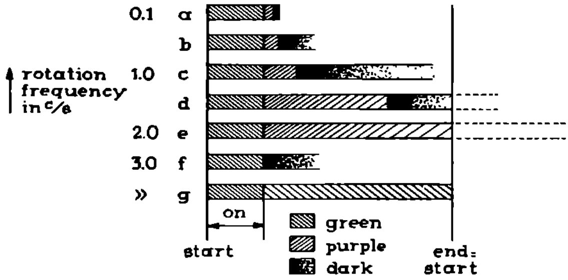

Fig. 21. Off-effects (stretched) following the bright not eccentrically rotating disk of fig. 12 C, as a function of the rotation frequency.

Let us now sum up the relevant properties of the off-activity found in all the experiments described, in order to try to understand why we see what we see.

1. Shortening the duration of the illumination during stabilization results in less black and less purple in the image at light-off. By reducing this duration more and more, first the purple is seen disappearing, and subsequently also the blackness of the after-image diminishes continuously (from experiment: totally stabilized image, § 1.).
2. The fact that purple is seen after the black in the off-trail does not mean that the black has a longer latency time than the purple. The first part of the off-trail consists in reality of two components: a purple and a black one;

only the black is not strong enough to suppress the purple there.

3. The decrement of the purple is greater than that of the black (from experiment: movement in one direction of a stabilized image, § 3.a.).

These findings may be brought in correlation with the results schematically shown in figure 21. The above points 2 and 3 are valid for the lines a to e in this figure, and point 1 applies to the lines f and g. Looking at these lines a to e the frequency increase, so to say, expands our time scale.

At high frequencies (line g) no off-activity at all is seen, but what we do see is an after-activity of green.

§ 5. THE REACTION OF THE PUPIL TO A STABILIZED IMAGE

What we expected was that the pupil reaction to a stabilized image could give some information about the locus in the nervous system where these effects of filling and disappearing activity are produced. The path of the pupillary light reflex is well known: part of the fibers coming from the retina cross in the chiasma. Subsequently part of the optic tract fibers leave this tract before reaching the lateral geniculate nucleus and arrive as a separate bundle at the pregeniculate nucleus in the pretectal region. From this nucleus onward the bundle follows its course to the nucleus of Edinger-Westphal in the oculomotor group. Before reaching this nucleus there is another partly crossing of fibers. The nucleus of Edinger-Westphal in its turn directs a number of fibers to the pupillary sphincter; i.e. the bundle that steers the pupil does not come from the lateral geniculate nucleus or occipital lobes, but directly from the retina. Therefore we expected the pupil to react to the loss of perception of the stabilized image, provided this loss had been caused by changes in the retina.

Figure 22 shows the experimental set-up. The consensual pupil reflex was used. The procedure is as follows: A light source illuminating a stabilized object upon the right eye is switched on. The left eye is in the dark. When the perception of the object has disappeared the subject gives a signal to the experimenter. At the same moment the pupil of the left eye is photographed by means of an electronic flash and a camera. The flash itself causes a pupil constriction after a latency of 200 ms (v.d. Tweel, 1956), but by then the picture has already been taken.

The influence of adaptation of the left eye after the flash, the necessary

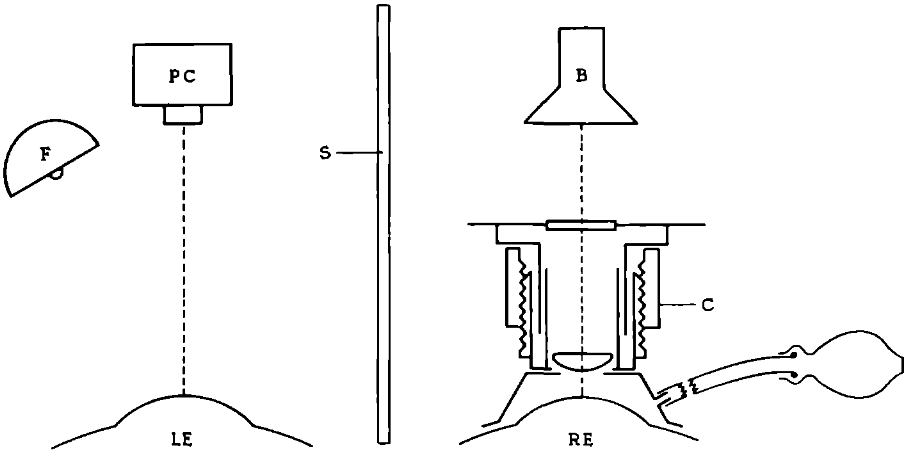

Fig. 22. Reaction of the pupil to a stabilized image.

RE	right eye	F	electronic flash
LE	left eye	PC	pupil camera
B	object illuminating source	S	screen
C	suction cap		

intervals between the pictures, the influence of the duration of the previous stabilization and so on, have been amply considered before these experiments were carried out. The diameter of the pupil has also been determined with the right eye viewing the same but non-stabilized object. In these experiments the cap with the object was not sucked on the eyeball but held by hand closely to the eye.

Various intensities were used for both types of experiments. Also intensity zero was included. The results showed that the diameter of the pupil as a function of the intensity of the stimulus is the same for the stabilized and for the non-stabilized image within the experimental error. At a high intensity of the stabilized stimulus the diameter of the pupil is small (± 2 mm), although this high intensity stimulus will not be perceived after some time.

Summarizing: The size of the pupil during constant illumination is the same in the stabilized and in the non-stabilized condition, in spite of the fact that the perception of the stimulus has faded in the stabilized condition.

CHAPTER III

DISCUSSION ON THE CONTINUITY AND COMPLETENESS OF DISAPPEARANCE OF THE PERCEPTION

§ 1. DISAPPEARANCE OF THE PERCEPTION; INFLUENCE OF TRAINING AND EXPERIMENTAL PRECAUTIONS

As has already been said there is a complete disagreement between Iarbus' (1957a, 1957b) and our own results on the one side and the experiences of the other experimenters on the other, as far as the continuity of the disappearance of perception is concerned. When the perception of a stabilized image has disappeared it does not come back as long as the subject is capable to avoid large rapid eye movements. Trained subjects lying supine can achieve an uninterrupted absence of perception during tens of minutes. As most experimenters (Barlow 1963) state that the image disappears for no longer than 3 to 30 seconds, we may ask ourselves whether other causes are responsible for this discrepancy, i.e. other than the obviously better elimination of eye movements by means of the suction cap.

These causes may be:

1. The use of a mydriatic to dilate the pupil and abolish most of the accommodating capacity of the subject. Periodic accommodation changes will cause periodic changes in the dimensions and sharpness of the retinal image. Changes of illumination of the retina may be caused by pupil fluctuations. We did not succeed in repressing the perception for a long time without the use of a mydriatic.
2. The subject has to lie down. When the subject is seated the downward pulling force of the cap's weight causes the eye to sag and this sagging is periodically

corrected by an upward flick, that shifts the cap over the eyeball.

3. A drop of the local anaesthetic (novesine) must be given periodically in order to prevent painful irritation of the conjunctivae.
4. At high illumination levels still more precautions have to be taken. One of them is the screening of that part of the sclera not covered by the cap. Eye movements cause a variable area of the sclera to become illuminated.
5. All the connections with the cap (3 very flexible rubber tubes) and the object (either flexible rubber tubes or electric connections) have to be fastened with plaster on the subject's forehead and cheek; they may under no circumstances pull the cap. The connectors for the flexible rubber tubes should be placed on the temporal side between the eyelids.
6. The underpressure must be well chosen. A low value of underpressure results in shift; too high a value of underpressure causes ischaemia and dull headache.
7. Periodic removal of the cap may be necessary, also to avoid hazy vision. In some cases, depending on the mood of the subject, a periodic rest may be very helpful.
8. And most important of all is a thorough training of the subject. He must be able not only to limit his eye movements, but also to describe his perception as objectively as possible. Regular experiments are absolutely necessary to maintain his ability. Each of our two experimenters has taken part in about 250 registered sessions of (on an average) $1\frac{1}{2}$ hour. A 3 months interruption of the experiments required renewed training during at least one week before the same level of eye control was reached again.

Since we were able to confirm most of Iarbus' results and have adopted all the precautions also taken by him, we have to conclude that the aforementioned discrepancies are attributable to the use of the better cap and to the better experimental conditions.

§ 2. RESIDUAL BRIGHTNESS

It has often been asserted in the literature, that some brightness remains even after stabilization for a long time. It is difficult to give a decisive opinion on this, because for a comparison of the brightness of the Eigengrau during the normal dark-adapted state with the brightness during stabilization the subject has to rely on his memory. If the stimulus intensity is not too high, but is well within the photopic range, the subject has the impression that the residual brightness of the stabilized image equals within about one minute that of the dark-adapted Eigengrau. After a much longer lapse of time, however, the subject observes that the brightness has decreased still further. But at high intensity levels even the most experienced subjects under the most favourable conditions (covered sclera and long stabilization) will perceive in the whole visual field a faint but nevertheless greater brightness than that of the Eigengrau. Corneal mist (Barlow, 1963) is not the cause of the low levels of residual brightness in our experiments. A misty haze will appear if the cap has been sucked too firmly or for too long a time on the eyeball. This haze may result from a shortage of oxygen supply to the cornea. Normally the corneal epithelium draws the oxygen it needs from the air. As a result of oxygen shortage the stroma swells and this swelling causes hazy vision.

Clouding can also be elicited by mechanical stress on the tissue or by high intra-ocular pressure raise. The clouding induced by stress, however, disappears immediately upon relaxation (Davson, 1962a). If our subject complains of hazy vision after a long period of observations, the suction cap is immediately removed, but this does not result in a direct improvement. This is indicative of the fact that oxygen shortage, and not the small intra-ocular pressure raise, disturbs vision in our experiments. This effect is avoided by removing the suction cap in the break between the experiments.

The origin of the faint residual brightness perceived in the experiments with higher illumination levels is still obscure. In our opinion it may be due to the statistical fluctuations in the steady-state discharge. Any crowding of spikes is likely to be transmitted to the higher system as a change. These bursts, which occur with low repetition rates, may be perceived as a consequence of the increased excitability of the central system in the stabilized condition (see Chapter VI, § 2.).

CHAPTER IV

MORPHOLOGICAL AND ELECTROPHYSIOLOGICAL DATA FROM THE LITERATURE

§1. CONNECTIONS IN THE VISUAL SYSTEM

A diagram of a number of the functionally or morphologically established connections in the visual system which will be used in our analysis is shown in figure 23.

