J. Physiol. (1984), **357**, *pp.* 219–240
With 13 *text-figures*
Printed in Great Britain

SPATIAL AND TEMPORAL CONTRAST SENSITIVITIES OF NEURONES IN LATERAL GENICULATE NUCLEUS OF MACAQUE

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(*Received 3 February 1984*)

SUMMARY

1. The discharges of single neurones in the parvocellular and magnocellular laminae of the macaque's lateral geniculate nucleus (l.g.n.) were recorded with glass-insulated tungsten micro-electrodes.

2. Linearity of spatial summation was examined using the test devised by Hochstein & Shapley (1976). 2 of 272 parvocellular units and 6 of 105 magnocellular units showed clearly non-linear spatial summation. A quantitative index of non-linearity did not suggest the existence of a distinct 'non-linear' class of magnocellular unit.

3. Spatial contrast sensitivity to moving gratings was measured by a tracking procedure in which contrast was adjusted to elicit a reliable modulation of discharge. With the exception of cells that were driven by blue-sensitive cones, measurements of contrast sensitivity did not reveal distinct subgroups of parvocellular units. All had low sensitivity, and those with receptive fields in the fovea could resolve spatial frequencies of up to 40 cycles deg^{-1}. Magnocellular units had substantially higher sensitivity, but poorer spatial resolution.

4. The higher sensitivities of magnocellular units led to their giving saturated responses to stimuli of high contrast. Responses of parvocellular units were rarely saturated by any stimulus.

5. At any one eccentricity the receptive fields of parvocellular units had smaller centres than did those of magnocellular units. Receptive fields of magnocellular units driven by the ipsilateral eye had larger receptive fields than did those driven by the contralateral eye.

6. Parvocellular units were most sensitive to stimuli modulated at temporal frequencies close to 10 Hz; magnocellular units to stimuli modulated at frequencies nearer 20 Hz. The loss of sensitivity as temporal frequency fell below optimum was more marked in magnocellular than parvocellular units.

7. Changes in temporal frequency altered the shapes of the spatial contrast sensitivity curves of both parvocellular and magnocellular units. These changes could be explained by supposing that centre and surround have different temporal properties, and that the surround is relatively less sensitive to higher temporal frequencies.

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INTRODUCTION

The macaque's performance on a variety of visual tasks is much like that of man (De Valois, Morgan & Snodderly, 1974; Harwerth, Boltz & Smith, 1980), and macaque and human visual pathways are anatomically very similar. It is therefore likely that neurones in the macaque and human visual pathways will have substantially the same physiological properties.

The aim of this paper is to characterize the spatial and temporal sensitivities of neurones in the macaque's lateral geniculate nucleus (l.g.n.), using techniques that permit comparison with psychophysical observations on man. A companion paper (Derrington, Krauskopf & Lennie, 1984) describes experiments to characterize the chromatic properties of neurones in the l.g.n.

METHODS

Preparation and recording

The main experiments were undertaken on twelve *Macaca fascicularis* and one *Macaca mulatta* that weighed between 4·5 and 7·0 kg. Each animal was anaesthetized with an injection of Vetalar (ketamine hydrochloride, 10 mg kg^{-1}, I.M.) and cannulae were inserted in the saphenous veins. Surgery was continued under Nembutal (sodium pentobarbitone) anaesthesia.

The trachea was cannulated, the head was placed in a stereotaxic frame and a small craniotomy was made above the right l.g.n. Pupils were dilated with atropine methonitrate and the corneae were protected with clear contact lenses. Artificial pupils (3 mm diam.) and, if necessary, supplementary lenses were placed immediately in front of the eye. The eyes were refracted by finding the lens that permitted resolution of the highest spatial frequencies by cells with receptive fields close to the fovea. Every 12 h the lenses were removed and the eyes washed in saline; every 24 h the lenses were removed and the eyes closed for 30 min.

