

THE CONTRAST SENSITIVITY, SPATIAL RESOLUTION AND VELOCITY TUNING OF THE CAT'S OPTOKINETIC REFLEX

By MICHAEL DONAGHY*

From the Physiological Laboratory, Cambridge CB2 3EG

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SUMMARY

1. Optokinetic nystagmus has been evoked from two cats using horizontally moving vertical grating patterns with sinusoidally modulated wave forms (mean luminance 8.5 cd/m^2). Eye movements were recorded by DC electro-oculography.

2. The velocity 'tuning' of the slow phase response was measured for high-contrast (0.8) gratings with spatial frequencies ranging from 0.18 to 2.8 cycles/deg. Irrespective of spatial frequency, the gain of slow phase tracking always declined as the stimulus velocity exceeded 5–8 deg/sec.

3. The effect of variations in grating contrast on the gain of slow phase tracking was investigated for spatial frequencies ranging from 0.04 to 2.8 cycles/deg. These gratings always moved at a velocity of 3 deg/sec. Reductions in grating contrast produced a fall in the gain of slow phase tracking. At any given contrast, the extent of the fall in gain depended on spatial frequency. At no value of spatial frequency was an optokinetic response demonstrable when the contrast fell below 0.02.

4. The above results have been used to derive the threshold contrast for evoking an optokinetic response at each spatial frequency tested. A contrast sensitivity function is plotted from these threshold contrasts, and this is compared with previous estimates of the cat's contrast sensitivity function derived from measurements of visual discrimination and cortical evoked potentials.

INTRODUCTION

Two types of smooth tracking eye movement are generally recognized: optokinetic slow phases and smooth pursuit movements. However the distinction between these two types of smooth tracking is rather blurred. Typically, the phylogenetically older optokinetic slow phase is evoked involuntarily by slow continuous motion of a large expanse of the visual field, whereas characteristic smooth pursuit is a volitional tracking of discrete targets moving relative to the rest of the visual field (Rademaker & Ter Braak, 1948). Obviously stimuli intermediate in quality between these two extremes are commonplace and the eye's smooth tracking response to them is not easily, or even usefully, categorized as either an optokinetic slow-phase or a smooth pursuit. Both voluntary pursuit of a moving spot (Westheimer, 1954; Robinson, 1965; Fuchs, 1967) and optokinetic slow phases (Dodge, Travis & Fox, 1930; Koerner & Schiller, 1972) become increasingly inefficient as the stimulus velocity

* Present address: Department of Renal Medicine and Immunology, Hammersmith Hospital, London W12 0H5.

exceeds 40 deg/sec in monkeys and men. However, the oculomotor system can generate eye movements of ten times these speeds, both in the form of saccades (Robinson, 1964; Fuchs, 1967), and as the continuous corrective movements of the vestibulo-ocular reflex (Donaghy, 1980). Clearly the low level at which the smooth tracking system shows velocity saturation must be determined by the processing capabilities of the visuo-sensory input to the oculomotor centres, rather than by the dynamics of the oculomotor plant. However, no studies have attempted to relate directly the stimulus conditions necessary for evoking optokinetic nystagmus to modern psychophysical and neurophysiological knowledge concerning the visual pathway.

Grating patterns of sinusoidal luminance profile are powerful stimuli for studying the analysis of spatial information in the visual system. They can be defined precisely in terms of their orientation, spatial frequency (cycles per degree of visual angle) and contrast. The threshold contrast, below which a grating is invisible, varies with spatial frequency and mean luminance (Schade, 1956; Campbell & Robson, 1968).

I have investigated the ability of moving gratings to drive optokinetic slow-phases over a wide range of spatial frequencies in conscious cats. The gain of slow-phase tracking has been measured as a function of grating contrast and velocity. These results are used to derive a contrast sensitivity function, which can be compared with the pre-existing functions that have been determined for the cat by visual discrimination or cortical evoked potentials. Such a comparison might reveal whether the visuo-sensory information reaching the cat's brain is filtered in any way before being made available to the oculomotor centres responsible for generating smooth tracking eye movements.

METHODS

Three adult female cats (C.B., M.B. and Fred), each weighing about 3 kg, were used in these experiments. Vertical and horizontal eye movements were transduced by chronically implanted silver-silver chloride electro-oculographic (e.o.g.) electrodes. The general methods and the calibration and reliability of this e.o.g. technique have been considered in a preceding paper (Blakemore & Donaghy, 1980). During experiments the cat lay in a comfortably padded box and its head was attached to a fixed headholder by means of chronically implanted skull screws.

Production of gratings of variable velocity. Film loops of gratings were back-projected on the outside of a Perspex hemisphere whose inner surface was viewed by the cat. The resulting gratings had a sinusoidal luminance profile in the direction perpendicular to their stripes. The harmonic distortion present in the waveform of the projected gratings was less than 10%. The space-average luminance of the gratings was kept at 8.5 cd/m² at all spatial frequencies. Contrast, which was calculated using the formula

$$C = \frac{L_{\max} - L_{\min}}{L_{\max} + L_{\min}}$$

where L_{\max} and L_{\min} represent the peak and trough luminances of the grating, was 0.8 ± 0.05 over the spatial frequency range used, which was 0.2–2.8 cycles/deg. The vertical gratings, which occupied a field of 80 deg horizontally and 50 deg vertically, were moved at constant velocities in a horizontal direction by means of a belt drive between a DC servo-motor and a spindle on the projector's film-strip carrier. At the projection distance used, grating velocity could be varied accurately in the range 1–150 deg/sec.

