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CAT COLOUR VISION: EVIDENCE FOR MORE THAN ONE CONE PROCESS

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SUMMARY

1. The ability of cats to distinguish colours was investigated at mesopic and photopic levels to test the hypothesis that cats discriminate wavelength by using rods in conjunction with a single type of cone.

2. Cats were trained to distinguish red from cyan, and orange from cyan at the mesopic level. They retained the ability to make this discrimination when the coloured stimuli were placed against a background bright enough to saturate the rods.

3. One cat was also tested after being exposed to a bright white light of 9000 cd/m^2 for a period of 5 min, and found able to distinguish red from cyan.

4. These results suggest that cats have more than one type of cone. Subsequent recordings from single units in the lateral geniculate nucleus showed that there are rare opponent colour units in layer B with input from a green-absorbing cone and a blue-absorbing cone.

INTRODUCTION

Recently we suggested that cats discriminate colour by using rods in conjunction with a single type of cone. The reason for this suggestion was our failure to find single units with more than one spectral sensitivity in the cat lateral geniculate body when a white background was used to saturate the rods. This evidence was not conclusive since it is possible that other cell types may be rare rather than non-existent, and it was clear that behavioural work was also required (Daw & Pearlman, 1969).

If cats do distinguish colour by using rods in conjunction with a single type of cone, then they should be able to distinguish colour in the mesopic range between cone threshold and rod saturation, but not at photopic

levels, above rod saturation. While some investigators have failed to train cats to distinguish colour (DeVoss & Ganson, 1915; Gunter, 1954; Meyer, Miles & Ratoosh, 1954), and others have been successful (Sechzer & Brown, 1964; Mello & Peterson, 1964; Meyer & Anderson, 1965), it is not clear that the former were working at photopic levels and the latter at mesopic levels. Indeed, the level of rod saturation, which is the dividing line between mesopic levels and photopic levels, has only recently been determined for the cat (Barlow & Levick, 1968; Daw & Pearlman, 1969).

The suggestion of more than one type of cone in the cat comes from the work of Granit and his colleagues (Granit, 1945; Granit & Tansley, 1948; Ingvar, 1959), and also from more recent work by Brown (1966). Granit measured the spectral sensitivity of ganglion cells in the cat retina in the light adapted state, then subtracted the spectral sensitivity of rhodopsin from the results. He called the resulting curves modulators, and found that they peaked at several different wavelengths. Remberg (1953) was the first to point out that one can obtain a variety of modulators like this with only one type of cone if the retina is not fully light-adapted, and the mesopic spectral sensitivity is the envelope rather than the sum of the rod and cone curves. It is quite easy to explain the red and green modulators in this way, but somewhat harder to explain the blue modulator (Daw & Pearlman, 1969).

Thus, the electrophysiological evidence for more than one type of cone in the cat is not completely satisfactory. No microspectrophotometric curves have been published from single cones in the cat, and no recordings obtained from single receptors, although reflexion densitometry does suggest a blue pigment (Weale, 1955). The behavioural evidence is also indefinite. Hence the existence of more than one type of cone has not hitherto been proved.

