BEHAVIOURAL CONTRAST SENSITIVITY OF THE CAT IN VARIOUS VISUAL MERIDIANS

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SUMMARY

1. The contrast sensitivity of the cat as a function of the spatial frequency of the visual stimulus was determined by using behavioural techniques.

2. No statistically significant difference was found for the contrast sensitivity thresholds at various orientations of the stimulus.

3. A comparison of the contrast sensitivity curve of the cat with that of the human shows that the two species have rather different characteristics of visual spatial resolution.

INTRODUCTION

The spatial performance of the visual system is best described by its contrast sensitivity function since this describes how the eye performs at all spatial frequencies. Recently Campbell & Maffei (1970) have been able to predict the psychophysical contrast threshold in man using electrophysiological methods. They recorded evoked potentials in response to a sinusoidal grating the phase of which was alternated in time. They found that the amplitude of the evoked potentials is linearly related to the logarithm of the contrast of the grating and that the extrapolation of the regression line between evoked potential amplitude and logarithm of contrast to zero voltage level, predicts the psychophysical threshold.

Campbell, Maffei & Piccolino (1973) have applied the same technique to the cat, finding again a linear relationship between evoked potential amplitude and the logarithm of contrast.

Assuming that the psychophysical threshold for the cat at each spatial frequency is represented by the contrast at zero voltage, as was the case for human subjects, they determined the contrast sensitivity function for the cat.

Following up this line of research we designed experiments to determine the contrast sensitivity function of the cat using behavioural methods. The results allow a comparison between the contrast threshold for the cat as predicted from the evoked potential data and the behavioural psychophysical threshold. The contrast sensitivity function has been determined for various orientations of the visual target to see whether the cat has a preference for a given visual axis, as man does for the vertical and horizontal meridians.

METHODS

Experiments were performed on four female cats; the results presented, however, are taken from only two of them. The subjects were restrained in a box, the walls of which were movable to fit the cat's body tightly (Fig. 1). The neck of the animal extended through an opening of the box and was partially fixed by a metallic collar rigid with the box which prevented gross head movements and maintained a constant orientation of the head toward the stimulus. A constant amount of liquid reward consisting of a mixture of milk, water and baby food, was delivered by a solenoid valve system through a metallic tube positioned in the mouth of the animal. The cat was free to push a pedal with its anterior paws (Fig. 1). The cats were under a 20 hr water and food deprivation schedule.

The animal faced an oscilloscope which was 30 cm from its eyes. The oscilloscope subtended 19°, and had an average luminance of 2 cd/m². Sinusoidal gratings of various spatial frequencies, contrast and orientation could be generated on the face of the oscilloscope using a modified version of the technique used by Campbell & Green (1965). The gratings were presented electronically for the desired periods, usually 2 or 4 sec. The contrast of the grating could be changed by means of a potentiometer from a value of 60 % to zero (blank stimulus) without changing the average luminance. The contrast of the grating is here defined as

$$C_0 = \frac{L_{max} - L_{min}}{L_{max} + L_{min}},$$

where L_{max} and L_{min} are the maximum and minimum luminance respectively.

Training of animals. Initially the subjects were trained daily, 7 days a week to push the pedal to receive a reward. In a second stage the animal was trained to push the pedal only when a grating of high contrast appeared on the scope and not to push it during intervals. This part of the experiment proved to be very laborious and took several months. It was very successful for two cats, partially successful for other two, but practically failed in three other cats. In this stage of training we used some types of punishment, such as prolongation of the intervals between presentations or interruption of the experiment for a few minutes. In a few instances we also used mild electric shocks delivered through the pedal.

The time of presentation of the grating was progressively shortened down to 4 or 2 sec, while the intervals were lengthened up to 20–30 sec. Also the contrast was progressively lowered. When the animal had learned to push the pedal during at least 90 % of the grating presentations and not to push it during intervals the data began to be collected.

Procedure. The experimenter started each cycle of the experiment with a warning acoustic signal to call the attention of the animal to the screen of the scope. From this moment the experiment proceeded automatically. After a random interval,

between 2 and 10 sec from the warning signal a grating selected randomly from six of various contrast (blank included) was presented for 2 or 4 sec. If the animal pushed the pedal during this period it received a reward (positive response).