Although many connections are known, and the specialists in this field may add numerous details, our diagram gives the main lines along which the visual signal is transmitted. In this schematic diagram (figure 23) the visual system can be divided into three parts:

a. a peripheral part comprising the eye;
b. a mesencephalic-diencephalic part comprising the lateral geniculate body,
the superior colliculus,
the reticular formation,
the pulvinar;
c. a telencephalic part comprising the visual cortex (Brodman's areas 17, 18, 19),
the temporal cortex,
the parietal cortex.

The most important line for vision undoubtedly is the chain: eye - lateral geniculate body - area 17 - pulvinar. The information content of the visual image falling upon the retina is encoded in patterns of nerve spikes and sent,

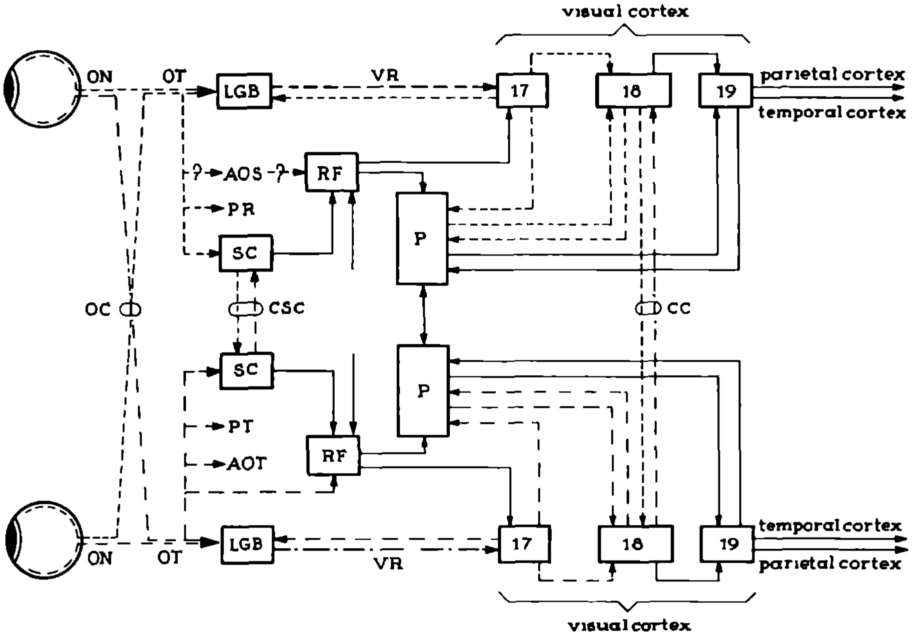

Fig. 23. Some connections in the visual system.

AOS	accessory optic system (probably not present in man and monkey)
CC	corpus callosum
CSC	commissure of the superior colliculus
LGB	lateral geniculate body
OC	optic chiasma
ON	optic nerve
OT	optic tract
P	pulvinar
PR	pretectal region
RF	reticular formation
SC	superior colliculus
VR	visual radiations
17, 18, 19	Brodman's areas 17, 18, 19 (visual cortex)

through the optic nerve, to the central nervous system. As is seen in the diagram, part of the fibers cross in the optic chiasma. The left and the right halves of the visual field of both eyes are represented in the right, respectively the left half of the brain. The lateral geniculate body, i.e. a part of the thalamus, receives part of the fibers of the optic tract. The lateral geniculate body is a 6-layered nucleus in man (3-layered in the cat), which not only sends fibers to the cortical area 17 but also receives corticothalamic fibers returning from this area.

The lateral geniculate body should be considered not only as a relay station, for it also participates in the regulation of the cortical excitability. In area 17 of the cortex many operations and correlations are performed and the results are sent to the pulvinar. But still no more than one half of the visual field is represented here since there is no input from area 17 of the other half of the brain. Probably the direct connections between the areas 17, 18 and 19 are not important, contrary to the connections of these areas with the pulvinar. The areas 18 and 19 are necessary for the recognition of objects. When these areas have been destroyed we distinguish the objects clearly but do not recognize them. Area 18 is the first cortical area in the chain in which both halves of the visual field are represented. This area receives fibers via the corpus callosum, which is the name given to the bundle of fibers connecting the cortical areas of both halves of the brain.

The pulvinar is a very important correlation center; it receives fibers not only from the visual cortices but also from other cortical sensory systems.

Another afferent to area 17 comes from the reticular system. In this reticular system two parts can be distinguished from the functional point of view. The first part is unspecific and provides a generalized cortical activation (waking, vs. sleeping); the second part is specific and is capable of exerting an activating influence upon more restricted areas of the cortex. The latter part probably subserves the regulation of attention. Part of the afferents for the reticular formation are to be found in the accessory optic system (uncertain for man and monkey) and in efferent fibers of the superior colliculus. This superior colliculus, which is also a correlation center, is far less important in man than in lower animals. Many functions of the superior colliculus in lower animals have been assumed by the cortical areas in man. Vision in animals is restored after destruction of the two areas 17 or cutting of both visual radiations: the animals are able to see with the help of their superior colliculi. If in man the visual area 17 has been excised or the visual radiation has been cut on one side, he is blind for the corresponding half of the visual field. If in man the areas 17, 18 and 19 are successively stimulated electrically, he will perceive dots and stars, triangles, hooks or complete familiar images. The more complex figures are provoked in area 19. This area borders the temporal and parietal cortex and sends fibers to these. As is found in some epileptic patients, stimulation of the latter areas causes them to go through many long forgotten events, but only in those details which had drawn the attention of the patient at that time. This suggests that area 19 is connected to an area which is strongly related with memory.

For constructing our diagram we availed ourselves of the information furnished by numerous articles and a number of handbooks, among others

Polyak (1948), Brodal (1950), Elliott (1954), Penfield and Jasper (1954), Buchanan (1957), Polyak (1957), Davson (1962b), Strong and Elwyn (1964).

§ 2. ELECTROPHYSIOLOGICAL INTRODUCTION

The names of Adrian, Hartline and Granit are closely associated with the earliest attempts to unravel the code sent through the optic nerve. The books written by Granit are still valued as standard works (Granit, 1947; 1955). The research on retinal ganglion cells of the frog and the cat started about 1935-1945, the research of Adrian concerning the eel in 1926 already, and other researches in this field are still going on.

The ganglion cells of the retina may be classified in several categories, according to their behavior on the illumination or darkening of the retina. Hence we discriminate:

on-cells, responding with an increase of their firing rate at light on (see figure 24);

on-off cells, responding with a short burst of spikes at light on, followed by a very low firing rate or total silence during subsequent continuous illumination, and with firing again at light off;

off-cells, which are nearly or completely silent at light on and answer the switching off of the light with a burst of spikes (see figure 24).

Hartline (1938), experimenting on frogs, found that in a given optic nerve fiber responses could be obtained upon illumination of a definitily restricted region of the retina. This area he called: "the receptive field".

In 1953 Kuffler published an important article on the organization of the receptive field of the retinal ganglion cells of the cat. Exploring the receptive fields with a small spot of light he found that the discharge pattern of a ganglion cell depends (among other things) on the state of adaptation of the retina and the location of the stimulating spot in the receptive field. Hence in the light-adapted retina, an on-cell which fires a burst of spikes at light on when stimulated in the center of its receptive field, may behave in the same manner as an off- or on-off cell when stimulated outside the center of its receptive field, i.e. in its surround.

Most of the retinal ganglion cells show this antagonistic surround activity in the light-adapted state and may be called: on-center off-surround cells or off-center on-surround cells. If the whole receptive field is illuminated they fire their center response. In the dark-adapted state the organizations of the receptive fields change and the antagonistic surrounds disappear (Barlow et al., 1957a, 1957b).

The definition of the receptive field given by Hartline for the retinal ganglion cells has also been used for the cells in the lateral geniculate body and the visual cortex. It becomes more and more obvious, however, that when defining the receptive field, the properties of the stimulus should be mentioned. So, for instance, the use of other than punctiform photic stimuli may largely increase the receptive field (McIlwain, 1966). This could be expected from the reports of the clinics. The scotomatic area for brightness, movement, color etc. in the brain-wounded may be different (Poppelreuter, 1917; Lashley, 1930; Teuber et al., 1960).

This means that, if projected back to the retina, one and the same cortical area is influenced by a retinal functional area that depends on the quality investigated. So it is known that the receptive fields for color are larger than those for black and white. MacNichol (see discussion, de Valois, 1965) suggested that the large number of color receptors connected to a single ganglion cell are responsible for this. In a recent publication by McIlwain (1966) the influence of a moving edge far outside the classical receptive field of the ganglion cell under consideration is shown, and this demonstrates once more the need of further specification when this notion is used.

In a series of brilliant articles Hubel and Wiesel have laid down their investigations on the cat's and the monkey's receptive field in the retina (Hubel, 1960; Hubel and Wiesel, 1960; Wiesel, 1960), the lateral geniculate body (Hubel and Wiesel, 1961; Wiesel and Hubel, 1964, 1966), the cat's visual cortex, area 17, (Hubel and Wiesel, 1959, 1962, 1963), and in the cat's visual cortex, areas 18 and 19 (Hubel and Wiesel, 1965). They showed that most of the cortical neurons in the areas 17, 18 and 19 respond best to line stimuli such as slits, edges and dark bars, the orientation of the stimulus then being critical for optimum responses. The same organization of neighbouring antagonistic areas as exists in the retina was found here, but the receptive fields were no longer circular. Generally there was little or no response when the entire receptive field was stimulated by diffuse light. This figure-analysing property of the cortex speaks to the imagination of many neurophysiologists as well as to that of psychologists. However, it does not solve the problem how to see constant diffuse light. The only publication on the monkey areas 17 and 18 with macroelectrodes (Cowey, 1964) and a communication of Wiesel at the Tübingen Meeting (1966) make it probable that the information transformation in this animal works along the same lines as the cat.

After the above findings many workers investigated retinal, geniculate or cortical receptive fields with stationary or moving borders and not with spots of light (Baumgartner, 1961a, page 45, OT; 1961b, page 296, LGB-cortex; Grüsser and Grüsser-Cornehls, 1961, page 313, LGB-cortex; Burns et al., 1962, cortex; Baumgartner, 1964, OT-LGB-cortex; Burns and Pritchard, 1964, cortex; Baumgartner et al., 1965, OT-LGB-cortex; Kozak et al., 1965, LGB; Rodieck and Stone, 1961a, 1961b, retina).

Baumgartner (1961b, page 306) and Jung (1961; 1964) correlated the neural activity with perception. They introduced the nomenclature D- and B-neurons for the off-cells and the on-cells respectively in the visual cortex, correlating the firing of the D-neurons with perception of darkness and that of the B-neurons with brightness. Other cortical neurons were called A-neurons (not influenced by visual stimuli), C-neurons (inhibited by light and darkness) and E-neurons (equivalent to on-off cells). In this way Jung succeeded in making several subjective phenomena, obtained in psychophysical experiments, easier to understand. So for example, he used the electrophysiological data obtained by one of his co-workers (Grüsser) to correlate the human after-images with the periodic firing of the B-, D- and E-neurons in the cat after light off.

