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CONTRAST SENSITIVITY AND ACUITY OF A CONSCIOUS CAT MEASURED BY THE OCCIPITAL EVOKED POTENTIAL

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Abstract—The contrast sensitivity of an alert cat was derived from measurements of occipital potentials evoked by phase-alternating gratings. This contrast sensitivity function agreed well with that obtained from the same cat when anaesthetised. Evoked potentials were obtained from gratings of spatial frequencies up to 8.5 c/deg, and this is therefore a lower limit to the visual acuity of the cat.

INTRODUCTION

The question of how well cats are able to see has been approached by three main lines of research. Behavioural estimates of contrast sensitivity and acuity have been made by several workers (see Jacobson, Franklin and McDonald, 1976). The distribution of contrast sensitivity in a population of single neurones may be used as an indication of the variation of sensitivity to contrast with spatial frequency (contrast sensitivity function) at various stages of the visual pathway (see Enroth-Cugell and Robson, 1966, for the retina; Ikeda and Wright, 1975, 1976; Maffei and Fiorentini, 1973, for the lateral geniculate nucleus and visual cortex). Measurement of the occipital evoked potential is, however, the only physiological technique that has been used to obtain a complete estimate of the contrast sensitivity function of a cat's visual system. Campbell, Maffei and Piccolino (1973), recording the evoked potential from cats with the brain stem transected immediately rostral to the exit of the fifth nerve, predicted a high spatial frequency cut-off above that indicated by any other method of measuring the cat's acuity. Berkley and Watkins (1971, 1973), using anaesthetised cats, obtained a much lower estimate of acuity from their studies of evoked potentials, but the differences in results can largely be attributed to differences in technique.

I have estimated the contrast sensitivity function from evoked potentials recorded in an awake, alert cat. By using a chronically prepared, conscious animal any possible effects of brain stem transection or anaesthetics have been overcome. The EEG electrodes used to record the potentials were allowed to stabilize over a period of weeks before recording. Evoked potentials were measured in the same animal in both an alert and an anaesthetised condition, permitting a direct comparison between the two states.

METHODS

Preparation and maintenance of the cat

A docile female cat was anaesthetised with pentobarbitone sodium (Nembutal) and silver/silver chloride electrodes (Bond and Ho, 1970) were inserted as tight-fitting plugs in holes in the skull directly in contact with the dura above the visual cortex. Recording was bipolar, with both electrodes over the postlateral gyrus of the left hemisphere. These electrodes were connected, by teflon-insulated silver wire, to a small connector plug fixed on the skull with dental acrylic. Four bolts were also fixed to the skull (Evarts, 1968) to provide a means of attachment to a head-holder. The animal was then allowed to recover and left for a few weeks, to allow the implants and electrodes to stabilize.

During experimental sessions the cat was gently restrained in a padded box and her head held by a clamp attached to the implanted bolts (Blakemore and Donaghy, 1974). The animal was placed facing an oscilloscope screen on which gratings were displayed. After a few practice sessions in which the animal was familiarised with the equipment she would remain in the head-holder for quite long periods, up to an hour, showing no evidence of discomfort. The animal appeared very interested in the display and would tolerate long sessions without obvious drowsiness or distress. The state of the cat was continuously checked throughout each experimental run and if she showed signs of inattention the computer program controlling the visual stimulus could be interrupted and continued after the cat had been aroused, or her attention redirected to the screen.

When measurements had been made for a complete range of spatial frequencies with the cat awake she was anaesthetised with halothane, maintained on intravenous methohexitone sodium (Brietal), administered as necessary, and another set of measurements was obtained.

Visual stimulation and measurements of the evoked potentials

The stimuli were vertical gratings of sinusoidal luminance profile whose spatial phase was reversed at 10 Hz (20 reversals per sec). They were generated by established methods (Schade, 1956; Campbell and Green, 1965) on an oscilloscope screen with a mean luminance of 300 cd/m^2. At this brightness the pupils were constricted to a width of 1–2 mm which is normal for this luminance (Wilcox and Barlow, 1974) and this made it simple to judge adequately the direction of gaze to be sure that she was looking towards the screen. In fact the screen subtended an angular width of 58 deg (height 48 deg) at the usual viewing distance of 28 cm: so, since the cat's eyes rarely deviate by more than ± 20 deg from the centre of the orbit (Stryker and Blakemore, 1972), it was extremely unlikely that the gaze could shift completely off the screen. For measurements at spatial frequencies of 5.0 and 8.5 c/deg (cycles per degree of visual angle) the screen was moved to 57 cm and particular care was taken to check the animal's direction of gaze.