Gratings of variable contrast. For a study of the influence of contrast on optokinetic slow-phase tracking, a television technique, rather than back-projection, was used for generating moving gratings. The virtue of back-projecting a moving film-loop is that it allows simple, rapid and accurate adjustment of grating velocity over a wide range but the contrast of the projected

gratings could not be varied accurately. In comparison, the contrast can be varied simply for gratings generated electronically on the face of a cathode ray tube, by the method of Campbell & Green (1965). The cathode ray tube used was a large-screen Hewlett Packard 1300 A oscilloscope with a P 31 (green) phosphor. It was placed 28 cm from the cat's eyes so that it covered the central 50 deg of the visual field horizontally and 40 deg vertically. Effectively uniform illumination of the tube screen, at 8.5 cd/m², was accomplished by means of a raster composed of a 1 MHz triangular wave form across the *Y*-plates and a 100 or 200 Hz sawtooth (time-base) waveform across the *X* plates. The field was converted into a vertical grating of sinusoidal profile by applying a sinusoidal voltage waveform to the *Z*-axis of the cathode ray tube. By changing the modulation depth of this voltage using a decade attenuator, the grating's contrast could be varied simply. The relationship between *Z*-voltage modulation depth and contrast deviated from linearity by less than 2% even at the relatively high contrast level of 0.71. The gratings were made to drift from left to right at a constant velocity of 3 deg/sec by adjustment of the ratio between the time base and *Z*-modulating frequencies.

The horizontal e.o.g. was calibrated by the peephole technique described earlier (Blakemore & Donaghy, 1980) using the Perspex hemisphere illuminated to a level of 8.5 cd/m², the same as the mean luminance of the screen of the cathode-ray tube. For this calibration, the periphery of the Perspex hemisphere was masked with black card to display a central field of 50 deg horizontally and 40 deg vertically, thereby equalling the angular subtense of the cathode-ray tube screen. Immediately following the eye movement calibration, the Perspex screen was wheeled away from the cat and replaced by the grating display.

RESULTS

Velocity tuning

Some authors have made a quantitative analysis of the optokinetic reflex in terms of the temporal frequency of light modulation at a fixed point in the stimulus field, rather than the absolute velocity of the grating (Bergmann, Chaimovitz, Gutman & Zelig, 1963; Pasik, Pasik & Valciukas, 1972). It is not known, however, whether the velocity tuning of optokinetic slow-phase tracking varies as a function of the spatial frequency of a grating stimulus. In order to answer this question, I have measured the gain of slow-phase tracking at different stimulus velocities over a wide range of spatial frequencies in two cats.

During each experimental session the 'velocity tuning curve' was determined at a single spatial frequency, using the back-projection technique to generate moving gratings at a fixed contrast of 0.8. Test velocities were presented to the cat in a pseudo-randomized order for a duration of about 1 min each. The gratings were moved from the cat's left to right: since viewing was binocular, no response asymmetry would be expected. After each test velocity presentation, the cat viewed a blank field of the same mean luminance for 1–2 min.

All moving gratings in the spatial frequency range tested, 0.18–2.8 cycles/deg, evoked typical optokinetic nystagmus (see examples for 2 cycles/deg in Fig. 1) in which the slow phases tracked the stimulus and the majority of the fast phases were aimed in the opposite direction. For each test velocity, a portion of the eye movement recording containing an unbroken stream of alternating fast and slow-phases was selected and the velocities of ten to fifteen consecutive slow-phases were measured. Mean slow-phase velocity is plotted as a function of stimulus velocity on the inset graph of Fig. 1. In this case slow-phase tracking started to become inadequate when the stimulus velocity exceeded 4 or 5 deg/sec.

The gain of optokinetic slow phases, expressed as the ratio of eye velocity to

grating velocity, is plotted in Fig. 2 as a function of grating velocity for all the spatial frequencies tested. There was a trend for unity-gain tracking to be maintained at slightly higher velocities as spatial frequency was reduced, but whatever