Later Grüsser and Grüsser-Cornehls (1962) published a detailed article on this periodic firing of the cortical neurons of the cat.

Besides the on-, off- and on-off cells hitherto considered there is another type: the <u>on-or-off cells</u>. These cells, found in the lateral geniculate body of the monkey by de Valois (de Valois 1960, 1965; de Valois and Jones, 1961; de Valois et al., 1963, 1966), respond with an on-discharge at light on of a certain wavelength range and with an off-discharge at light off of another wavelength range. These cells behave very much nearly as they should according to Hering's opponent-color theory. So blue-on yellow-off cells, red-on green-off cells, and the reversals of these types were found by de Valois. Recently Wiesel and Hubel (1966) confirmed the presence of these cells (although with slightly different response maxima). These cells are almost unresponsive to white light. Wiesel and Hubel (1966) found various other types of cells as red on-center green off-surround cells, red off-center green on-surround cells and so on. These cells behave in a similar way as those found by Wolbarsht et al. (1961a, 1961b) in the fish retina. All these types are believed to carry color information to the brain. A response nearly independent of the stimulus wavelength is obtained from the broadband on-cells and broadband off-cells in this nucleus. The response curve of the first group as a function of wavelength is seen to have the same form as the CIE photopic luminosity function; these cells are thought to carry the brightness information (de Valois, 1965). Jacobs (1963, 1964, 1965, 1966) and Brooks (1966) have investigated the properties of the geniculate cells with regard to their brightness discriminative abilities. In addition to numerous studies on color coding by the cells of the lateral geniculate body there exist several reports concerning color coding in the cortex (Lennox and Madsen, 1955; Madsen and Lennox, 1955; Ingvar, 1959; Lennox-Buchthal, 1961, page 191, 1962, 1965; Anderson et al., 1962; Motokawa et al., 1962) and superior colliculus (Ingvar, 1959; Wolin et al., 1966).

We started this introductory excursion by mentioning the spatial characteristics of the receptive fields in the retina, and will finish it with the investigations of their temporal properties. Grüsser and Rabelo (1958) and Grüsser and Kapp (1958) examined the response of the on-, off- and on-off cells of the cat as a function of the repetition frequency of a short flash of light and as a function of the interval time between the two flashes using double pulse stimulation. They were able to decompose the responses, found from the different types of neurons, in oscillating excitatory and inhibitory phases, which they consider to be the most probable components.

Hughes and Maffei (1966) used sinusoidal instead of square wave light stimulation, and studied the phase lag of the response. At low frequencies this response (in spike counts) is found to follow the stimulus closely.

For studying the ganglion cell response Enroth-Cugell and Jones (1963) make use of light intensities that change exponentially in time.

Ogawa et al. (1966) published the post-stimulus time histograms from on-center units in cats in response to 100 flashes at 0.2 c/s and at 3 intensity levels. These authors show that the latency time shortens, that the mean peak firing rate increases and the sustained level of discharge decreases with increasing intensities of the stimulus. One cell only showed an increase in the steady-state firing level (maintained discharge) for increasing intensities. Their conclusion from these observations is that the retinal coding of information about absolute levels of illumination remains obscure.

Kuffler et al. (1957) studied the maintained activity in the cat's retina for very long constant stimuli.

This necessarily very incomplete "review", in which certainly a number of important publications have been omitted, mainly gives the basic facts necessary for correlation with our results. Moreover, these facts emphasize the conclusion that the on- and off-systems in the retina and the B- and D-systems in the cortex provide us with the necessary information concerning transient temporal or spatial changes and the color content of the local retinal illumination. It is not clear, however, how these systems will give us any information on the constant diffuse brightness levels which are found inside the contour of every picture exposed to the retina.

Since our experiments and the conclusion drawn from them are directly related to this problem, we will now give a detailed account about the attempts made to overcome this difficulty.

§3. ATTEMPTS TO EXPLAIN THE PERCEPTION OF CONSTANT BRIGHTNESS BY THE STEADY-STATE ACTIVITY

Figure 24, which shows schematically the response of on- and off-cells at light on and light off, may be helpful to understand what the experimenters mean to say.

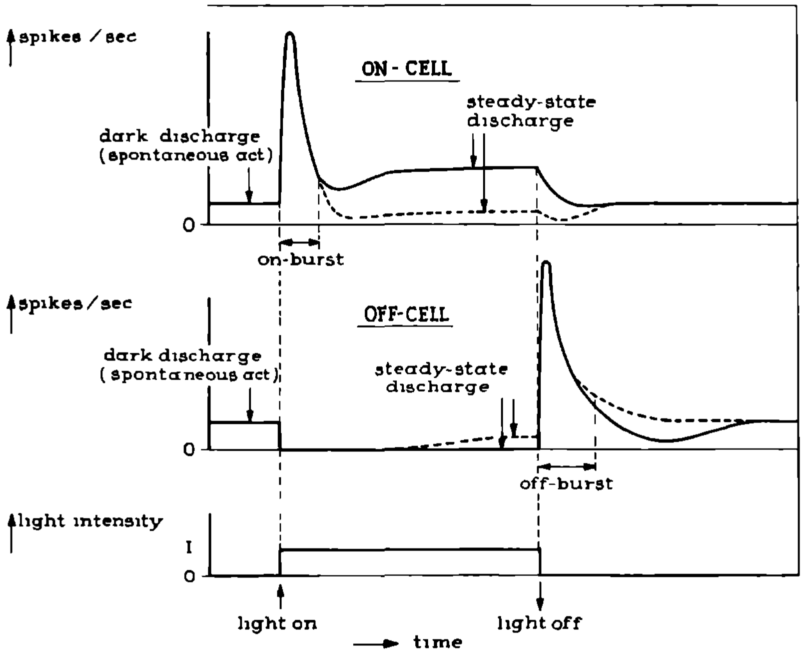

Fig. 24. Schematic diagram of the on- and the off-cell response at light on, during constant illumination and at light off.

The bottom line shows at which moments the light is switched on and off. The stimulus has a duration of several minutes.

On-cell response

The upper line of fig. 24 gives the on-cell response (spikes per second) as a function of time. As can be seen, the cell fires already before the light is switched on. This is the spontaneous activity or dark discharge. At light on the cell responds with a transient burst of spikes, after which the response slowly falls to a fairly constant value of spike firing, called the steady-state discharge. The steady-state firing rate may be lower (dotted line) or higher (solid line) than the rate of firing in dark. At light off the cell may return slowly or in an oscillatory mode to the earlier dark discharge level.

Off-cell response

The central line of fig. 24, representing the behavior of the off-cell, also indicates a spontaneous activity or dark discharge of this cell. At light on this discharge is partly or completely inhibited, sometimes temporally, in which case it gradually reaches a higher steady level during illumination (solid or dotted line). However, at light off the cell fires a strong off-burst, which, often slowly, sometimes in an oscillatory mode, passes to the original dark discharge level.

Summarizing: Both cells exert a spontaneous activity in dark. Both cells fire a burst of spikes: the on-cell at light on, the off-cell at light off. Both cells reach a steady-state firing level during illumination.

The mean dark discharge of the cortical cells is lower than that of the cells in the lateral geniculate body, which in turn is lower than that found in the retinal ganglion cells. The retinal on- and off-bursts activate the cells of the lateral geniculate body and cortex which respond also with lower burst firing rates. As the on-burst is a short-lived phenomenon (from some milliseconds up to a few seconds, depending on what part is taken to belong to the burst) the attempts to explain the perception of constant diffuse brightness have been concentrated on the steady-state part of the on- and off-cell responses.

At unit level, i.e. if only one ganglion cell is considered, there seems to be no correlation between the direction of the change in the steady-state firing rate (increase or decrease) and the direction of the change in light intensity. As can be found, for example, in the article of Ogawa et al. (1966) most cells respond with a decrease, but others with an increase in their steady-state firing rate with increasing intensities.

Arduini (1961a, page 184) showed that, although there are large fluctuations in the firing rates and in the number of discharges per individual unit, the total number of discharges, derived from many units, is constant with minor fluctuations. This number decreases with increasing light intensities, and the change of this (what he calls) "tonic activity" (=steady-state activity) is a linear function of the intensity. According to Arduini this is the manner in which the information of constant brightness is transmitted to the brain.

Instead of coding the brightness of a constant stimulus by means of the firing frequency of the individual unit or the massed discharge, it may be transmitted in the time-distribution of the spike discharges of the units. Herz et al. (1964) and Fuster et al. (1965) have published articles containing not only interesting data concerning the spontaneous and the steady-state activity of on- and off-cells in the optic tract, in the lateral geniculate body and in the striate cortex of the cat, but also concerning the interval distributions of these responses.
The latter investigators found three types of distribution. The Poisson-like distribution of intervals of the retinal response was not found in the cells of the lateral geniculate body and cortex, which tend to maintain a grouped spike activity. The cortical cells change their mean firing rate and interval distribution for different levels of intensity only very slightly. According to these authors it is doubtful whether the cortex will react on these minor changes, and it seems more probable that brightness is perceived by comparison of the activities of neighbouring points in the retina by making use of eye movements.

Jung (1964) stated that the response of the B-system (representing the retinal on-cells) is mainly a transient one while there is always a difference in the constant firing rate of the D-neurons (representing the off-cells) in light vs. darkness. According to Jung the difference between these firing rates of the D-neurons (in darkness and light) may inform the brain as to the intensity of the constant illumination.

In a recent article Straschill (1966) has published the results of his investigations on the optic tract and the lateral geniculate body of the cat. He found the on-neurons to fire faster during continuous light (steady-state) than during darkness (spontaneous activity), this in contrast with the off-neurons. He tried to describe the relation of light intensity and neuronal response with power and logarithmic functions.

These theories, although clever in their attempts to explain how the system works, start from a completely wrong point: they suppose that the animal (cat, monkey) will see by means of this steady-state activity. Our experimental results, obtained under the same stabilized conditions as for the animals, prove that man in reality sees nothing during the steady-state firing.

A completely different manner of operation of the system to see constant brightness has been revealed by our results and will be described now.

CHAPTER V

THE STABILIZATION EFFECTS

§1. RETINAL OR CENTRAL ORIGIN

Before giving any theory we would discuss the question of whether these effects of spreading and disappearance of the perception are of retinal origin or whether they are due to properties of the central nervous system.