For each session forty-eight trials, eight of each contrast, were made. The total number of trials, the number of trials for which the animal received a reward, and the number of mistakes (presses during intervals) were counted by a special-purpose device. The experimental sessions during which the animal made more than 10% mistakes (presses during intervals) were discarded.
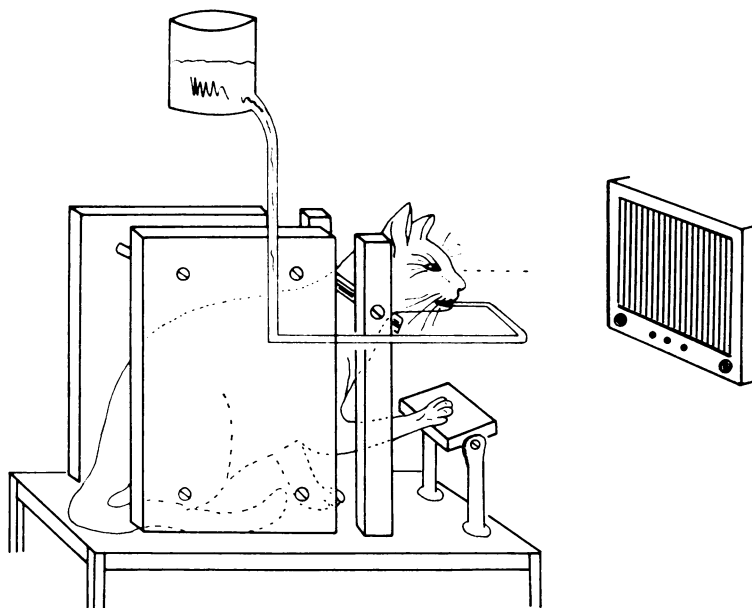

Fig. 1. Schematic diagram of the experimental set up
(for explanations see text).

The animals were not prevented from making small head or eye movements. Thus no valid statement concerning the exact retinal locus of the stimulus can be made. The experimenter did observe, however, that all cats maintained their gaze oriented toward the test stimulus.

RESULTS

Contrast sensitivity function

We have reported in Fig. 2, for one animal, the psychometric functions relating percent positive responses to the contrast of vertical gratings of various spatial frequencies. Each point of the curves is the probability of a positive response, computed over at least forty trials performed in four or five experimental sessions. The percentage of positive responses is plotted on the ordinates in a normal probability scale and the contrast

on the abscissae in a linear scale. The lines through the experimental points were fitted by the least-squares method. We have taken as contrast threshold, at every spatial frequency, the value of the contrast corresponding to a 50 % probability of positive responses.
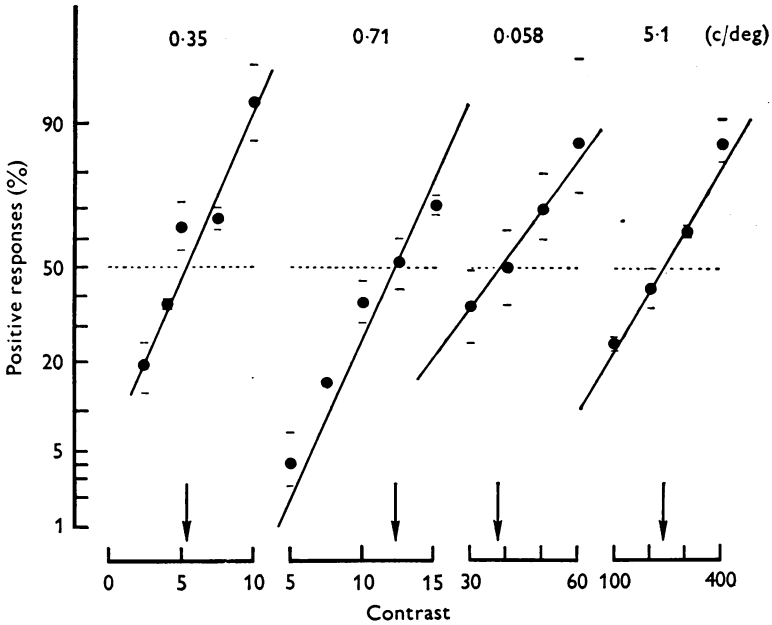

Fig. 2. Psychometric functions at various spatial frequencies for one animal. Each point is the probability of a correct response computed over forty-eight trials subdivided in six sessions. Standard errors among the six sessions are shown by horizontal lines reported. The arrows indicate the contrast thresholds and correspond to a probability of 50 % of positive responses. The line through the points has been calculated by the least-squares method.