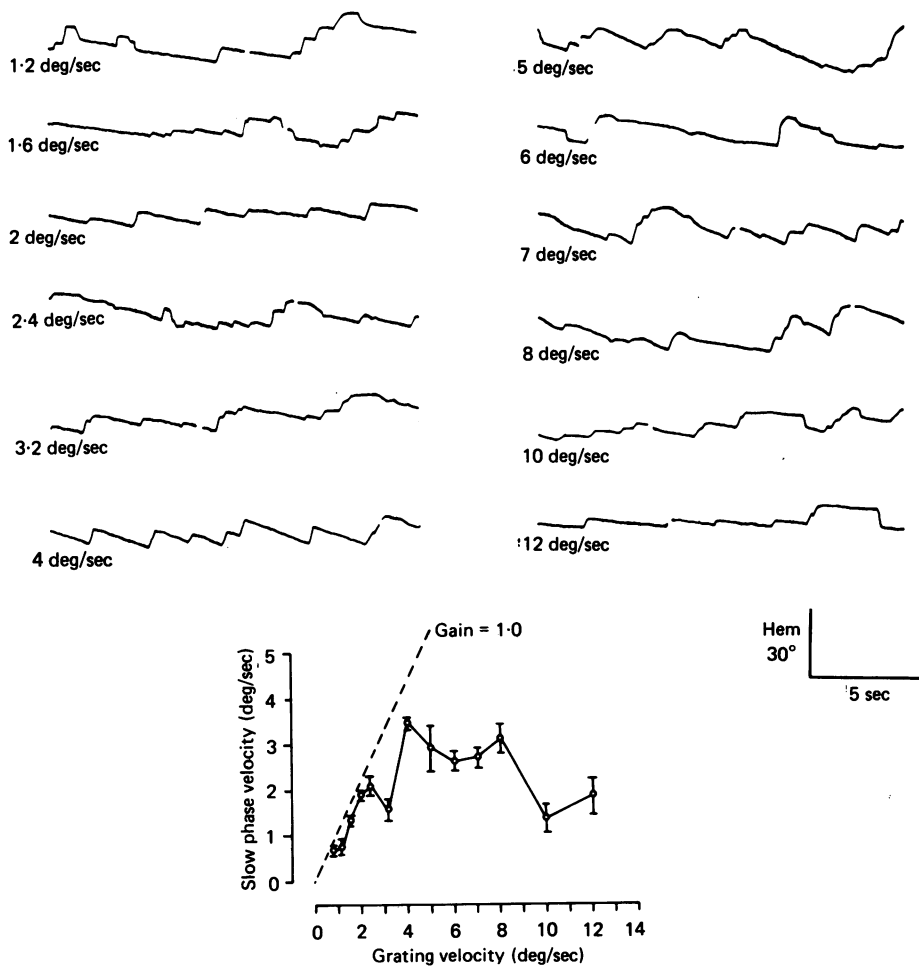


Fig. 1. E.o.g. traces (downward deflexion = rightward movement) showing optokinetic nystagmus elicited by a vertical, 2 cycles/deg grating moving from left to right. Grating velocity is indicated beside each trace. The graph below the e.o.g. records shows the mean slow phase velocity (± 1 s.e.) at different pattern velocities. Cat Fred. Hem = horizontal eye movement calibration.

the spatial frequency the slow-phase tracking gain had always dropped by at least 3 db when the stimulus velocity exceeded 10 deg/sec. Clearly the attenuation of slow-phase gain was determined primarily by the absolute velocity, rather than by the temporal frequency (spatial frequency \times velocity) of the grating stimulus.