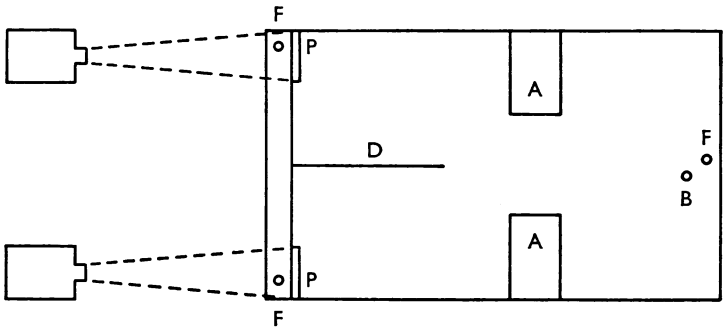
METHODS

The apparatus used for the behavioural experiments was designed by Dews & Wiesel (1970) and has been described by them. The discrimination was made in a box (Text-fig. 1), 5 ft. long with two translucent Plexiglas doors (P) at one end and a lighted button (B) at the other. At the beginning of each trial, the cat pressed the lighted button whereupon food was presented through a nearby hole in the floor (F). The two Plexiglas doors were then illuminated from behind, one by a positive stimulus, the other by a negative stimulus. If the door with the positive stimulus was pushed, food was presented through a hole (F) in the floor behind the Plexiglas door. The stimulus light remained on for the 10 sec of food presentation. The cat then turned around, moved down the runway and received food again when the lighted button was pressed. If the negative stimulus was pushed the stimulus light went out immediately and no food was presented. When the lighted button was then pressed again no food was delivered, but the doors were re-illuminated to start another trial.

The slides and the programme for advancing from one slide to the next were

arranged in an order that penalized any consistent position strategy, such as continuous choice of one side or the other, or an alternation between one side and the other (see Dews & Wiesel, 1970). Each series of trials consisted of thirty trials and three to six series were completed each day. The cats were deprived of food before the first trials were begun and maintained at approximately 80 % of their free-feeding weight throughout the course of the experiment.

The stimuli were projected on the backs of the Plexiglas doors by two Kodak Carousel projectors that were advanced and controlled by Grason-Stadler equipment. The background lights were two appropriately masked high-intensity desk lamps, also directed at the backs of the doors. Since the transmission of the translucent Plexiglas doors was directional, the luminance of the stimuli and back-



Text-fig. 1. Diagram of the behavioural test box. A, arch; B, lighted button; D, divider; F, food holes; P, Plexiglas doors.

grounds from the cat's side depended somewhat on the angle of view. Therefore the cat was required to pass through an arch (A) after pressing the lighted button, and a long divider (D) was placed between the two Plexiglas doors so that the cat had to make his choice from a place close to the centre of the arch.

Most of the results were obtained with two cats. One cat was a normal 1-year-old female, with no prior experience in the apparatus. The second cat was a 1-year-old male, whose right eye had been closed at birth and reopened at 3 months. He had previously been trained to use the apparatus in tests for acuity, but had not been trained to distinguish colours. There was no difference in the results obtained from this cat when tested with or without a black contact lens over the eye that had been closed.

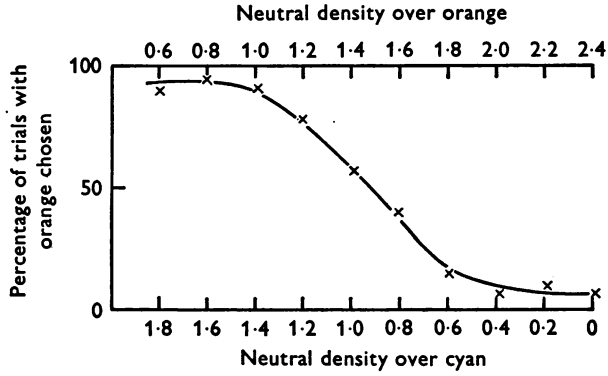
The methods for recording from single units in the lateral geniculate body with tungsten micro-electrodes were adapted from those developed by Hubel & Wiesel (1961), and have been described in detail in earlier papers (Daw & Pearlman, 1969; Pearlman & Daw, 1970).

RESULTS

Purkinje shift. First we determined the relative brightness, for the cat, of the various colours used. This was necessary to eliminate brightness as a cue in the colour discrimination tests. Relative brightnesses were determined at several levels through the mesopic and photopic ranges. Red (Wratten No. 24) was compared with blue (Wratten No. 47) and orange (Wratten No. 22) was compared with cyan (Wratten No. 64).

The stimuli were two circles about 6 cm in diameter. The cat was first trained with white circles, the brighter circle being rewarded. Then the cat was tested with a set of ten orange/cyan (or red/blue) pairs of slides. There were ten orange slides spanning a range of 1·8 log units, in steps of 0·2 units, and ten cyan slides, also spanning a range of 1·8 log units, in even steps. The brightest cyan slide was paired with the darkest orange slide and so on.

