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THE CONTRAST SENSITIVITY OF THE CAT

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SUMMARY

1. The experiments were carried out on pretrigeminal cats.

2. By recording potentials evoked from the visual cortex by a grating stimulus, it was established that there was a linear relation between the voltage generated and the logarithm of the contrast of the grating.

3. The voltage evoked by the grating was independent of the orientation of the grating.

4. It has previously been shown in man that, if the contrast is determined by an extrapolation to the point at which a zero voltage occurs, this value corresponds to the psychophysical threshold. On the assumption that the threshold of the cat also occurs at zero voltage, thresholds for a number of spatial frequencies and orientations were determined.

5. When the threshold sensitivity function for the cat is compared with man it is found to be displaced to lower spatial frequencies by a factor of about ten. This means that while the cat cannot see such high spatial frequencies as man, it can see lower frequencies better than man.

INTRODUCTION

By means of a behavioural method, Smith (1936) found that cats could distinguish between vertical and horizontal gratings composed of equal width black and white bars at a spatial frequency of 5·5 c/deg. Although he did not test with gratings of higher spatial frequency, it seems unlikely that the cat's resolution limit was much higher for the performance of the cat appears to have been impaired at this frequency compared with coarser gratings. Man can resolve such a grating at a frequency of 50 c/deg.

Using a grating stimulus and measuring the response of single ganglion cells, Enroth-Cugell & Robson (1966) estimated that their cell with the highest resolving power might well be able to just detect a spatial frequency of about 5·5 c/deg. Campbell, Cooper & Enroth-Cugell (1969) extended these studies to the responses of geniculate fibres and to cortical neurones. They likewise found that the upper limit was about 4 c/deg. Recently it has been established that the neurones which are selective to spatial frequency are the simple neurones and not the complex neurones (Fiorentini & Maffei, 1973).

A valid objection to these studies on single neurones is that the experimental recording technique might be such that neurones responding to much higher special frequencies could be missed because, for example, higher frequencies might be transmitted by neurones from which it is difficult to record. An alternative approach, free from this objection, has been developed by Campbell & Maffei (1970). Using the evoked potential, they were able to show that there was very good agreement between the psychophysical measure of contrast threshold and the objective measure obtained with the evoked potential in man.

In this paper we extend the evoked potential technique to the cat in order to investigate the spatial characteristics of its visual system. We discuss the relevance of comparing the performance of the cat with that of the human.

METHODS

The experiments were performed on ten adult cats in which the brain stem was sectioned immediately rostral to the exit of the fifth nerve (Batini, Moruzzi, Palestini, Rossi & Zanchetti, 1959). To prevent eye movements, the animals were paralysed by curare and, therefore, artificial respiration was used. The CO_2 content of the expiratory air was continuously monitored by means of a Beckman gas analyser.

Pupils were dilated with atropine and contact lenses applied. One of the advantages of using a contact lens is that it removes any corneal astigmatism. Artificial pupils of 6 mm diameter were used. The refraction of the cat's eye was carefully determined by means of retinoscopy and corrected with suitable spectacle lenses in front of the eye. Great care was taken to keep the contact lens and the cornea clear throughout the experiment. The refraction was determined electrophysiologically by finding the lens power which gives the best resolution for a high frequency grating.

The optic nerve head of one eye was projected, by means of an inverting ophthalmoscope, on to a tangent screen 24 cm from the cat's eye. The position of the area centralis was computed from data provided by Bishop, Kozak & Vakkur (1962). Once the position of the area centralis was determined, the tangent screen was replaced by the screen of the oscilloscope. Great care was taken to place the centre of the oscilloscope screen on the area centralis of one eye. The other eye was covered.

On the screen of the oscilloscope a sinusoidal grating was generated, the contrast and spatial frequency of which could be varied. The phase of the sinusoidal grating was electronically alternated by 180 degrees with a temporal frequency of 8 Hz. The mean luminance of the screen was 2 cd/m^2 and was kept constant in all the experiments. The potential evoked by such stimuli was recorded by means of screws implanted in the skull above the cortical projection of the area centralis (area 17).

The recording was usually bipolar, and contralateral to the stimulated retina. Classical methods of amplification were used. The potentials were fed into a band-pass filter with a peak at 16 Hz. An averaging computer (CAT 400 C) was used to improve the signal-to-noise ratio.