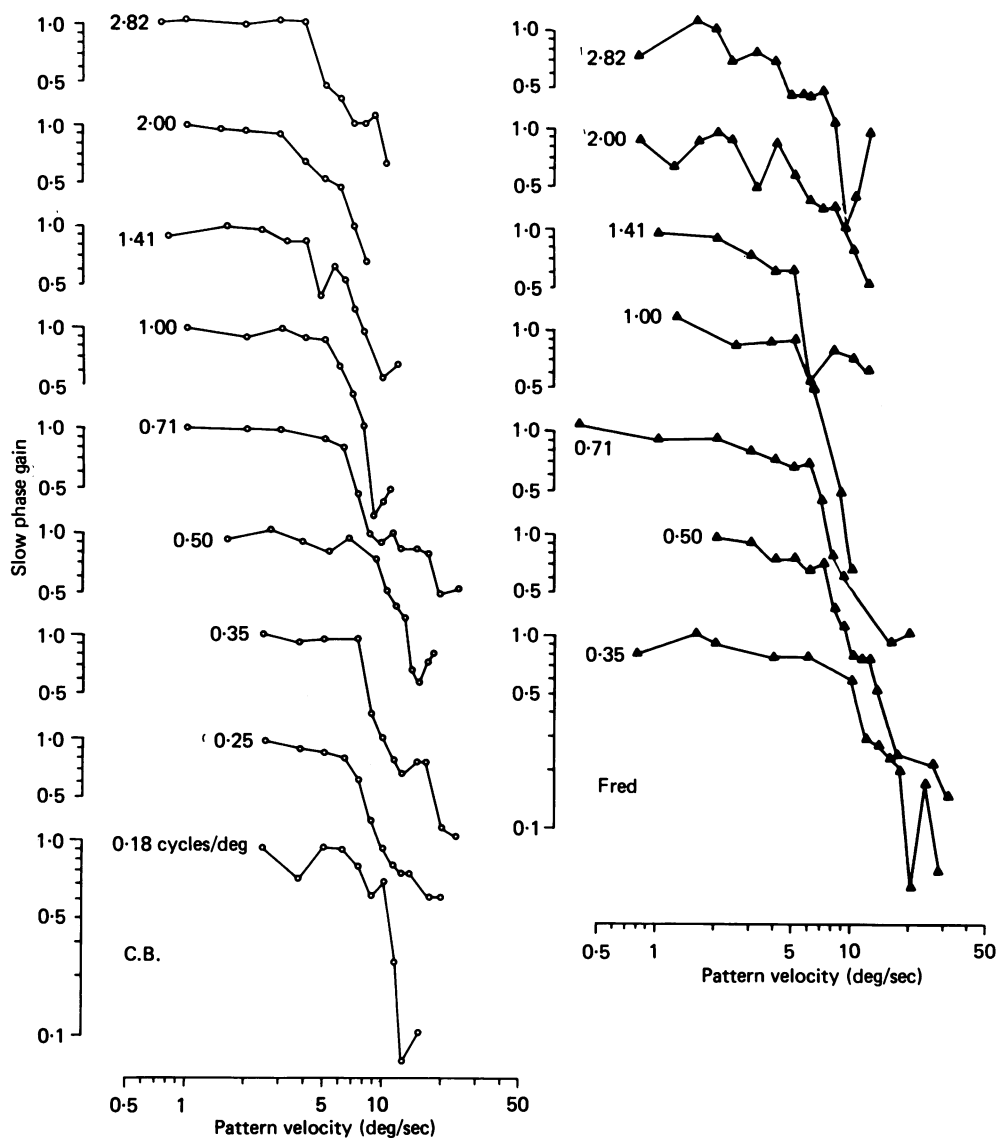


Fig. 2. Optokinetic slow-phase gain as a function of pattern velocity at a number of spatial frequencies (indicated next to each curve) in two cats. Cat Fred died before data were obtained at spatial frequencies of 0.25 and 0.18 cycles/deg.

Variation of grating contrast

The following experiment examined how the gain of optokinetic slow-phase tracking was influenced by changing the contrast and spatial frequency of the grating stimuli, which were generated by the television technique. Grating velocity was held constant at 3 deg/sec, a speed that the previous experiment had shown to be comfortably situated in the high-gain portion of the slow-phase velocity tuning curve whatever the spatial frequency. Contrast was varied from 0.01 to 0.71 in steps of

3 or 5 db and each contrast was presented for a minute's viewing. The different contrast levels were exposed to the cat in order of ascending value rather than by a randomized sequence. This was done to avoid adaptation effects due to viewing gratings of high contrast before seeing those of low contrast. The cats were kept alert throughout by noises.

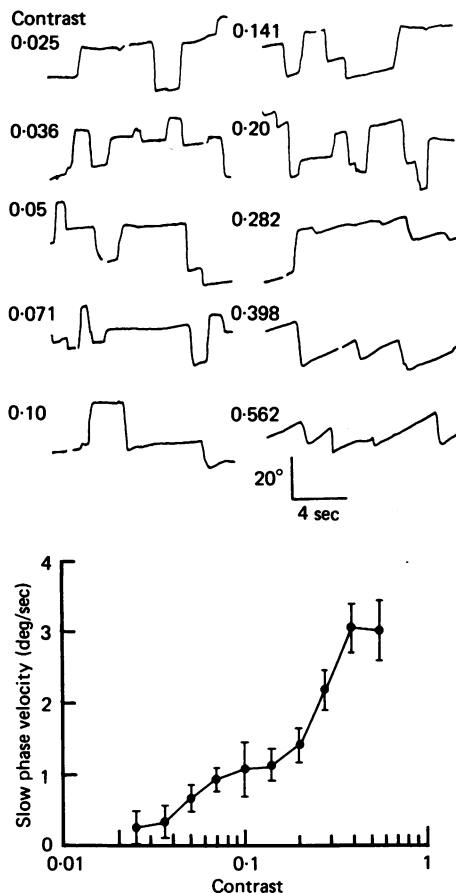


Fig. 3. Horizontal optokinetic nystagmus in response to moving gratings of various contrasts. Spatial frequency was constant at 0.35 cycles/deg and velocity was constant at 3 deg/sec. The graph shows mean slow phase velocity (± 1 s.e.) at different contrasts. Cat C.B.

Inspection of the resulting eye movement recordings showed that the gain of slow-phase tracking fell as the grating's contrast was reduced (Fig. 3). The extent of this fall in gain was assessed quantitatively by the following method. First, the eye movement recording at each contrast level was scrutinized to determine whether an optokinetic response was present. The criterion for judging this was the existence of a stretch of record containing at least three obvious slow-phases in the appropriate direction within ten successive intersaccadic fixations. This criterion eliminated all recordings below a certain contrast level at each spatial frequency. However, due

