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THE ABSOLUTE THRESHOLD FOR VISION IN THE CAT

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In recent investigations of vision in animals the methods of electrophysiology have proved an invaluable tool for the elucidation of functions of the visual apparatus. Action potentials in optic nerve fibres, as well as electro-retinograms, have been employed to this end; so that we now have a body of accurate and objective information regarding the capacities of the animal's peripheral visual system.

Much of this information has been obtained by taking as an index of retinal sensitivity the relative energy in different parts of the spectrum necessary to produce a constant physiological effect, such as the height of the *b*-wave of the retinogram (Chaffee & Hampson, 1924), or a constant retinal potential (Graham & Riggs, 1935), or a constant number of optic nerve impulses (Graham & Hartline, 1935).

By plotting sensitivity as the reciprocal of the amount of light energy necessary to produce a threshold response (or any other constant response) against wave-length, luminosity curves for various animals under different conditions of adaptation have been obtained. These curves, which describe the sensitivity of the eye to lights of various wave-length show, in most cases, fairly good agreement with the spectral distribution of sensitivity of the human eye obtained by subjective methods under similar conditions of adaptation. It is reasonable to suggest that the luminosity curve as a psychophysical function corresponds to a reaction of the retina, which manifests itself as a measurable electrical response. This quantitative electrical response has often been assumed to be the likely physiological basis of the sensation of brightness, so that, on this assumption, a constant retinal potential can be taken as a measure of the sensitivity of the retina to lights of different wave-length. This method has been widely used as a means of investigating colour vision. From the point of view of physiology, however, we are merely dealing with the spectral distribution of sensitivity under various conditions of adaptation, while properties of colour, such as brightness and hue, are purely psychological concepts, a quantitative estimation of which can only be obtained by considering the reaction of the living animal to various spectral stimuli, and it would be of interest to compare the data obtained by this method with those obtained by means of electrophysiology.

Employing the method of behavioural discrimination, the present author has undertaken a series of investigations into the question of colour vision in the cat, an animal for which a reliable body of information has already been obtained by electro-physiological and other methods.

The experiment reported in this paper was designed as a preliminary step in this direction, and was intended to supply information as to the limits of the animal's absolute retinal sensitivity. In this case the minimal amount of white light which the animal is capable of discriminating from darkness, under conditions of complete dark-adaptation, has been taken as an index of the absolute threshold.

METHOD

Discrimination apparatus

The apparatus used was a Y-shaped discrimination box; its dimensions are given on the general plan in Fig. 1. The dark-adapted animal was released from the restraining chamber, *R*; pushed open door D_1; and faced doors D_2, which were hinged on either arm of the box. In the middle of these doors was a 3 × 3 in. milk glass panel, one of which (the positive stimulus) was illuminated from behind by white light from the light box *L*. The stimulus panel on the other door remained dark. A glass partition, *G*, which separated one stimulus panel from the other, was found useful during the initial stages of training by increasing the time needed by the animal to obtain its food behind the positive stimulus, once it had made the wrong choice and had gone to the non-illuminated door. The whole box was painted flat black inside. Removable covers could be fitted light-tight over all sections of the apparatus.

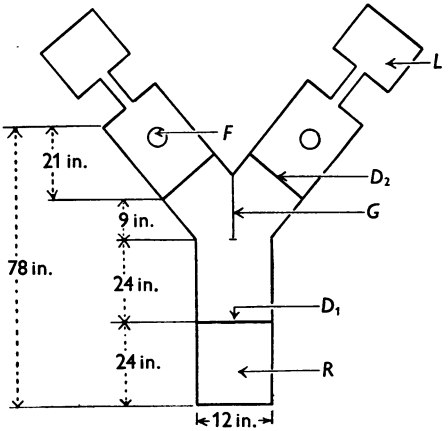

Fig. 1. Ground plan for discrimination box. *L*, light box; *F*, food; D_1, hinged door; D_2, hinged door with 3 × 3 in. opal glass panel; *G*, glass partition; *R*, Restraining chamber. The box is 13 in. high.

Controls

(1) *Olfactory.* To equalize the olfactory stimuli, dishes containing milk were placed behind both doors, but only the one behind the door bearing the positive stimulus was accessible to the animal.

(2) *Switches.* In order to avoid conditioning the animals to the click of the contacts when changing the light stimuli, Mutac silent switches were employed.

(3) *Prevention of light-adaptation.* In order to avoid light-adaptation while the animal was eating its reward, the doors were wired in such a way as to cut out the stimulus light as soon as the animal opened them.

