The Dependence of the Photopupil

Response on Flash Duration and Intensity

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ABSTRACT   The changes in pupil size were recorded by infrared pupillo-
graphic methods in response to light flashes of different durations and inten-
sities for a 13 degree 34 minute centrally fixated circular field. For such stimuli,
the threshold intensities for (rod) vision and for the pupil response were found
to be about the same. The response amplitudes were related to the logarithm
of the flash energy, the reciprocity law remaining valid up to about one-half
second. The curve relating flash energy and pupil response was clearly divisible
into two parts commensurate with the duplex character of the human retina.
A similar dichotomy appears in curves relating response amplitude to response
latency. Since the pupil response is determined by total flash energy, intense
long flashes produce larger pupil responses than shorter (and perceptually
brighter) ones of the same intensity.

INTRODUCTION

Light incident on the human retina results both in vision and a reduction in
the size of the pupil. There are many similarities in these two different con-
sequences of retinal excitation. For example, the directional sensitivity of
certain pupillomotor photoreceptors is quite like that of the "visual" cones
(Alpern and Benson, 1953). Furthermore, the dark adaptation curves of the
visual cones and of the "pupillomotor" cones have an identical time course
(Alpern, Kitai, and Isaacson, 1959). Finally, the visual photoreceptors and
the "pupil" photoreceptors have essentially the same spectral sensitivities
(Alpern and Campbell, 1962).

   In the present series of experiments we have attempted to see how the
amplitude of the pupil response changes as the energy of the incident light
is varied. Rectangular light pulses with different intensities and durations
have been used. Such experiments are important not only for what they have
to say about the photokinetics of the pupil light reflex. The intensity factor
in vision is much less easily quantified than other visual characteristics (e.g.
directional and spectral sensitivities, dark and light adaptation, etc.). Be-

cause of the similarities of many of the retinal processes both in vision and photopupillary motility, statements as to how the amplitude of the pupil response increases with increased light intensity may help also to provide insights into the physiology of perceived brightness.

METHOD

Experiments were carried out in seven young males using the method of infrared pupillography already described (Alpern *et al.*, 1959).
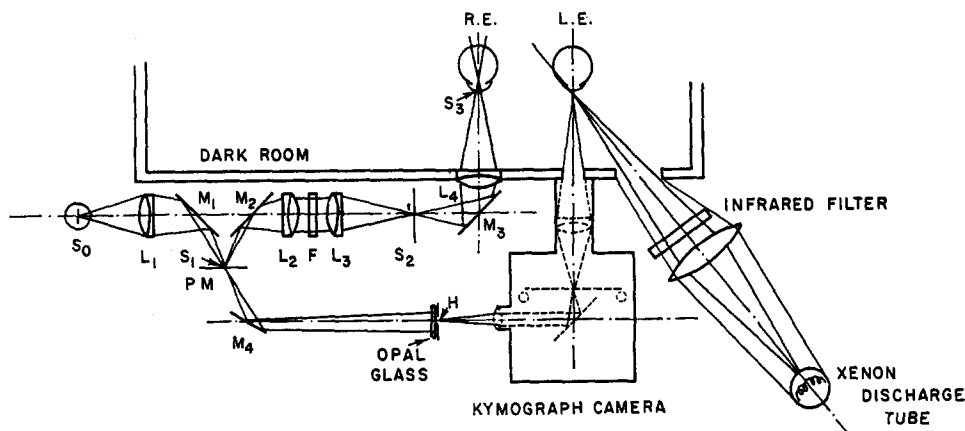

FIGURE 1.   Schematic diagram of the apparatus.

The arrangement is illustrated in Fig. 1. The tungsten ribbon filament (S_0) was imaged in three planes $(S_1, S_2,$ and $S_3)$ by a lens relay system $(L_1, L_2, L_3,$ and $L_4)$. This provided a Maxwellian view optical system having a 13 degree 34 minute circular field centered along the line of sight of the right eye. The image of the aperture stop (S_2) in the plane of the entrance pupil of the right eye was smaller than the smallest natural pupil size and in this way fluctuations of the latter had no influence on the intensity of retinal illuminance. Between lenses L_1 and L_2 the optical path was diverted by mirror M_1, reflected by mirror PM, and again by mirror M_2.