Pressing either orange or cyan doors led to food during the test period. When one colour was a log unit or more brighter than the other, the cat went to the brighter colour more than 90% of the time (see Text-fig. 2).



Text-fig. 2. Percentage of trials in which orange was chosen for each of ten pairs of orange and cyan slides.

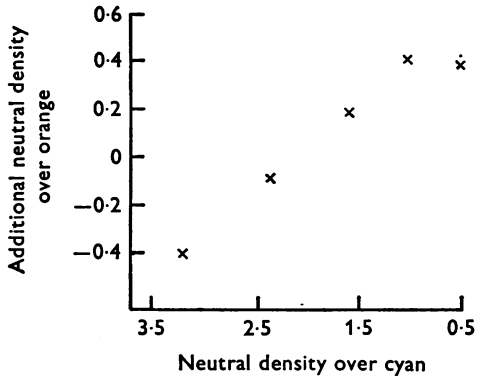
When there was less than a log unit difference in brightness, the cat was less certain. Each pair of slides was presented a total of 30 times over a period of 4 days. Text-fig. 2 shows the percentage of times that the cat chose orange rather than cyan in one of these experiments. An Ogive curve was drawn through the points. The pair of slides where orange and cyan were chosen equally often by the cat (where the Ogive curve crosses the 50% line) was considered to be equally bright to the cat.

The experiment of Text-fig. 2 was repeated at four other levels of brightness. The 50% points for all five experiments are plotted in Text-fig. 3. This Figure shows the additional neutral density required over the orange for various levels of neutral density over the cyan. If there were no Purkinje shift, that is, if the ratio of orange to cyan for equal brightness was the same at all levels, the points on this graph would fall on a horizontal line. The points show that orange has more brightness for the cat at higher levels and cyan has more brightness at lower levels. The points also show that the Purkinje shift is complete at the highest level used. These results agree with physiological determinations of the Purkinje shift (Barlow &

Levick, 1968) and the level at which the shift is complete is close to that producing rod saturation (Daw & Pearlman, 1969). Similar curves were obtained in the brightness matches comparing red with blue.

Colour discrimination. One cat was trained initially to distinguish red from blue and then transferred to a red/cyan discrimination. The other cat was trained to distinguish orange from cyan. The initial training was done at a high mesopic level with circles of colour against a dark background.

Two methods were used to train the cats. In the first method there were three sets of slide pairs. Some pairs had reds of brightness equal to that of the blue, some pairs had reds 4 times as bright as the blue, and some pairs



Text-fig. 3. Plot of the Purkinje shift. Horizontal axis shows the neutral density over the cyan filter. Vertical axis shows the additional neutral density required over the orange filter to match the cyan filter in brightness.

had blues 4 times as bright as the red. Red was always the positive stimulus. The cat was given 100 trials per day until the red was pressed 90% of the time.

In the second method a cat previously trained to make a brightness discrimination was given a set of slides in which the oranges were all 10 times as bright as the cyan. Orange was the positive stimulus, and the cat was immediately able to choose the correct stimulus in more than 90% of the trials. The brightness of the orange was then reduced in steps and the trials continued, with orange being rewarded at each step, until the cat had learned to press the orange 90% of the time. After a number of series, the orange was equal in brightness to the cyan and eventually dimmer than the cyan. The cat was then able to perform at above criterion levels on a series of slides, one third of which had orange equal in brightness to the cyan, one third with orange 4 times as bright as the cyan, and one third with cyan 4 times as bright as the orange. More than 1500 trials were required to train the cats to make reliable colour discriminations by

either training method. A third cat was trained to discriminate red versus blue by the first method with equally slow results. Other investigators have also found that many trials over a long period of time are required to train cats to discriminate colour (Sechzer & Brown, 1964; Mello & Peterson, 1964).

After the initial period of training to colour was complete, a white background was introduced. The cat was then asked to distinguish a red or orange circle against a white background from a cyan circle against a white background of the same brightness. The coloured circles were much brighter than the white background and the discrimination was an easy one for a human observer. At first the cats found it very difficult and several hundred more trials were required before performance was again over 90 %.