Action potentials were recorded with glass-insulated tungsten micro-electrodes (Merrill & Ainsworth, 1972) placed in the l.g.n. The l.g.n. in these relatively large animals commonly lay 3–5 mm anterior to the position indicated by the stereotaxic atlas of Shantha, Manocha & Bourne (1968), and after it had been located Pavulon (pancuronium bromide) was infused rapidly to induce paralysis; this was maintained by a continuous infusion of 60 $\mu g\ kg^{-1}\ h^{-1}$ in a saline solution containing dextrose (5 %). The monkey was ventilated artificially at 25–30 strokes min^{-1} at a tidal volume adjusted to keep the end-tidal CO_2 close to 4·5 %. Throughout the experiment the level of anaesthesia, maintained by small doses of Nembutal, was monitored by the electroencephalogram (e.e.g.); the electrocardiogram (e.c.g.) was monitored as an indicator of the animal's general health. A heated blanket regulated by a subscapular thermistor prevented body temperature falling below 37 °C.

At the beginning of the experiment, and every few hours thereafter, the positions of the foveas, established by reversed ophthalmoscopy, were plotted on a tangent screen 1·2 m in front of the animal.

Visual stimuli

The receptive fields of well-isolated units were located on the tangent screen. A mirror was then used to place the receptive field on the centre of a more distant (5·6 m) screen. Slide projectors and interference filters (red, 625 nm; yellow, 575 nm; green, 554 nm; and blue, 462 nm) were used to present white and coloured spots and backgrounds on this screen. By listening to the responses to onsets and offsets of small spots presented against backgrounds of different colours it was possible to assign neurones to one of the four types described by Wiesel & Hubel (1966).

The tangent screen was then removed, exposing an oscilloscope display on which sinusoidal grating patterns were presented. This had a constant space and time average luminance of 200 cd m^{-2} and appeared white (P4 phosphor). At the usual viewing distance (5·6 m) it subtended 3·3 deg by 2·7 deg. Grating patterns could be moved steadily across the screen at rates between

0·16 and 41·8 Hz or their contrast could be modulated with temporal sinusoids at the same rates. The technique used for generating these displays is described in Derrington & Lennie (1982). In the present experiments 167 frames of the display were presented every second.

Analysis of response

Action potentials were amplified, then used to trigger rectangular pulses that were recorded by the computer. In some experiments these records were converted into histograms of average discharge rate against time. Every histogram contained the discharge to at least 1·5 temporal cycles of the stimulus, so after discarding the early part of the histogram that contained a fractional cycle of response, the amplitudes and phases of the component responses at different temporal frequencies were measured by taking the Fourier transform of the remainder of the histogram.

For on-line measurement of the amplitude of the component of response at a single temporal frequency we used a simplified procedure: the response to a single presentation of a stimulus was convolved with a square wave of the frequency of interest and the peak of the resulting function was taken as the amplitude. The odd harmonic components of response, to which this technique is also sensitive, are very small, and we checked that the relative amplitudes of responses to moving gratings measured by this procedure were the same as those obtained from the Fourier transform.

Measurement of contrast sensitivity

Contrast sensitivity was taken as the reciprocal of the contrast that produced a criterion modulation of discharge on 50 % of trials. The criterion was calculated for each cell as the amplitude of response that exceeded by two standard deviations the mean amplitude of the same component frequency in the maintained discharge to a uniformly illuminated screen. For most cells the criterion modulation was close to 10 impulses s^{-1}; this was usually audible. A computer-controlled staircase procedure (Derrington & Lennie, 1982) was used to keep the contrast close to threshold, which was calculated by fitting a regression line to the relationship between contrast and response. In most experiments contrast sensitivities to gratings of several spatial or temporal frequencies (or both) were measured concurrently, and trials containing the different stimuli were randomly interleaved.

We have interpreted contrast sensitivity functions in terms of Rodieck's (1965) model of the retinal ganglion cell receptive field. This represents centre and surround of the receptive field by concentric Gaussian sensitivity profiles, of opposite sign, which combine signals linearly from different parts of the receptive field. From Enroth-Cugell & Robson (1966), the contrast sensitivity function $F(f)$ will then be the difference of two Gaussian spectra

$$F(f) = C(f) - S(f), \tag{1}$$

where

$$C(f) = k_c \pi r_c^2 e^{-(\pi f r_c)^2} \tag{2}$$

and

$$S(f) = k_s \pi r_s^2 e^{-(\pi f r_s)^2} \tag{3}$$

and k_c is centre sensitivity, k_s is surround sensitivity, r_c is centre radius, and r_s is surround radius. A general-purpose minimization routine (Chandler, 1965) was used to find values of k_c, k_s, r_c and r_s that minimized the squared differences between measured and predicted values of the logarithm of contrast sensitivity at different spatial frequencies.