The mirror PM was mounted on a bob at the end of a vertical free swinging pendulum rod about 1 ft in length. The stimulus light reached the eye only when some part of this mirror intercepted the filament image S_1. The duration of exposure of the stimulus was varied by changing: (a) the height at which the bob was held at the moment of its release and (b) the width of the pendulum mirror PM. Two different sizes of mirrors were used. This method gave virtually rectangular light flashes with durations from 4 to 150 msec. In a few experiments the flash duration was prolonged up to 7.5 seconds. For such experiments, the longest flashes could be regulated manually, and intermediate durations were obtained by an electromagnetic shutter triggered by a pulse generator.

The intensity of the flash was varied by placing Wratten No. 96 filters (cemented in

B glass) in the collimated light beam between lenses L_2 and L_3. The intensity of retinal illuminance varied from 7.03×10^{-3} to 7.03×10^5 trolands.

A Grass model C_4 kymograph camera photographed the iris of the observer's left eye. During photography the camera shutter was left open and the film moved continuously at a speed of 250 mm/sec. Every time the film advanced three-fourths of an inch the camera triggered a General Electric Ft. 220 xenon flash tube (General Radio Company strobolume 1532-c). Light from this tube illuminated the anterior segment of the left eye after passing through a Wratten No. 89B infrared filter. High speed infrared film (HIR-4-21) was used to obtain pictures of this eye every 76 msec.

In order to get a record of the stimulus on the film the light from S_0 was reflected to illuminate a piece of opal glass directly behind the pinhole H, whenever the pendulum mirror PM did not intercept the image of the filament at S_1. This pinhole was imaged on the film alongside the picture of the observer's eye. As the pendulum mirror intercepted the film image it also occluded the light illuminating the pinhole H and the line on the film made by the image of H was interrupted for exactly the duration of the stimulus flash.

Each observer was dark-adapted for 30 minutes before measurements were made. Only one intensity of stimulus light was used for any given experimental session. A sufficient time interval (at least 3 minutes) was always allowed between flashes to permit full recovery of dark adaptation.

To obtain a dark adaptation curve a calibrated neutral wedge was mounted in the stimulus beam just before the aperture S_2. Just behind this aperture was mounted an episcotister attached to a synchronous clock motor. This provided 50 msec. test flashes once a second. The subject adjusted the wedge for threshold visibility at various time intervals in the dark while fixating the center of the field.

RESULTS

Quantification of the changes which the pupillograph records can be done in one of several different ways and there is not very much evidence available to allow an *a priori* prediction as to the response criterion most closely related to physiological changes in the iris muscles. Moreover, there were no obvious differences in the inferences one could make with variation of intensity and duration of light flashes when the criterion was (a) change in pupil area, (b) change in pupil diameter, (c) the percentage changes of either of these, or even (d) an estimate of the work done by the muscles based on reasonable assumptions as to their mechanical attachments. Since the change in diameter of the pupil is directly proportional to the change in length of the muscle, it has been used as the measure of response.

(a) Reciprocity of Duration and Intensity

Typical pupillographs which illustrate the responses to light flashes of different intensities and durations are given in Fig. 2. Increasing either the duration or the intensity of the light is associated with a shorter latent period and