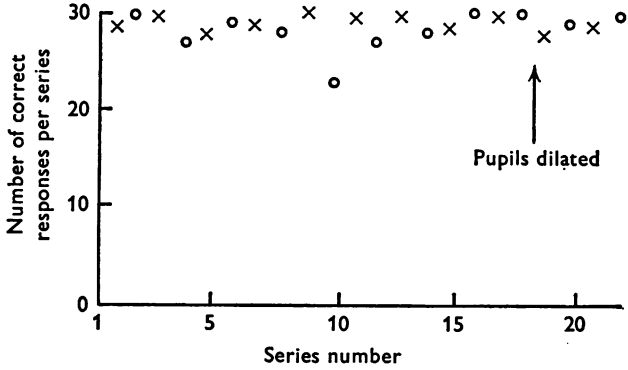
Eventually both cats gave a performance of better than 90 % with a set of slides against a white background of 2 cd/m^2. The set of slides was similar to that described before, with some reds or oranges equal in brightness to the cyan, some 4 times as bright, and some one quarter as bright. The stimuli were all between 10 and 100 times as bright as the background.

The brightness of the background was then increased by two log units to raise it above rod saturation. The brightness of the coloured circles was also increased by about 2 log units, so that the contrast between the coloured circles and the white background would not be reduced. Because of the Purkinje shift, the brightness of the coloured circles was not increased by exactly 2 log units; in fact, the brightness of the orange stimuli was increased 1·7 log units and the brightness of the cyan stimuli was increased 2·2 log units. After a few hundred trials against this high level of white background, both cats went to the positive stimulus more than 90 % of the time.

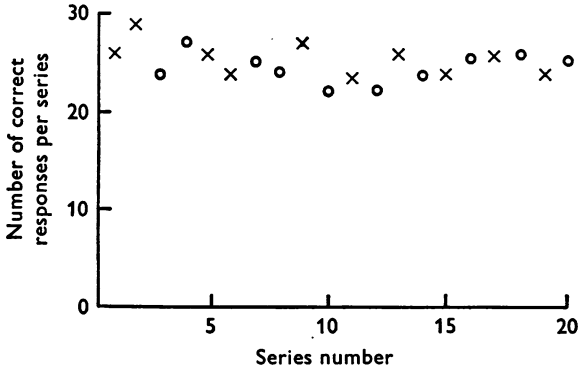
Each cat was then given alternate series against bright and dim white backgrounds. Text-fig. 4 shows the results for the second cat, trained to discriminate orange from cyan. The Figure is a plot of the number of correct responses per run of thirty trials. The crosses give the results for the stimuli seen against a background of 2 cd/m^2, which is a mesopic level, and the circles give the results for the stimuli seen against a background of 200 cd/m^2, which is a photopic level. The results show that the cat went to orange more than 90 % of the time at both levels.

Reducing the contrast between the coloured stimuli and the surrounding illumination produced a decrease in the cat's level of performance. To increase the ambient illumination, the testing box was lined with white paper and illuminated by white light of about the same intensity as the white background: this also added to the intensity of the white background by reflexion from the front surface of the Plexiglas, particularly

for directions of view other than from the centre of the arch. The cat's performance was reduced from 95 to 80%, at both the mesopic level and the photopic level (see Text-fig. 5). Thus it would seem that the ability to discriminate wave-length is weak for the cat if the stimuli are not much brighter than the background.



Text-fig. 4. Number of correct responses per series of thirty trials in a discrimination between orange and cyan, the orange being rewarded. Crosses give the results at a mesopic level; circles give the results at a photopic level. The last four points were taken with pupils dilated and accommodation paralysed with atropine.



Text-fig. 5. Number of correct responses per series of thirty trials with same stimuli as Text-fig. 4, against a slightly brighter background and with brighter ambient illumination.

One cat was also tested after being exposed to a bright white light of 9000 cd/m^2 for a period of 5 min. The pupil of one eye was dilated with atropine; the other eye was covered by a black contact lens. The uncovered eye was held open, facing a white card in sunlight. Upon transfer back to the test box and retesting on the red-cyan discrimination, there was satisfactory performance during the course of the first 5 min.