Linearity of spatial summation

This was examined in all cells by application of the 'null' test described by Hochstein & Shapley (1976).

Identification of recording sites

Small electrolytic lesions were made at intervals along electrode penetrations to allow reconstruction of the tracks. At the end of the experiment the animal was perfused through the aorta with 0·9 % saline followed by 10 % formalin in saline. A block was cut in the plane of the electrode tracks. This was kept in formal saline and then transferred to 30 % sucrose/formal saline 24 h before being frozen and cut into 50 μm sections that were mounted and stained with Cresyl Violet.

RESULTS

Parvocellular layers

In the parvocellular layers of the l.g.n. we encountered cells of Wiesel & Hubel's (1966) types I, II and III. Cells of types I and III have receptive fields with centre–surround organization; centre and surround of type I units have obviously different spectral sensitivities, while those of type III units appear to have the same spectral sensitivity. This centre–surround organization of antagonistic regions leads us to expect that both types will respond well to achromatic gratings of appropriate spatial frequency. Receptive fields of type II units contain two mechanisms of differing spectral sensitivity, but these mechanisms are co-extensive. If both have the same distribution of sensitivity to white light then no achromatic grating will elicit a response; an imbalance of sensitivities will render type II units responsive to achromatic stimuli. In the sections that follow B–(R & G) opponent units (i.e. those receiving signals from blue-sensitive (B) cones opposed to some combined signal from red-sensitive (R) and green-sensitive (G) cones) are distinguished from 'red–green' (R–G) ones. Mostly this distinction was made using the very precise methods developed in the following paper, but even less precise exploration of the receptive field with coloured spots and backgrounds revealed B–(R & G) units unambiguously.

An initial aim was to establish whether the cell types identified by Wiesel & Hubel (1966) could be distinguished by their sensitivities to achromatic gratings.

Linearity of spatial summation. If a cell responds to the sum of light-evoked signals from different parts of its receptive field then a stationary sinusoidal grating can be positioned on the receptive field so that modulation of its contrast elicits no response (Enroth-Cugell & Robson, 1966; Hochstein & Shapley, 1976). The absence of a response at this 'null' position is not caused by balanced centre–surround antagonism but by the delivery of equal increments and decrements in signal to both surround and centre; indeed, at the high spatial frequencies typically used in this test the large size of a linear surround renders it insensitive to the grating in any spatial phase.

Fig. 1 shows the results of applying this test to two parvocellular units, one type I and the other type III. The stimulus in each case was a stationary grating of spatial frequency 1·5 times optimum for the cell. The stimulus was modulated at 5·2 Hz. Open circles show how the amplitude of the 5·2 Hz component in the average discharge depended upon the spatial phase of the grating. For both cells response amplitude varies approximately sinusoidally with spatial phase, as would be expected from a cell with linear spatial summation. The 10·4 Hz (second harmonic) component of the response is plotted as filled circles; it is negligibly small at all spatial phases. This pattern of results, which indicates that light-evoked signals are summed linearly within the receptive field, was found in all but two parvocellular neurones studied. The ratio of the mean amplitude of the second harmonic (averaged across all spatial phases) to the amplitude of the fundamental at the best phase, provides a useful index of non-linearity (Hochstein & Shapley, 1976), a value greater than 1 indicating a substantial non-linearity of spatial summation. Fig. 2*A* shows the distribution of this index for 272 parvocellular units; it confirms Blakemore & Vital-Durand (1981) and Kaplan & Shapley (1982) in showing that the overwhelming bulk of parvocellular units have linear spatial summation.

Spatial contrast sensitivity. Fig. 3*A* and *B* shows contrast sensitivities to sinusoidal gratings moving at 5·2 Hz (which is close to the optimum temporal frequency), plotted as functions of spatial frequency for a type I cell (Fig. 3*A*) and a type III cell (Fig. 3*B*) encountered in the same penetration. Both curves have the shapes expected for a receptive field with centre–surround organization, and to that extent