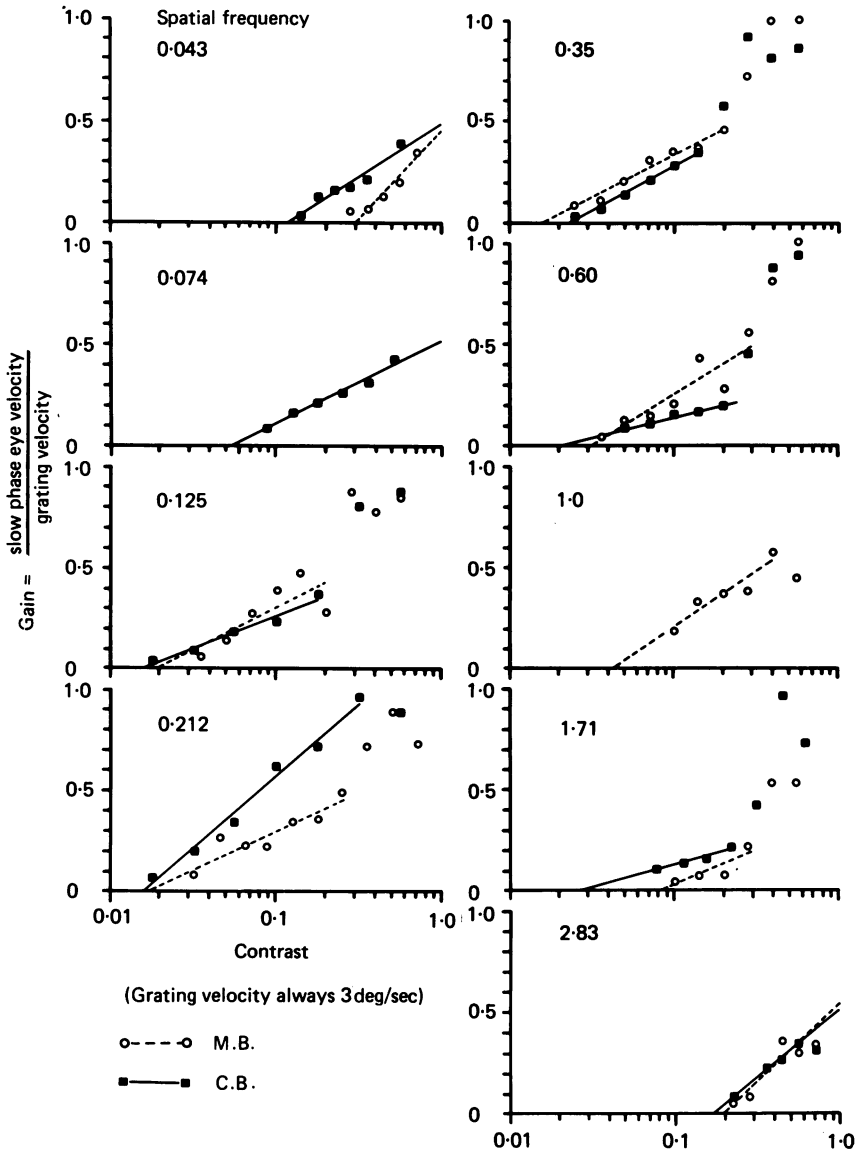


Fig. 4. The dependence of optokinetic slow-phase gain on grating contrast at nine different spatial frequencies from 0.043 to 2.8 cycles/deg. Grating velocity always 3 deg/sec. Cats C.B. (○ --- ○) and M.B. (■ — ■). The method of fitting regression lines is described in the text.

to the arbitrary nature of this criterion, that contrast level was not regarded as the threshold contrast for eliciting optokinetic nystagmus. Instead, the threshold was determined by a method of linear regression and extrapolation that will be outlined later.

At those contrast levels at which optokinetic nystagmus had been adjudged to be

present, the slope of the eye movement in *all* of the ten intersaccadic intervals was measured. This measurement was made irrespective of whether the eye movement was obviously recognizable slow-phase, an apparently steady fixation, or rarely, a drift in the opposite direction to the stimulus. These ten values were averaged and the gain of slow-phase tracking was calculated. Fig. 4 shows how the gain deteriorated as the contrast was reduced at all spatial frequencies in the range tested. The standard error values shown on the graph of Fig. 3 give an indication of the variability

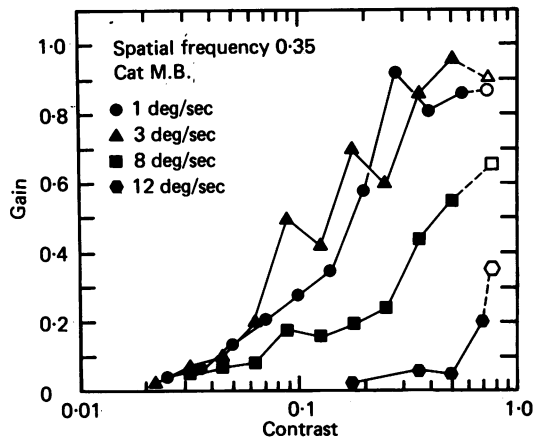


Fig. 5. The gain of slow-phase tracking as a function of contrast for grating velocities of 1, 3, 8 and 12 deg/sec. Grating spatial frequency was 0.35 cycles/deg. The open symbols represent gain values derived from the 0.35 cycle/deg velocity tuning curves in Fig. 2 (cat Fred) while the filled symbols were obtained from experiments involving moving gratings generated by the television technique (cat M.B.).

of slow-phase velocity at different contrast levels. At any contrast level, the standard error of the ten values of slow-phase velocity generally lay in the range 0.1–0.4 deg/sec. Neither cat produced a clear optokinetic response to gratings of 4 cycles/deg, even at a contrast of 0.71. The gain of slow-phase tracking was least rapidly attenuated by reductions in contrast at spatial frequencies of 0.125 and 0.21 cycles/deg.

The relationship between slow-phase gain and grating contrast has also been investigated at a number of stimulus velocities other than 3 deg/sec. Fig. 5 shows how the slope of the curve relating slow-phase gain to grating contrast is decreased by increasing the velocity of a 0.35 cycle/deg grating. At each of the four stimulus velocities (1, 3, 8 and 12 deg/sec) the slow-phase gain at high-contrast levels was directly comparable to the corresponding points on the slow-phase velocity tuning curves presented in the previous section (see 0.35 cycle/deg velocity tuning curves in Fig. 2).