The disappearance of the perception of a constantly illuminated object after stabilization can be explained on the ground of complete adaptation of cells in the visual system. Electrophysiological evidence shows that some of the retinal ganglion cells respond continuously to a constant illumination (steady-state), while others completely adapt (Granit, 1947). The proportion of completely to partly adapting elements seems to depend on the animal species. However, it has been shown over and over again (see above) that the cells in the visual cortex do not give a response to a constant afferent activity, but obviously only to changes in the activity of the input. This suggests that the loss of perception is rather a cortical than a retinal phenomenon.

In the cat, the retinal (Grüsser and Rabelo, 1958) and the cortical neurons (Jung, 1961, page 418; Grüsser and Grüsser-Cornehls, 1962) show periodic activities after a stimulus has been switched off. These activities presumably are the correlates of the periodic changes of the after-images observed after a stabilized image has been switched off (Chapter II, §1.).

These periodic neural activities are usually explained on the ground of inhibitory and excitatory interactions of the retinal cells. The after-images of non-stabilized fixated stimuli also show these periodic fluctuations. This suggests that the retinal activity is the same irrespective of whether stabilized or non-stabilized stimuli are employed.

In Chapter II, §5. we have shown that the static pupillary light reactions to stabilized images are the same as those to non-stabilized images. We know that the fibers subserving the pupil reaction leave the optic tract before the lateral geniculate body, so that they do not reach the visual cortex. If we can assume that the retinal elements serving the perception are also acting as input elements for the pupil reaction (in which case the pupil fibers may be collaterals as well as separate fibers in the optic tract), then we may conclude that the loss of perception by stabilization is not of retinal origin. This assumption seems plausible, but has not been proven.

Figures consisting of lines, e.g. a cross, a triangle and a circle, generally fade and often reappear in fragments during stabilization in the first second(s), as if the figure were built up of separately acting units. The same happens in the after-image when the light is switched off after a period of stabilization. This effect has also been found by others (Pritchard et al. 1960; Pritchard, 1961; Eagle and Klein, 1962; Evans and Piggins 1963; Evans, 1965). It is possible that the fixed form- and direction-sensitive units found by Hubel and Wiesel (1959, 1962, 1963) in the cortex of the cat and of the monkey, are correlates of this perceptual phenomenon. If this fading takes place at retinal level, we should expect the image to fade in areas of the retina, but certainly not in specific units. The cells which represent more specific units have to be sought in the more central levels of the visual system. This would exclude the retina, the lateral geniculate body and probably even Brodman's area 17 as the possible site of the stabilization effects.

Walsh (1957), Teuber et al. (1960) and Gassel and Williams (1963) described many patients with scotomata, caused by lesions in the occipital cortex. A small stimulus imaged on that part of the retina which projects to the defective part of the visual cortex will not be observed. But a large retinal stimulus, the projection of which covers and surrounds the scotoma, is seen completely filled in after some time. The patient then does not notice his scotoma. Similar phenomena occur with migraine scotomata (Lashley, 1941; Walls, 1954; Walsh, 1957). These migraine scotomata often start in one half of the field of vision and subsequently enlarge slowly. Since the two half fields of vision do not project to a common hemisphere as far as at least Brodman's area 18 or the pulvinar (see figure 23), an enlargement of these scotomata across the border of the two fields of vision might indicate where this process develops. Unfortunately the reports considering the limitation of this spreading are contradictory (Walls, 1954; Ahlenstiel, 1958).

Galbraith (1964) has shown that, in stabilization experiments, the computer-averaged ERG's during the disappearance and regeneration periods are identical, and thus he concluded that the perceptual impairment during the time of disappearance is not caused by retinal mechanisms.

Recording the electroencephalogram from the skull (electrode positions $Q_2 - C_0 - F_{p1}$ in the 10/20 electrode-system) we always found α-waves during the period of the subjective disappearance of the object.

Lehman et al. (1965) tried to correlate the on-set of these α-waves with the verbal reports of the subject concerning the disappearance and the regeneration of the perception. He found that the α-wave trains <u>precede</u> the subjective report of fade-out of perception of the stabilized image. In other experiments the image was viewed in normal vision but faded out by the experimenter. In this case the subject reported fade-out of perception <u>before</u> the appearance of the α-wave train in his EEG. The experimenter's conclusion is that the fade-out by stabilization is a central process not induced by retinal changes.

Our conclusion from these arguments is that the origin of these stabilization effects of spreading, disappearance and filling-in is not to be sought in the retina but rather in a higher center of the visual system. In the following discussion we shall indicate this locus by the words "higher center", because at this stage of our knowledge we can only say that it is central to the retina and the lateral geniculate body.

§2. HYPOTHESIS CONCERNING THE FUNCTION OF THE ON- AND THE OFF-SYSTEM

On the basis of our experimental results and the correlating data obtained from the electrophysiological experiments, we would propose the following functional theory:

The on-system (brightness)

Switching on continuous illumination appears to give rise to no more than a brief deviation from the mean firing-frequency of the cells in the visual cortex and to an immediate perception of brightness, contours and color. The relevant electrophysiological input from the retina to the cortex is the transient activity of on-fibers in the optic nerve, which rapidly build up a corresponding activity in the projection areas of the higher center. If the illumination is kept constant and the image stabilized, the contour blurs and the stimulus seems to spread into its surroundings. The electrophysiological correlate would be that after the release of the on-activity of the retinal ganglion cells the activity in the higher center starts to spread also outside the originally activated part; moreover, the brightness and the color fade. This means that the steady-state response of the retinal ganglion cells do not give rise to a similar response of neurons of the higher center.

This spreading and fading take place within a few seconds (for the color and most of the brightness) up to a few minutes (for the residual brightness), depending on the initial brightness of the object as well as on the subject's appreciation of the darkness momentarily perceived. At any rate this spreading and fading take much more time than the time necessary to build up a perception-representing activity in the higher center by the on-bursts.

The movement of a stabilized image in one direction causes a similar effect: the on-activity released at one side of the moving edge gives rise to perception of a bright, colored border which again diffuses and fades when the movement is stopped. The spreading of the on-activity mentioned above can be stopped by a barrier of off-activity (see below).

Summarizing: Presumably the retinal on-bursts rapidly build up an activity in the higher center. This activity slowly diminishes through local adaptation if not compensated for by a new supply. Moreover, this activity tries to spread to all sides if not blocked by a barrier (the off-activity). In the case of a stabilized image there are no new on-bursts and off-bursts, and hence no new supply and no remaining barrier.

The off-system (darkness)

Normally, if a stimulus is turned off, a sudden decrease in brightness is perceived. Presumably this is not due to the decrease of the steady-state activity of the on-fibers, but rather to the off-bursts of the off-fibers in the optic nerve.

Owing to this off-activity of the retina, an activity is rapidly build up in the higher center, and this activity "neutralizes" the activity that exists there, and which has been caused by the on-bursts. When this neutralization is complete, the perceptual effect is Eigengrau. For this reason one of the purposes of the off-activity is the rapid cancellation of the brightness activity previously built up by the on-discharge. This is one of the four possibilities suggested by Barlow (1961, page 375). Another task assigned to the off-activity is the formation of a barrier to stop the spread of the on-activity (see above). The activity in the higher center, generated by the off-bursts in the retina, has the same properties of spreading and local adaptation as the activity caused by the on-bursts (see above). This off-activity spread can be halted by a barrier of on-activity.

<u>Summarizing</u>: The activity of retinal off-elements rapidly builds up a new activity in the higher center, which cancels the existing activity caused by the on-bursts. This activity slowly diminishes by local adaptation if not compensated for by a new supply. Besides, this activity tries to spread to all sides if not blocked by a barrier (the on-activity).

Two more remarks concerning this matter:

We are fully aware of the fact that the on-bursts and off-bursts do not build up an activity in the higher center directly, but by means of the cell-firing in the lateral geniculate bodies and perhaps the cortical areas 17. This should be kept in mind when, in our later explanations we disregard these steps in order to avoid lengthy discriptions.

It is not (yet) possible to conclude which kind of action is involved in the prevention of the on- and off-activity spreading: a barrier action of the on-activity or off-activity against the spread off-activity or on-activity, or on the other hand a cancelling action of these activities, whereby the activity is not arrested in its spread, but cancelled locally. The one action or the other will probably make no difference in the direct perception of the effect, but is of great theoretical (functional) importance.

§3. THE PERCEPTION OF BRIGHT, CONSTANTLY ILLUMINATED FIELDS

As has been shown in Chapter IV, §3., the attempts to explain the continuous perception of brightness have been focused on the significance of the steady-state discharges of the ganglion cells. We made clear however that like man, the animal does most probably no longer see the stimulus, when all the retinal ganglion cells are firing their steady-state discharges.

It should be emphasized that the eye movements are not necessary for seeing the object at the very moment it is presented. They are indispensable, however, in order to continue seeing the object. Even if the duration of the stimulus is so short that the influence of eye movements is negligible, or if short light flashes on the stabilized eyes are given, the image is perceived in its entirety. This is due to the on-bursts firing elements which almost immediately build up an activity in the higher center. Although the experiment described in Chapter II, §3.b.3. proves that for filling-in and perceiving the inside field homogeneously it suffices to move no more than the border, this process takes relatively much time.

Thanks to the short-lasting on-burst of every single element in the whole field we profit of the fact that the level of activity in the higher center is at once raised over the whole field projection, and so this field is instantly perceived as being homogeneous. If this activity were not supported it would extinguish. The local adaptation in the higher center would cause the perception of this field to disappear completely. This effect is counteracted, however, by the activity that spreads in the higher center from the border of the field to the inside.

The activity along the border of the field in the higher center is built up there again and again by the retinal on-bursts caused by the small movements of the eye with respect to the object.

So the steady-state discharge of the ganglion cells situated on the inside of the field has nothing to do with the continuity of perception. But, as will be discussed in Chapter VI, § 2., the steady-state discharges probably do have a function in the regulation of the cortical excitability and in this way affect the perceptual intensities.

Our results also hold the solution to a problem raised in the discussion between Arduini and Jung (1961a, page 205). It is difficult to understand how we can obtain a continuous sensation of brightness from the short transient activities of cortical neurons. Responsible for the preservation of the central activity, and thereby for the perception of continuous brightness over the stimulus field are rather the continuously generated transient activities of on- and off-cells along the stimulus border caused by the continuous image movement over the retina and the spreading of these activities to the inside of the field.

§ 4. INFLUENCE OF THE CONTOUR; STABILIZED VS. NON-STABILIZED FIELDS

From the above reasoning the influence of the contour around a field is perfectly clear. With non-stabilized images sharp contours are seen while blurring of the contour and spreading of the activity are perceived when observing stabilized images. When the center of a large bright field is being fixated, all the retinal elements situated at the inside of the field behave, in fact, as in the case of stabilization of the field. These elements fire an on-burst at light on and subsequently fall to their steady-state firing rate.

