

## THE RESPONSES OF THE PUPIL OF GEKKO GEKKO TO EXTERNAL LIGHT STIMULUS

By E. J. DENTON\*

(From the Department of Physiology, University of Aberdeen, Aberdeen, Scotland)

PLATES 1 AND 2

(Received for publication, April 11, 1956)

The eyes of the nocturnal geckos are in one important respect simple and therefore useful for physiological experiment; their retinas have only rods (Walls, 1942; Detwiler, 1943; Rochon-Duvigneaud, 1943) and thus the interpretation of results obtained upon their vision is not made difficult by the uncertainty as to the relative roles of rods and cones. A study of the responses of the pupil of *Gekko gekko* to external light stimulus, in itself a subject of great interest because the gecko's pupil responses are exceptionally efficient ones, is used here to give information about the properties of the gecko's retina.

The gecko's pupil differs markedly from the human in that: the pupil is a slit pupil (Fig. 1) not a circular one; the two irises are completely independent: if one is brightly illuminated and the other in darkness the first pupil will be very tiny whilst the second remains very large; the pupils are under independent voluntary control, the gecko can close a pupil tightly independently of the stimulating light intensity. The last facility is sometimes, but not often, a nuisance during the experiments.

### *Methods*

#### *Fixation of the Eye*

The gecko can make only very small movements of the eye within its orbit; the problem of fixing the eye can therefore be reduced to that of keeping the head still. A piece of cylindrical glass 6 cm. in diameter and 28 cm. long was taken; half of the tube was cut away for 6 cm. at one end and the glass replaced by centimeter wire netting. A flat glass plate was placed in the tube to make a platform for the gecko to stand upon and a wedge-shaped piece of cork was placed on top of this platform under the netting with the broader part of the wedge near the end of the tube. When the gecko was placed on the platform at the open end of the tube he ran along to the closed end of the tube, putting his head firmly on the wedge-shaped space formed by the cork, platform, and netting (Fig. 2). A piece of soft rubber foam sheet was pushed behind the gecko to prevent his escaping. Even in this confined space the gecko

\* Present address: The Laboratory, Citadel Hill, Plymouth, England.

could move and even turn round but it very rarely did so, usually staying quite still (probably shamming dead when the observer was nearby).

The glass tube containing the gecko was held on to the movable block of a Palmer adjustable stand by two curved friction tight springs. The tube could thus be raised or lowered with the block on the stand and turned along its axis in the springs.

#### *Light Sources*

Two types of light source were used. The first (type A) was identical with those previously described (Denton and Pirenne, 1954 *a*), a tungsten filament 12 volt, 12 watt opal bulb being the source of light, its intensity being controlled by two neutral wedges and its spectral composition by placing combinations of glass and gelatin colour filters in the light beam. The second source (type B), used for experiments in which a higher intensity of light was required, was made of a tungsten filament 12 volt, 80 watt opal bulb enclosed in a light-tight, water-cooled box, the box being closed by holders for neutral and colour filters. The intensity of the second source could be changed only in steps of about 0.1 log unit by changing the neutral filters.

The light sources were calibrated for brightness and colour temperature and the filters for spectral transmission by the methods previously described (Denton and Pirenne, 1954 *a*).

#### *Methods of Observation*

In these experiments visual observations (sometimes through a telescope), which were always used when possible, were supplemented by measurements of photographs of the pupil. Infrared photographs were made using Kodak I.R.E.E. plates; the infrared light for the photographs was given by a source type B, the radiations other than the infrared being filtered out by a Chance OX 5 filter. With only the infrared source, the pupil was shown to have the same area when the distance from the source to the gecko's eye was halved; again, at higher intensities where visual observations could be made, cutting on and off the infrared source had no effect on the pupil. From these observations it was concluded that the infrared light used to take photographs did not significantly change the pupil responses. For the higher intensities of stimulating light photographs were made using Ilford H.P.3 plates.

The eye and pupil of the gecko were so still that exposures of several seconds could be used to take the photographs. The area of the pupil was measured from the photographic plates by projecting a greatly enlarged image of the eye on to graph paper, drawing round the image of the pupil, and counting the squares contained in the outline of this image. This method makes no allowance for corneal refraction and the pupil areas given below are the apparent pupil areas as seen from outside the eye, not the real pupil areas. The photographs were taken along a line which made an angle of 20° with the perpendicular to the gecko's iris.

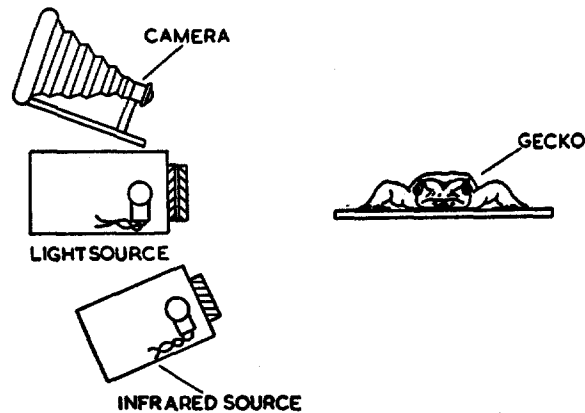
#### *Variation of Pupil Area with Angle of Incidence of the Light*

The relative positions of the eye and the light source could be changed in moving the light source and also by changing the position of the tube holding the gecko. Visual observations and photographic measurements of the changes in area of the

pupil with angle of incidence were made for lights differing in spectral composition and in intensity.

