A number of investigators have studied the relationship between the intensity of a light stimulus and the degree of contraction of the pupil. This relationship has been most extensively studied for stimuli of long duration and the experimenter usually chooses one point in time after onset of the stimulus and plots the diameter at this point in time against log intensity of the stimulus. Talbot in 1938 made an extensive parametric study of the total time course of pupillary diameter during continuous presentation of light at several stimulus intensities.

In general, the pupil contracts more extensively to more intense stimuli though there is some controversy as to the exact shape of the curve describing this relationship. It completes its contraction within five seconds and then begins to dilate despite the continuous presentation of the stimulus. The dilation of the pupil begins earlier with less intense stimuli, later with more intense stimuli, and slowly heads back towards its dark adapted diameter. The reaction to short stimuli is also a function of the intensity of the stimulus. This type of reaction has been studied by Lowenstein and Lowenfeld and also by Talbot. In a recent series of experiments, Lowenstein and Lowenfeld studied the reaction to short pulses of light during the course of dark adaptation. At the beginning of dark adaptation, the pupil will not contract to short low intensity pulses, but as dark adaptation progresses the pupil recovers its ability to contract to such stimuli. Similarly, the effectiveness of a short stimulus in eliciting a pupillary contraction has been shown by Talbot to be influenced by the state of light adaptation of the retina.

All these investigators (except Stark who worked primarily with repetitive light stimuli), studied the reactions of the pupil in its normal physiological state, that is to say, the contraction or dilation of the pupil increases or decreases the luminous flux reaching the retina. While this is in fact the way the pupil normally functions, it complicates understanding of input-output relations, since even during continuous stimulation with constant light intensity, the output, that is the diameter of the pupil, changes the input, that is the flux density at the retina. It has never been clear, therefore, to what extent the course of contraction and subsequent dilation under constant stimulus conditions is due to the changing amount of flux reaching the retina which is brought about by the changing diameter of the pupil.

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In our own work with the pupillary reflex, we became concerned with the problem of knowing the contribution of this factor to the shape of the contraction and dilation curve of the pupil. We had found, as had Lowenstein and Westphal in 1933, abnormal pupillary reactions in schizophrenic patients. However, even in the resting state, in other words in the dark adapted eye, schizophrenics showed smaller pupils. It was therefore not clear to what extent the abnormal shape of the pupillary reaction of the schizophrenic was due to the fact that beginning with a smaller pupil, the effective light stimulus differed from that reaching the retina of the normal.

We, therefore, undertook a parametric study of the pupillary reflex to light under conditions where the size of the pupil could not alter the light input or in what Stark has called by analogy with servomechanism theory, the open loop condition. This would provide a baseline of information for work in which the pupil is measured under physiological conditions, or for studies with schizophrenics, or with normals under chlorpromazine, in which reactions are elicited from an already constricted pupil.

The optical system by which we obtained the open loop condition was a Maxwellian view system. In this system, the beam of light has its focal point in the plane of the cornea. The diameter of the beam at the point of focus was 1.8 mm, that is smaller than the smallest possible pupillary opening. The optical system was arranged so as to stimulate a 3⁰ centrally fixated retinal area. Two sources of light, independently controlled with respect to intensity and duration, were superimposed to form the final beam of light at the cornea. The subject perceived the short flashes as a momentary increase in the brightness of the 3⁰ field he viewed.

We used infrared photography to obtain pictures of the eye. A 35 mm motion picture camera gave us ten exposures per second. The combination of a fast lens system and a highly sensitive film made it possible to use extremely low infrared illumination. Talbot's work with which this study is most comparable had to put up with more visible light from his infrared sources in order to get good pictures in 1938.

Since the reactions of the pupils are consensual under these conditions, we stimulated the left eye and photographed the reactions of the right eye. Pupillary diameter was measured from the developed film with a total error from all sources of ± .05 millimeters.