Several control experiments were carried out in order to be certain that the discrimination was based on colour and not on other cues. Cues related to some optical property such as chromatic aberration were eliminated by putting the coloured circles out of focus, and also by dilating the pupils and paralysing accommodation with atropine placed in the conjunctival sac. Points on the far right in Text-fig. 4 were obtained with pupils dilated; neither putting the stimuli out of focus nor dilating the pupils altered the cat's performance at mesopic or photopic levels.

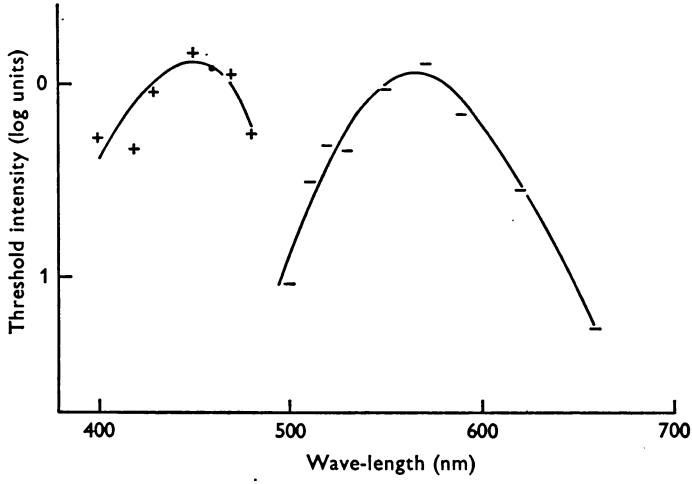
Altering the order of slide presentations or completely exchanging the slides in the left projector with those in the right projector had no effect on performance. Finally, to eliminate the possibility that the cat was responding to some extraneous cue such as noise from the relay racks or projectors, the cyan slides were all replaced with orange, while the original orange slide in the pair continued to be the rewarded stimulus. When this substitution was made, performance fell to 60%.

Lateral geniculate recordings. The behavioural experiments show that the cat can make a colour discrimination as easily at the photopic level, above rod saturation, as he can at mesopic level between cone threshold and rod saturation. This result indicates that there is more than one type of cone involved, contrary to the suggestion made by us in a previous paper (Daw & Pearlman, 1969). We therefore undertook further micro-electrode recordings from single units in the lateral geniculate and optic tract.

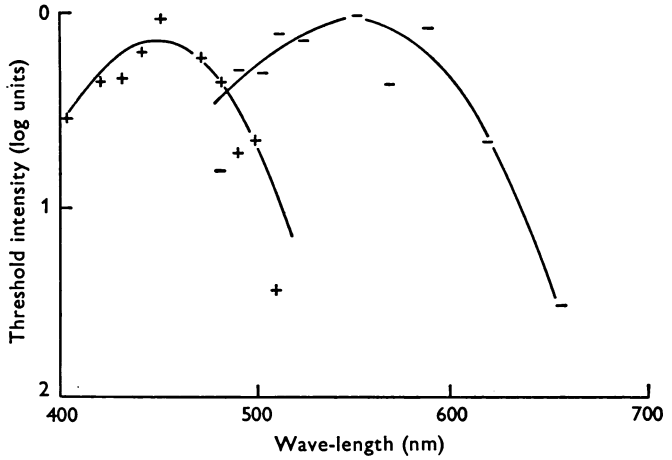
A preliminary report of these results has been made elsewhere (Pearlman & Daw, 1970). The vast majority of single units in the lateral geniculate body are found to have input from a single type of cone with spectral sensitivity peaking at 556 nm. However, an occasional unit is found with input from two cone types, connected to the unit in an opponent manner. Four such units were found in a sample of 434 units recorded in thirty-one electrode penetrations in nine cats. All four gave an 'on' response to blue light in the centre of their receptive fields and an 'off' response to green and red light. Two were double opponent cells like those described in the goldfish retina (Daw, 1968), and in the monkey cortex (Hubel & Wiesel, 1968); they were also inhibited by blue light and excited by green light in the periphery of their receptive fields. One of the other two may also have been a double opponent cell, but definite evidence was not obtained on this point.