a larger change in pupil size. The curves are so arranged that the amount of energy in the stimulus flash is about the same for responses illustrated along diagonal lines from the upper left to the lower right. Flashes of light with about the same amount of energy produce about the same amount of change in pupil size. This was an invariable finding in experiments of this kind and it emphasizes the fact that between 5 and 150 msec. the reciprocity law (intensity × time = constant) remains valid for the photopupil response.
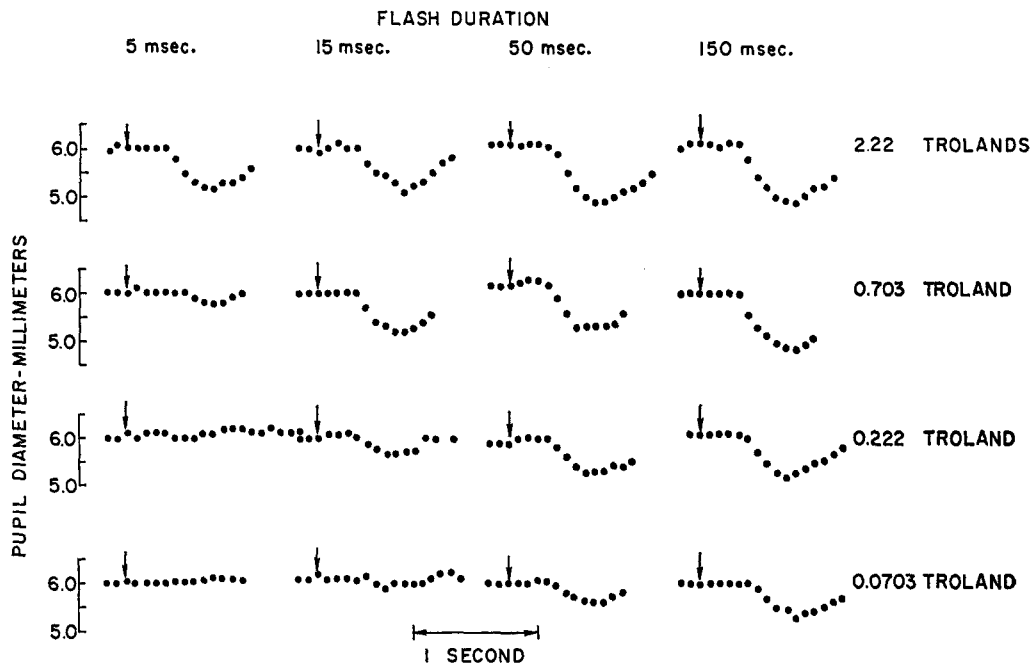

FIGURE 2. Pupillographs for W. S. at four different illuminance levels and flash durations. The curves are so placed that responses to a nearly constant product of intensity and duration are arranged along diagonals from the upper left to the lower right of the figure. These responses are approximately constant for any given level. Note the extent of "spontaneous variation" in pupil diameter.

Fig. 3 substantiates this conclusion in a different way. In this figure are plotted the intensities and durations of stimulus flashes required to produce a constant criterion response (1.0 mm change in pupil size). These data were interpolated from the results in the following way: for each flash duration the relation between pupil response and intensity was plotted and from these curves the intensity required to produce the criterion response could be read off the curve. The line is drawn through the points in Fig. 3 according to the reciprocity law.

While the same result is obtained independent of the response criterion

employed, the validity of reciprocity becomes progressively harder to prove by this method for the larger criteria without estimating the responses to shorter flashes by extrapolation. Since it is important to be certain that increasing the intensity of the light stimulus does not significantly alter the relations illustrated in Figs. 2 and 3, a supplementary experiment was carried out at a level sufficiently bright to produce about 2.0 mm change in pupil size. The size of the response was measured for a variety of different flash durations with intensities so selected that the product of intensity and dura-
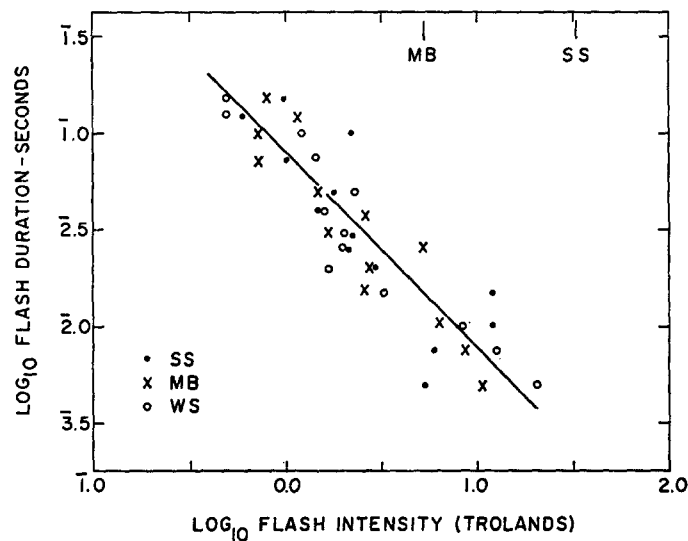