#### *Effect of Intensity of Light*

Photographic measurements were made of the pupil area for a series of light intensities. The two types of light source were used to give an extended range of intensities. In this experiment the source was placed at a distance such that it subtended  $5^\circ$  at the gecko's eye. These measurements were made only for white light coming to the gecko's eye in a direction perpendicular to the iris.



TEXT-FIG. 1. Diagram of the apparatus used to study the effect of light intensity on the pupil area of the gecko.

#### *The Degree of Spatial Summation of the Response*

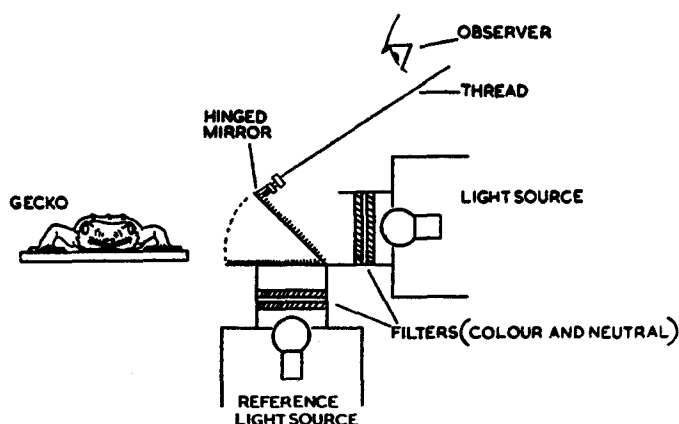
Only two angular fields were used: the source itself at a distance such that it subtended  $5^\circ$  at the gecko's eye and a source subtending  $140^\circ$  formed by placing a circular opal glass between the  $5^\circ$  source and the gecko. A circular opal glass and circular neutral filters could be placed side by side in a slide carrier borrowed from a slide projector. In one position of the slide carrier the gecko saw the light source itself through a neutral filter and subtending  $5^\circ$  at the eye, and in the other the opal illuminated by the same source subtending  $140^\circ$  at the eye. The neutral filter was changed until upon moving the slide carrier from one position to the other there was no change in the size of the pupil. This comparison was made for a number of intensities and colours of light.

*The Losses in the Opal.*—Two pieces of the flashed opal glass used in the experiment were taken, one larger than the other. In front of the larger opal a large neutral filter density 1.0 was placed. One-half of this neutral filter was covered with the smaller opal and the other by a second neutral filter. This whole assembly was placed perpendicularly between the light source and the eye of the experimenter with the larger opal towards the experimenter. The value of the second neutral filter was changed until the two fields corresponding to this neutral filter and to the smaller

opal appeared equal. The joining edge of these fields was hidden with black paper. The absorption of the "matching" neutral filter, whose density was about 0.4 log unit, was taken as equal to the losses in the opal. In this calibration the conditions are very close to those used in the experiment upon the gecko, the larger opal corresponding to the plane of the gecko's eye. The density 1.0 filter was used to make the effects of successive reflections between the opals unimportant.

#### *The Determination of Spectral Sensitivity*

Two light sources of type A were placed perpendicular to each other. A mirror, made of stainless steel polished on one side and blackened on the other, could be moved quickly with a piece of thread between two stops in such a way that one source



TEXT-FIG. 2. Diagram of the apparatus used to measure the spectral sensitivity of the gecko's eye.

could be replaced by the other in the gecko's field of view. In one position, the mirror lay flat, cutting off the horizontal light source and the gecko saw directly the vertical source. In the other position, with the mirror raised to 45°, the vertical light source was cut off from the gecko's eye and the gecko saw the reflection of the horizontal source (Text-fig. 2).

The reference horizontal light source was kept constant in intensity and in spectral composition, the light being that transmitted by a reddish orange combination of the Chance OR 2 filter and the Corning 2412 filter.

The vertical light was varied in spectral composition by placing coloured filters in the light beam. For each combination of filters used the intensity of the source was changed using its neutral wedges until a "match" was made between the two sources, that is, on switching from one source to the other the pupil of the gecko neither constricted nor dilated. The spectral sensitivity of the gecko was determined in this way for wave bands from 370 to 720  $m\mu$ . Matching methods such as this one have the advantage that their accuracy depends only upon the constancy of the differential sensitivity and not upon the constancy of the absolute sensitivity of the response.

The intensity chosen for the comparison source was one for which the rate of change of the pupil area with change in intensity was very high. The calibrations of light intensities at the eye were simple because the vertical light source upon which the measurements depended shone directly onto the eye.

Two types of experiments were performed. First the approximate curve was determined by making measurements for all the filters in turn without any allowance for a possible change in differential sensitivity of the retina during the experiment. Such series were made by two observers. The second method was to make successive measurements for a given filter and the filter Ilford 604. In this way each filter is compared in turn against the Ilford 604 and the small effects of change in differential sensitivity during the experiment can thus be almost eliminated.

#### RESULTS

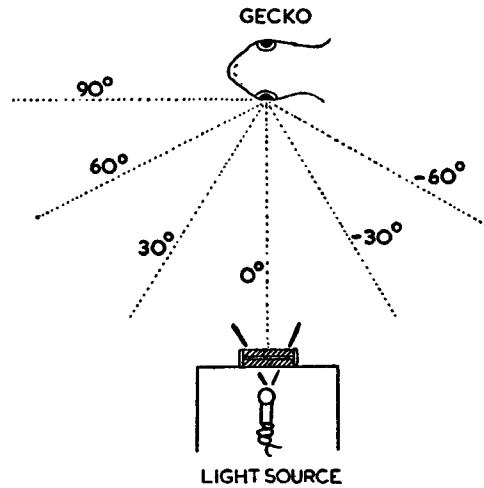
The external diameter of the gecko's eye along its optical axis was estimated to be 1 cm. This compares with the corresponding figure of 2.4 cm. (Le Grand, 1946) for the human eye.