All the contrast sensitivities (1/threshold) for two animals seeing vertical gratings are reported in Fig. 3 as a function of spatial frequency. The interrupted curve is the line fitting the contrast thresholds for the cat determined with the evoked potential technique (Campbell *et al.* 1973). Apart from some difference in the low spatial frequency range, the agreement between the electrophysiological and the behavioural results is remarkable. In Fig. 4 the experimental points of Fig. 3, have been replotted and fitted by eye with a continuous curve which represents the behavioural overall contrast sensitivity function for the cat. The maximum of contrast sensitivity is around 0·2 c/deg, while the fusion frequency is slightly above 5 c/deg. This figure is in a good agreement with electrophysiological results obtained both with evoked potentials

(Berkley & Watkins, 1973; Campbell *et al.* 1973) and single cell recordings. Indeed Maffei & Fiorentini (1973) have found that the maximum of visual resolution for the simple cells of the cat's striate cortex is 5 c/deg. In Fig. 3 we have reported also the contrast sensitivity for a human subject (L.M.) obtained in exactly the same experimental conditions. In these conditions our visual acuity is around 30 c/deg. On the other hand the
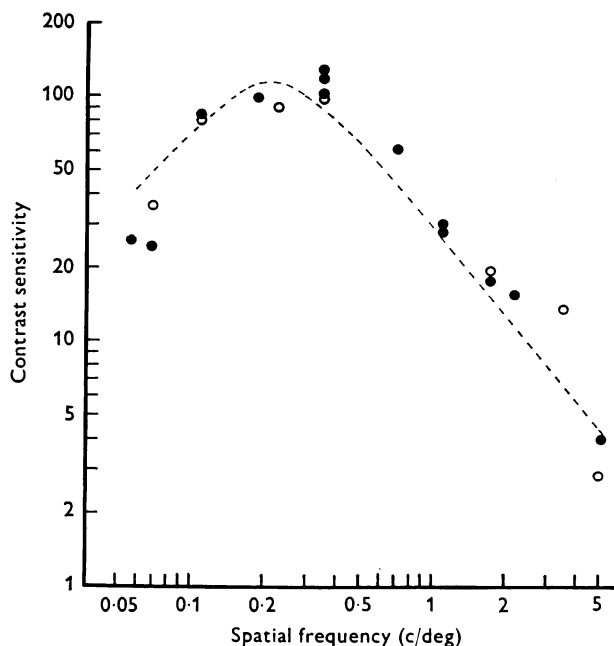

Fig. 3. Contrast sensitivities for two animals (filled and open circles) at various spatial frequencies. For 0·35 and 1 c/deg the contrast sensitivity has been tested 3 and 2 times respectively, with intervals of several weeks. The dotted line through the points is the contrast sensitivity curve determined with evoked potentials. It has been replotted from Campbell *et al.* 1973.

spatial resolution of the cat is better than ours at low spatial frequencies. In comparison with the human curve, that of the cat is displaced to lower spatial frequencies by a factor slightly less than ten; otherwise the two curves run approximately parallel. Our maximum contrast sensitivity, however, is better than the cat's (compare the peaks of the two curves in Fig. 3). This difference probably does not depend on the cat's having a different threshold criterion, since its maximum contrast sensitivity obtained with behavioural and the evoked potential techniques is very similar.