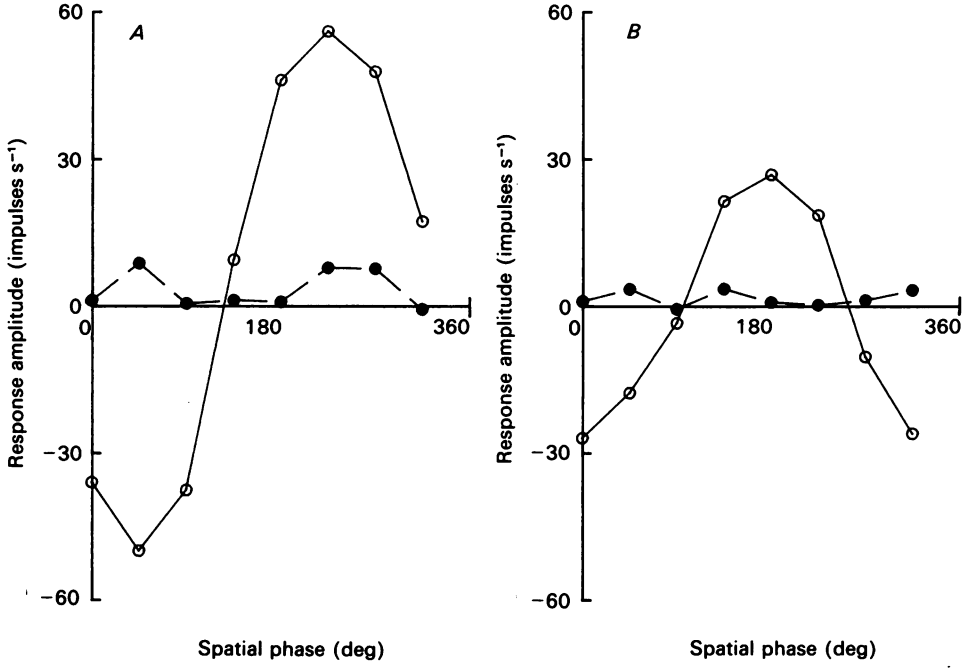

Fig. 1. Linearity of spatial summation. Open circles show the amplitude of the fundamental Fourier component of the response to a grating presented in different spatial phases while its contrast (0·6) was modulated sinusoidally in time at 5·2 Hz. By convention, response amplitude is negative when its phase is greater than 180 deg. Filled circles show the amplitude of the second harmonic (10·4 Hz) component of discharge. *A*, type I unit 8G; *B*, type III unit 9A.

resemble curves obtained from ganglion cells and l.g.n. cells in cat. However, the peak contrast sensitivity is substantially lower than is found in cat, and the spatial resolution (the highest spatial frequency that can be resolved by a unit) is much higher. The smooth curves drawn through the points are the best-fitting solutions to eqn. (1). At any one eccentricity units of types I and III were not distinguishable by their spatial contrast sensitivity curves.

Within our sample of type I/type III units there was considerable variation in the form of the contrast sensitivity function at low spatial frequencies; some cells showed little or no loss of sensitivity to low spatial frequencies while others showed a steep decline. (Repeated measurements on any one cell showed very little variation in the shape of its contrast sensitivity function.) Fig. 3*C–E* shows further examples.

The continuum of low-frequency sensitivity losses represented in Fig. 3*A–E* prompts one to explore the distinction between type I/type III and type II cells. Fig. 3*F* shows the contrast sensitivity curve of a unit identified, by preliminary

observations, as a type II unit that had clear R–G opponency but no discernible surround. The graph shows very little loss of sensitivity as spatial frequency falls below optimum, but the contrast sensitivity function is not otherwise distinguishable from the curves in Fig. 3*A–E*.

The variation from cell to cell in the loss of sensitivity to low frequencies could be due to variations in the sensitivity of the surround and in its dimensions relative