On projecting a small light image onto the gecko's eye and moving it across the eye it was shown that the pupil response was only to light entering the pupil of the eye; no response of the pupil to light falling only on the iris could be seen. It is therefore probably safe to assume that the pupil response of the gecko is mediated by way of the absorption of light by the photosensitive pigments of the retinal receptors.

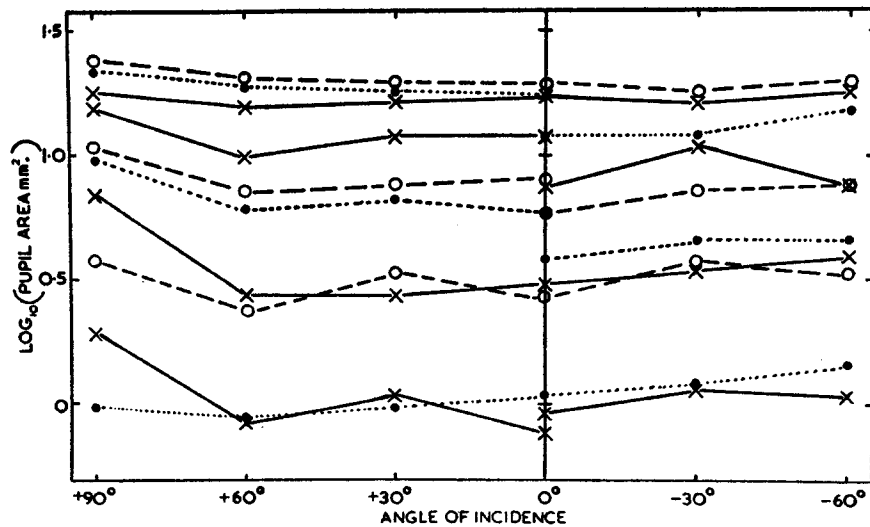
#### *Variation of Pupil Area with Angle of Incidence of the Light*

For a given intensity and colour of light the gecko's pupil area was found by visual observation to be very constant for changes in the direction of incidence of the light at the eye; there was no suggestion of a specialized pupil reflex localized in a particular part of the retina. Using the same apparatus the human subject was seen to have, as is well known, a more powerful pupil reflex for light falling on the fovea than for light falling on the periphery of the eye, and an anesthetized cat gave a much stronger pupil reflex for light striking the eye in one direction (probably for light falling on the area centralis) than for light striking it in other directions.

For the gecko photographs were made as the angle of incidence of the stimulating light was varied across one "meridian" in 30° steps (Text-fig. 3). Three spectral bands and several intensities for each band were used. The three spectral bands were those isolated by the red Corning cut off filter 2408, transmitting wave lengths greater than about 620 m $\mu$ , the green filter Ilford, 604, maximum transmission about 520 m $\mu$ , and the blue filter Corning 5113, maximum transmission about 420 m $\mu$ . The results of these measurements are shown in Text-fig. 4. The area of the pupil varied for a given light very little with angle of incidence, the lines showing sensitivity to different colours are seen moreover to be everywhere approximately parallel to one



TEXT-FIG. 3. Diagram of angles used to study the variation of pupil response with angle.

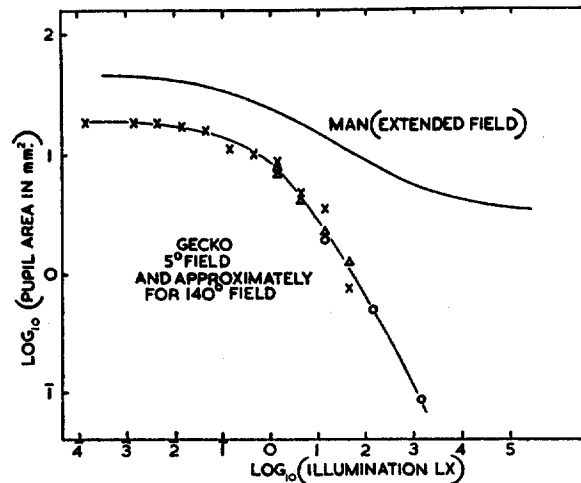


TEXT-FIG. 4. Variations of pupil area with angle of incidence of the source for several different intensity levels for three colour filters. Ilford 604 ( $\lambda_{ms} = 0.52 \mu$ )— $\times$ — $\times$ — $\times$ . Corning 5113 ( $\lambda_{ms} = 0.42 \mu$ )  $\dots \bullet \dots \bullet \dots$  Corning 2408 (cut-off filter transmits wave length greater than  $0.61 \mu$ )— $\circ$ — $\circ$ — $\circ$ — $\circ$ . One line across the graph is for a given filter at a given intensity. Several different intensity levels are used for each filter; these intensity levels are spaced approximately 1 log unit apart.

another; this means that if there are changes in relative spectral sensitivity of the pupil reflex across the gecko's retina these changes must be exceedingly small.