The e.e.g. was monitored throughout the experiment. As is well known, the pre-trigeminal preparation shows a desynchronized e.e.g. pattern, sometimes replaced by slower waves. It was found that for a better repeatability of the evoked responses the cat's e.e.g. had to be desynchronized.

RESULTS

The basic principle of the method is the empirical finding of Campbell & Maffei (1970) that there exists a linear relation between the logarithm of the contrast of the grating used to evoke the response and the amplitude of the evoked voltage, and that if the relation is extrapolated to zero voltage it indicated the appropriate psychophysical threshold. Campbell & Kulikowski (1972) have re-examined these empirical findings with a better technique and they confirm that, in the human, this empirical technique is justified. We now investigated the use of this approach in the cat.

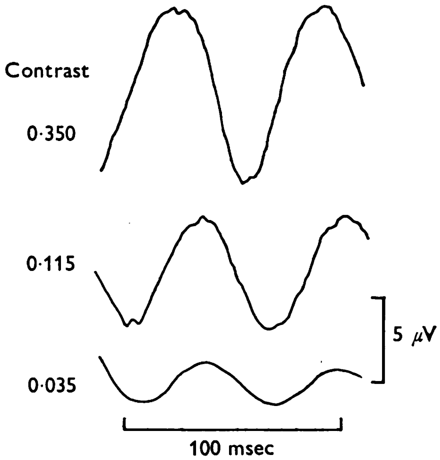

Fig. 1. Shows examples of the evoked responses obtained at various contrast levels. These are marked by arrows in Fig. 2.

The relation between contrast and the evoked potential

In this initial experiment the amplitude of the evoked potential was determined for a number of contrast levels over a range of spatial frequencies. Care was taken to ensure that the grating was always centered on the area centralis. A few examples of the wave forms that we obtained after averaging are shown in Fig. 1. The peak-to-trough amplitude of the voltage was measured in arbitrary units.

In Fig. 2 are shown the results obtained for various contrasts and various spatial frequencies. In Fig. 2*a* the three arrows indicate the three sample records shown in Fig. 1. In Fig. 2*b* the experiment was repeated for a second time (0) to show the degree of repeatability. A good indication of the reproducibility of these results is given by the regression coefficients found when the regression lines were fitted by the least-squares method. These were *A* 0·982; *B* 0·989; *C* 0·949; *D* 0·989.

We may conclude that the behaviour of the evoked potential in the cat is similar to that found in the human. That is, $V = \log (C/C_0)$, where V is the voltage evoked, C is the contrast used and C_0 is the contrast where the voltage is zero.

The over-all contrast sensitivity

In the human it was possible to determine the threshold and thus confirm this objective approach. Ideally we should now measure behaviourly the threshold for at least one spatial frequency for the cat. Assuming that the psychophysical threshold for the cat is represented by the contrast at zero voltage, we can proceed to determine the contrast sensitivity function for the cat.

It is important to note that we have used what we believe to be a threshold measurement to get the contrast sensitivity function for the cat. If a fixed contrast level is used and if the amplitude of the resulting evoked potential is taken as a measure of sensitivity, the same result would occur

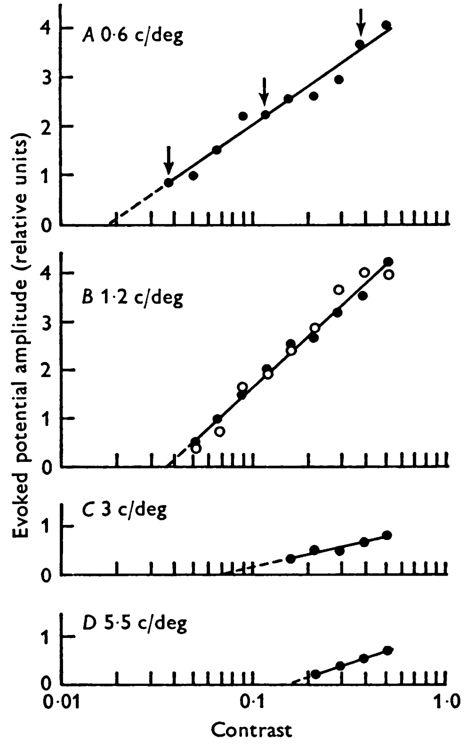

Fig. 2. Four examples of the relation between the voltage evoked by gratings at different contrast levels and at four spatial frequencies. In *B* the experiment was repeated twice to show the reliability of the data.