(4) *Test of light-tightness of box.* To test whether light, unobservable by the experimenter, could enter the box from the outside, or whether the light providing the positive stimulus could penetrate between the sides of the stimulus door D_2, and the sides of the box, the whole of the apparatus in front of the doors D_2 was laid out with bromide paper, the stimulus panels were blacked out with various layers of black paper, and the lids were placed over the box. Both light boxes were switched on, and the whole of the apparatus illuminated from the outside, both from above and below, by four 1000 W. lamps for 24 hr. When the bromide paper was developed, no traces of fogging were shown.

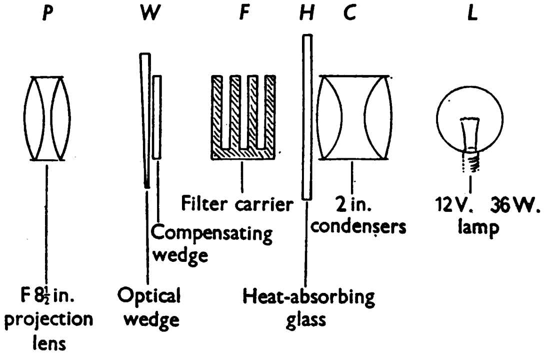

Fig. 2. Plan of optical system.

(5) *Test experiments.* To test for the absence of secondary clues, experiments were done both with stimulus intensities of below threshold value and with absence of illumination on both stimulus panels. Completely random responses by the animal to these tests revealed that the cats were responding to the light stimulus, and not to any other clues.

Optical system

A line-drawing of the optical system is shown in Fig. 2. The light from lamp *L* is focused at the condenser lens *C*. From here it passes through heat-absorbing glass *H* (Chance O.N. 20), and its intensity is reduced by means of one or more Ilford neutral tint filters, *F*. An optical wedge with compensator, *W*, can be adjusted to give the required further small changes in intensity. The projector lens *P* forms an image of the condenser lens on the stimulus panel of the discrimination box.

Control of voltage across the light source

The current was supplied by 230 V., 50 cycles, a.c. mains and passed through a constant voltage transformer which reduced the normal (10%) a.c. mains fluctuations to voltage fluctuations of 0·5%. The current was then fed into a step-down transformer. To ensure that the lamps were at all times run at their rated value, a voltmeter was put across the lamp-circuit, and by means of an adjustable rheostat, the voltage was kept constant at 12 V. Fig. 3 shows an outline of this arrangement.

Procedure

Six animals (four females, two males) were used in this experiment, and were trained to discriminate between white light of high brightness and colour temperature 2950–3100° K. (the positive stimulus) and darkness (the negative stimulus). According to a predetermined random order, either glass panel was illuminated and the animal had to show its ability to discriminate by opening the door containing the positive stimulus, where it obtained milk. No punishment was given for the wrong choice. A correct response in twenty-five successive trials was taken as the criterion for learning and was reached by all cats from between 110 and 250 trials (Table 1). As soon as the animals were trained to the high intensity level used during training, the brightness of the positive stimulus was decreased to a suitable low level by means of Ilford neutral tint filters and the experiment began.

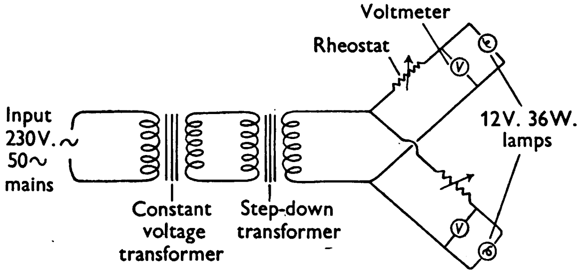

Fig. 3. Control of voltage.

All animals were completely dark-adapted for 1 hr. before the experiment, which was run in a dark room, with the stimulus panels as the only source of illumination.

TABLE 1. Number of trials required by six cats to learn the discrimination of light versus darkness.

Cat	Luminance of positive stimulus during training (f.c.)	No. of trials required
1	80	110
2	80	125
3	40	250
4	40	160
5	10	150
6	10	180

This table shows that between 110 and 250 trials were necessary to establish the response to light in all animals. The data also show that the magnitude of the intensity of the light stimulus does not seem to be a significant factor in the process of learning the discrimination.

