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THE SIZE AND SHAPE OF THE PUPIL IN LIGHTLY ANAESTHETIZED CATS AS A FUNCTION OF LUMINANCE

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Abstract—The S-shaped relation between pupil area and illumination is similar in this preparation to that of the human, with a mid-point just below 1 cd/m^2. The range of pupil areas is, however, at least 10 times greater in the cat, ranging from more than 120 mm^2 to less than 1 mm^2.

The following study of the size and shape of the cat's pupil was undertaken for two reasons. First we wanted to verify that consistent changes in pupil size with luminance occurred under the conditions of experiments in which the discharge of visual neurones is studied neurophysiologically, since the majority of retinal ganglion cells do not give signals monotonically related to mean luminance (Barlow and Levick, 1969). Second, we wished to compare the range of adjustment in the cat with that in the human, both with respect to the luminance levels at which adjustments occur and with regard to the range of pupil area in the two species. We found that the cat lightly anaesthetized with N_2O controls its pupil area in a way very similar to the human but that the cat's range of pupil areas is at least ten times greater.

The dependence of the human pupil upon illumination has been much studied, and a fairly clear picture emerges in spite of the great variability (see De Groot and Gebhard, 1952; Loewenstein and Loewenfeld, 1969). Our measurements of pupil area as well as width in N_2O-anaesthetized cats supplement and agree quite well with the measurements by Kappauf (1943) of the width of the pupil in restrained unanaesthetized cats.

METHODS

The cats were prepared in the manner customary at Berkeley for neurophysiological recording. Briefly, induction was done with Metofane, surgery under intravenous surital (thiamyl sodium), and the cat was then paralyzed with gallamine triethiodide (Flaxedil) (5 mg/Kg) and maintained on 75% N_2O, 22·5% O_2, 2·5% CO_2, with continuous infusion of Flaxedil at 7·5 mg/kg. hr and D-tubocurarine at 0·5 mg/kg–hr.

The cat's right eye, covered by a contact lens, was at the centre of a translucent plastic hemisphere about 1 m dia providing a 180°–200° field (see Fig. 1). The translucent hemisphere was surrounded by an outer cylinder of white art board which was illuminated by a set of variac controlled tungsten photoflood lamps positioned to provide uniform illumination of the outside of the hemisphere. This was achieved to within 0·3 log units, usually considerably better.

The cat's eye was observed by means of an i.r. sensitive image converter tube (RCA 1-P-25) and a lens mounted in the hemisphere. Where necessary the i.r. illumination of the eye was increased by radiation reflected from a separate source above the cat's head that focussed a filament image on a small mirror mounted on modelling clay in the hemisphere. The arrangement is indicated in Fig. 1. Observation from the position of the cat's eye revealed a uniform hemisphere of light except for the observing lens and illuminating mirror, which could be seen as a dim red glow only at the lowest luminance settings.

Light calibration

The luminance at 18 settings of the variacs that controlled the photoflood lamps was measured with a calibrated photon multiplier (Gamma Scientific 721) and an SEI visual photometer. The luminance covered a range of 9 log units. In spite of the great change in colour temperature, the difference between scotopic and photopic luminance is an unimportant fraction of this scale. In the figures SEI values are used above 2·0 log cd/m^2, scotopic Gamma 721 below 1·0 log cd/m^2, and photopic Gamma 721 in the intermediate range. The Gamma instrument is provided with a tungsten lamp for standardization and the

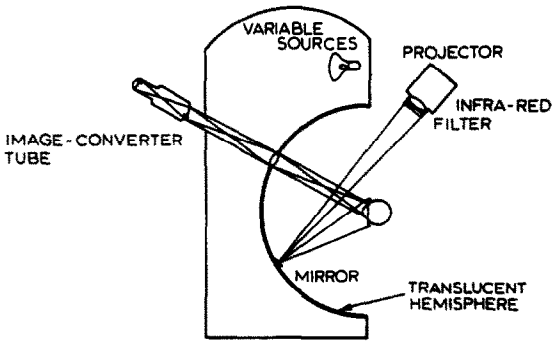

Fig. 1. Diagram of method of measuring the pupillary area. Illumination was provided by several sources controlled by variacs. At low luminances i.r. illumination was provided by the projector. Scales, placed in the plane of the pupil, were used to calibrate the image seen or photographed in the image converter tube. The angle of observation was about 15° above the visual axis of the eye (see Vakkur, Bishop and Kozak, 1963).

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scotopic and photopic measurements are obtained with screening filters. At the low colour temperatures there was little difference between scotopic and photopic values, and the SEI readings agreed well in the range of overlap.

Measurements

The measurements were made on the right eyes of four normal cats viewing the hemispheric field through both eyes. A stable pupil size was usually reached within a minute of changing luminance, somewhat longer if the luminance change was large. For these measurements we typically waited 5 min at each level, so a sequence of 19 readings from 3500 to 0 cd/m^2 occupied about 1·5 hr. Results on some animals were excluded because the pupil showed excessive unprovoked excursions and did not settle down to a stable size. It should be noted that unanaesthetized and even lightly N_2O anaesthetized cats, show very mobile pupils and dilation can readily be produced by a loud hand-clap or firm pressure on a paw. Extraneous stimuli were of course avoided during measurement.

The major and minor diameters of the pupil could be measured directly from the image convertor tube by reference to mm scales which were placed horizontally and vertically alongside the cat's eye, as nearly as possible in the plane of the pupil. In addition, the display was photographed and the negatives were projected at about 10× enlargement to permit measurements and tracings. Areas were either calculated as if the pupil was a true ellipse or measured in various ways from the tracings. No allowance has been made for the pigmented pupillary fringe, and since the viewing axis was within about 15° of the optic axis of the eye, corrections for obliquity were not thought to be necessary (see Spring and Stiles, 1948; Jay, 1961).