When the cat was anaesthetised the pupils were dilated by homatropine and her eyes were protected with best-fitting contact lenses containing 1.5 mm artificial pupils. The refractive state was corrected for the viewing distance by the addition of spectacle lenses whose power was determined by maximising the amplitude of the occipital potential evoked by a stimulus of fixed contrast and spatial frequency (Berkley and Watkins, 1973). The oscilloscope screen was centred on the projection of the area centralis of the right eye, determined by a reversible ophthalmoscope. The left eye was covered to avoid any complication of the results due to misalignment of the visual axes. This means that stimulation was monocular when the cat was anaesthetised and binocular when it was alert.

The constricted pupils had the added advantage of guaranteeing sharp imagery (Bonds, 1974) with good depth of focus; therefore the exact accommodative state of the cat was unlikely to have been a limiting factor.

The signal from the silver/silver chloride electrodes was amplified 10,000 times by an optically coupled EEG amplifier and the signal was then fed through a filter (Kemo VBF/3/J) with a passband of ± 3 Hz centred on the second harmonic (20 Hz) of the frequency of phase reversal. The filtered signal was fed through an analogue to digital converter (resolution 2.5 mV) into a PDP 11/10 computer which averaged the responses to successive phase reversals of the stimulus each sweep of the histogram including two reversals.

The computer maintained separate averages of the signals for each value of spatial frequency and contrast used.

The computer also controlled the spatial frequency and contrast of the patterns, which were varied randomly, in an interleaved sequence. Each particular presentation only lasted for 50 sweeps of the histogram, therefore every stimulus appeared 50 times in the sequence to produce a full histogram of 500 sweeps. Thus averaged evoked potentials for several stimuli were obtained simultaneously, minimizing the effects of any changes in the sensitivity of the preparation.

Sessions were included in which the screen was blank to determine the background noise level. The stimulus display and averaging procedure are the same as those previously described for measurements of evoked potentials in human infants (Harris, Atkinson and Braddick, 1976).

RESULTS

The evoked potential was measured for gratings having spatial frequencies between 0.14 and 8.5 c/deg, and for a rangee of Michelson contrasts from 0.02–0.5 for each spatial frequency. Contrast is defined as $(L_{max} - L_{min})/(L_{max} + L_{min})$, where L = luminance. The same animal was used in both alert and anaesthetised conditions and the same range of spatial frequencies and contrasts and number of sweeps were used in the two states.

Campbell and Maffei (1970) and Campbell and Kulikowski (1972) have shown in adult humans that extrapolation to zero potential of a graph of the amplitude of the evoked potential against the logarithm of the contrast of the stimulus produces an estimate of threshold contrast which agrees well with psychophysical estimates. The same seems to hold in infant humans, where evoked potentials and behavioural methods produce similar estimates of contrast sensitivity (Harris *et al.*, 1976).

Figure 1 shows typical plots relating the amplitude of the evoked potentials in the cat to the logarithm of the contrast of the stimulus. Results are illustrated for two spatial frequencies (0.4 and 8.5 c/deg) in both the anaesthetised (1a) and alert (1b) conditions. Also shown are 95% confidence limits, defined as $t_{n-2}\sqrt{\sigma^2}$ where t is the Student's t distribution for the 0.95 level, σ is the standard deviation for each value of the log. contrast and n is the number of points for each condition. The regression lines have been extrapolated to zero potential and these intercepts are taken as estimates of the contrast thresholds.