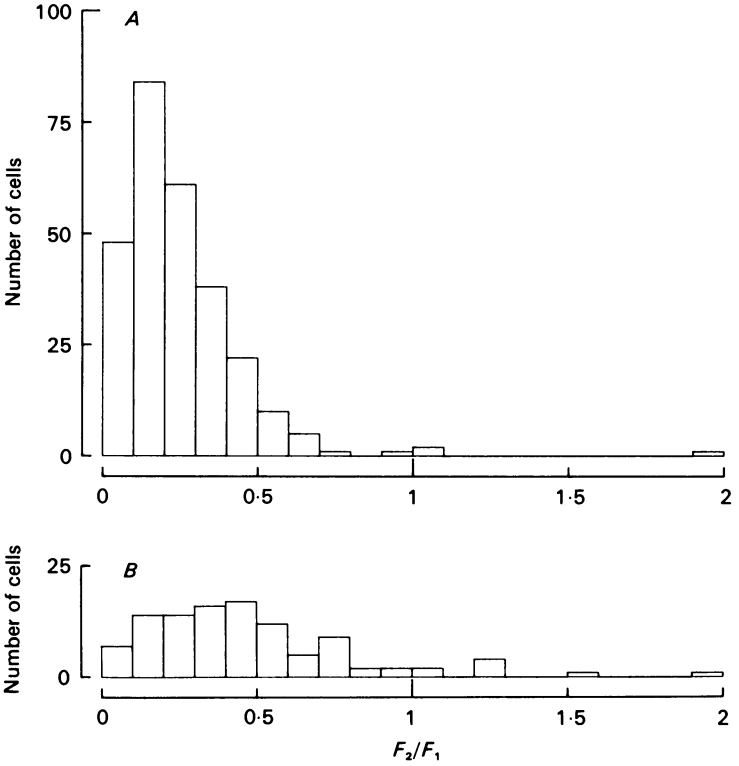

Fig. 2. Distribution of index of non-linearity of spatial summation. The ratio of the amplitudes (F_1/F_1) of the second harmonic (10·4 Hz) to the fundamental (5·2 Hz) component of discharge was calculated using the F_1 amplitude obtained for a grating in the spatial phase giving the greatest response and the F_2 component averaged across all spatial phases. Cells with an index greater than 2 are placed in the final bin of the histogram. *A*, parvocellular neurones; *B*, magnocellular units.

to those of the centre. Table 1 shows, for the units of Fig. 3, the values of the parameters of the best-fitting solutions to eqn. (1). The variation in loss of sensitivity to low spatial frequencies can be adequately represented by variation in the strength of the surround (k_s) and in its space constant (r_s). On the basis of contrast sensitivity measurements we have no reason to draw a qualitative distinction between type I/III units and type II units with R–G colour opponency.

Units that received inputs from B cones were particularly insensitive to achromatic stimuli, and we were unable to obtain any thoroughly satisfactory measurements of their spatial contrast sensitivities. The contrast sensitivity curve of the most sensitive