*Variation of Pupil Area with Intensity of Light*

The change of pupil area with light intensity for white light (that of a tungsten filament opal lamp of colour temperature 2400°K.) is shown in Text-fig. 5. The curve of log pupil area against log intensity for the gecko is here



TEXT-FIG. 5. Pupil area against intensity of light. The symbols +,  $\Delta$ , and  $\circ$  represent different experiments all made with 5° sources. The curve for man is taken from Le Grand (1948) and is for an extended field. The illumination scale at the bottom applies both to man for an extended field and to the gecko for a 5° and approximately for a 140° field.

compared with a similar curve given for man by Le Grand (1948) on the basis of the experimental results of Crawford (1936) and Flamant (1948). The lower limit of pupil area was not reached in these measurements for on holding the gecko with its eye towards a "brightly" lit Aberdeen summer sky the pupil was seen to be smaller in area than the smallest area measured photographically. The smallest pupil seen was made up of four very tiny holes, the largest being estimated, by comparison with holes of known size, to be about  $\frac{1}{10}$  mm. in diameter.

*The Degree of Summation of the Response*

The source itself was 16.5 cm. from the eye; the diffusing surface of the opal (radius 4 cm.), when placed between the source and the gecko's eye,

was 15 cm. from the source and 1.5 cm. from the eye. If such a source has a candle power of  $L$  cd in the direction of the center of the opal, then the illumination at the center of the opal will be  $\frac{L}{(0.15)^2}$  lx. Assuming the opal to be uniformly illuminated (at its edge its illumination will in fact be about 7 per cent less) and that all the light striking the opal is perfectly diffused on the other side in the direction of the gecko's eye, then the illumination at the gecko's eye would be

$$\frac{L}{(0.15)^2} \times \frac{4^2}{4^2 \times 1.5^2} \text{ lux} \quad (\text{Walsh, 1953}).$$

This would be greater by 0.12 log unit than the direct illumination of the eye by the source which is

$$\frac{L}{(0.165)^2} \text{ lux}$$

The above calculation neglects the losses by reflection and absorption in the opal. These were found (see *Methods*) to be of the order of 0.4 log unit. Thus simply replacing the  $5^\circ$  field of the source by the  $140^\circ$  field of the opal would have reduced the illumination at the eye by about 0.3 log unit.

It was found over the whole range of pupil response, within which visual observations could be made, that the  $5^\circ$  source viewed directly through a 0.2 to 0.3 density neutral filter had the same stimulating action on the pupil reflex as a source of  $140^\circ$  made by substituting between the source and the gecko's eye an opal glass for the neutral filter. For a given pupil response the total amount of light flux entering the pupil of the gecko was then 0 to 0.1 log unit more for the  $140^\circ$  source than for the  $5^\circ$  source. The calculations upon which this result depends were simplified by the assumption that the opal perfectly diffused the transmitted light. The method used for finding the losses in the opal glass was, however, one which averaged the transmitted diffused light and the use of the value so given for these losses largely corrects for the errors which the assumption of perfect diffusion would otherwise give. The curve of log pupil area against log light flux entering the eye for a  $140^\circ$  source was then of the same form as the curve for a  $5^\circ$  source, being perhaps a little displaced along the intensity axis.

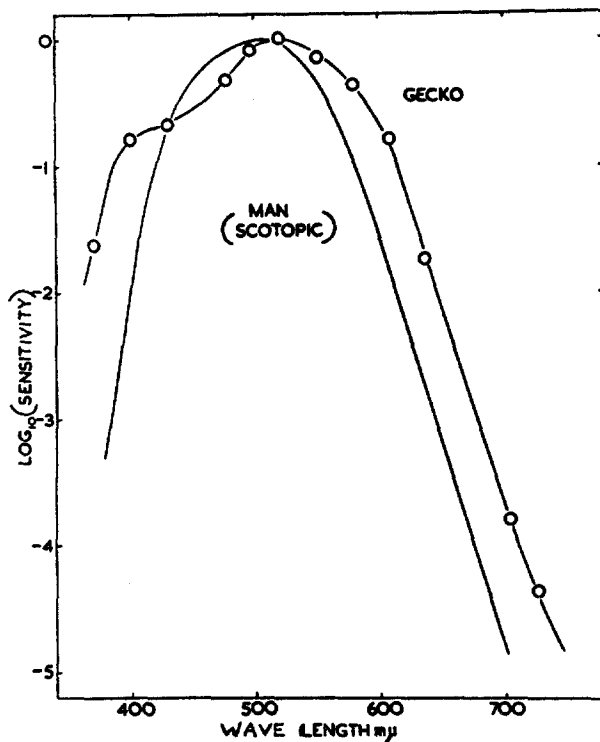
#### *The Determination of Spectral Sensitivity*

Measurements made using the second method were, for this type of experiment, very accurate and the results were always reproducible within a range of 0.1 log unit.

In Text-fig. 6 the spectral sensitivity curve for the gecko is compared with the C.I.E. scotopic sensitivity curve for man (C.I.E., 1951). It can be seen



that the gecko's curve is similar in shape to the human scotopic curve but is displaced between 20 to 30  $m\mu$  towards the longer wave length end of the spectrum, this displacement appearing greater for the red end of the curves than around the maxima. The latter fact may be caused by a higher density of photosensitive pigment in the gecko's rod than in human rods.



TEXT-FIG. 6. The spectral sensitivity curve of the gecko as compared with the C.I.E. scotopic curve for man. The ordinate is of log sensitivity; a constant has been arbitrarily added to the ordinate values to make the maximum sensitivities equal to unity.

In the near ultraviolet the gecko appears to be more sensitive than the human subject. There is, however, some uncertainty about the meaning of the value given for  $\lambda = 370 m\mu$  because the crystalline lens gave a bluish green fluorescence for light of this wave length. This is a well known effect for other vertebrate lenses and Le Grand (1938) has measured the spectral composition of the light given by such a fluorescence. If the light given by the fluorescence of the lens were the effective stimulus to the pupil response the direct sensitivity to the near ultraviolet must be even less than that shown in Text-fig. 6.