Threshold contrast. It was of interest to determine from the data in Fig. 4 the threshold contrast below which optokinetic slow-phases would not be evoked, at each spatial frequency. The threshold contrast can be defined as that level at which the gain of optokinetic slow-phase tracking has fallen to zero. It has been estimated by fitting linear regression lines to the data. The question of how many data points to include for calculating the linear regression lines was overcome by using a com-

puterized regression line program that calculated the best linear relationship between gain and contrast (C):

$$\text{gain} = a_1 + a_2(\log C) \tag{1}$$

and the best quadratic fit:

$$\text{gain} = a_1 + a_2(\log C) + a_3(\log C)^2. \tag{2}$$

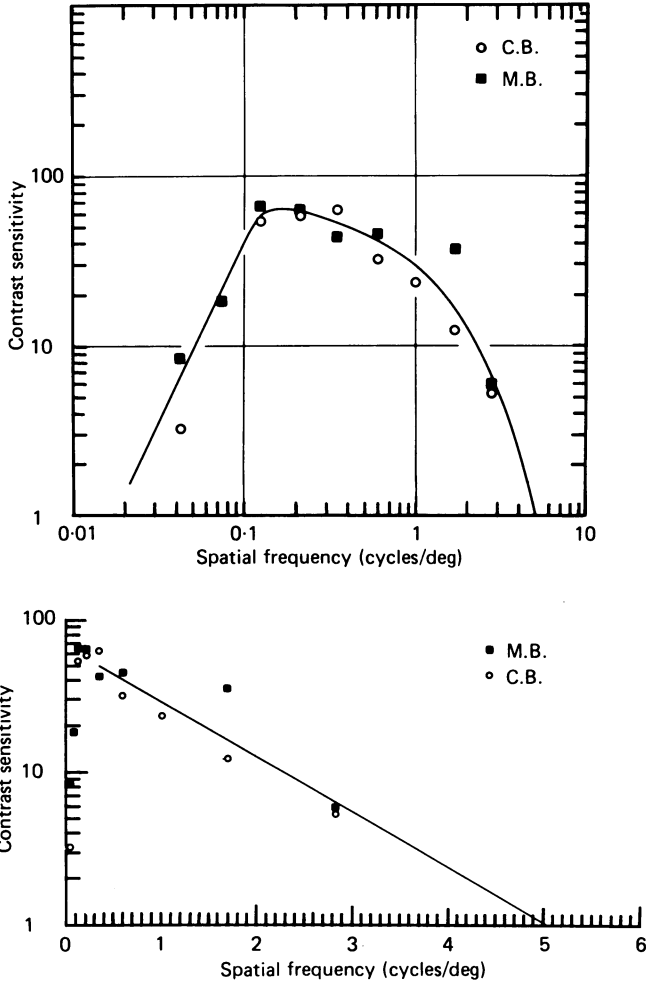


Fig. 6. The optokinetic contrast sensitivity function. The symbols plot the reciprocals of the optokinetic contrast thresholds determined in Fig. 4 against log (upper graph) and linear (lower graph) spatial frequency. The high spatial frequency asymptote of both graphs is the same.

The data points obtained at high contrasts were eliminated one by one in descending order from both curve-fitting calculations until the correlation coefficients of the linear and quadratic fits were the same to two decimal places. At this point, since the linear fit was as good as the quadratic fit, the $a_3(\log C)^2$ term in eqn. (2) had

become insignificant. These linear regression lines are shown in Fig. 4 and their intercepts on the abscissa represent empirical estimates of the threshold contrasts.

The curve relating the reciprocal of threshold contrast to spatial frequency is called the *contrast sensitivity function* (Schade, 1956; Campbell & Robson, 1968). Such functions have been plotted in Fig. 6 with spatial frequency as a linear co-ordinate on the lower graph and as a logarithmic co-ordinate on the upper graph. Comparison of these two graphs shows that the high spatial frequency asymptote is best described by a straight line when spatial frequency is plotted linearly. The computed regression line extrapolates to a cut-off spatial frequency of 5 cycles/deg when the grating contrast is 1.0 (the maximum possible contrast). This same regression line has been replotted on the logarithmic spatial frequency axis of the upper graph of Fig. 6.

DISCUSSION

Slow-phase velocity tuning

The gain of optokinetic slow-phase tracking in the cat starts to fall when the stimulus velocity exceeds 4–8 deg/sec. Spatial frequency, within the range explored, is not an important determinant of slow-phase tracking ability. The equivalent high velocity cut-off point in rabbits is 1.5 deg/sec (Collewijn, 1969), and in monkeys or men it is 45–50 deg/sec (Dodge *et al.* 1930; Koerner & Schiller, 1972). In rabbits the velocity tuning of slow phases probably reflects the tuning of 'on-type' directionally selective retinal ganglion cells (Oyster, Takahashi & Collewijn, 1972). Stimulation of the nucleus of the optic tract in the pretectal area of the rabbit's midbrain evokes a vigorous ipsiversive nystagmus (Collewijn, 1974). The neurones of this nucleus have peak velocity sensitivities of less than 10 deg/sec in rabbit (Collewijn, 1975) and cat (Hoffmann & Schoppmann, 1975).

Once an optokinetic slow phase has started, the velocity of retinal image motion will drop with a resultant fall in the output of directionally selective neurones. Yet each slow phase does not progressively decelerate. Clearly the maintenance of optokinetic slow-phases must depend in part on the output of a memory element which records the speed of the preceding portion of the slow phase. The presence of such a memory element means that the peak velocity attainable by slow phases could be higher than the stimulus velocity range which is most accurately transduced by the directionally selective neurones. In view of this possibility, caution is required when attempting to relate the velocity tuning of optokinetic slow phases to that of directionally selective visual neurones studied while the eye is immobilized.