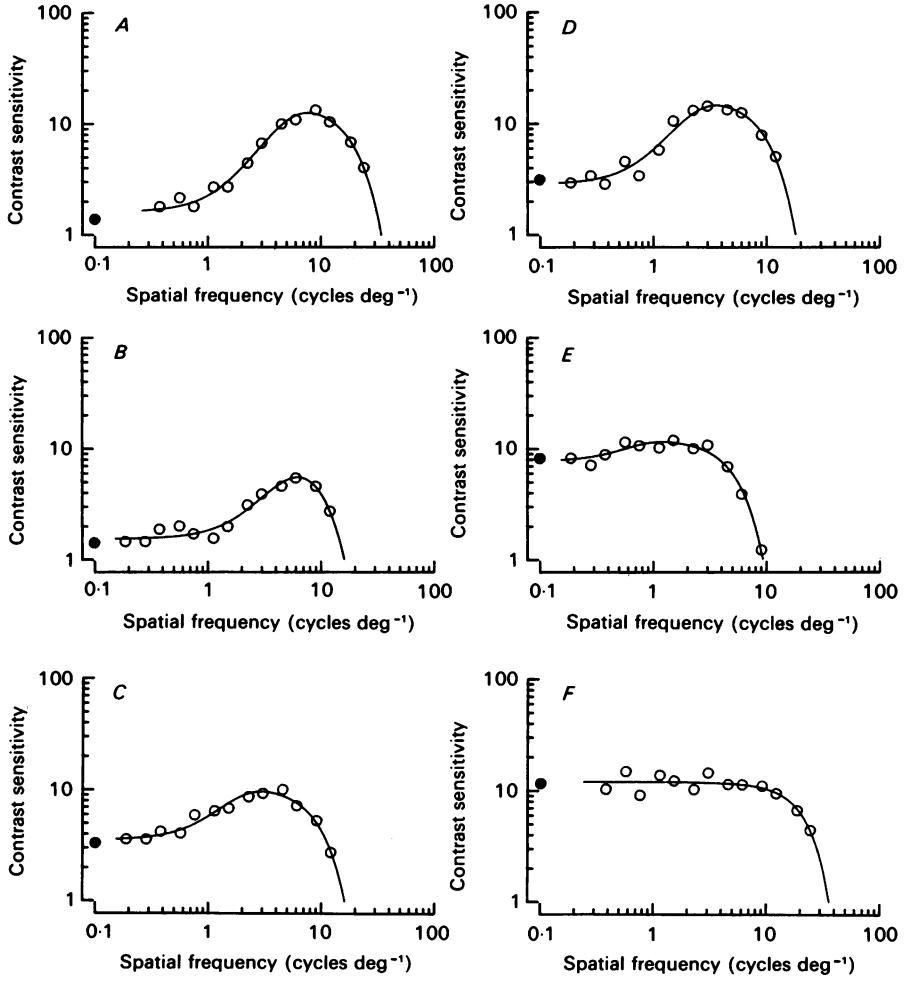

Fig. 3. Spatial contrast sensitivity of parvocellular units to sinusoidal gratings moving at 5·2 Hz. Filled circles on the ordinates mark the sensitivity to modulation of a spatially uniform field. *A*, *C* and *E*, type I units; *B* and *D*, type III units; *F*, type II unit driven by R and G cones.

TABLE 1. Best-fitting parameters for eqn. (1)

Cell	k_c	r_c	$k_s r_s^2 / k_c r_c^2$	r_s
A (8D)	15·03	0·015	0·89	0·072
B (14G)	9·51	0·029	0·84	0·069
C (15M)	10·74	0·030	0·67	0·202
D (15A)	16·87	0·029	0·83	0·159
E (13D)	12·18	0·054	0·37	0·494
F (8E)	17·63	0·015	0·31	0·020

of these units is shown in Fig. 4. Like other similar units, it differs from the curves of Fig. 3 in preferring relatively low spatial frequencies, though it should be noted that chromatic aberration, which in these experiments was uncorrected, probably causes at least a dioptre of defocus of the image to which the B cones are sensitive. No unit that received inputs from B cones showed a substantial loss of contrast sensitivity to low spatial frequencies. This confirms Wiesel & Hubel's (1966) observation that the chromatically opponent mechanisms are nearly spatially co-extensive.

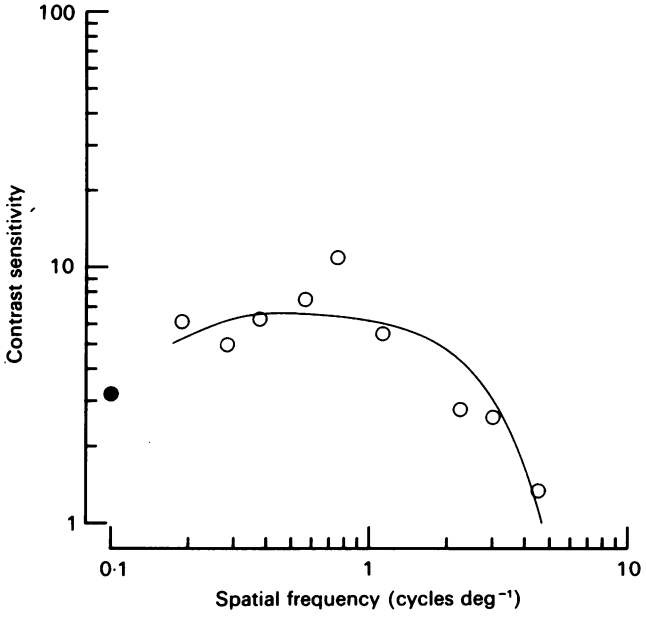

Fig. 4. Spatial contrast sensitivity of a B–(R & G) unit measured with a grating moving at 5·2 Hz. This example was the most sensitive on which measurements were made.