## DISCUSSION

In many of the arguments which follow the assumption is made that the pupil response, which depends upon light entering the pupil, is mediated by the retinal receptors.

The eye of the gecko has two features of special interest: one of the most efficient irises found in nature and the large rods of its pure rod retina.

The function usually attributed to the human iris is one of protecting the retina against sudden changes in illumination (Le Grand, 1948). This function is, however, very inefficiently fulfilled; the minimal area of the human pupil is only one-sixteenth of the maximal and, even at its best, the response to a tenfold increase in illumination is a decrease in the area of the pupil to three-fifths of its original value leaving a large increase (about sixfold) in retinal illumination.

The gecko's iris is altogether better than the human iris in protecting the retina against increase in illumination. The minimal area of the pupil is less than one-three hundredth of the maximal and, at its most efficient, the response to a tenfold increase in illumination is a reduction of the pupil area to about one-sixth its former value, the retinal illumination being therefore not even doubled.

Aguilar and Stiles (1954) have shown by a most ingenious experiment that "at a field intensity of about 100 scotopic trolands the sensitivity of the (human) rod mechanism to stimulus differences begins to fall off rapidly and that at 2,000-5,000 scotopic trolands (corresponding approximately to daylight luminances of 120-300  $cd/m^2$ ) the rod mechanism becomes saturated and is no longer capable of responding to an increase in stimulus." (100  $cd/m^2$  is the illumination in a room lit by moderate artificial lighting.)

The gecko's pupil continues, however, to contract sharply for an increase in intensity of a 5° source of luminance 100,000  $cd/m^2$  and since the gecko has only rods as retinal receptors this source, which is about 1,000 times brighter than that required to "saturate" completely the human scotopic visual system, gives a retinal illumination insufficient to saturate the gecko's rod visual system. The gecko's eye, lacking cones, is clearly adapted to allow the rods to be useful for vision at much higher external illuminations than are the human rods. Part, but by no means all, of this adaptation is the reduction of the intensity of light reaching the retina by a very efficient pupil.

The retinal illumination is given for the human eye by the formula  $D = 0.36 B.S.\tau_\lambda$  (Le Grand, 1948) in which  $D$  is the retinal illumination in lux,  $S$  the area of the pupil in  $cm.^2$ ,  $B$  the brightness of the external source in  $cd/m^2$ ,  $\tau_\lambda$  the transmission of the ocular media.

Taking account of the difference in size of the human and gecko's eye, the formula  $D = 0.36 B.S.\tau_\lambda$  for the human eye becomes approximately  $D =$

$2.25 B.S.\tau_\lambda$  for the gecko. For  $B = 10^5 \text{ cd/m}^2$ ,  $S$  is for a  $5^\circ$  source,  $9.8 \times 10^{-4} \text{ cm}^2$ . Taking  $\tau_\lambda = 1$ ,  $D = 2 \times 10^2 \text{ lux}$ .

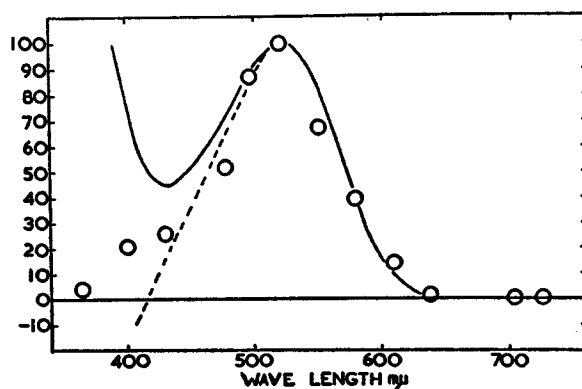
The gecko's rod has a cross-section about 16 times that of the human rod and it can be calculated as described by Denton and Pirenne (1954 *b*) that the gecko's rod is not saturated when approximately  $10^6$  quanta/sec. of the wave length  $520 \text{ m}\mu$  fall upon it. Unpublished measurements (Denton) upon two other species of gecko gave for  $\lambda = 530 \text{ m}\mu$  densities of about 0.5 for the photosensitive pigment *in situ*; this means that of the light of this wavelength striking the retina about 70 per cent is absorbed. We have then the remarkable fact that the gecko's rod, which probably like the human responds to the absorption of 1 quantum, is not saturated even when absorbing almost  $10^6$  quanta/sec.

A more important function of the human iris than that of shielding the retina against changes in light intensity is to give to the pupil the optimum diameter for visual acuity. The minimal diameter of the human pupil of about 2 mm. is a value for which the limits to acuity set by the fineness of the retinal mosaic and size of the pupil are approximately the same (Shlaer, 1937). When the external illumination is high the human pupil is made as small as is useful within the limits set by the diffraction of light in order to cut down the effects of the eye's spherical and chromatic aberrations. At lower levels of illumination the acuity is probably limited not by the fineness of the retinal mosaic but by the number of quanta reaching the retina (Pirenne and Denton, 1952) and it is then useful to increase this number by increasing the pupil area even though the distortions caused by optical defects of the refractive system of the eye will become more disturbing.