Optokinetic contrast sensitivity function

There are differences between the cat's contrast sensitivity function as determined by this optokinetic method and the corresponding function estimated from evoked potentials (Campbell, Maffei & Piccolino, 1973) or behavioural discrimination (Bisti & Maffei, 1974) at similar luminance levels. To facilitate comparison, these contrast sensitivity functions are all plotted together in Fig. 7. The peak contrast sensitivity determined by the optokinetic method was only 60. This is roughly half the value of 110 that has been obtained using cortical evoked potentials (Campbell *et al.* 1973; Harris, 1978) or behavioural discrimination (Bisti & Maffei, 1974; Blake, Cool &

Crawford, 1974). There are a variety of possible causes for this difference. Possibly the contrast sensitivity of the visual input to the optokinetic slow-phase generator is inferior to that of the input to the visual cortex. This could be verified by measuring the visual evoked potential in the nucleus of the optic tract, assuming that this is the source of optokinetic slow-phase control. Poor accommodation to the oscilloscope

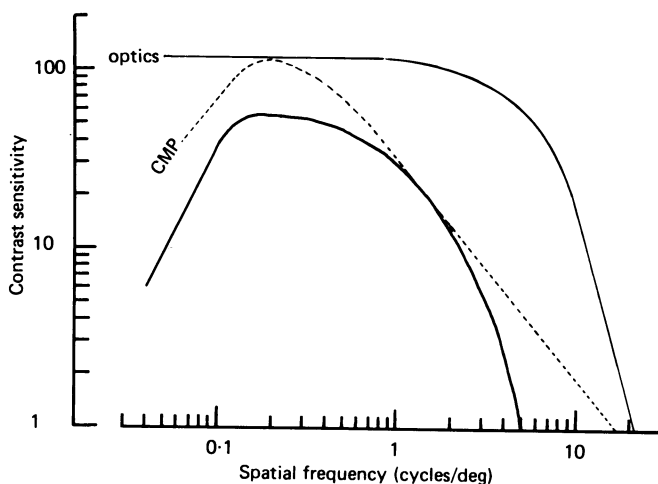


Fig. 7. Comparison of cat contrast sensitivity functions determined by different techniques. The thick curve is the optokinetic function of the present study. The curve labelled CMP is the function determined by evoked potentials (Campbell *et al.* 1973) and also by behavioural discrimination (Bisti & Maffei, 1974). The transfer function (labelled 'optics') of a cat's dioptries through a 3 mm pupil, arbitrarily displaced on the ordinate to touch the CMP curve, is also shown (Bonds, 1974).

screen at low contrasts is unlikely to have been responsible for the low-contrast sensitivities obtained in this study since its distance lay within the cat's accommodative range (Elul & Marchiafava, 1964) and the screen's dark surround provided an ample accommodative stimulus. Indeed, at low grating contrasts, this stationary dark border could have been a stronger stimulus to fixation than the moving grating that it surrounded; however, examination of the horizontal e.o.g. showed that the cats did *not* spend an appreciable amount of time fixating the edge of the screen, even when they were not making optokinetic responses.

Using the optokinetic method, the peak contrast sensitivity occurred at a spatial frequency of 0.16 cycles/deg. This value is similar to that of 0.2 cycles/deg obtained by Campbell *et al.* (1973) and Harris (1978) using cortical evoked potentials, and by Bisti & Maffei (1974) using behavioural discrimination.

When measured optokinetically, the cat's contrast sensitivity declined roughly exponentially as the spatial frequency was increased above 0.3 cycles/deg. Notably, all the previous studies that have measured the cat's high spatial frequency asymptote, using evoked potential or discrimination methods, found that spatial frequency was best related to threshold contrast by a power law (Berkley & Watkins, 1973; Campbell *et al.* 1973; Bisti & Maffei, 1974; Blake *et al.* 1974; Harris, 1978). A consequence of this difference is that the optokinetically determined function extrapolates

to a cut-off of 5 cycles/deg, whereas other methods (Fig. 7) have produced functions that extrapolate to spatial frequencies three times higher (Campbell *et al.* 1973; Bisti & Maffei, 1974; Harris, 1978), although the functions obtained in some other studies also extrapolate to only 4–7 cycles/deg (Berkley & Watkins, 1973; Blake *et al.* 1974; Muir & Mitchell, 1973). It cannot be over-emphasized that these high spatial frequency cut-off values are hypothetical in that they are derived by extrapolation from results obtained at lower spatial frequencies. There is no confirmation as yet that cats can actually resolve spatial frequencies exceeding about 10 cycles/deg, although Jacobson, Franklin & McDonald (1976) have demonstrated that cats can certainly see gratings as fine as 9 cycles/deg when the contrast is 0.8 and the luminance is very high (325 cd/m²).

If there is a genuine, but small, difference between the optokinetically determined contrast sensitivity function and those derived from the evoked potential or behavioural methods, can it be explained by the different response properties of two separate populations of visual neurones? If so, the optokinetically determined function should represent the threshold behaviour of a group of movement-sensitive neurones that are incapable of responding to such low contrasts, or such high spatial frequencies, as the cells giving rise to cortical evoked potentials. These two subsets of visual neurones could be located anatomically in the geniculo-cortical system and the nucleus of the optic tract. The contrast sensitivities of these two brain areas cannot exceed those of their afferent visual inputs and there is evidence that separate subsets of retinal ganglion cells project to these two systems (Fukuda & Stone, 1974; Hoffmann & Schoppmann, 1975) although their relative contrast sensitivities are as yet unknown.