We presented the subject with light stimuli of 10 millisecond duration before, during, and after the presentation of a steady light which was on for 80 seconds. (Figure 1)

A few words on the nomenclature we are using: We call the long stimuli adapting lights. The short 10 msec flashes are pulse stimuli. The pulse stimuli here are presented in the pre-adaptation period, early adaptation period, late adaptation period, and post adaptation period. Adaptation here refers to light adaptation.
Eight different adapting luminances were used. The luminances of the adapting stimuli ranged over 5 log units from 6600 mls to .066 ml. The pulse had a luminance of 12,600 ml.

The main purpose of this study was to determine in what way the response of the pupil to a pulse of light depends upon the state of light or dark adaptation of the retina. The data obtained also lent themselves to the examination of two further questions: (1) What is the effect of continuous exposure to light on pupillary diameter, and what is the effect of the removal of light after prolonged exposure on the pupillary redilation in the ensuing dark period?

Following fifteen minutes of dark adaptation the first of the 10 msec flashes was presented.

In Figure 2 the reaction curves of the dark adapted eye to two pulse luminances are shown. Each of these curves is the average of 56 reactions. The more extensive contraction is to the 12,600 millilambert pulse. The shallower curve is a contraction to a pulse 3 log units dimmer.

Next, we determined the effect of each of the eight adapting lights on the size of the pupil during the first 10 seconds of stimulation. (Figure 3) Each curve shown is the average of 14 presentations. An inspection of this figure leads to the following observations:
1. The minimum size reached by the pupil under the influence of the adapting stimuli varies with the luminance of the stimulus: The higher the luminance, the greater the contraction.
2. The velocity of contraction increases with increase in luminance although the rate of increase is smaller with higher luminances.
3. When the adapting stimuli of low luminance are presented the pupil begins to dilate soon after it has reached its minimal diameter. The dilation is relatively rapid for a short period, about two seconds, and then levels off. When the brighter adapting stimuli are presented, there is a slow dilation from the minimum diameter with no discernable rapid phase.

In summary, the effect of the continuous stimulus during the first ten seconds of its application is as follows: there is (1) an increase in the amount of contraction of the pupil with increases in luminance, (2) increased velocity of contraction with increases in luminance, and (3) also depending on the luminance of the stimulus, various degrees of dilation.

It is clear from this figure that the dilation of the pupil during continuous stimulation is not due to a decrease in visual flux reaching the retina. Rather, the dilation of the pupil seems to parallel an increase in retinal sensitivity as a result of retinal adaptation. Further evidence for this statement will be given below.

Figure 4 shows the responses of the pupil to the high luminance pulse during the early adaptation period, that is ten seconds after onset of the step stimulus. Each of these curves is the average of seven re-
actions. The diameter at the onset of the pulse stimulus is at a level which results from the ten second exposure to the adapting light. The pulse stimulus presented against the background of the ongoing adapting stimulus produces an additional response, the size of which is a joint function of the pulse luminance and the level of adaptation. When the pulse is superimposed on the brightest adapting stimulus, no clear contraction can be observed against the fluctuating baseline. At those levels of luminance at which a contraction occurs in response to the pulse stimulus, the contraction is more extensive and the contraction curve steeper as luminance of the adapting stimulus decreases.

Figure 5 shows reactions to the same luminance pulse sixty seconds later. It should be remembered that the adapting light is still on. At this stage of light adaptation the pulse stimulus elicits more extensive contractions. Even with the brightest adapting light, a small contraction can be seen. Also compared with the early adaptation period, the curves here are now closer together.

The greater effectiveness of the pulse stimulus in eliciting a contraction late in light adaptation evidently represents the increasing sensitivity of the retina under continued exposure to light.

The next question we had asked was: How does light adaptation affect the redilation curve of the pupil in darkness?