Figure 2 shows the estimated contrast sensitivity (reciprocal of the extrapolated threshold contrast) as a function of spatial frequency for both conditions (cat alert, cat anaesthetised). Included on this graph are the 95% confidence limits for the extrapolated threshold points. These were obtained by extrapolating by eye the 95% confidence limits boundaries for each spatial frequency (examples of which are shown in Fig. 1) until they crossed the abscissa. The estimates of sensitivity agree well with Campbell *et al.*'s (1973) derived contrast sensitivity function, shown as a continuous curve, and are in good agreement with some behavioural observations (Bisti and Maffei, 1974). The contrast sensitivity at 8.5 c/deg on this curve is predicted by an extrapolation of Campbell

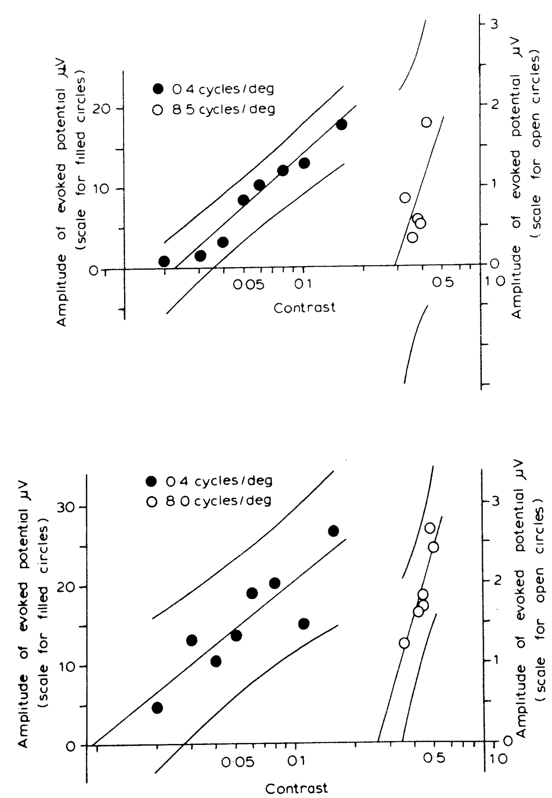

Fig. 1. This shows the relationship between the amplitude of the evoked potentials and the log contrast. Filled circles are from a spatial frequency of 0.4 c/deg and the open circles are from a spatial frequency of 8.5 c/deg. Fig. 1a is with the cat anaesthetised and Fig. 1b is with the cat awake and alert. The data points are bounded by 95% confidence limits (see text). Note the vertical scales are different for the open and filled circles.

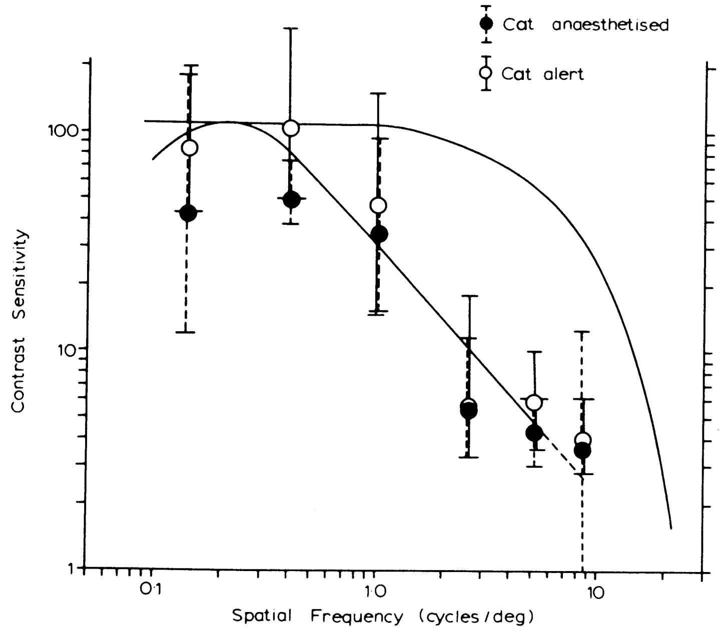

Fig. 2. The contrast sensitivity of the cat derived from measurements of the evoked potential (open circles: cat awake; filled circles: cat anaesthetised). The lower solid curve, through the points, has been redrawn from Campbell *et al.* (1973) and extrapolated (dotted section) to 8.5 c/deg. The 95% confidence limits (see text) are shown as solid lines for the awake condition (open circles) and as dotted lines for the anaesthetised condition (filled circles). The upper solid curve plots the optical transmission of the cat's eye measured through a 2 mm pupil (Enroth-Cugell and Robson, 1977) displaced on the ordinate to bring the two curves into contact at the peak of the contrast sensitivity.