Contrast sensitivity in different meridians

The previous experiments were done with the grating in the vertical position. The next question is to investigate whether the contrast sensitivity varies with the orientation of the grating, as is the case for man (Campbell & Kulikowski, 1966; Campbell, Kulikowski & Levinson, 1966). We have tested four orientations (vertical (0°), horizontal (90°), 45° and −45°) at three spatial frequencies (0·35; 1·1; 2·2 c/deg). We have not found any statistically significant difference in the contrast sensitivity
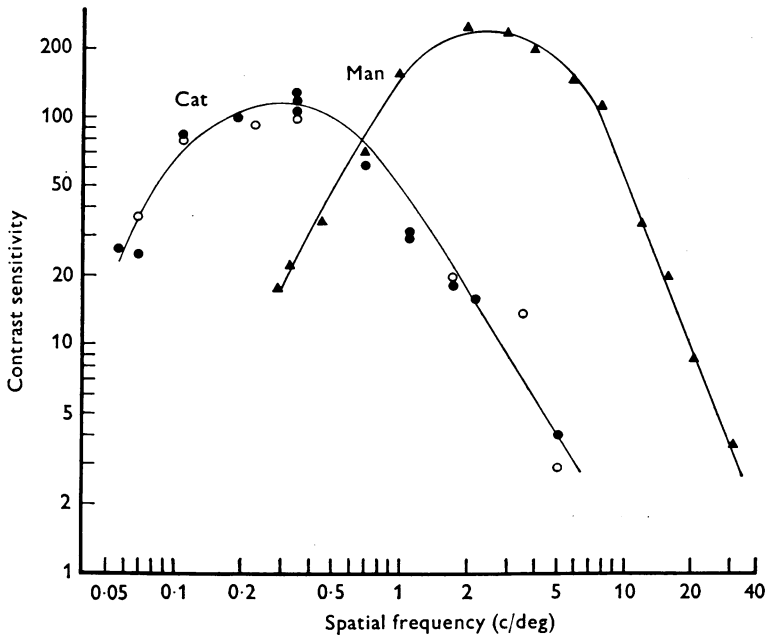

Fig. 4. Comparison of the contrast sensitivity curves of the cat and of a human subject (L.M.) in similar experimental conditions.

thresholds at the various orientations. The psychometric functions for the spatial frequency 1·1 c/deg at different orientations are reported in Fig. 5 for one animal. Similar results have been obtained in another one. The contrast thresholds for the oblique (45° and −45°), the vertical (0°) and the horizontal orientations are remarkably similar. The results for various spatial frequencies are summarized in Fig. 6 where the log contrast threshold has been reported in polar co-ordinates.

In bright light the cat shows a very narrow slit pupil which could affect differently the visual performance in the various meridians. In our experiment the animal pupil was approximately elliptical with a

horizontal diameter of about 5 mm and a vertical diameter of about 8 mm. This pupil size in close to that used when recording evoked potentials (artificial pupil with a diameter of 6 mm). Such anisotropy of the pupil could still theoretically impair visual performance by a
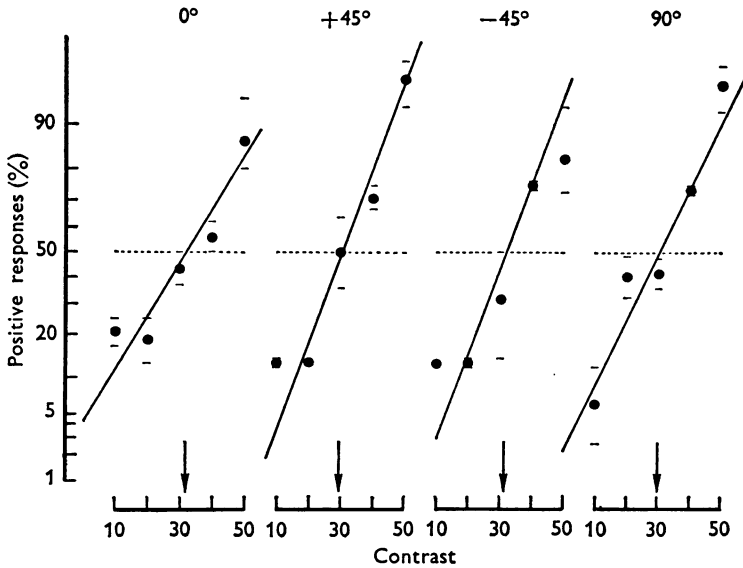
Fig. 5. Psychometric functions for different orientations of the stimulus (0°, +45°, −45°, 90°) in one animal. Spatial frequency 1·1 c/deg. For other explanations see Fig. 2.
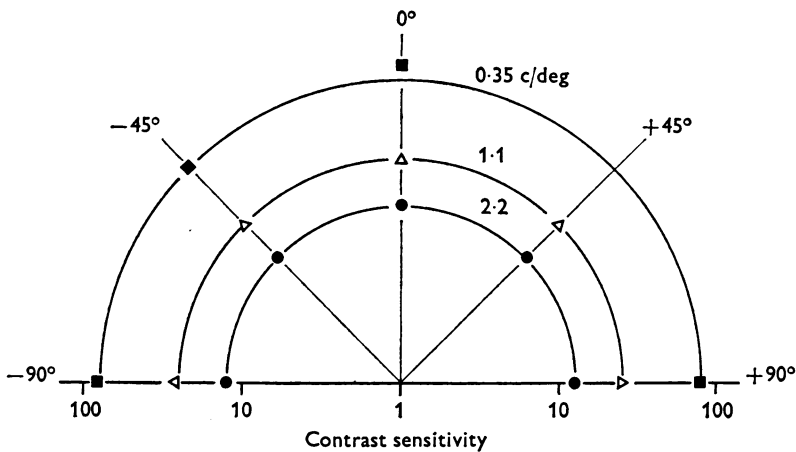
Fig. 6. Contrast sensitivities for various orientations at three different spatial frequencies.