only if there was a linear relation between the evoked voltage and the contrast used to elicit the potential. But we know that the voltage is logarithmically related to the contrast. Furthermore, the slope of logarithmic function decreases with an increase in spatial frequency, as shown in Fig. 2. Berkley & Watkins (1971) used a fixed contrast and assumed linearity of response to obtain a Modulation Transfer Function. Their incorrect assumption makes it difficult to compare their results with ours. Agreement is expected, however, at the high spatial frequency cut-off point providing they started with a high contrast, which they did. They obtained 5 c/deg for this point. Because of the non-linearity they could not, and did not observe the low frequency attenuation.

The over-all contrast sensitivity for three cats is shown in Fig. 3. No significant difference was found between the cats. The Figure also shows the well established low and high frequency attenuation found in man and shown as open circles. In the cat the attenuation at higher frequencies is not so steep as in man. In both, the low frequency attenuation has a slope of 1. The results could be summarized by saying that the contrast sensitivity function for the cat is displaced to lower spatial frequencies by a factor of about 10.

Thus for a cat and a human to just detect an object of a given physical dimension, the cat would have to be 10 times closer to the object than the human. Because the contrast sensitivity of the cat is slightly less, the contrast of the object would have to be slightly greater.

As the posterior nodal distance of the cat is 12·5 mm (Vakkur, Bishop & Kozak, 1963) and the human is 16·7 mm, the size of the retinal image of the cat will only be 1·29 smaller than in the human; this factor is not great enough to account for our results.

The retinal image could become degraded by optical aberrations. While this could not account for the attenuation found at low spatial frequencies it might account for the attenuation at high frequencies. The most recent reviews and measurements of the quality of the retinal image formed by the dioptrics of the cat (Bonds, Enroth-Cugell & Pinto, 1972) lead to the conclusion that the attenuation of the contrast sensitivity at 5 c/deg is only slightly influenced by the quality of the optics. Bonds (1972) has kindly supplied us with a typical optical transfer function for a cat with an artificial pupil diameter of 3 mm. He used the technique developed by Campbell & Gubisch (1966) for measuring the line spread function in man. His result is shown as a thick continuous line in Fig. 3. Note that there is practically no attenuation for spatial frequencies lower than 0·5 c/deg. The optical transfer function has been positioned on the ordinate so that the flat, low frequency, section agrees with the peak contrast sensitivity for the cat. The optical quality of the retinal image in the cat is not so good as the human (Campbell & Gubish, 1966) but it is much better than the resolving power of the cat's visual system. Even at 5 c/deg the optics are attenuating the contrast only slightly.

In addition to the present electrophysiological evidence that the cat can respond to these spatial frequencies there is also direct neurophysiological evidence. For comparison, the results from single neurone studies have been added to Fig. 3, as follows:

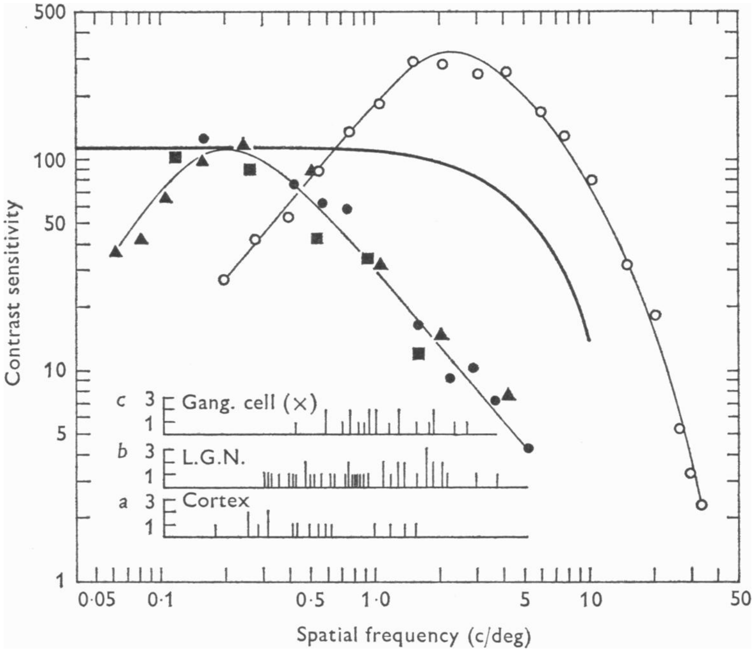

Fig. 3. The filled triangles, squares and circles are the 'contrast thresholds' (zero voltage contrast) for three cats. The curve has been fitted by eye. The open circles represent the contrast sensitivity measured monocularly in subject F.W.C. The thick line represents the optical transfer function of the dioptrics of a cat with a 3 mm diameter pupil as measured by A. B. Bonds. The inset is fully described in the text. The luminance of the screen used to obtain the data from the human was 500 cd/m^2, while that for the cat was 2 cd/m^2.

a is the position in the spatial frequency spectrum for a number of cortical neurones that were also selective to orientation (Campbell, Cooper & Enroth-Cugell, 1969). Neurones to the left responded to low spatial frequency gratings and neurones to the right responded to high. *b* is a similar plot of the spatial tuning of neurones from the lateral geniculate neurones by the same authors. *c* is likewise the position of ganglion cells that have a steady discharge and behave linearly (X-type, linear and sustained) from Enroth-Cugell & Robson (1966).

There appear to be neurones present at all frequencies in the range from 0·2 to 4 c/deg; that is, the high frequency region.

Sensitivity to different orientations

The previous experiments were done with a vertical grating. Now the grating is rotated in steps of 10° or 15° and the amplitude of the evoked potential is measured for each orientation. The results for these spatial frequencies are shown in Fig. 4. It is rather difficult to see the details of the fluctuations in the data for the higher frequencies. This difficulty can be overcome by finding the mean voltage generated for each spatial frequency and normalizing the data. This has been done in Fig. 5. The line is drawn through the normalized mean. It will be noted that the data fluctuate randomly around the mean and that there is no difference between each of the three frequencies. More important, the oblique orientations 45° and 135° are not different from the other orientations.

DISCUSSION

Contrast sensitivity in different orientations

In man, many psychophysical studies have shown that visual resolution in the vertical and horizontal axes of the visual field is slightly better than in either of the oblique axes (see Howard & Tempelton, 1966 for review). This also applies to grating targets, providing the spatial frequency is higher than 3 c/deg; the contrast sensitivity is higher for a vertical or horizontal grating when compared with either oblique orientation (Campbell, Kulikowksi & Levinson, 1966). These authors also demonstrated, by laser interferometry, that this phenomenon cannot be due to the properties of the optics of the eye. Maffei & Campbell (1970) have strengthened this evidence by showing that the orientation of a grating does not affect the amplitude of an evoked electroretinogram, although it does affect the amplitude of the evoked potential recorded from the occipital scalp. In the latter instance the change in amplitude agreed quantitatively with the change in threshold for the different orientations of the grating. They concluded that this orientational phenomenon must arise between the site of origin of the electroretinogram and the electrocorticogram.

In the cat and monkey, the discovery by Hubel & Wiesel (1959, 1962, 1965 and 1968) of cortical neurones selective to orientation has suggested to many that the psychophysical effects in man may be due to an increased number of neurones subserving the vertical and horizontal orientations compared with the oblique orientations. Alternatively, the vertical and horizontal orientations may have a superior performance because the neurones in these orientations are more highly selective for orientation – a suggestion that would fit with psychophysical measurements of this orientational selectivity (Campbell & Kulikowski, 1966).