But for the elements along the contour the situation in the normal and in the stabilized condition is quite different. In the stabilized condition the firing rate of the contour elements falls to their steady-state level, and so does the firing rate of the center elements. In normal vision, however, these contour elements are switched on and off over and over again by the movements of the eye. This is a most powerful stimulus. The barrier of off-activity prevents (or cancels) the spread of the on-activity in the higher center to the outside (see figures 15 and 16). The spread to the inside compensates the loss of activity (by local adaptation) at the inside.

§ 5. THE COLOR SYSTEM

The same conception like that of a balance between the B- and the D-system (see electrophysiological introduction) is also applicable to the color system. de Valois (1960, 1965) and de Valois and Jones (1961) investigating the response of the cells in the layers of the monkey lateral geniculate body found there green on - red off cells, red on - green off cells, yellow on - blue off cells, and blue on - yellow off cells. Recently Wiesel and Hubel (1966) published an article concerning these color coding cells (monkey LGB). They found green on center - red off surround cells, blue on center - green off surround cells and so on (their type I), and, besides blue on - green off cells, blue off - green on cells, (probably) also red on - green off cells, and green on - red off cells (their type II). Their type I cells are most responsive when the receptive field center is stimulated with the color complementary to that which stimulates the receptive field's surround. So these cells have the appearance of opponent color contrast cells. Their type II cells resemble the opponent color-cells found by de Valois.

In our opinion a fiber in the visual system sends quantitative information concerning one quality only to the higher center. That is to say, a red on - green off cell transmits only the quality red, the amount of redness being encoded in the cell's firing frequency. Hence the red on center-green off surround cell signals red, the red off center-green on surround cell signals green and so on. This holds for all the opponent color cells and the opponent color contrast cells.

In our opinion these cells mediate the color information in a similar manner as the brightness system with regard to the function of the off-response. So, for instance, if we switch off the red light, the red build up in the higher center by the activity of the red on - green off cells is rapidly neutralized by the activity of the green on - red off cells. Several authors believe that the inhibition of the spontaneous activity of the off-fibers at stimulus on carries important information to the higher center, both in the brightness system (Granit, 1955, page 93) and in the color system (de Valois and Jones, 1961, page 197, question of Baumgartner). In their opinion the on-fiber sends the information black in case of inhibition of its spontaneous activity. In the same way green should be signalled in the case of inhibition of the spontaneous activity of the red on - green off cell. In our opinion only the spontaneous brightness activity, or the spontaneous red activity (noise), as the case may be, is inhibited in the above-mentioned cases.

§6. THE OTHER EXPERIMENTS

The results of the experiment in which a black stabilized image on a non-stabilized illuminated background was given (Chapter II, §2.) will now be understood more easily. When the illumination is switched on, the subject perceives a black disk on a green surrounding field. The on and on-or-off elements of the retina, illuminated by the green field, fire on-bursts which rapidly build up an activity in the higher center, causing the perception of the green surroundings. The neural projection of the retinal image of the black stabilized field, however, lies within this region of the higher center. The retina does not send then any activity from this part of the visual field, and consequently there exists no activity coming directly from the retinal activity in the projection area of the black disk in the higher center. But the activity in the higher center will spread when it is not prevented from doing so by a moving contour. Hence, since the contour of the black stabilized field does not move, the activity in the higher center from the projection of the green surroundings diffuses to the projection area of the black field. This manifests itself as a filling-in until a completely homogeneous green field is perceived. However, by switching off the illumination, off-activity is generated in the higher center, and this neutralizes the activity caused by the on-bursts. But no retinal off-activity occurs at the image of the black field, and therefore the activity in the higher center projection of the black field, caused by spreading from the surrounding higher center area, is not neutralized. Consequently, the black field is still seen as green until this activity in the higher center has been dissipated by local adaptation.

At high illumination levels, however, the stray light reaching the retinal projection area of the disk through the sclera, which will be switched off, has some influence. The off-effect of this stray light causes a reduction of the filled-in brightness and color at the location of the disk. Besides, the influence of the off-effect from the neighbouring non-stabilized background on the filled-in brightness will also increase with higher illumination levels.

This is evidenced by the better results obtained at higher illumination levels when using the sclera screening black film or by turning the eye to a black field, instead of switching off the light. In these ways the disturbing effect of stray light was strongly reduced or overcome.

In this experiment, an activity in the higher center is observed which is not derived directly from the retina.

The filling-in of this "artificial scotoma" described above is exactly the same as the experience of some patients with lesions in their visual cortical areas (Walsh, 1957; Teuber et al., 1960; Gassel and Williams, 1963).

In the experiments described in Chapter II, §3.b.3., only a green border was moved in all directions, and this proved sufficient to fill in the inside of the disk until it was seen as homogeneous bright green. Low rotation frequencies failed to make it homogeneous. The most efficient frequency to reach that goal was somewhere between 2 and 3 c/s, depending on the intensity of the light. Efficient has to mean here: greatest activity spreading property. In 1962, Burns et al. published some recordings regarding cortical cells of the cat. In view of the close correlations with our results we will discuss some details of Burns' article.

Burns showed first (his fig. 1) that the difference in the mean firing rate of these cells stimulated with continuous illumination and in darkness is negligible. He used a non-moving black-white border situated in the receptive field of the cell as a stimulus. When this stationary border was illuminated intermittently (frequency 2 c/s), the meanfiring rate increased from about 10 to 28 spikes per second, i.e. considerably above the spontaneous activity in dark (about 10 spikes per second). He also determined that position in the receptive field of the cell where he got maximum response from it by stimulating with a spatially oscillating light-dark boundary with an amplitude of movement of 42 min. arc and at a frequency of 2 c/s.

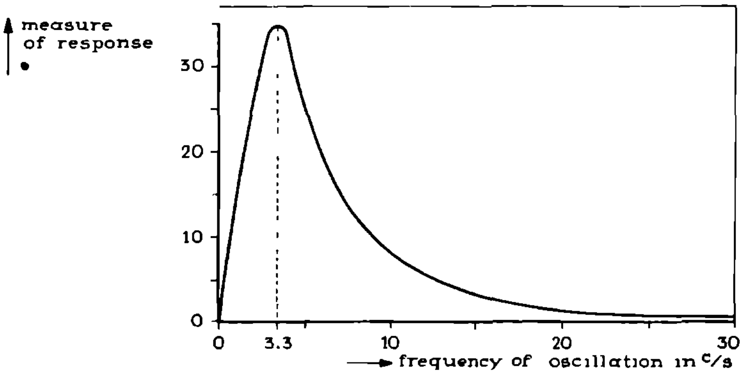

Fig. 25. Responses of a cortical neurone to retinal excitation by a horizontal light-dark boundary oscillating at various frequencies. Amplitude 50 min. arc (Burns et al., 1962, figure 7).

In this optimum location for this cell he varied the frequency of oscillation of this light-dark boundary, the amplitude being set at 50 min. arc.

His figure 7 (here redrawn as fig. 25) shows that the response of this cortical cell was greatest at an oscillation frequency of about 2-4 c/s. The correlation with our results (most efficient frequency 2-3 c/s) is striking, although Burns' results were obtained from the cat and ours from man. This suggests that a basic property of some cortical cells has been discovered.

Burns' curve shows the same trend as that found by us for the efficacy of the frequency of rotations for obtaining a homogeneous field: low frequencies (0,2 - 0,8 - 1 c/s) and higher frequencies (>4 c/s) were less effective than the 2-3 c/s range. Obviously, the maximum cell activity causes maximum spread. Probably it is very difficult, if not impossible, to determine with our subjective measures the bandwidth of this curve in more than a few points. Undoubtedly the use of a rotating stimulus border instead of a stepwise moving border like that of Burns or of the normal eye movements is less efficient in its activity spreading properties.

We already evidenced this earlier (see Chapter II, §3.b.8.), but it may as well be seen from fig. 16. In our experiments point d of this figure is illuminated during a shorter period than point c, which in its turn is stimulated during a shorter period than point b, and so on. This means that the duty cycle for light on is very small for point d and increasingly larger for the inside points. In Burns' experiments, however, the duty cycle is the same for all points and equal to one half. This is most probably the cause of the necessity of the fairly critical rotation frequency setting for obtaining the best results in the experiments with the regular eccentric movement of a bright and dark object (§3.b.3. and 3.b.6.). Argueing along the same lines we might expect (and indeed have found) that the setting of the frequency was even more critical in the experiment with the regular, non-eccentric movement of a bright object (§3.b.7.). In his figs. 8 and 9 Burns shows how the responses of the cells depend on the amplitude of movement when the frequency of oscillation is set constantly at 2 c/s. There is little or no increase of the cell response above about 50 min. arc of movement amplitude. This must be an indication of the cell's own field of activity. On the other hand the cell may be influenced in its firing rate from up to a distance of 20 degrees (see Burns' fig. 6). This is undoubtedly caused by the activity spreading from remotely activated cells to the cell under observation. Contrary to our own experiments (in which retinal activity spread would not be of any help), we found no indication in Burns' article whether this spread is a retinal or a cortical phenomenon. It is known that it may take place either in the retina or in the cortex.

All the observations in the various experiments can be understood by means of this model, including the experiments with other colors and those replacing the background illumination by another color instead of merely switching off. Only one observation is still difficult to understand: When a stimulus consisting of a green annulus surrounding a black field is stabilized, it disappears completely. When the stimulus is switched off the retina will fire off-bursts only over the annulus, and this should be perceived by the subject as a purple annulus solely. But the subject sometimes observes a purple annulus surrounding a green field (fig. 3). This effect cannot yet be explained by the model.

CHAPTER VI

REFLECTIONS ON THEORY AND EXPERIMENTS

§1. FIXATION VS. STABILIZATION

Fixation may be considered as a first step to stabilization. Suppose the center of a black disk on a red surround is rigidly fixated. After 12-15 seconds a faint red light can be seen filling the black disk. At the same time the subject notices a dark black and greenish sickle on the inside border of the disk and a bright red sickle opposite it, but situated outside the disk. The sickles can be seen moving with the subject's eye movements. These sickles, as will be understood, represent on- and off-effects, and the red faint light inside the disk is caused by some spreading of red into the disk, starting from the bright red on-border. Owing to the fixation, part of the efficiency of the on- and the off-system is lost, and the consequences of this are the results described. These same effects, obtained with real stabilization, are of course much more pronounced. When after such a period of fixation the illumination is switched off, the black object reappears in the color of the formerly illuminated surround (in the example mentioned above: red). This effect can also be seen when the area of the black object is instantaneously enlarged.