The intensity of the stimulus was measured by means of an Autophotometer (Everett Edgcumbe) which was periodically checked against an N.P.L. standard source. The intensity was decreased in gradual steps by means of calibrated wedges and neutral filters, until the animal, by giving random responses, showed that it could no longer distinguish between the illuminated and the dark stimulus panel. No limit was given to the exposure time. The panel remained illuminated at one particular intensity level until the animal had made its choice. The animal was given twenty runs at each intensity level, and each experimental session required sixty runs a day, i.e. three intensity levels were explored daily. Before experiments on a new intensity level were started, the animal was re-tested at the intensity at which it had previously given a 100% correct response, so that, in fact, each new session consisted of (i) a pre-test, and (ii) the crucial experiment. In order to avoid the interference of the experiment with the test, the data for the near-threshold responses were collected by interspersing the crucial test intensity with an intensity to which the animals had consistently responded positively at previous experiments, so that the twenty test results were collected from approximately forty trials. By this method a state of high motivation was maintained and a situation of mental stress avoided, because a negative, non-rewarded difficult choice was soon followed by a positive and well-rewarded one.

The animals were kept under normal living conditions and allowed to eat as much as they liked after the day's experiments.

RESULTS

In order to make the present results comparable with similar data presented by other workers, the 80% level of correct response to the positive stimulus has been chosen as the criterion of successful discrimination. On this basis the threshold values obtained ranged from $6{\cdot}32 \times 10^{-8}$ mL. to $12{\cdot}21 \times 10^{-8}$ mL. within the population studied. The arithmetic mean of these values is $9{\cdot}92 \times 10^{-8}$ mL., with a standard error of $\pm 0{\cdot}92 \times 10^{-8}$ mL.

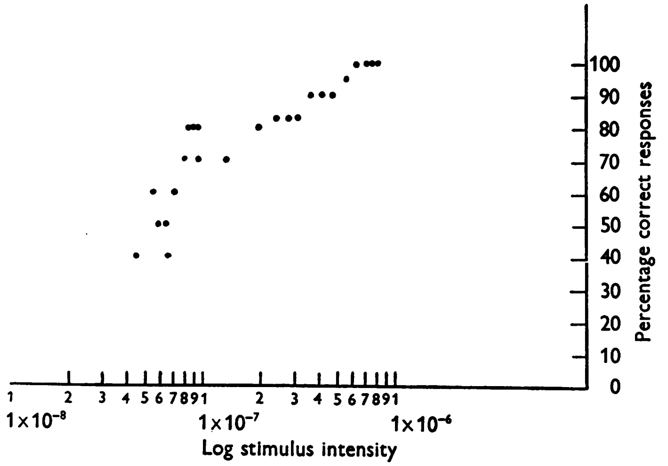

Fig. 4. Points represent the number of correct responses in 10 trials by one animal, chosen at random.

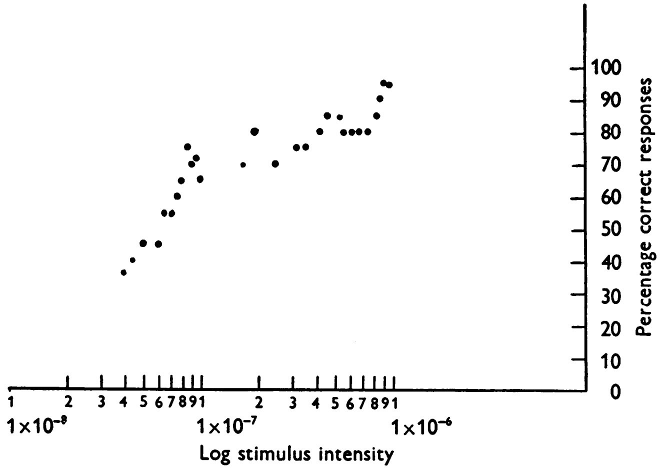

Fig. 5. Points represent average results for 5 series of trials for one cat.

In order to get some idea of the variations around the threshold, all animals were re-tested at frequent intervals, and it was interesting to note the day-to-day fluctuations of the threshold values. However, these oscillations were strikingly similar in the same animal when tested twice on the same day with 1 hr. interval between them.

Human thresholds. Under the conditions described above, the absolute threshold for two human observers was determined and the same computation was applied to the aggregate data. It was found that the 80% level of correct response to the positive stimulus corresponded to a mean intensity value of $5{\cdot}47 \times 10^{-7}$ mL. with a standard error of $\pm 0{\cdot}37 \times 10^{-7}$ mL.

The transition from 'seeing' at one brightness level to 'not seeing' at a level one-half of a log unit below, was found to be very abrupt.

DISCUSSION

Bridgeman & Smith (1942) found the absolute threshold of six cats to white light to lie between $5{\cdot}8 \times 10^{-8}$ and $2{\cdot}4 \times 10^{-7}$ mL. with an average value of $8{\cdot}2 \times 10^{-8}$ mL. They, however, were using a different method. Their animals were trained to press a lever when a glass panel was illuminated. They received a slight electric shock if they responded when no light was presented. This method seems to produce a sharper point of transition from 'seeing' to 'not seeing'. In view of the differences in experimental method the values obtained by the present writer are not strictly comparable to those given by these investigators, who, unfortunately, do not state a measure of reliability attaching to their estimate. In spite of these differences in procedure, their mean value falls just outside the limits covered by the writer's standard error.