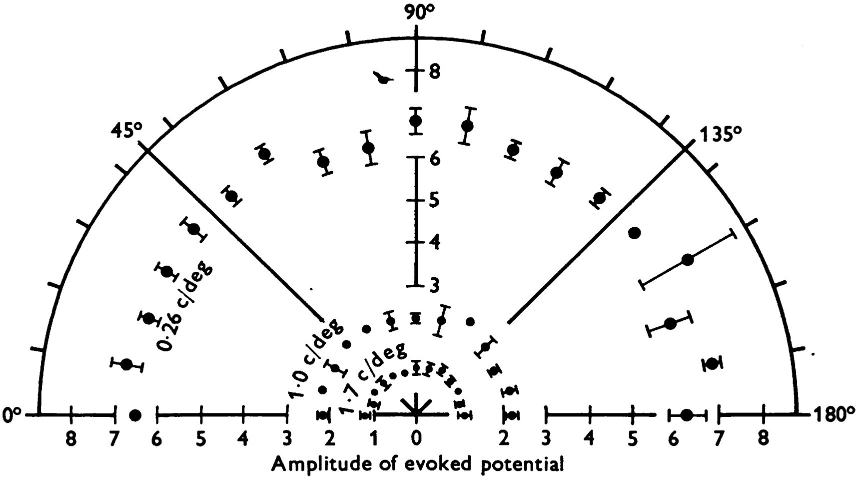

Fig. 4. Shows the amplitude of the evoked potential measured when the grating was at different orientations, for the three frequencies 0·26, 1·0 and 1·7 c/deg. The contrast was fixed at 0·5. The lines represent ± 1 S.E. When no line is present the S.E. was very small or zero. N varied from 3 to 5.

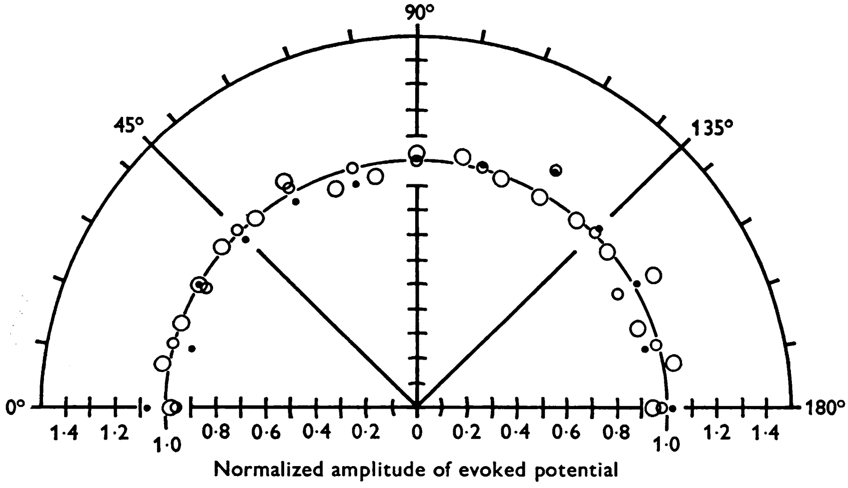

Fig. 5. Shows the same data as Fig. 4. but the results have been normalized to the mean of each spatial frequency to show better the scatter of the data. The line is the normalization ratio of 1.

Indeed in the cat, Pettigrew, Nikara & Bishop (1968) have found slightly more neurones subserving the vertical and horizontal axes. Hubel and Wiesel, with a much larger sample, have not found this axes preference in cortical neurones in the monkey or in the cat. A difficult sampling problem arises here because, as the electrode runs vertically down a column, neurones are recorded with a very similar preferred orientation and thus non-random sampling is occurring which makes statistical analysis difficult. The evoked potential technique is at an advantage here for it is likely to sample evenly all orientations. Indeed, the agreement between the evoked potential findings and the psychophysics in man supports this assumption (Maffei & Campbell, 1970).

Our present finding that this orientational preference is not found in the cat suggests that there exists a real species difference, although it is still possible to criticize this conclusion on the grounds that the evoked potential in the cat is arising mainly from the terminations of the geniculate fibres in the cortex and hardly at all from the cortical neurones selectively sensitive to orientation. This is unlikely, for if a cat is adapted to a high contrast grating at a given orientation and spatial frequency for some minutes, the potential evoked by this grating decreases considerably; it then slowly recovers with a time constant of 25–30 sec. This adaptation does not occur if the test grating differs either in orientation or spatial frequency (M. Piccolino & L. Maffei, in preparation). Thus, in the cat, some of the potential evoked with grating patterns must be arising at, or subsequent to, the site of these orientation selective neurones – a conclusion also reached by Campbell & Maffei (1970) in the human where they depressed the sensitivity of a given orientation by adaptation to a high contrast grating of that orientation.

Can one account for some cats having more neurones tuned to vertical and horizontal and others not? It has been established that if a kitten is brought up in a visual environment containing a grating of one given orientation only the neurones subserving that orientation develop. These remain functional into adult life (Hirsh & Spinelli, 1970, 1971; Blakemore & Cooper, 1970). It is conceivable therefore that some kittens, growing in say a cage with vertical and horizontal bars, could show some dominance of these orientations. This may account for the findings on the Canberra cats. The Boston and Pisa kittens may have matured in a natural visual environment containing objects with a random distribution of orientations.