Creed (1931) and Straschill (1964) have carried out and described many experiments of this type, the after-images of which resemble very much those of our experimental result, which has not yet been explained (see page 75). An investigation of these after-images in our laboratory is in progress. The most difficult problem is to design the experiment in such a manner that it permits us to establish with certainty which aspect of the after-image is of central and which aspect is of retinal origin. By applying pressure on the eye (ischaemia)

Cibis and Nothdurft (1948) were able to distinguish between images generated in the retina and those generated centrally. So far we have not succeeded in making the desired distinction by following this method.

Besides these enhanced after-images rigid fixation entails another experience, known as the "Troxler effect". When a large, not too bright, field is fixated by the subject, he will temporarily lose the perception of the peripheral parts of the field. He gets the impression that the field shrinks periodically. The receptive fields are much larger in the peripheral part of the retina than in the foveal area. The temporary abolishment by fixation of the largest of the whole range of eye movement amplitudes will therefore have a relatively stronger influence on the peripheral cells with the larger receptive fields, which need these larger movements in order to be activated. Fixation is not able to cancel the smaller eye movements. The Troxler effect has been investigated most recently by Clark (1960, 1961) and Clark and Belcher (1962) who conclude these effects to take place in the lateral geniculate body.

§ 2. PROBABLE INFLUENCE OF CHANG'S EFFECT; FUNCTION OF THE STEADY-STATE ACTIVITY

It may be taken for granted that, when being illuminated, the retina provides two opponent activities. In the first place it fires the on-bursts which cause the immediate perception of the light. Secondly it prepares, during the illumination period, an activity which is necessary for rapid neutralization of the activity that causes the perception. This off-activity is released at light off. During normal perception the off-activity effects the rapid disappearance of perceived brightness and color after the switching off of the illumination. In the stabilized condition the off-effects are more pronounced causing a blackness darker than Eigengrau or after-images in the complementary color. These more pronounced off-effects are not only to be observed after fixation or stabilization. A trained subject is able to perceive clearly purple off-activity of a green stimulus even if this stimulus did not last longer than 1 ms physically. We may ask ourselves, however, why the perception of these off-effects is so strongly enhanced under stabilizing conditions. In our first article on stabilized images (Gerrits et al. 1966, page 436) we argued that this might be caused by an "overshoot" of perception: the retina fires its normal off-bursts when the stimulus is turned off, but the activity, build up in the higher center at light on, has by then disappeared owing to the local adaptation (stabilization). The ensuing off-activity causes an "overshoot" which is experienced as an uncommon perception, i.e. intense black. Although this "overshoot" may be real in the overall descriptive sense, further research in the literature suggests some correlation with Chang's potentiation.

Chang (1952) stimulated the optic tract of the cat electrically, recording from neurons in the lateral geniculate body and the visual cortex. He found a large increase in the responses to this electric stimulation as soon as the dark retina was flooded with light. This increase of excitability by the constant retinal illumination is called: potentiation. Its full development takes at least 5 seconds, it shows no sign of decline of strength and it influences not only the neurons in the lateral geniculate body but also the cortical neurons. Its effect is restricted to the visual area.

According to Arduini and Hirao (1960) and Arduini (1961a, page 184; 1961b, page 117) this excitability increase is not conditioned by a direct facilitatory influence of the diffuse illumination (the steady-state discharge), as was thought by Chang, but by the elimination of an inhibitory action, which occurs under the influence of the spontaneous activity in the dark. Also retinal ischaemia results in potentiated responses. As already discussed, the total number of discharges in the steady-state firing, integrated from many units, decreases with increasing intensities of light (Arduini, 1961a, page 184). In other words: a higher retinal illumination is accompanied by a lower rate of steady-state firing and a higher state of excitability of the lateral geniculate body and cortex. These potentiation experiments have been carried out with anaesthetized and paralyzed animals and consequently under stabilized image conditions. We expect the integrated retinal firing rate to be higher in the normal than in the stabilized condition because of, firstly, the addition of the on-bursts and off-bursts fired everywhere along the borders; secondly, on the ground of the experimental results of McIlwain (1966) who demonstrated the influence (increase of firing) on elements situated as far as 29 degrees from a moving source; thirdly, on account of Arduini's remark in his discussion with Bremer (1961b, page 124), quoted as follows: "On the other hand the striking effects obtained in our experiments by changing the direction of the light beam (as far as EEG synchronization is concerned) suggest that under continuous illumination there is an excitatory component counteracting and occasionally overwhelming the effects of the abolition of the dark discharge".

On these grounds we may conclude: The state of cortical excitability is most probably higher in the stabilized than in the normal condition.

We are permitted to extend the effects of this excitability increase to responses on flashes of light because not only the response to an electric stimulus supplied to the optic tract is enhanced by constant illumination. Steriade and Demetrescu (1966) investigated in the cat the influence of constant light on the cortical response to short flashes of light. They found a diminution of the a-wave amplitude, but an amplitude increase of the b- and c-waves. In their terminology the a-, b- and c-waves constitute the primary responses. According to these investigators constant light exerts a specific facilitatory effect on the b- and c-waves, due to intracortical reverberations.

Chang (1952) succeeded in decomposing the change in excitability, after illuminating the retina, in 4 different processes. His figures 9, 10 and 15 are redrawn here as the figures 26, 27 and 28.

In the figures 26 and 27 the solid line and the dotted line represent the average size of excitability during continuous illumination and in dark respectively. The measure of excitability is the amplitude of the cortical response to electric stimuli applied to the optic tract. As can be seen from these figures there is a very short depression (post-excitatory depression) both at the on-set and at the off-set of the illumination. Subsequently there is a considerable excitability increase, especially after the off-set of the light. These oscillatory excitability changes die out in about 1 second (see curve 3 of figure 28, which is equivalent to the curve of figure 26); they are due to the activity in the corticothalamic reverberation circuits. As can be seen in figure 28 a constant level of excitability increase (curve 1), be it modulated with a spontaneous oscillation (curve 4), is reached after about 5 seconds.

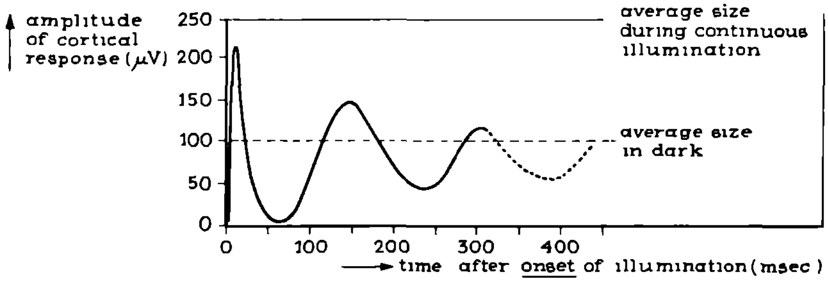

Fig. 26. Response to electric stimulation of the optic tract in the dark, during illumination and at the on-set of the illumination. This curve is the same as that numbered 3 in figure 28 (Chang, 1952, figure 9).

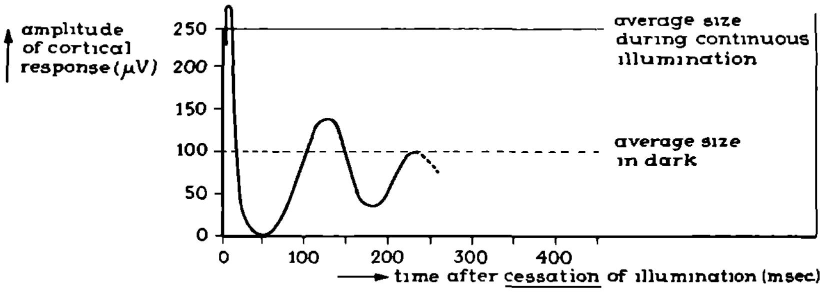

Fig. 27. Response to electric stimulation of the optic tract in the dark, during illumination and at the off-set of the illumination (Chang, 1952, figure 10).

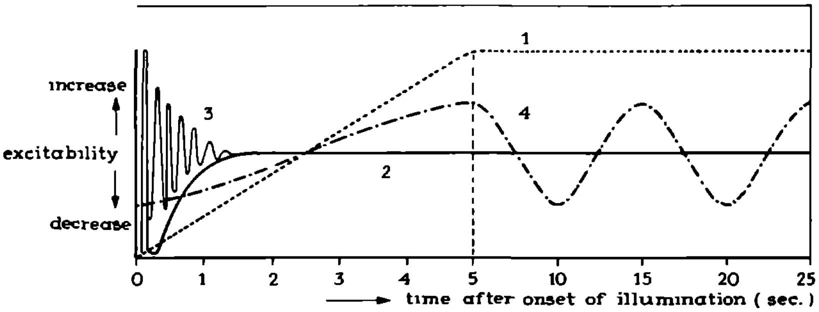

Fig. 28. Four different processes of excitability change of the visual system immediately after and during illumination of the retina.

1. progressive facilitation
2. post-excitatory depression
3. periodic variation of excitability accompanying corticothalamic reverberation
4. slow spontaneous periodic variation of excitability (Chang, 1952, figure 15).

According to Steriade and Demetrescu (1966), who stimulated the animal with light flashes and not with electric shocks, the time necessary to reach a constant level of the facilitatory effect of steady light may be 15-60 seconds.

The increased level of excitability in the stabilized condition compared with that in the non-stabilized condition for the same intensity level of constant illumination may account for the perception of stronger off-effects in the stabilized condition. Although the retinal transient response in both conditions may be slightly different, we believe that the increase in cortical excitability, as found in the electrophysiological response, plays an important role in the intensification of the perceptual effects in the stabilized condition.

The minor effect of the shorter durations of the stabilizing light on the perception of the off-effect (see Chapter II, § 1.) can be explained on the ground of the smaller increase of the excitability than would be reached with stimuli of longer duration. It could also be due, however, to a decreased retinal output for short durations.

An increased perceptual effect of the on-response as well as of the off-response might be expected. We carried out some preliminary experiments, investigating the increment threshold during stabilization. However, we did not find a decrease but an increase in the increment threshold in the stabilized condition. In our opinion this was due to an inadequate manner of stimulation; hence more experiments will be performed in the future.

Ditchburn and Fender (1955), on the contrary, reported that their subjects complained of the brightness of illumination at high interruption rates of the stabilized field. These subjects overestimated the brightness up to a factor 100, which may be due to the increased excitability of the brain.