RESULTS

The results of 12 sets of measurements (some ascending, some descending) on four cats are shown in Fig. 2. Figures for the human from De Groot and Gebhard (1952) are shown for comparison. It will be seen that the largest area for the cat (123 mm^2) is three times that for the human (40·5 mm^2). The smallest area for the cat is probably an overestimate, since the pigmented fringe of the pupil, which obstructs the entry of light, is included in the measured area. Even so, at 0·9 mm^2, it is less than one third the smallest human pupil area (3·1 mm^2). Thus the pupil area of the cat varies by a factor of at least 135, more than 10 times that for the human.

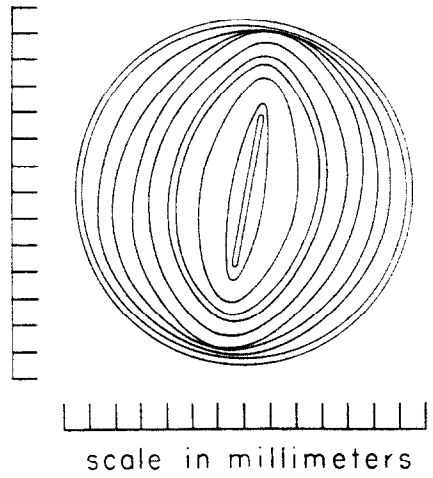

Fig. 3. Tracings of photographs of the converter image of a cat's pupil showing how it changes in shape as it constricts. The pigmented iris fringe was not distinguishable from the true pupil, which must therefore be slightly smaller than shown here.

Figure 3 shows traced outlines of the pupil at various diameters in one cat, showing the sequence of changes in shape. Measurements of these tracings by planimeter, and by direct counting of squares, showed that the calculation of area from major and minor axes [$A = \pi d(\max) \times d(\min)/4$] is accurate.

Figure 4 shows the measured area of the tracings of Fig. 3 as a function of pupil width. Since width is a relatively easy quantity to measure this curve may be found useful in calculating retinal illumination.

DISCUSSION

The pupil must play a more important role in adaptation to a varying visual environment for the cat than it does in the human. The ability to improve sensitivity by factor of more than 100× within a few

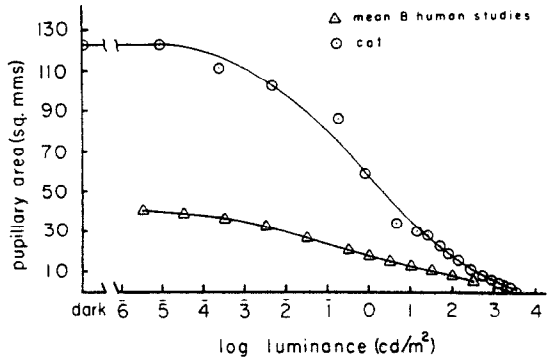

Fig. 2. Pupillary area of the N_2O-anaesthetized cat as a function of illumination, compared with the human. For the cat, 12 runs on four cats were averaged. Scotopic luminances are used below 10 cd/m^2, photopic above. The human data are from De Groot and Gebhard (1952) who averaged the results of eight studies.

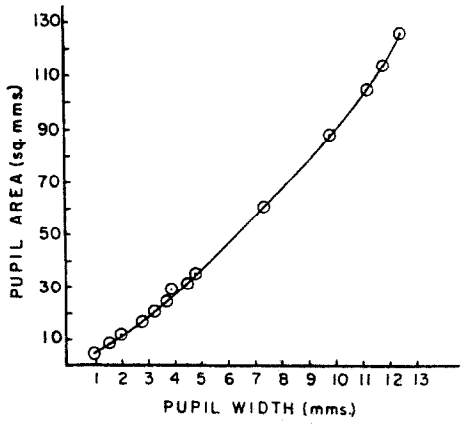

Fig. 4. The relationship between pupillary area and pupillary width obtained from tracings such as those shown in Fig. 3 (no corrections for pigmented iris fringe).

seconds of moving from a bright to a dim environment must be of considerable advantage. Perhaps even more important is the ability to protect the retina from bright bleaching and adapting lights when emerging from a dim environment to a bright one (Barlow, 1972). Some of the adaptation-preventing advantages of pupillary constriction can be seen in the experiments of Woodhouse and Campbell (1975) in the human and LaMotte and Brown (1970) in the cat.

Looking at the range of luminance over which the change takes place it will be seen that cat and human are very similar. One cannot of course be sure that the anaesthetic has no effect. Kappauf, on restrained, unanaesthetized cats, found that the pupil width was reduced to half its maximum value at $10\,cd/m^2$, whereas the present results give $6\,cd/m^2$ for the same figure. For the human, the figure is about $30\,cd/m^2$ according to De Groot and Gebhard.

It should be noted that mydriatics can dilate the pupil above the figure of $130\,mm^2$ we found in darkness. After 1% mydriacil LaMotte and Brown (1970) found up to $230\,mm^2$, although the figures of Vakkur and Bishop (1963) would not suggest quite so large a maximum possible pupillary area.

We have no measurements of the width of the pigmented fringe. If it is 100 μm wide, then at the highest luminance the pupil is completely closed and admits no light. It must certainly reduce the effective area considerably below our measured figure, so the range of control of retinal illumination is certainly considerably greater than our figure of 135×. A method is required for measuring effective pupil area, that is the area that actually admits light, rather than the apparent pupil area we have measured, which includes the pigmented iris fringe. The difference is only important at small pupil areas, but there it may be all-important.

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