We know that the early visual environment in man is also important, for recent studies of patients with a history of astigmatism, uncorrected in childhood, show that the orientation that gives the best acuity coincides with the orientation of the focal line that is closest to the retina when the eye was uncorrected. Conversely the poorest acuity is obtained for gratings whose orientation is at right angles to that of the most focused of the focal lines (Freeman, Mitchell & Millodot, 1972). They used the technique of Campbell & Green (1965) to bypass the effects of the dioptrics with Thomas Young interference fringes. Thus, it may be that the early visual environment may account for some cats being different from other cats and for most cats being different from man.

Contrast sensitivity at different spatial frequencies

We now consider what the visual environment looks like to the cat. Start with the familiar situation where we inspect an optician's test chart from a distance of 6 m. With normal eyesight we can easily read the 6 m line; that is, our visual acuity equals 6/6. The maximum resolving power of the cat is lower by a factor of about 10, so the cat 'could read' only the large letter at the top – the letter that can be read by us at 60 m (V. A. = 6/60). Now we can readily test a simulation of this situation by placing + 3 dioptre lenses in front of our eyes, in order to render them so myopic that we can only discern the 60 m letter at 6 m.

But is this a fair simulation of what the cat sees? When we look at a distant scene with this degree of myopia, we note that everything is very blurred, even the objects that we can discriminate. The reason for this is that the myopic optics acts as a spatial filter which attenuates the higher spatial frequencies relatively more than the lower frequencies (Green & Campbell, 1965). Thus, the sensation of blurring can be interpreted as a lack of activity in those neurones which transmit the higher spatial frequencies relative to the activity in the neurones attuned to the lower spatial frequencies. But the cat does not possess neurones attuned to these higher frequencies and therefore its distant view cannot be blurred and cannot be simulated by our artificial myopia.

Instead of blurring our vision, let us look at the test chart through a pair of binoculars with a magnifying power of 10 times, but on this occasion look through them via the object lenses so that we get a reduction in size. Now we will only be able to read the 60 m letter and there will be no blurring as in the previous simulation. To read the 6 m line we would have to go 10 times closer to a distance of about half a metre, taking care to refocus the binoculars for the new distance to avoid blurring.

This optical analogy of cat vision is better than the blurring analogy for it describes mathematically the 10 times displacement of the sensitivity curves along the logarithmic spatial frequency axis in Fig. 3. The difficulty with a direct optical magnification transformation is that it introduces the complication of changes in perspective. At this stage it might be assumed that cat vision, just like our vision, is quite sharp and clear but that it is different from ours in that it is attuned to seeing objects well at a much closer range. If 'seeing well' means a mechanism for detecting low contrast objects at close range then the cat requires neurones responding to low spatial frequencies. We have noted that it does have neurones sensitive to spatial frequencies as low as 0·2 c/deg and that it does have a high contrast sensitivity at these lower frequencies (Fig. 3).

Comparison with human performance shows that the cat can see well down to much lower spatial frequencies than those to which we are able. It is difficult to accept that the visibility of some objects decreases as they come closer to our eyes. This point can be illustrated by examining the sinusoidal grating shown in (Pl. 1). The contrast of the grating is decreasing exponentially from a contrast of about 0·3 down to a contrast of about 0·001. These contrasts represent sensitivities of 3·3 and 1000 respectively. First view the grating from about 9 m and note that the high contrast portion of the grating can just be resolved (24 c/deg). Now approach the grating slowly and note that more and more of the grating becomes visible. Between 1 and 2 m most of the grating is visible (3–6 c/deg). Approach even nearer and note that the low contrast section becomes less visible.

A number of empirical facts are known about the resolving power of man for a variety of targets. While the contrast sensitivity function can predict some of the resolution limits, such as the threshold for thin lines (Campbell, Carpenter & Levinson, 1969), it cannot yet do so for all. However, it seems reasonable to consider how the cat might detect other types of objects using the simple assumption that only the factor of 10 displacement in its contrast sensitivity function is relevant.