The slow spontaneous oscillations (curve 4, figure 28) have probably been observed by Fiorentini and Ercoles (1963, 1965). They published reports on the fluctuating perception of a stabilized object. Apart from a rapid decline of the visibility of the object a periodic fluctuation with a period of about 10 seconds has been found with constrained accommodation. One would be inclined to correlate these fluctuations with those found by Chang in the cat (see figure 28). Like Barlow (1963), we did not find the fluctuations described here. The reason for this may be the use of Iarbus' suction cap and a mydriatic, as well as the influence of long training, as is evidenced by Conticelli (1962) in prolonged fixation experiments.

It has been stated often in this thesis that a great deal of the observations described have a bearing on effects brought about on the cortical rather than on the retinal level. We may emphasize the fact that many of these observations are not limited to particular experimental situations, but may be common-day experiences as well. Evidence for this is for instance the filling-in of the blue-blind fovea and the blind spot which are never observed if not tested with small spots of light (Walls, 1954). There are also several clinical reports concerning the filling-in of scotomatous areas in brain-wounded patients (see page 65).

We have also shown the likelihood of an increased or decreased perceptual effect of the retinal output to be obtained as a result of a change in the level of the cortical excitability.

Reports from the clinics suggest that these changes have taken place in some patients. So for example Critchley (1951) reports on his case 4:

> "If he looks at a thing and looks away, he may continue to see it somewhere else, as if it did not get cut off quickly."

On his case 6:

> "She would find that after looking at an object she might continue for a minute or 2 to see this object even after its removal."

Also Kinsbourne and Warrington (1963, page 469) report:

> "As the object was replaced by its persisting image, so would its color change, usually into a roughly complementary hue ...... rapidly moving objects may leave a trail, like the tail of a shooting star."

See also the reports of Le Beau et al. (1952).

One of the functions we assigned to the off-activity is the rapid cancellation in the higher center of the activity (and with it of the perception) built up there previously by the on-bursts (see Chapter V, §2.).

When this off-activity in the higher center is decreased by some excitability change the on-activity existing there is not fully cancelled and so the perception is not switched off entirely (see also the observations described in Chapter II, §2.a.). This may be an explanation for the perception described by the patients of Critchley and Kinsbourne. Also the trail seen to follow rapidly moving objects (Kinsbourne's patient) may be explained by an excitability change. By the movement of the object a formerly illuminated retinal area (firing on-bursts) is now darkened (firing off-bursts). If in one way or another the cortical excitability is changed, the on-activity built up in the higher center may not be completely neutralized. The on-activity left fades away slowly. This gives the impression of a trail following the object (compare with the trails in figure 9).

In spite of the resemblance of the effects, their origin may still be quite different, of course.

§3. CONCLUDING REMARKS

In the normal eye movements a whole range of frequencies are to be found. According to the data most used, there is a high frequency tremor, with an amplitude smaller or equal to 0.5 min.arc and a frequency range up to 80 to 150 c/s. This high frequency tremor is superposed on a slow drift of the eye, which shifts with a speed of 1 min.arc per second. We correct this drift periodically with flicks, which rapidly shift the image over the retina with a maximum amplitude of about 50 min.arc and at intervals of 0.03 to 5 seconds.

If we try to eliminate the large amplitude eye movements by rigid fixation, it is the peripheral part of the visual field with the larger receptive fields that becomes dark (Troxler effect). From theory and experiments it is obvious that cells with smaller receptive fields are restimulated by smaller movements.

We are convinced that different cells inform the brain about different qualities of the stimulus; that is to say, the cells are specific. Nevertheless, the cell which belongs specifically to the color system is able to make a contribution to the brightness system. This idea is not new; Hillebrand and Hering (1888) already gave evidence of it. In our experiments it is the bright purple off-effect which proves that there is an influence of the specific color cell on the brightness system. This means that the efferent from the cortical color cell on its way to the (or a) higher center sends a collateral into the layer of brightness cells. In this way the color cell does not lose its specificity, for it still projects on a specific color element in the higher center, but moreover it influences the brightness. In fact efferents giving collaterals are found in abundance in area 17. As may be understood from the above, we believe the different layers of area 17 to be specific too. The idea is that the smaller cells (situated in the layers 2 and 3 of area 17) may influence the larger cells (situated in the lower cortical layers 5 and 6). These larger cells may transfer activity, received by means of collaterals from the efferents of the smaller cells, to neighbouring cells in the same layer (spreading). These smaller cells should have smaller receptive fields and be color-specific and "contour-specific" cells. By "contour-specific" is meant that they are responsive mainly to narrow, small stimuli.

From the experimental results described, as well as from the literature data, it is clear that changes are most important in the visual system and, as we have proved, are even capable of transferring information about the brightness of not changing parts of the field, that is, of constantly and homogeneously illuminated fields. Besides, it is very probably the integrated "constant" activity (the steady-state discharge) which sets the state of excitability of the information receiving elements.

We fully agree with the suggestion that the brain stores the given visual pattern. The retina only transmits new changes to the brain and counteracts central adaptation. This suggestion has been made and evidenced by Mackay (1958).

SUMMARY

Considerable information concerning the function of the visual system has been obtained by electrophysiological experiments on anaesthetized animals which consequently do not move their eyes during the experiment. In order to correlate these experimental data with visual perception in man, psychophysical experiments have to be carried out on a subject under equivalent conditions, i.e. with abolition of the influence of his eye movements. One of the methods to reach that goal is to suck the object to be observed on the eyeball of the subject. This is called stabilization.

Some of these stabilization experiments have been described in Chapter II. If the image is completely stabilized (§ 1.) the subject observes a fading of the contours, the colour and the brightness during a few seconds. The perception disappears completely notwithstanding the constant illumination of the retina. The sequence of disappearance of the perception stages is always the same: firstly the contours, secondly the color, thirdly the brightness. At the moment of switching off the stimulus (after the fading by stabilization), the subject perceives a very bright after-image in the complementary color.

In § 2.a. a black stabilized image against a normal non-stabilized background is presented to the subject. Again the stabilized part fades in a few seconds and is filled in with the color and brightness of the adjacent background.

Upon switching off the background illumination the part filled in is observed to fade away slowly. Instead of switching off the background after the filling-in has taken place it may be replaced by a background of another color (§ 2.b.). In the latter case the subject observes the part filled in with the first background color contrasting against the new background. The stabilized part changes its appearance once more and adopts the hue and brightness of the new background.

In § 3.a. the subject's perception has been described when a stabilized image is moved in one direction. He perceives only those borders which are moved and thereby cause a change in the illumination of the retinal elements. The activity is spreading, however, far outside the area where it has been generated (the border). It is in no way possible to restore the perception of the original image by unilateral displacements.

A movement of the image in various directions might be necessary in order to regenerate the original perception. A very small electric synchronous motor which can be fitted in the object holder sucked on the eye has been used to obtain multidirectional movements of the image (§ 3.b.2.). The object forms part of the rotor of this motor. By moving the contour of the field in various directions using this motor it appeared possible to bring back into vision the field perceived homogeneously illuminated with the color and the brightness of the moving contour elements. By these contour movements it was found possible to regenerate bright fields (§ 3.b.3.) as well as black fields (§ 3.b.6.).However, a pattern situated in the center of the field does not come back.

An analysis of the observations is given in § 3.b.4., and is checked by an experiment using a specially shaped object. The results predicted were indeed obtained from this experiment (§ 3.b.7.).

The differences between the movements of the image applied in the various experiments and the real eye movements are discussed in § 3.b.8. In this paragraph a better method to imitate the real eye movements is given.

§ 5. of Chapter II describes the reaction of the pupil on the stabilized image. The pupil reaction might give some information about the locus where the stabilization effects are produced. It was found from the experiments that the pupil diameter is the same in the stabilized and in the non-stabilized condition, i.e. the pupil diameter does not change by the fading of the perception in the stabilized condition.

In Chapter III the influence of the subject's training and of several experimental precautions on the observations is discussed.

Chapter IV reports a number of literature data necessary for correlating the psychophysical results with morphological and electrophysiological facts. The most important nuclei and tracts of the visual system are discussed in § 1., while § 2. deals with electrophysiological data.

It is obvious from these electrophysiological data that the visual system responds vigorously to stimulus changes but only faintly or not at all to stimuli which are constant in time and space. It has been accepted, however, that the anaesthetized animal continues to perceive a constant (stabilized!) stimulus. The animal is considered to make use in one way or another of the low firing rate found in the optic nerve after the decay of the strong response to the switching on of the stimulus for the perception of constant brightness (§3.).

Chapter V, § 1. deals with the question of whether the perceptual changes caused by stabilization are produced in the retina or whether they are due to properties of the central nervous system. Most arguments indicate a central origin of these effects.

In § 2. a hypothesis is given concerning the function of the two cell systems, i.e. the on- and off-cells which are responsible for the perception of brightness and darkness at the moment of switching on, respectively of switching off the stimulus. This hypothesis is helpful to understand why a constant non-stabilized stimulus does not fade from perception (§ 3.), what is the influence of the moving contour (§ 4.), and why the perception in stabilized condition is quite different from that in non-stabilized condition (§4.). The color system most probably functions in an analogous manner as the brightness system (§ 5.). In § 6. a further explanation of the observations is given. The strong correlation between these observations and electrophysiological data is also shown in this paragraph (6). From the above it is clear that the eye movements are indispensable, not for seeing but in order to continue to see.

The most important part of Chapter VI is formed by § 2., in which the regulation of the excitability of the central nervous system is discussed. The stabilization experiments have shown that the low firing rate in the optic nerve does not lead to constant perception. This low firing rate has another function, however. As is known from electrophysiological experiments this retinal activity regulates the excitability of the central nervous system for the incoming retinal signals. This could mean that also the perception may be influenced by this low firing rate. Several effects caused by changes in excitability, and revealed by electrophysiological experiments on the cat, correlate with perceptual effects in the stabilization experiments on man. This is shown in § 2. However, the presence of these corresponding perceptual effects is probably not bound to experimental situations, but can also be found in certain patients with disturbances in their visual system.

The correlations found indicate the manner in which new experiments have to be carried out in order to obtain more information concerning the working of the visual system.

SAMENVATTING

Zeer veel gegevens over de werking van het visuele systeem zijn verkregen uit electrofysiologische experimenten op dieren. Deze dieren zijn veelal geanaesthetiseerd, waardoor hun oogbewegingen zijn opgeheven. Wil men de gegevens verkregen uit deze experimenten correleren met de visuele perceptie van de mens, dan moeten psychofysische experimenten worden uitgevoerd met een proefpersoon onder soortgelijke condities, d.w.z. met opheffing van de invloed van zijn oogbewegingen. Deze z.g. stabilisatie kan onder meer worden bereikt door het aangeboden object (stimulus) in een kapje aan de oogbol van de proefpersoon vast te zuigen.