different amount in the horizontal meridian as compared with the vertical, especially when the eye is not well focused on the target. In our experimental conditions, however, this effect does not seem to be detectable.

DISCUSSION

Campbell & Maffei (1970) showed in man the existence of a linear relationship between amplitude of evoked potentials in response to oscillating grating and log contrast. The extrapolation of the regression line between the amplitude of evoked potentials and log contrast crossed the contrast axis in a value corresponding to the psychophysical threshold. Campbell *et al.* (1973) found the same logarithmic relationship between amplitude of evoked potentials and contrast in the cat and, assuming that the extrapolation of the regression line had the same properties as in man, determined the contrast sensitivity function of the cat. The present results (Figs. 3 and 4) which show a remarkable agreement between the contrast thresholds obtained using behavioural techniques and those predicted on the basis of evoked potentials demonstrate that their assumption was, at least from the operational point of view, correct. We consider that the technique of evoked potentials in response to sinusoidal gratings is a promising, powerful tool, much faster and simpler than behavioural techniques to study the spatial visual performance of many other animals.

The comparison of the contrast sensitivity curve of the cat with that of the human has shown that the two species have rather different characteristics of visual spatial resolution. However, the displacement to lower spatial frequencies of the contrast sensitivity curve of the cat with respect of that of man does not mean that cat's vision is poorer than ours. It rather means that he uses another range of spatial frequencies, most probably matched to the distance at which the visual world appears to the cat more relevant. This point and the possible limits introduced by the optics of the eye (Bonds, 1972; Bonds, Enroth-Cugell & Pinto, 1972; Wässle, 1971; Wässle & Creutzfeldt, 1973) have been thoroughly discussed in a previous paper (Campbell *et al.* 1973).

Contrast sensitivity in different visual meridians

The resolving power of the human visual system is better in the vertical and horizontal orientations than in the two oblique ones. Maffei & Campbell (1970) have shown that in man the change in the amplitude of the evoked potentials in response to the presentation of a grating agrees quantitatively with the changes in the psychophysical thresholds

for the different orientations of the same stimulus. In the cat Pettigrew, Nikara & Bishop (1968) recording single neurons from the striate cortex found more neurones subserving the vertical and horizontal axes than the oblique ones. The behavioural experiments reported here (Fig. 6) show that the cat has an equal contrast sensitivity in every visual meridian that we have tested. The result is again in good agreement with evoked potentials (Campbell *et al.* 1973). It disagrees, however, with the single cell recordings by Pettigrew *et al.* (1968). The correlation between single cell recordings and behavioural results has been, however, often over emphasized. Let us consider, for example, the results of Blakemore & Cooper (1970) and Hirsch & Spinelli (1970, 1971). They have 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, the situation remaining practically invariant in the adult animal (Hirsch, 1972). The behavioural experiments, on the other hand, either have failed to show any preferred orientation for these animals, or have shown only a slight preference for the orientation to which the animals were adapted (Hirsch, 1972; Muir & Mitchell, 1973). In our opinion these and similar findings raise the question whether the orientational selectivity of cortical striate neurones is the only essential feature in the elaboration of the perception of orientation.

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Note added in proof. R. Blake, S. J. Cool & M. L. J. Crawford (personal communication) have recently obtained similar results for the contrast sensitivity of the cat.

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