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REFERENCES

- BERGMANN, F., CHAIMOVITZ, M., GUTMAN, J. & ZELIG, S. (1963). Optokinetic nystagmus and its interaction with central nystagmus. *J. Physiol.* **168**, 318–331.
- BERKLEY, M. A. & WATKINS, D. W. (1973). Grating resolution and refraction in the cat estimated from evoked cerebral potentials. *Vision Res.* **13**, 403–415.
- BISTI, S. & MAFFEI, L. (1974). Behavioural contrast sensitivity of the cat in various visual meridians. *J. Physiol.* **241**, 201–210.
- BLAKE, R., COOL, S. J. & CRAWFORD, M. L. J. (1974). Visual resolution in the cat. *Vision Res.* **14**, 1211–1217.
- BLAKEMORE, C. & DONAGHY, M. (1980). Co-ordination of head and eyes in the gaze changing behaviour of cats. *J. Physiol.* **300**, 317–335.
- BONDS, A. B. (1974). Optical quality of the living cat eye. *J. Physiol.* **243**, 777–795.
- CAMPBELL, F. W. & GREEN, D. C. (1965). Optical and retinal factors affecting visual resolution. *J. Physiol.* **186**, 558–578.
- CAMPBELL, F. W., MAFFEI, L. & PICCOLINO, M. (1973). The contrast sensitivity of the cat. *J. Physiol.* **229**, 719–731.
- CAMPBELL, F. W. & ROBSON, J. G. (1968). Application of Fourier analysis to the visibility of gratings. *J. Physiol.* **197**, 551–566.
- COLLEWIJN, H. (1969). Optokinetic eye movements in the rabbit: input–output relations. *Vision Res.* **9**, 117–132.

- COLLEWIJN, H. (1974). Oculomotor areas in the rabbit's brainstem. *Brain Res.* **66**, 362-363.
- COLLEWIJN, H. (1975). Direction selective units in the rabbit's nucleus of the optic tract. *Brain Res.* **100**, 489-508.
- DODGE, R., TRAVIS, R. C. & FOX, J. C. (1930). Optic nystagmus. III. Characteristics of the slow phase. *Archs Neurol. Psychiat., Chicago* **24**, 21-34.
- DONAGHY, M. (1980). The cat's vestibulo-ocular reflex. *J. Physiol.* **300**, 337-351.
- ELUL, R. & MARCHIAFAVA, P. L. (1964). Accommodation of the eye as related to behaviour in the cat. *Archs ital. Biol.* **102**, 616-644.
- FUCHS, A. F. (1967). Saccadic and smooth pursuit eye movements in the monkey. *J. Physiol.* **191**, 609-631.
- FUKUDA, Y. & STONE, J. (1974). Retinal distribution and central projections of Y-, and X-, and W-cells of the cat's retina. *J. Neurophysiol.* **37**, 749-772.
- HARRIS, L. R. (1978). Contrast sensitivity and acuity of a conscious cat measured by the occipital evoked potential. *Vision Res.* **18**, 175-178.
- HOFFMANN, K.-P. & SCHOPPMANN, A. (1975). Retinal input to direction selective cells in the nucleus tractus opticus of the cat. *Brain Res.* **99**, 359-366.
- JACOBSON, S. G., FRANKLIN, K. B. J. & McDONALD, W. I. (1976). Visual acuity of cat. *Vision Res.* **16**, 1141-1143.
- KOERNER, F. & SCHILLER, P. H. (1972). The optokinetic response under open and closed loop conditions in the monkey. *Exp. Brain Res.* **14**, 318-330.
- MUIR, D. W. & MITCHELL, D. E. (1973). Visual resolution and experience: Acuity deficits in cats following early selective visual deprivation. *Science, N.Y.* **180**, 420-422.
- OYSTER, C. W., TAKAHASHI, E. & COLLEWIJN, H. (1972). Direction selective retinal ganglion cells and control of optokinetic nystagmus in the rabbit. *Vision Res.* **12**, 183-193.
- PASIK, P., PASIK, T. & VALCIUKAS, J. A. (1972). Quantitative studies on optokinetic nystagmus in the monkey. *Bibl. ophthalm.* **82**, 317-326.
- RADEMAKER, G. J. J. & TER BRAAK, J. W. G. (1948). On the central mechanisms of some optic reactions. *Brain* **71**, 48-76.
- RASHBASS, C. (1961). The relationship between saccadic and smooth tracking eye movements. *J. Physiol.* **159**, 326-338.
- ROBINSON, D. A. (1964). The mechanics of human saccadic eye movement. *J. Physiol.* **174**, 245-264.
- ROBINSON, D. A. (1965). The mechanics of human smooth pursuit eye movement. *J. Physiol.* **180**, 569-591.
- SCHADE, O. H. (1956). Optical and photoelectric analog of the eye. *J. opt. Soc. Am.* **46**, 721-739.
- WESTHEIMER, G. (1954). Eye movement responses to a horizontally moving visual stimulus. *Archs Ophthalm., N.Y.* **52**, 932-941.