Figure 6 shows the redilation of the pupil in darkness during the first ten seconds after the eighty second adapting light had been turned off. There is little possibility of additional dilation after exposure to the two lowest levels of illumination since the pupil under these conditions has almost reached the dark adapted size while the stimulus light was still on. The six other curves seem to run parallel, although the diameter at the beginning is still a function of the luminance of the adapting stimulus.

Ten seconds after the adapting light has been turned off the pulse stimulus is again presented. (Figure 7). Note that the clustering observed in late light adaptation is even more pronounced. The shape of all eight curves is now essentially the same. There is a tendency to maintain the relative position of the curves in accordance with the luminance of the preceding adapting light. This indicates the presence of a residual effect of the earlier light adaptation.

The whole experiment was repeated with a pulse stimulus 3 log units dimmer. It is obvious that a less intense pulse will be less effective in eliciting a response against the background of the adapting light. However, as with the high luminance pulse, the low luminance pulse is more effective late in light adaptation. Ten seconds after turning off the adapting light, the reaction to the low luminance pulse reflects more visibly the residual effects of the different luminances of the adapting lights.
In order to demonstrate more clearly the relationship between luminance of the adapting light, and the diameter of the pupil at different points in time, Figure 8 was prepared. These four curves give pupillary diameter plotted against log luminance at the following points in time: (1) at the minimum diameter after onset of the adapting light. (2) ten seconds after onset of the adapting light. (3) eighty seconds after onset and (4) ten seconds after cessation of the adapting light.

The relation between pupillary diameter and log I at the point of minimum diameter seems to be a linear one. The change in diameter during the next several seconds is more rapid with the lower luminances than with the higher luminances. The curve is therefore sigmoid and resembles the curves described by Wagman, Reeves and others. After eighty seconds of stimulation, the total curve however is displaced to the right which indicates the dilation of the pupil during continuous illumination. Ten seconds after the cessation of the adapting light, the pupil has recovered almost completely to its dark adapted diameter but this recovery is slightly less complete after the higher adapting luminances.

The redilation curves after cessation of stimulation are in line with those described by Reeves, Wagman, and Brown and Page. It seems that variations of luminance in the adapting lights of long duration do not influence the general shape of the redilation curves in darkness. Different luminances merely displace these curves on the time axis. It is interesting to note that a similar relationship has been reported by Hecht, Haig and Chase with respect to the foveal threshold sensitivity in their study of dark adaptation. This similarity has been interpreted as support for an "all cone" theory of pupillomotor receptors.

The main problem in this investigation was to study the effect of light adaptation on the pupillary response in the open loop condition. The function relating pupillary diameter to intensity of adapting light has been described. In general, the brighter the adapting light the smaller the pupillary diameter. When the pulse stimuli are presented against the background of different adapting luminances, several observations can be made. The effectiveness of the pulse stimulus in contracting the pupil further depends on the state of light or dark adaptation of the retina at the instant of pulse presentation. The pupil dilates slowly during the presence of the adapting light. This dilation of the pupil is accompanied by an increase in the sensitivity of retinal receptors to effect pupillary contraction to pulse stimuli. When the adapting stimulus is bright and the pupil correspondingly contracted the presentation of a pulse does not elicit a further contraction of the pupil. The presentation of the identical pulse 60 seconds later with the adapting light still on results in a substantial contraction. In darkness, following light adaptation, the effectiveness of the pulse stimulus to elicit a contraction is a direct function of the intensity of the preceding adapting light.
It is not argued that the sensitivity of the retina with respect to pupillary reactivity is identical with its sensitivity with respect to visual functions, but rather that these processes seem to follow parallel courses.

Bibliography


SCHEMATIC OF PROGRAMMED SEQUENCE IN THE EXPERIMENTAL RUN

Fig. 1

Fig. 2
Fig. 3

PUPILLARY CONTRACTION DURING FIRST 10 SECONDS OF LIGHT ADAPTATION

Fig. 4

REACTIONS TO HIGH LUMINANCE PULSES IN EARLY ADAPTATION PERIOD