Figure 3.   The relation between flash duration and flash intensity required to produce a 1.0 mm change in pupil diameter for three observers. The abscissa scale is correctly positioned for W. S. but shifted laterally for the other two observers. The vertical lines at the top of the figure indicate the extent of these shifts by marking the correct positions for 100 trolands in these other two cases. The line drawn through the empirical points has unit slope and is the theoretical prediction of the reciprocity law.

tion remained essentially the same. In all, the experiment was repeated ten times on separate days. The results are tabulated in Table I and verify the fact that reciprocity holds for energies of the light at least as large as $\log_{10}$ troland seconds = 3.2.

These experiments prove that pupil responses to constant light energy ($I \times t$) are constant for different observers (Fig. 3), for different response criteria (Fig. 2, Table I), and for flashes at least as long as 150 msec. What is the critical duration?

The dark-adapted observer was exposed to various durations and intensities of light flashes which were so selected that their energies were always about the same. A more or less typical experimental result is illustrated in

Fig. 4. It is clear that there are no systematic deviations from the reciprocity law, at this level, for flashes shorter than about 0.6 second. Longer flashes appear to produce progressively smaller responses. Presumably this is because the event in the response studied in the experiment (*i.e.* appearance of the smallest pupil size) occurs at a given time after the onset of the stimulus. Clearly, that part of a long flash which occurs after the reaction time for this event cannot influence the response (Hartline, 1934; Talbot, 1938).
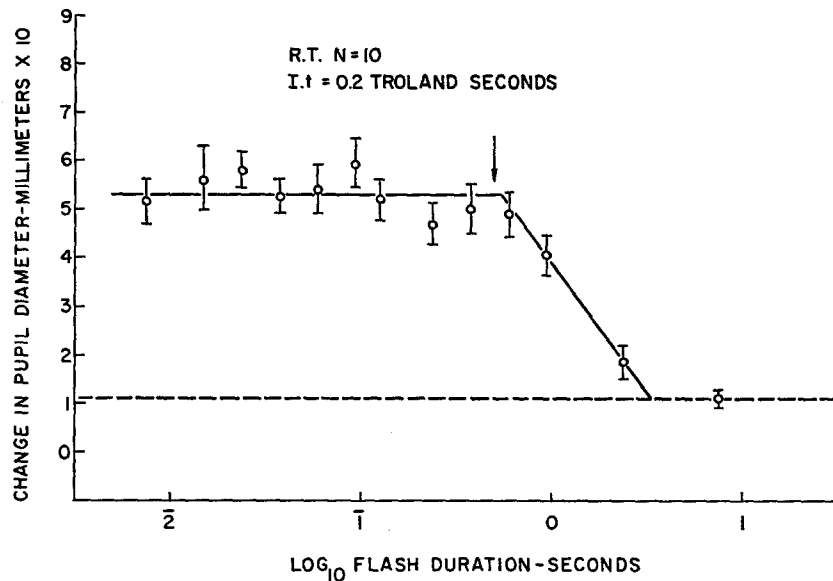

FIGURE 4. The means ± standard errors of the means of the responses to flashes of different durations with intensities so selected that the flash energy was constant at about 0.2 troland second. Observer R. T.—ten repetitions at each duration. The solid straight horizontal line is what is to be expected as long as the reciprocity law remains valid. The response to the longest flash is about the same as the spontaneous variation in pupil diameter in the dark (shown by the dashed line) for this observer. The arrow indicates the critical interval at threshold predicted by the latent period data of W. S. (Fig. 7). Note that there is no systematic deviation from reciprocity below about 0.59 second.

(*b*) *Response Amplitude Energy Relation*

The way pupil response changes with change in the energy of the stimulus light is illustrated in Fig. 5. All the data in this figure are for flash durations ≤ 150 msec. The longest flash is at least 30 msec. less than the shortest latent period recorded.