The spectral sensitivity of one of these units tested against a white background of 30 cd/m^2 is shown in Text-fig. 6. When the spectral sensitivity is measured against a coloured background, it gives a better indication of the cone pigments involved. Spectral sensitivity for the 'on' process for the unit of Text-fig. 6 was therefore measured against a bright orange background, and the spectral sensitivity for the 'off' process was measured

against a bright blue background. The results are shown in Text-fig. 7. The curve drawn through the points for the 'on' process is the Dartnall nomogram for a pigment peaking at 455 nm. The curve drawn through the points for the 'off' process comes from measurements on non-colour-



Text-fig. 6. Spectral sensitivity of a lateral geniculate opponent colour unit against a background of 30 cd/m². Plusses give thresholds for 'on' responses; minuses give threshold for 'off' responses.



Text-fig. 7. Spectral sensitivities for a lateral geniculate opponent colour unit against coloured backgrounds. Unit same as in Text-fig. 6. Plusses give thresholds for 'on' responses against an orange background (Wratten No. 22). The associated curve is the Dartnall nomogram for a pigment peaking at 445 nm. Minuses give the 'off' responses against a blue background (Wratten No. 47). The associated curve is the curve for non-colour-opponent geniculate cells in the light adapted state.

coded geniculate cells in the light adapted state. This curve is slightly narrower than the Dartnall nomogram for a cone pigment peaking at 556 nm (Daw & Pearlman, 1969).

The sample of 434 single units included 128 cells from layer A, 131 from layer A_1, eighty-seven responding to stimuli in the contralateral eye in layer B (layer C of Guillery, 1970), four cells below this responding to the ipsilateral eye (layer C_1 of Guillery, 1970), forty-four fibres in the optic tract and four fibres in the optic radiation. The anatomical position of thirty-six units could not be identified, in most cases because they were fibres recorded within the lateral geniculate. The position of the four colour-coded units was determined in each case by making a lesion, and observing the lesion in Nissl stained serial sections (Pl. 1). All four units were found to be in layer B, and all responded to the contralateral eye.

DISCUSSION

The behavioural results show that the cat can discriminate colour at a photopic level above rod saturation. Explanations of the discrimination based on chromatic aberration or some other optical effect associated with wave-length were ruled out by appropriate controls. Consequently, the cat must have more than one type of cone.

The subsequent search for physiological evidence demonstrated rare opponent colour units in layer B of the dorsal nucleus of the lateral geniculate body with input from blue-absorbing cones as well as input from green-absorbing cones. These green-absorbing cones have the same spectral sensitivity as those which provide input to the vast majority of lateral geniculate cells which are not opponent colour. No evidence was found for any input from red-absorbing cones in our sample of 434 units, although the possibility remains that further study might demonstrate their existence.

The paucity of opponent colour units in the lateral geniculate of the cat agrees with Granit's early results on the ganglion cells of the retina. Granit measured the spectral sensitivity of a number of units in the light and dark adapted state and found only one modulator when the measurements were made against an achromatic background (Granit, 1945, 1950). In his later work he found dark-adapted units which had a lower threshold for 460 nm than 650 nm of equal brightness for visual purple. These units may have reflected the activity of blue-absorbing cones (Granit & Tansley, 1948). It is interesting that only on-elements showed this property, and that all the lateral geniculate units which we found to be colour-coded gave an 'on' response to blue in the centre of their receptive fields. The blue-absorbing pigment may well be that revealed by Weale (1955) in reflexion densi-

tometry measurements. Granit's so-called 'red modulators' in the cat were probably measurements made in the mesopic state with the visual purple curve subtracted.