Man can detect a 1′ black disk against a bright background. The cat should detect a disk of 10′ against the sky. Thus it should be able to detect the presence of a bird with a wing span of about 20 cm at a range of 60 m, although the details of the bird should not be visible. Likewise, at dusk, the cat should see the moon quite distinctly as a disk but the details on the surface of the moon will not be resolved. The moon subtends 30 min. The stars and the planets will all be less than the cat's effective point-spread-function so that they will all look the same and only vary in their brightness.

Although the analogy of looking through a 10 times optical glass the wrong way round takes us some way towards understanding the cat's visual system it does not answer the question of whether the cat sees everything 10 times smaller. Its visual system could well be wired up so that its perspective is just like ours.

The vision of the cat cannot be simply related to its body size for the squirrel monkey is smaller and yet has neurones covering a higher range of spatial frequencies (Campbell, Cooper, Robson & Sachs, 1969). It might be fruitful to use the evoked potential technique to study the visual performance of a number of animals, particularly ones that are assumed to have higher resolution than man, such as the eagle (Schlaer, 1972).

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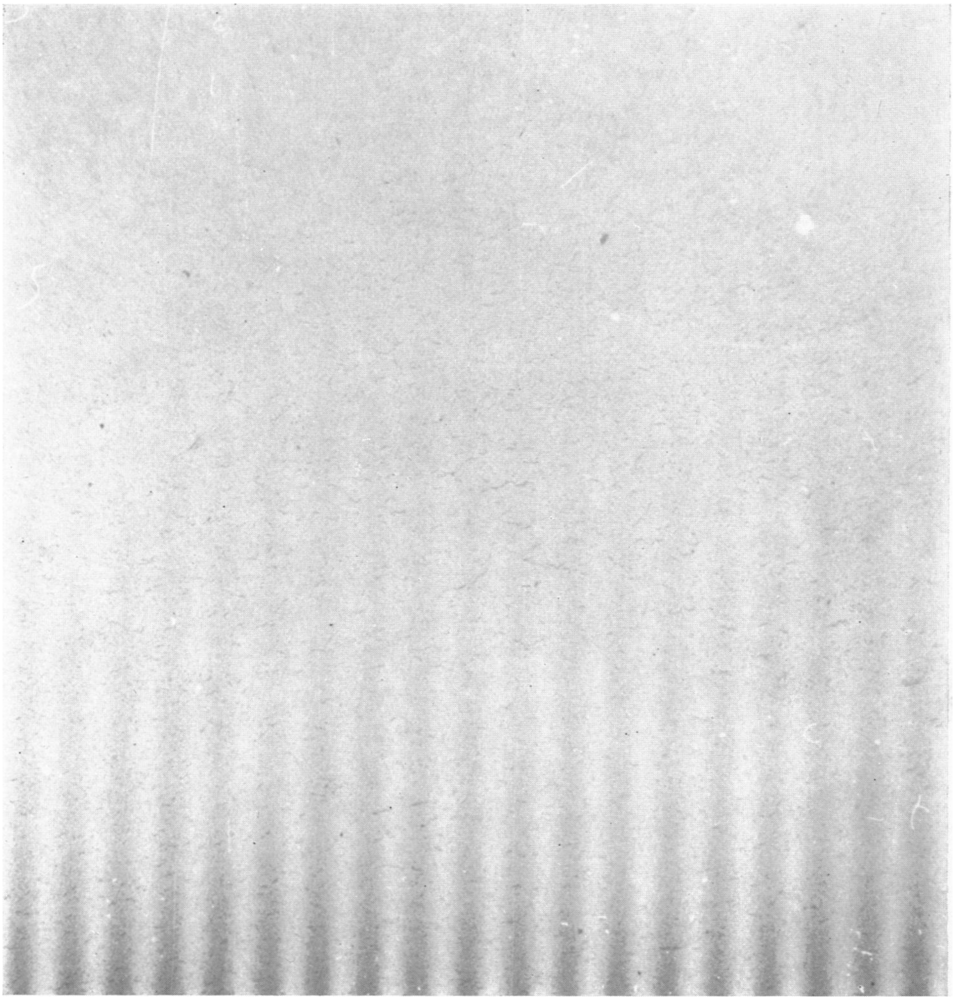

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EXPLANATION OF PLATE 1

The contrast of the sinusoidal grating is decreasing exponentially from a contrast of about 0·3–0·001. There are 1·5 c/cm.