An outstanding characteristic of psychophysical measurements of vision (visual acuity, dark adaptation, critical flicker frequency, brightness discrimination) is the way in which the curves relating such measurements to the logarithm of the light intensity are divisible into two distinctly different

TABLE I

PUPIL RESPONSES TO CONSTANT ENERGY FLASHES
OF DIFFERENT DURATIONS

(T.P.; N = 10)

Flash duration	Flash intensity	Flash energy	Mean response ± SEM
sec.	*trolands*	*troland sec.*	*millimeters*
0.0074	222,000	1,640	2.02±0.042
0.0150	112,000	1,680	1.95±0.062
0.0234	70,300	1,645	2.00±0.066
0.0375	44,400	1,660	2.02±0.122
0.0600	28,200	1,690	1.96±0.073
0.0940	17,700	1,660	2.01±0.062
0.1330	11,200	1,490	2.00±0.042
0.2340	7,030	1,645	1.97±0.117

parts. Hecht (1937) emphasized the importance of this observation in terms of the duplex character of the vertebrate retina. The data in Fig. 5 are noteworthy because they are a demonstration of the same result for the pupil response to brief flashes of light.

Under the stimulus conditions of this experiment, the threshold pupil response occurs at about 0.0003 troland second. The change in pupil size evoked by a suprathreshold flash increases approximately linearly with the logarithm of the amount of light over about 3.0 $\log_{10}$ units. In this range a
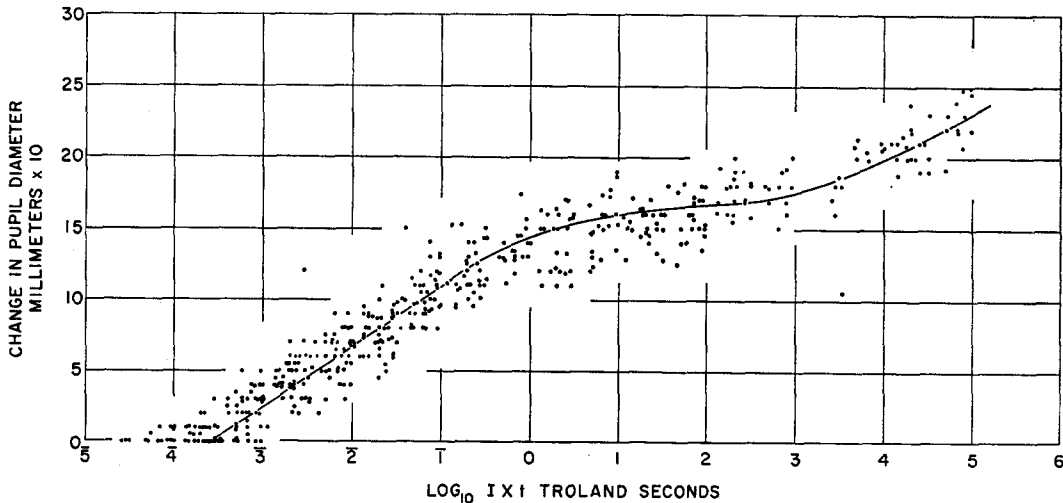

FIGURE 5. The relation between the amplitude of the pupil response and the energy of the stimulus light (W. S.). The smooth curve has been drawn arbitrarily to show the trends. All flashes are between 4 and 150 msec. long.

tenfold increase of the energy of the flash is associated with about 0.42 mm increase in the amplitude of response.

Further increases in energy after this are associated with progressively smaller increases in response until about 100 troland seconds when the curve becomes almost flat. Increasing the flash energy still further, however, is again associated with increased amplitudes of responses. It seems as though the pupil response is again increasing linearly with the logarithm of the flash energy. Extrapolation for higher flash energies is dangerous, but quasi steady-state measurements (Flamant, 1948) suggest that the curve does become linear before a final plateau is reached.

(c) Relation to Psychophysical Responses

In order to relate the curve in Fig. 5 to aspects of retinal excitation which give rise to vision, the dark adaptation curve for the same test arrangement has been measured psychophysically.