Contrast–response relationships. We have not yet considered the dependence of contrast sensitivity upon the amplitude of the criterion response. This is of particular interest in view of the low sensitivity found in parvocellular units: if the relationship between contrast and response is non-linear, a small shift in the criterion amplitude will produce a disproportionate change in the contrast required for threshold. For a large number of cells the relationship between contrast and response was measured with gratings of optimum spatial frequency, moving at 5·2 Hz. Fig. 5 shows two examples, one of type I (Fig. 5*A*), one of type III (Fig. 5*B*). The smooth curves drawn through the points in Fig. 5*A* and *B* are the best-fitting solutions to the equation

$$A = Kc/(c+c_0), \tag{4}$$

where A is response, c is contrast, and K and c_0 are constants. Eqn. (4), which characterizes the stimulus–response relationships of more distal neurones in the visual pathway, provides a satisfactory description of the contrast–response relationships for parvocellular units. For values of c appreciably smaller than c_0, A varies linearly

with c; the threshold criteria used in the present experiments fell within this linear range. Over the range of contrasts used in these measurements the phase of the response to the grating was almost constant.

The characteristic radius of the centre of the receptive field (r_c) was estimated from measurements of contrast sensitivity. Fig. 6 *A* and *B* shows, separately for cells driven

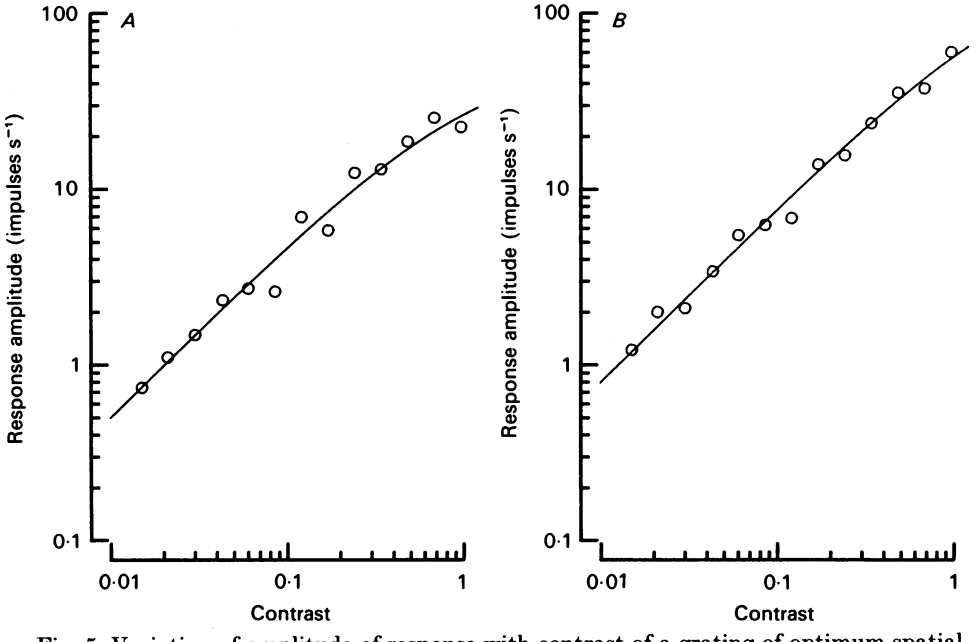

Fig. 5. Variation of amplitude of response with contrast of a grating of optimum spatial frequency, moving at 5·2 Hz. Histograms from which the amplitudes were measured contained responses to progressively larger numbers of stimulus cycles as contrast was reduced from its maximum: for the lowest contrasts 1800 cycles of the response were accumulated. Smooth curves drawn through the points are best-fitting solutions to eqn. (4). *A*, type I unit; *B*, type III unit.

from nasal and temporal retina, how r_c of 220 parvocellular units that received no discernible input from B cones varied with the eccentricity of the receptive field.

The straight lines on the graphs of Fig. 6 are solutions to the regression equation:

$$r_c = e^{(kx+c)}, \tag{5}$$

where k and c are constants and x is eccentricity in degrees. Since successive plots of foveal position were up to 1·5 deg apart, the relationship between r_c and eccentricity is correspondingly imprecise. Moreover, small eye movements, or defocus, or misalignment of the artificial pupil will all act to increase the estimate of r_c, especially at small eccentricities. Consequently the most reliable values of r_c are probably those that lie near the lower bounds of the distribution. The units with the smallest receptive fields could resolve over 40 cycles deg^{-1}, comparable to the psychophysical performance of *M. fascicularis* (De Valois *et al.* 1974).