*et al*s original curve and is consistent with behavioural observations by Jacobson *et al.* (1976) and Mitchell, Giffen and Timney (1977) that such high spatial frequencies are about the highest that can be resolved by the cat.

It is interesting to note that the estimates of contrast sensitivity are consistently slightly lower for the anaesthetised state (filled circles): the mean difference is 0.15 log units (S.D. = 0.09 l.u.). It is probable that this small discrepancy is not attributable to the state of the animal but to the fact that one eye was covered when the cat was anaesthetised. Campbell and Maffei (1970) have, in fact, shown that, in humans, the contrast threshold estimated by evoked potentials is reduced by a factor of $\sqrt{2}$ (0.15 l.u.) when one eye is covered. This point deserves further investigation in the conscious cat, but in this experiment it was thought to be an unacceptable distraction to the animal to cover one eye when it was conscious and restrained.

An extrapolation of this contrast sensitivity function (Fig. 2), obtained with the conventional zero potential criterion of contrast threshold (Campbell and Maffei, 1970) predicts a high spatial frequency cut-off of about 20 c/deg. Even if the criterion of contrast threshold is considerably increased, this value is only slightly affected. For example, if an extremely generous criterion of 10 times the background noise (the amplitude of the averaged potential when there was no stimulus present) is used, a cut-off of approximately 10 c/deg is predicted, although it is important to emphasize that extrapolation beyond the data points is not necessarily valid.

DISCUSSION

Jacobson, Franklin and McDonald (1976) using the behavioural technique of conditioned suppression (in which cats were required to stop licking a food bowl upon presentation of a grating to avoid an electric shock) found that they could respond on at least 50% of stimulus presentations to a square wave grating of spatial frequency 8.15–8.85 c/deg. They also reported that the highest spatial frequency to which responses occurred more frequently than on blank trials was 9.3–14.5 c/deg. Many previous behavioural tests (Smith, 1936; Muir and Mitchell, 1973; Blake, Cool and Crawford, 1974) have suggested a best acuity of only 6 c/deg.

However, as Mitchell, Giffin and Timney (1977) have pointed out, it is important to take luminance and pupil size into account when comparing behavioural studies since the mean retinal illumination certainly affects contrast sensitivity and acuity in man (Van Nes and Bouman, 1967; Leibowitz, 1952). Mitchell *et al.* demonstrated that the acuity of kittens is dependent on luminance and obtained an estimate of 9.4 c/deg for a $4\frac{1}{2}$ month old kitten with a stimulus luminance of 35 cd/m^2, using their jumping stand technique. They conclude that, in order to obtain optimum performance from a cat, the luminance of the stimuli should be at least 50 cd/m^2. In the present study the screen had a luminance of 300 cd/m^2 and it is therefore unlikely that this imposed a limit of acuity.

Evidence is scarce that neurones anywhere in the cat's visual system can resolve spatial frequencies close to the behaviourally determined acuity. Ikeda and Wright (1975) found cells in the cat visual cortex that responded above 5 c/deg, and reported neurones in the lateral geniculate nucleus responding as high as 8 c/deg (Ikeda and Wright, 1976). However, population distributions of sensitivity from small samples of single units are not necessarily reliable indicators of the proportion of neurones responding at particular spatial frequencies. There is a possibility of biased sampling characteristics of the microelectrodes used (Levick and Cleland, 1974).

An extrapolation of the curve used by Campbell, Maffei and Piccolino (1973) to describe the cat's contrast sensitivity suggests a high spatial frequency cut-off (acuity) of 15–20 c/deg. This curve is included in Fig. 2 and describes the present observations well in the range of spatial frequencies studied. The upper curve in Fig. 2 shows the modulation transfer function of the optics of the cat's eye with a 2 mm pupil, computed from the measured linespread function (Enroth-Cugell and Robson, 1977). It is clear that there is no appreciable optical attenuation of the quality of the image over the range of spatial frequencies considered here. The performance of the cat's visual system is probably even less restricted by the quality of its optics than is the vision of man (Campbell and Green, 1965).

I am therefore able to conclude from this study that an alert, awake adult cat has a contrast sensitivity function much like that estimated from a pretrigeminal preparation. It is valid to extrapolate this function to at least 8.5 c/deg and therefore, in agreement with estimates obtained of behavioural methods at high luminance, this is a lower limit to the visual acuity of the cat.

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