A typical curve obtained in this way is presented in Fig. 6. The horizontal line drawn on this graph illustrates the level of the pupillary threshold as obtained from Fig. 5. The absolute visual (rod) threshold is not significantly below the pupil threshold as Schweitzer (1956) claimed for areas of this size nor is it true that the pupil threshold and the cone threshold coincide as de Launay (1949) maintained. Rather, the rod threshold and the pupil threshold agree reasonably well within the precision of the measurements. The difference between this result and that of the earlier investigators is undoubtedly to be related to the different characteristics of the stimulus flashes used, but the present finding is unequivocal evidence against the hypothesis (Talbot, 1938; de Launay, 1949; Harms, 1949) that only excitation of the cones can produce a contraction of the pupil. In fact, in this experiment pupillary responses are evoked by flashes of light with less than one-hundredth of the energy of the least amount of light which can excite the cones.

(d) Latent Period

The data in Fig. 2 show a progressive decrement of latent period with increase in flash intensity or duration and in fact it is possible to specify such a relation in a quantitative way. However, a better understanding of the latent period process is afforded by plotting the reciprocal of the latent period as a function of amplitude of the response (Fig. 7). It is clear from this figure that the results are again easily divided into two distinct parts, each showing a fairly reasonable linear relation between reciprocal of the latent period and amplitude of the response. It should be pointed out that the two lines intersect at a response amplitude of 1.2 mm which is about the level at which the curve in Fig. 5 begins to depart from a straight line, although this level is about 10 times as high as the absolute threshold for the cones.

A second feature of the results illustrated in Fig. 7 is the fact that the extrapolation to the latent period reciprocal for a zero amplitude response does not pass through zero. This is a somewhat surprising result since it implies that as the response amplitude approaches zero the latent period does not approach infinity as might be expected. Apparently there is some limiting
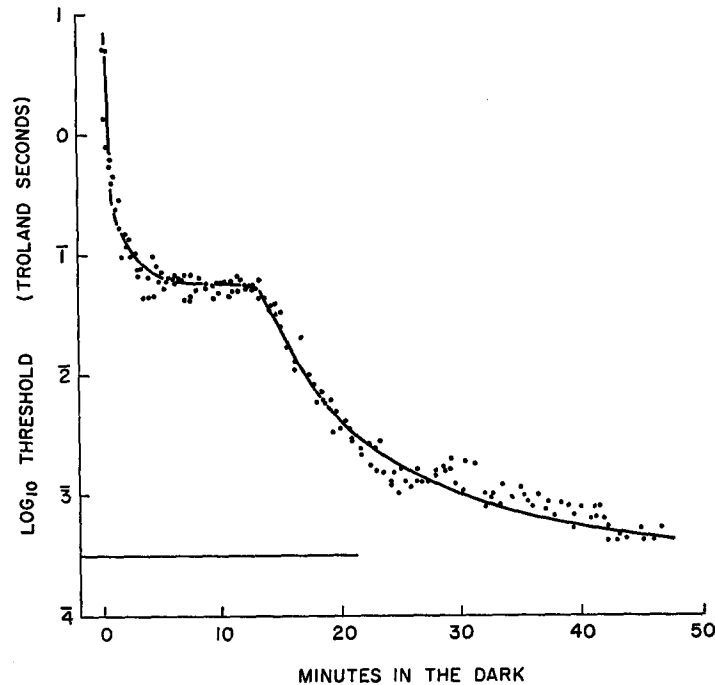

FIGURE 6. The dark adaptation curve measured psychophysically using the same stimulus field with which the pupillographic data were obtained. The subject dark-adapted for 5 minutes, then light-adapted to a large (about 50°) field of luminance 5610 foot-lamberts prior to the beginning of the experiment. The abscissa shows time in the dark after this adapting light was viewed with natural pupils for 7 minutes. The plotted points are from two successive experimental runs on separate days. Observer D. M. The horizontal line shows the level of the pupil threshold from Fig. 5.

value to the latent period such that if a given amount of excitation has not occurred within it, the response cannot occur at all. Thus the latent period data predict that for threshold, the pupil response has a critical interval of about 0.5 second. This is almost precisely the critical duration of the stimulus obtained slightly above threshold in the experiment illustrated in Fig. 4. Since the ways in which these independent estimates of the stimulus critical duration were obtained are so different, the agreement between them seems noteworthy.