When their criterion of choosing as the threshold the lowest brightness level to which the animal responded correctly with a score of 80% in any series of twenty trials, and ignoring all other responses of the animal to the same and other brightness levels, was applied to the present data, it was found that the actual values thus obtained were comparable to those found by Bridgeman & Smith (1942). It is interesting to note, however, that the threshold values for two human observers obtained by these workers under the same conditions as for the cats was found to be $5{\cdot}8 \times 10^{-7}$ mL., i.e. the human threshold was higher by a factor of 7 as compared with that found for the cats.

Comparing the human threshold value obtained by the author to that found for his cats, it will be seen that their absolute threshold is lower by a factor of almost 6.

Hecht & Pirenne (1940), working on the owl, and taking the minimal observable pupil contraction in response to green light as their criterion, report an absolute threshold of $1{\cdot}5 \times 10^{-7}$ mL. Their own threshold measured by the same criterion under the same conditions is stated as approximately $4{\cdot}0 \times 10^{-7}$ mL.

The most representative value for the human threshold, as cited by Bridgeman (1938) in his survey of the literature, is given as $5{\cdot}8 \times 10^{-7}$ mL.

Mead (1942) reports an absolute lower threshold in two of his cats of approximately $1{\cdot}3 \times 10^{-7}$ ml. His method was essentially similar to that of the present author. As a criterion of the absolute threshold Mead took the inability of the animal to distinguish the intensity level of the standard (brighter) stimulus from zero illumination on the negative stimulus panel. Mead's absolute threshold differs from that reported by Bridgeman (1938) for the average value of six normal cats and from that obtained by the present author by less than one log unit.

There are many factors in the cat's visual system which may contribute to a greater than human retinal sensitivity, such as, for instance, the higher rod-cone ratio and the finding of Glees (1941), who reports that in the cat 30–40 terminals are related to each geniculate cell and that there is a considerable degree of overlap. In spite of this, the relatively lower sensory threshold can be adequately accounted for by a combination of reflexion from the tapetum lucidum (Brücke-Helmholtz phenomenon) and the greater amount of light which reaches the cat's retina owing to the increased aperture of its dioptric system. A comparison of the '*f*' value (signifying speed) of the human eye with that of the cat's eye shows that the efficiency of the latter is markedly superior.

The retinal sensitivity of the human subject is, therefore, not necessarily any less than that of the cat, it may be only that the cat's dioptric mechanism is adapted for lower visual stimuli, and the work of Smith (1936) and of Mead (1942) on brightness discrimination in the cat bears out this contention.

A lower absolute threshold was vividly illustrated in the present experiment where the cat gave consistently correct responses to an illuminated stimulus panel invisible to the writer, who was as dark-adapted as the experimental animals.

SUMMARY

1. By the method of behavioural discrimination the absolute lower threshold to white light of colour temperature 2950–3100° K. was determined for six cats.

2. The threshold values at the 80% level of successful response to the positive stimulus were found to lie between $6{\cdot}32 \times 10^{-8}$ and $12{\cdot}21 \times 10^{-8}$ mL. (mean $9{\cdot}92 \times 10^{-8}$ mL. with S.E. $\pm 0{\cdot}92 \times 10^{-8}$ mL.).

3. The absolute threshold for two human observers was obtained under the same conditions as for the cats, and a value of $5{\cdot}47 \times 10^{-7}$ mL. (S.E. $\pm 0{\cdot}37 \times 10^{-7}$) computed.

4. Comparing this human threshold value to that of the cats the animals' absolute threshold is lower by a factor of almost 6.

5. As possible reasons for the low threshold in cats, an explanation is offered in terms of the greater speed of the animals' dioptric mechanism ('*f*' value) and the reflexion of the tapetum lucidum.

6. The threshold values found by the writer are compared with estimates of the minimal amount of white light perceptible by the cat as cited in the literature, and some possible reasons for the discrepancies in the results are discussed.

The writer wishes to express his thanks to his colleague Dr L. C. Thomson for many valuable discussions and to Dr Westgarth for his help with the statistical part of this investigation. Dr K. S. Bridgeman has been kind enough to make his results, contained in a thesis, accessible to the writer. The greater part of the work was carried out at the Imperial College of Science, London, and the writer wishes to express his thanks to the College authorities for putting the laboratory facilities at his disposal.

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