Een aantal van deze stabilisatie-experimenten wordt beschreven in hoofdstuk II. Wordt een beeld geheel gestabiliseerd (§1.), dan verdwijnen de contouren, kleur en helderheid in enkele seconden en wordt er niets meer waargenomen, ondanks de constante belichting van de retina. De volgorde van het verdwijnen van de aspecten van de stimulus is altijd gelijk: eerst de contour, dan de kleur, vervolgens de helderheid. Schakelt men de stimulus na het verdwijnen uit, dan neemt de proefpersoon een bijzonder sterk nabeeld waar in de complementaire kleur.

Wordt een zwart gestabiliseerd beeld aangeboden tegen een achtergrond welke niet is gestabiliseerd (§2.a.), dan verdwijnt eveneens het gestabiliseerde deel in enkele seconden en wordt het ingevuld met de kleur en helderheid van de aangrenzende achtergrond. Wordt vervolgens de achtergrond uitgeschakeld, dan blijft het ingevulde deel achter en zakt langzaam weg. Wanneer men echter de achtergrond niet uitschakelt doch vervangt door een achtergrond van een andere kleur, dan ziet de proefpersoon het met de eerste kleur ingevulde deel afsteken tegen de nieuwe achtergrond. Ook nu neemt het gestabili-

seerde deel weer de kleur en helderheid van de (nieuwe) achtergrond aan (§2.b.).

Vervolgens wordt beschreven wat de proefpersoon waarneemt als een gestabiliseerd beeld wordt bewogen in één richting (§3.a.). Het blijkt dat slechts die randen worden waargenomen die door de beweging een verandering in de belichting van de retinale elementen veroorzaken. Vanuit deze randactivering spreidt echter een activiteit uit naar alle zijden. Het is niet mogelijk met deze beweging in één richting het oorspronkelijke beeld (gepercipieerd vóór de stabilisatie) weer op te wekken.

Om te onderzoeken of een beweging van het beeld in verscheidene richtingen in staat is om de oorspronkelijke perceptie weer op te roepen, is gebruik gemaakt van een zeer kleine electrische synchroon motor (§3.b.2.), welke wordt gemonteerd op een kapje dat aan de oogbol wordt vastgezogen. Het object is gevat in het draaiende deel van deze motor. Het bleek nu mogelijk te zijn de proefpersoon een vlak geheel egaal te doen zien door uitsluitend de randen in verscheidene richtingen te bewegen. Dit vlak wordt dan gezien in de kleur en met de helderheid van de bewegende randelementen. Zowel gekleurde heldere vlakken (§3.b.3.) als zwarte vlakken (§3.b.6.), welke door stabilisatie niet meer zichtbaar waren, konden door deze randstimulatie worden geregenereerd. Een figuur gelegen in het vlak binnen de bewegende rand blijft echter onzichtbaar.

In § 3.b.4. is een analyse gegeven van de waargenomen verschijnselen. Ter verificatie van deze analyse werd een experiment uitgevoerd met een ander object van een bepaalde vorm (figuur 20 B en C), dat zich op een voorspelbare wijze zou moeten gedragen. Experimenten met dit object (§3.b.7.) leverden inderdaad het voorspelde resultaat.

§ 3.b.8. behandelt de verschillen tussen de bewegingen gegeven in bovenvermelde experimenten en de werkelijke oogbewegingen en de wijze waarop deze oogbewegingen nog beter nagebootst kunnen worden. Ten slotte beschrijft §5. van dit hoofdstuk de reactie van de pupil op het gestabiliseerde beeld. De pupilreactie kan een indicatie geven over de plaats waar deze stabilisatie-effecten optreden. Uit de experimenten werd gevonden dat er geen verschil is in de reactie van de pupil op gestabiliseerde en ongestabiliseerde beelden. De pupildiameter verandert dus niet door het wegvallen van de perceptie.

Hoofdstuk III behandelt vervolgens de invloed van training van de proefpersoon en van de verschillende experimentele voorzorgen op de waarnemingen.

Om verband te leggen tussen de psychofysische resultaten en morfologische en electrofysiologische gegevens wordt van deze laatste in hoofdstuk IV een kort overzicht gegeven.

De voornaamste kernen en banen van het visuele systeem zijn geschetst in §1., terwijl §2. de nodige electrofysiologische gegevens verschaft.

Uit deze electrofysiologische gegevens blijkt duidelijk, dat het visuele systeem sterk respondeert op veranderingen van de stimulus, doch nauwelijks of niet op een constante stimulus. Tot nu toe wordt aangenomen dat een geanaesthetiseerd dier een constant aangeboden stimulus (gestabiliseerd!) blijft zien. Het zou hiertoe onder deze omstandigheden op een of andere wijze gebruik maken van de lage stationaire activiteit welke in de nervus opticus overblijft nadat de sterke responsie op het aanschakelen van de stimulus is verdwenen. De verschillende theorieën waarin getracht wordt de perceptie van constante helderheid te verklaren met behulp van deze lage activiteit zijn beschreven in §3.

In hoofdstuk V, § 1. wordt nagegaan of de veranderingen welke in de perceptie plaats hebben ten gevolge van stabilisatie zich afspelen op retinaal niveau of verderop in het centrale zenuwstelsel. Er zijn zeer vele aanwijzingen voor dat hier eigenschappen van centrale processen in het spel zijn.

In § 2. wordt een hypothese gegeven betreffende de functie van twee celsystemen, de z.g. "on-" en "off-cells", voor het ontstaan van de perceptie van helderheid en het afschakelen van deze perceptie op het moment dat de stimulus aan- resp. uitgeschakeld wordt. Tevens is met deze hypothese te begrijpen hoe men een constante ongestabiliseerde stimulus kan blijven zien (§3.), wat de invloed van de bewegende contour is (§4.) en waarom de perceptie in gestabiliseerde toestand zo geheel verschillend is van die in ongestabiliseerde toestand (§4.).

Het wordt aannemelijk gemaakt dat het kleurensysteem op analoge wijze werkt als het helderheidssysteem (§5.).

Een verdere verklaring van de waargenomen verschijnselen wordt in §6. gegeven. De sterke correlatie tussen deze waarnemingen en verschillende electrofysiologische uitkomsten wordt eveneens in deze paragraaf (6) aangetoond.

Uit het voorafgaande is het duidelijk dat de oogbewegingen onontbeerlijk zijn, niet om te zien, maar om te blijven zien.

Het belangrijkste deel van hoofdstuk VI is § 2., waarin de regeling der gevoeligheid van het centrale nerveuze systeem wordt besproken. Alhoewel de stabilisatie-experimenten hebben aangetoond dat de overblijvende stationaire lage activiteit in de nervus opticus niet leidt tot de constante perceptie van de aangeboden stimulus, wil dat niet zeggen dat aan deze lage activiteit in het geheel geen functie kan worden toegekend. Uit de electrofysiologie is bekend dat met deze retinale activiteit de gevoeligheid van het centrale nerveuze systeem voor de hierin aankomende retinale signalen wordt geregeld. Dit houdt in dat hiermee ook de perceptie in aanzienlijke mate zou moeten kunnen worden beinvloed. In § 2. is aangetoond dat verschillende electrofysiologisch gemeten effecten t.g.v. gevoeligheidsveranderingen, gevonden in experimenten op de kat, daarmee corresponderende perceptuele effecten ten gevolge hebben bij stabilisatie-experimenten op de mens. Dit geldt waarschijnlijk niet alleen in de hierboven beschreven en door andere onderzoekers uitgevoerde experimenten, maar ook in het geval van sommige patiënten met storingen in hun visueel systeem.

Deze gevonden correlaties tussen electrofysiologische en psychofysische waarnemingen geven een inzicht op welke wijze nieuwe experimenten moeten worden ingericht om verdere informatie omtrent de werking van het visuele systeem te verkrijgen.

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STELLINGEN

I

Een correlatie van menselijke waarnemingen met electrofysiologische gegevens verkregen uit een proefdier is slechts dan waardevol indien het mogelijk is de anatomische verschillen in de beschouwde systemen van beide species redelijk te evalueren.

II

Ten behoeve van de kennis van zintuigen en zenuwstelsel zal veel meer dan tot nu toe gebruik moeten worden gemaakt van pathofysiologische gegevens uit de kliniek. Dit temeer daar bij de mens de mogelijkheid om electrofysiologische experimenten uit te voeren zeer beperkt is.

III

De ischaemie experimenten van Cibis zijn niet zo goed uitgevoerd als algemeen wel wordt aangenomen.

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IV

Om tot een begrip van de werking van het complexe menselijke visuele systeem te komen is de samenwerking van onderzoekers uit geheel verschillende disciplines nodig. Zij moeten in een groep op één laboratorium verenigd worden om elkaars "taal" te leren verstaan en aldus tot efficiënte samenwerking te komen. Incidentele contacten op vergaderingen of werkbesprekingen zijn daartoe absoluut onvoldoende.

V

De veelheid van mathematische modellen betreffende biologische systemen die worden gepubliceerd zonder aan te geven wat hun waarde is om gevonden experimentele gegevens te verklaren, werkt de bestudering en het gebruik van deze modellen door zintuigfysiologen tegen.

VI

Een opleiding aan een Technische Hogeschool is door zijn karakter meer aangepast voor het verrichten van zintuigfysiologisch werk dan een opleiding aan een Universiteit.

VII

Het effect van het gebruik van verschillende soorten anaesthetica op de electrofysiologische responsies van een proefdier is nagenoeg onbekend. Een systematisch onderzoek hiernaar is van het grootste belang, zowel om de mislukking van experimenten te beperken als om verschillen in gevonden resultaten te begrijpen.

VIII

De efficiency van informatie overdracht door een voordracht in een tijdsbestek van 10 minuten op congressen is bijzonder gering. Inplaats van deze voordrachten te houden, welke in ieder geval reeds kort in het rondgestuurde programma moeten zijn samengevat, zouden deze sprekers zich beschikbaar moeten stellen om met geinteresseerden over hun werk te spreken gedurende een tijd en op een plaats als aangegeven in het programma.

IX

De aanschaf van computers voor de verwerking van electrofysiologische gegevens moet, ondanks de grote uitgave hiervoor, gepropageerd worden. Het is hiermee mogelijk meer gegevens, verkregen uit één experiment, te verwerken en zodoende het aantal benodigde proefdieren belangrijk te beperken. Dit is niet alleen op ethische gronden wenselijk doch komt bovendien het laboratoriumbudget weer ten goede.

X

In vele in de literatuur beschreven electrofysiologische experimenten blijken de gegeven fysische stimuli dermate slecht te zijn gedefinieerd dat voor de fysische beschouwingen van het onderzochte systeem de verkregen resultaten weinig betekenis hebben.

H.J.M.Gerrits   Nijmegen, 12 mei 1967