DISCUSSION

One outcome of the present set of experiments is the clear demonstration that the curve relating change in pupil size and stimulus energy is divisible
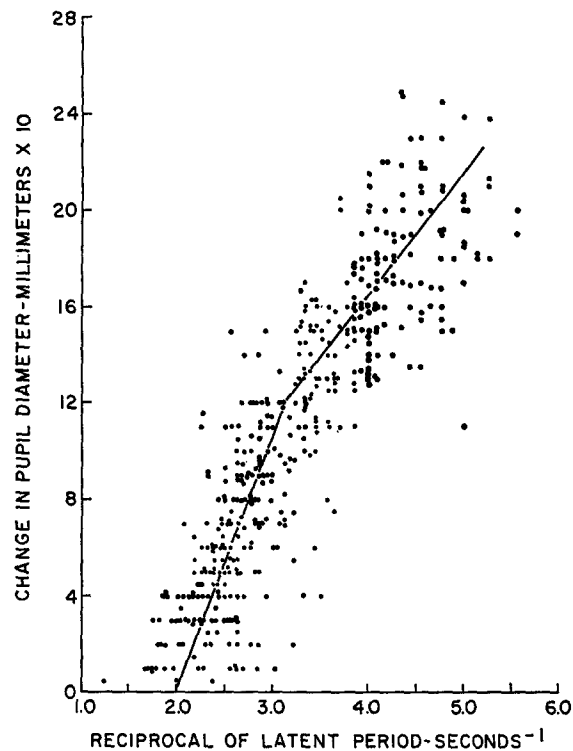

FIGURE 7. The relation between latent periods of the responses and their amplitudes. These responses are the same ones illustrated in Fig. 5. Note that the extrapolated latent period for zero response is not infinitely large but about 0.5 second. The latent period was determined by drawing a horizontal straight line through the pupillographic data at the time of onset of the light and a sloping straight line through the linear part of the pupillographic curve after the pupil size had obviously begun to decrease. The time interval between the onset of the stimulus and the point of intersection of these two lines was taken as the measurement of the latent period.

into two parts. This is different from the S-shaped curves usually drawn following the pioneer experiments of Reeves (1918). Flamant (1948) studied the size of the pupil of thirty-seven subjects under conditions of normal vision out-of-doors; that is, with the subject viewing the sky during the evening as the light was failing. Her curves also show a discontinuity at intermediate light levels but it remains a question of whether this discontinuity was due to artifacts related to variation in the time of day (Le Grand, 1948), or to

more complex adaptation effects with natural pupils rather than to variation in the retinal illuminance *per se*. The present conditions rule such artifacts out in so far as the responses to flashes are concerned and it is unlikely that the matter is very different in the case of responses to steady-state stimuli (Alpern, Falls, and Lee, 1960; Alpern and Campbell, 1962).

To what are the two different curves in Fig. 5 to be attributed? It is almost axiomatic following Hecht (1937) to say that they are reflections of the duplex photoreceptor character of the human retina. Any other explanation is, in fact, quite unlikely but the inference only becomes convincing after consideration of additional evidence. The evidence is of two types: (a) The demonstration that the pupillary threshold and the rod threshold virtually coincide (Fig. 6) and that the cone threshold occurs before the inflection in the re-response *vs.* log *It* curve. (b) The spectrum analysis which demonstrated that the low intensity part of this curve has the action spectrum of rods while the high intensity part of this curve has the action spectrum in which the ordinate (on a logarithmic scale) is determined by the weighted mean of the logarithms of the rod and cone sensitivities at each wave length (Alpern and Campbell, 1962).

In Fig. 5 the cone threshold is exceeded at a level where no detectable change in the form of the curve is to be observed. Presumably this is due to the fact that although there are cones now responding they are much less numerous than the rods. Since the pupil lacks the facility (characteristic of vision) of differentiating between focal and non-focal light, any slight contribution of the cones to the response is effectively obscured by the rod contribution at these low light levels. Detectable cone effects on the pupil response only first appear about one $\log_{10}$ unit higher than the cone threshold. At this point, Fig. 5 begins to depart from linearity and the slope of the line relating latent period reciprocal and pupil response (Fig. 7) suddenly changes.