For man then the minimal pupil diameter of approximately 2 mm. and a retinal mosaic of cones 2 to  $2.5 \mu$  apart (Pirenne, 1948) set approximately the same limit to acuity (Shlaer, 1937). The gecko has a minimal pupil diameter of about 0.1 mm. Such a pupil will probably set the same diffraction limit to angular acuity as would a 0.1 mm. pupil in man, that is 14 times that of man with a 2 mm. pupil (Lister, 1913). Again for the gecko a retinal mosaic of rods  $10 \mu$  apart (Detwiler, 1943) in an eye of external diameter two-fifths the dimension of the human eye gives a limit to angular acuity 12 times as great as does the human retinal mosaic. For the gecko the two limits to acuity may not therefore be of exactly the same value, but they are nevertheless still close to one another and for the gecko's eye we see almost the same elegant economy in design as for the human eye.

For the human eye external objects situated at a distance for which the eye is not accommodated will be blurred. An example taken from Listing (1851) is that for a circular pupil of 4 mm. diameter and an eye accommodated for infinity a point object at 9.4 cm. from the human eye will give not a point retinal image but a circular retinal image (circle of diffusion) of di-

iameter 0.58 mm., corresponding to a circular external field of diameter  $2^\circ$ . For the gecko when the pupil is a narrow slit the retinal images of external objects for which the eye is not accommodated will be sharper horizontally than vertically; when its pupil consists of a vertical series of holes, such an object will give a series of retinal images, one for each hole, displaced vertically from one another. (This effect is seen for the human eye in the well known experiment of Scheiner.) The gecko with an eye two-fifths the linear dimension of the human eye had for the higher external experimental illuminations used a pupil made up of a series of holes spaced along a 4 mm.



TEXT-FIG. 7. Comparison of the absorption spectra of extracts from the retinas of *Phyllurus milii* (Crescitelli) and the spectral sensitivity curve (plotted on a quantum basis) of *Gekko gekko*. Solid line, relatively pure unbleached spectrum and broken line,  $\text{NH}_2\text{OH}$  difference spectrum of *Phyllurus milii*; open circles, sensitivity on a quantum basis of *Gekko gekko*. Each curve is scaled so that its maximum is 100 per cent.

line, and hence in the conditions described above, the circular retinal image corresponding to  $2^\circ$  for the human becomes a series of retinal images corresponding to an arc of approximately  $5^\circ$  in the external field.

Dr. F. W. Campbell (private communication) has suggested that the gecko might use this effect to judge the distance of external objects either by finding what degree of accommodation is required to bring the vertically spaced images into coincidence or that "the gecko might for example wait until the 4 flies coming toward it become one fly and then bite."

Unless the absorption spectrum of the ocular media is very anomalous, the rod vision of *Gekko gekko* is mediated by a photosensitive pigment similar to rhodopsin but with its maximum displaced between 20 and 30  $m\mu$  towards the red end of the spectrum. (The lenses of other geckos examined were quite colourless.) This conclusion is confirmed by the careful measurements of Crescitelli (1956) upon several species of geckos. He found in particular that the

photosensitive pigment extracted from a closely related species of gecko, *Phyllurus milii*, has an absorption curve similar to that of rhodopsin but its maximum is displaced to 524  $m\mu$ . The present measurements of spectral sensitivity when plotted on a quantum basis (Dartnall and Goodeve, 1937) agree well with his results (Text-fig. 7). Again, difference curves measured upon the fresh retinae of two Egyptian geckos, *Tarentola annularis* and *Ptyodactylus hasselquistii*, had maxima displaced about 30  $m\mu$  towards the long wave length end of the spectrum with respect to the corresponding maxima for the frog and salamander (Denton, unpublished observations, using a method similar to that described by Denton and Wyllie (1955)).

The geckos seem then to be exceptions to the general rule given by Wald (1945 *a*) that all terrestrial animals have a scotopic vision mediated by rhodopsin. Wald noted, however, that there was then no information on the rod vision of reptiles. The biological significance of these results is discussed by Crescitelli (1956).

The measurements of absorption obtained upon extracted pigments are very precise around the wave length of maximum absorption but become inaccurate when the absolute absorption becomes low; there is also a difficulty in interpreting the results for the shorter wave lengths because the products of bleaching are not colourless. Measurements such as those described here, although they are less precise than measurements upon pigments in solution around the maximum of absorption, are equally precise for every wave band used and their chief interest lies in the information they give for wave lengths at the extremities of the visual spectrum.

The logarithm of the spectral sensitivity of the gecko, plotted on a quantum basis against the reciprocal wave length  $1/\lambda$ , falls approximately linearly in the long wave end of the spectrum as  $\lambda$  increases. A similar fall is observed for the human rod and cone systems (Stiles, 1948) and *Xenopus* (Denton and Pirenne, 1954 *b*). A theoretical interpretation of the shape of the sensitivity curves in this region is given by Stiles (1948) and Lewis (1955). It is an interesting example of how biological measurements may give information on a physicochemical problem inaccessible to conventional physical chemical experimental methods.

The fall in sensitivity may be described (Stiles, 1948) by equations of the type

$$\log_e \frac{hv}{W_\lambda \tau_\lambda} = \text{a constant} + K \frac{hv}{kT}$$

in which  $W_\lambda$  is the threshold energy entering the eye for radiation of wave length  $\lambda$  (frequency  $\nu$ ) measured at the cornea of the eye;  $\tau_\lambda$  is the spectral transmission of the eye media between cornea and retina,  $h$  is Planck's constant,  $k$  is Boltzmann's constant,  $T$  the absolute temperature (here 291°K.).

$K$  is a constant depending upon the particular photosensitive pigment mediating vision.  $K$ , which is 0.79 for human rod vision, 0.87 for human cone vision, 0.75 for *Xenopus*, is found here to be 0.76 for the gecko.