It is interesting that the cat could not make colour discriminations unless the colours were very much brighter than the white background and the level of ambient illumination. Colour discriminations were poor when the colours were as much as 5–10 times as bright as the background and appeared highly saturated to a human observer. At this level light passed by the cyan filter is approximately ten times as bright as the white background in terms of its effect on the blue-absorbing cones. It may well be that the blue cones do not function strongly enough for the cat to make a colour discrimination unless the stimulus is several times as bright as the background, although threshold for the non-opponent units in the lateral geniculate which receive input from green-absorbing cones alone is reached when the stimulus is only 1/30 as bright as the background. Unfortunately, we were not able to measure the Weber fraction for the blue process in the colour opponent cells accurately.

Recent fibre degeneration studies by Guillery (1970) indicate that the cat lateral geniculate has five layers rather than three. Within the most ventral layer, which has conventionally been called layer B (Thuma, 1928), Guillery describes a layer of cells with input from the contralateral eye (C), another with input from the ipsilateral eye (C_1) and a third with no direct input from the optic tract (C_2). We recorded from four cells in layer B that received input from the ipsilateral eye, thus confirming Guillery's anatomical evidence for layer C_1. Two of these cells were found in the electrode track shown in Pl. 1: both were recorded after the lesion was made and the electrode advanced slightly.

None of the four cells in layer C_1 was colour-coded, and only four of the eighty-seven cells found in layer C were colour-coded. None of the 259 cells recorded in layers A or A_1 were colour-coded. While there appears to be some aspect of colour associated with the layering, it is clearly not the case that layer C is exclusively concerned with colour (Le Cros Clark, 1949).

The presently available evidence suggests that the cat is a dichromat, and a tritanomalous protanope. Now that the level of rod saturation is known with some certainty, the spectral sensitivity of the green pigment is known very accurately, and the spectral sensitivity of the blue pigment is known approximately, it is possible to devise further behavioural studies to test whether the cat is a dichromat or a trichromat. If the latter proves to be the case, a more strenuous search for physiological evidence of a red cone may be justified.

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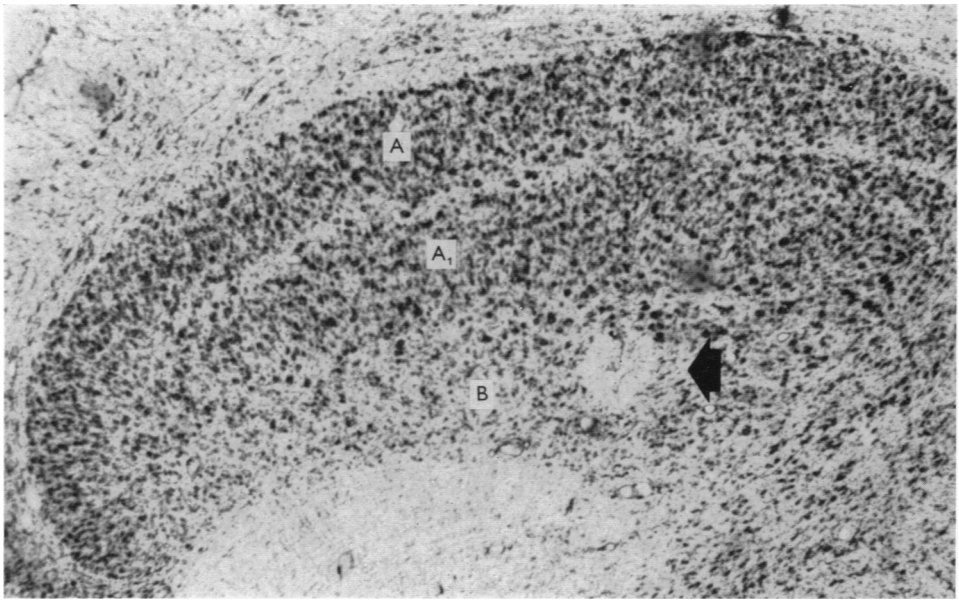
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EXPLANATION OF PLATE

Coronal section through cat lateral geniculate body. Arrow points to a lesion, made where recordings were taken from a colour-coded cell. The electrode track can be seen above the lesion. Just below the lesion two cells responding to stimuli in the ipsilateral eye were recorded. Letters A, A_1 and B mark the layers of the body.