The way in which the intermediate part of Fig. 5 is produced, presumably by some complex interaction of rod and cone contributions, is still not clear. The question is central to the problem of the transition from scotopic to mescopic vision and its understanding may well be furthered more by psychophysical than it will by pupillographic experiments. At the moment it is evident only that in this range two processes are probably important: (a) a reduction in the size of the increments of the response produced by rods above about 1 troland second, and (b) a greatly increased contribution from the cones above about 1000 troland seconds. Neither full bleaching of the rhodopsin in focal rods (Rushton, 1961) nor their saturation (in the manner of Aguilar and Stiles, 1954) can account for the first of these changes. The light level is much too low (Campbell and Rushton, 1955; Fuortes, Gunkel, and Rushton, 1961).

It might be inferred that the two lines drawn through the latent period

data (Fig. 7) represent a separation of the latent periods of rod and cone responses. Since the action spectrum data prove that none of the responses is exclusively determined by cones, the statement that the intersection of the lines in this figure represents the transition from latent periods determined by rods to those determined by cones, must mean that the latent period is determined by the fastest receptor system and that for responses larger than 1.2 mm, cones are much quicker in responding than are rods.

The present results show that in two important ways photopupillary and psychophysical results of retinal excitation are strikingly different. First, the critical stimulus duration for pupil response (0.5 to 0.6 second) is much longer than is the case for vision under comparable stimulus conditions (0.027 to 0.06 second) (Brindley, 1960; Talbot, 1938). Because the pupil attains a minimum diameter in less than a second after onset of the flash, however, the critical duration for a criterion minimum diameter is much shorter than that imposed by rhodopsin kinetics (Campbell and Rushton, 1955). Second, when the flashes are sufficiently intense, longer (150 msec.) flashes of equal luminance are less effective than shorter ones (50 msec.) in brightness-matching experiments (Broca and Sulzer, 1902; Alpern, 1963). However, as a corollary of the first difference, the longest flashes evoke the largest pupil responses. The increased brightness of 50 msec. flashes is not associated with an increased ability to constrict the pupil when compared to the longer (and subjectively dimmer) flash.

It might be imagined that the differences between vision and photopupil activity just described might in some way be related to the slow time characteristics of the pupil responses. For example, it is known that intermittent light at high intensity can be seen to flicker at rates above 60 cycle/sec., but movements of the pupil no longer continue to follow alternations much above 3 cycle/sec. (Stark and Sherman, 1957). The differences between vision and pupil response, enumerated above, differ from those in this last example, however, in that the comparison between different durations here is made between motor responses which are not essentially different from each other in time characteristics. Indeed the essence of the critical duration results is that the response produced by a long flash is the same as that produced by a short one of the same total energy for time values in which the brightness-detecting system no longer continues to integrate intensity and duration (Brindley, 1960, p. 185). Suppose, however, that if the mechanism underlying brightness judgments is much less sluggish than is the system underlying control of the pupil responses, it might well be capable of displaying transients in retinal output to which the pupil control systems were insensitive. The "sluggishness" postulated here implies one not due to time characteristics of the muscles themselves but of the control system to the muscles.

The following experiment strongly suggests that this interpretation cannot

be the explanation for the differences between vision and pupil responses obtained in the present experiments. Clynes (1962) found that the pupil control system can detect a (non-gradual) change ". . . in the frequency of light [flashes] of constant intensity from 30 cycles to 15 cycles say and can react to this with a single contraction and redilation response, although no intensity change is perceptible to vision." This means that the pupil control system is capable of responding to transients in retinal output to which mechanisms underlying brightness judgments are insensitive. Moreover, the durations of these stimuli are precisely within the range (*i.e.* 33 to 66 msec.) that would be needed for the pupil to show a Broca-Sulzer effect. The fact that it does not do so, therefore, cannot be attributed to sluggishness in the pupil control system. In the Broca and Sulzer experiment the information utilized by the control system of the pupil must be very different indeed from that utilized by the system underlying brightness judgments.

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