The sudden drop in sensitivity found in the near ultraviolet is probably principally caused by a sudden decrease in the transmission of the crystalline lens. This is the explanation of the similar fall found in man (Goodeve, Lythgoe, and Schneider, 1942; Wald, 1945 *b*). Denton (1955, 1956) has shown that for 27 species of fish, the frog, and the squid, the fall in transmission of the lens on moving towards the shorter wave length end of the spectrum is always sharp but that the wave length around which the fall takes place varies greatly from one species to another. This wave length varies from 440  $m\mu$  for *Chlorophthalmus agassizii* to 310  $m\mu$  for *Anguilla vulgaris*. Here for the gecko there is probably such a fall in transmission around 370  $m\mu$ .

#### SUMMARY

1. The responses of the pupil of a nocturnal gecko (*Gekko gekko*) to external light stimulus were studied.
2. The responses of the pupil are determined by light entering the pupil and not by light acting directly on the iris.
3. The responses of the pupil are very uniform in sensitivity including spectral sensitivity for light coming in different directions to the eye.
4. The possible change in area of the pupil is more than 300-fold and probably represents an effort to shield the pure rod retina from saturating light intensities.
5. The pupil continues to contract sharply for changes in external light intensity which give retinal illuminations corresponding to  $10^6$  quanta/sec. striking a retinal rod.
6. There is a large degree of spatial summation of the response; circular external light fields subtending 5 and  $140^\circ$  giving the same illumination at the pupil give approximately the same pupil response.
7. The spectral sensitivity curve agrees with the absorption curve of an extracted pigment from a closely related gecko described by Crescitelli in the followig paper. It is similar to the human scotopic curve but its maximum is displaced about 20 to 30  $m\mu$  towards the red end of the spectrum. The fall in sensitivity towards the red end of the spectrum is described by the equation

$$\log_e \frac{hv}{W_{\lambda}\tau_{\lambda}} = \text{a constant} + 0.76 \frac{hv}{kT}$$

I wish to thank Mr. J. Lester, Curator of the Reptile House, Regent's Park Zoological Gardens, London, for the loan of the *Gekko gekko*, Professor A. Hassan of

Ein Shams University, Cairo, for the gift of Egyptian geckos, and Dr. M. H. Pirenne for the loan of colour filters bought with a grant from the Medical Research Council. I am grateful to Mr. A. E. A. McLeod for excellent technical assistance.

## REFERENCES

1. Aguilar, M., and Stiles, W. S., *Optica Acta*, 1954, **1**, 59.
2. Crawford, B. H., *Proc. Roy. Soc. London, Series B*, 1936, **121**, 376.
3. Crescitelli, F., *J. Gen. Physiol.*, 1956, **40**, 217.
4. Dartnall, H. J. A., and Goodeve, C. F., *Nature*, 1937, **139**, 409.
5. Denton, E. J., *Bull. muséum nat. hist., Paris*, 1955, **28**, 418.
6. Denton, E. J., *Bull. inst. Oceanog. Monaco*, 1956, **53**, 1.
7. Denton, E. J., and Pirenne, M. H., *J. Physiol.*, 1954 *a*, **123**, 417.
8. Denton, E. J., and Pirenne, M. H., *J. Physiol.*, 1954 *b*, **125**, 181.
9. Denton, E. J., and Wyllie, J. H., *J. Physiol.*, 1955, **127**, 81.
10. Detwiler, S. R. *Vertebrate Photoreceptors*, New York, Macmillan, 1943.
11. Flamant, F., *Rev. Opt.*, 1948, **27**, 751.
12. Goodeve, C. F., Lythgoe, R. J., and Schneider, E. E., *Proc. Roy. Soc. London, Series B*, 1942, **130**, 380.
13. *Proc. Internat. Commission on Illumination*, (Halbertsma and Jansen, editors), New York, Central Bureau C.I.E., 1951, 3.
14. Le Grand, Y., *Compt. rend. Acad. sc.*, 1938, **207**, 1128.
15. Le Grand, Y., *Optique physiologique*. Vol. 1. La Dioptrique de l'oeil et sa correction, Paris, Editions de la Revue d'Optique, 1946.
16. Le Grand, Y., *Optique physiologique*. Vol. 2. Lumiere et couleurs, Paris, Editions de la Revue d'Optique, 1948.
17. Lewis, P. R., *J. Physiol.*, 1955, **130**, 45.
18. Lister, J. J., *J. Roy. Micr. Soc.*, 1913, **32**, 34.
19. Listing, J. B., 1851, quoted by Helmholtz, H., in *Optique physiologique* (translated by Javel and Klein), Paris, Masson et Fils, 1867, 136.
20. Pirenne, M. H., *Vision and the Eye*, London, Chapman and Hall Ltd., 1948.
21. Pirenne, M. H., and Denton, E. J., *Nature*, 1952, **170**, 1039.
22. Rochon-Duvigneaud, A., *Les Yeux et la vision des vertebres*, Paris, Masson et Fils, 1943.
23. Schlaer, S., *J. Gen. Physiol.*, 1937, **21**, 165.
24. Stiles, W. S., in *Transactions of the Optical Convention of the Worshipful Company of Spectacle Makers*, London, Spectacle Makers Co., 1948, 97.
25. Wald, G., The chemical evolution of vision, Harvey Lectures, 1945 *a*, **41**, 117.
26. Wald, G., *Science*, 1945 *b*, **101**, 653.
27. Walls, G. L., *The Vertebrate Eye and its Adaptive Radiation*, Bloomfield Hills, Michigan, The Cranbrook Press, 1942.
28. Walsh, J. W. T., *Photometry*, London, Constable & Co., 1953.

## EXPLANATION OF PLATES

## PLATE 1

FIG. 1. Photographs of the eye of the gecko for six different intensities of stimulating light ( $5^\circ$  source). These intensities increased from a to f. Photographs a, b, and c were made using infrared-sensitive plates, d, e, and f were made using panchromatic plates.



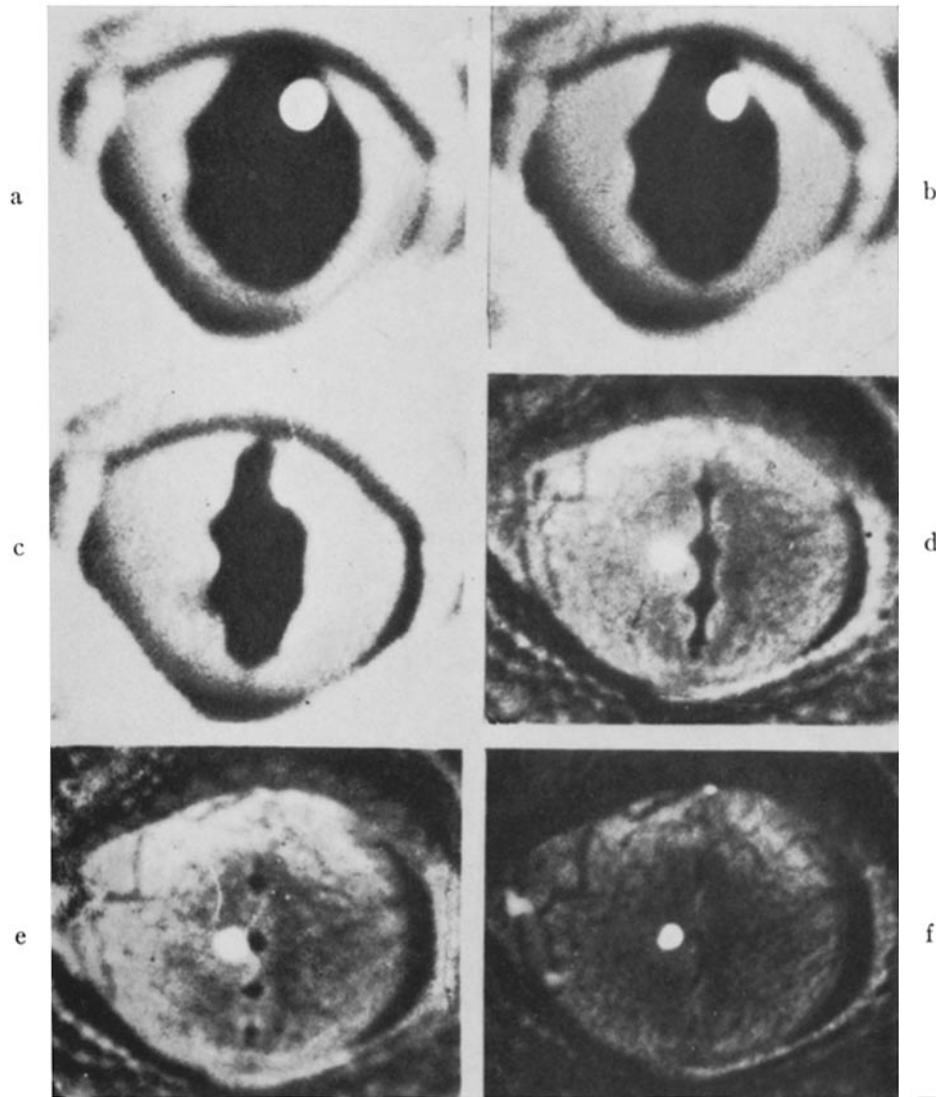


FIG. 1

(Denton: Pupil responses of *Gekko gekko*)

PLATE 2

FIG. 2. The gecko in position for the experiment.

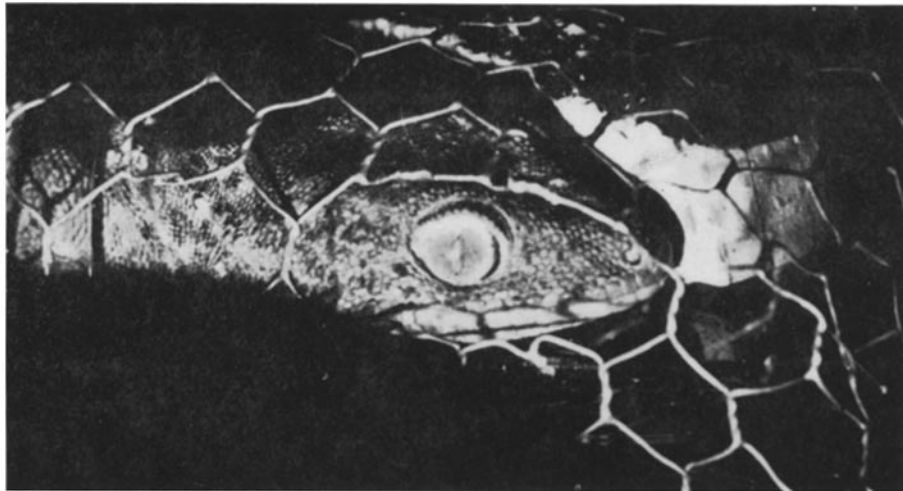


FIG. 2

(Denton: Pupil responses of *Gekko gekko*)