Temporal contrast sensitivity. Variations in temporal frequency affect contrast

sensitivity measured psychophysically in man (Robson, 1966) and monkey (Merigan, 1980) and can have substantial effects upon the contrast sensitivity of ganglion cells in cat (Derrington & Lennie, 1982; Enroth-Cugell, Robson, Schweitzer-Tong & Watson, 1983). The contrast sensitivities of eighty cells were measured using gratings of optimum spatial frequency, moving at a series of temporal frequencies. Fig. 7

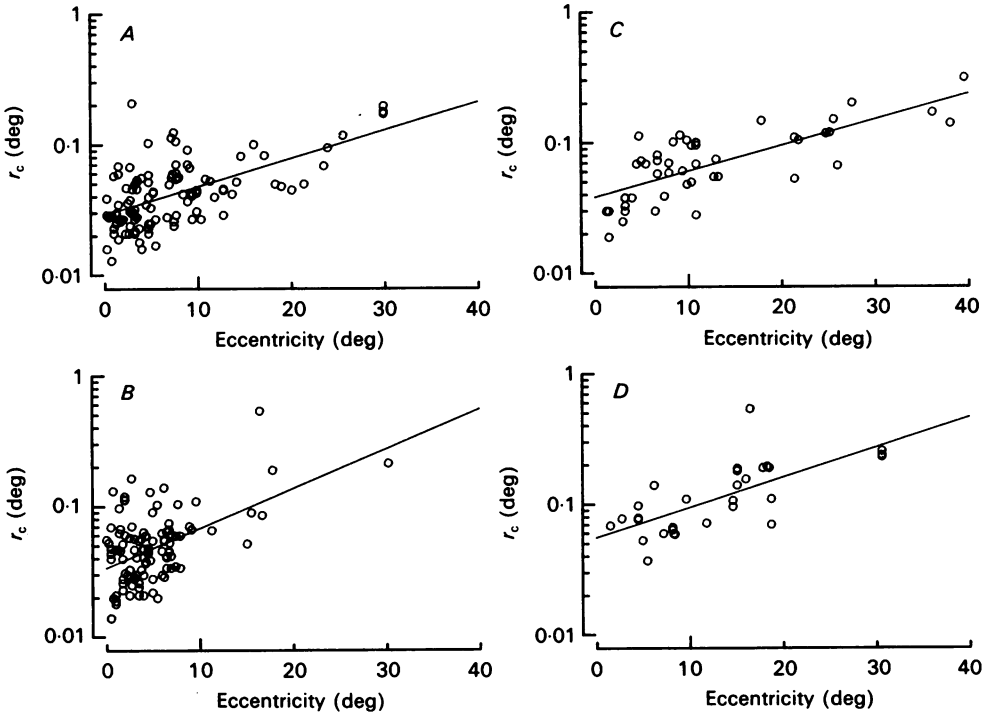

Fig. 6. Variation of receptive field dimensions with eccentricity. The characteristic radius (r_c) is estimated from the solution of eqn. (1) that best describes the spatial contrast sensitivity function. Straight lines are solutions to the regression equation $r_c = e^{(kx+c)}$. The estimates of r_c are least reliable for small values of r_c. *A*, parvocellular units with receptive fields in contralateral retina; *B*, parvocellular units with receptive fields in ipsilateral retina; *C*, magnocellular units with receptive fields in contralateral retina; *D*, magnocellular units with receptive fields in ipsilateral retina.

shows, for two units that represent the range found in the parvocellular laminae, how sensitivity to the optimum spatial frequency (measured at 5·2 Hz) depends upon temporal frequency. For all parvocellular units contrast sensitivity peaks at around 10 Hz, with a gentle loss at lower temporal frequencies and a much more rapid loss at higher temporal frequencies. It is helpful to have an analytic expression to characterize the temporal properties of a cell. One that provides a satisfactory description of the temporal contrast sensitivity function of parvocellular units represents it as the difference between two exponentials, thus

$$F(\omega) = S_1 e^{-k_1\omega} - S_2{}^{-k_2\omega}, \tag{6}$$

where S_1 and S_2 are scale factors and k_1 and k_2 the time constants of the two processes. The smooth curves drawn through the points in Fig. 7 *A* and *B* are best-fitting solutions to eqn. (5), the parameters of which are given in the caption to the Figure. Temporal contrast sensitivity curves were obtained from two B–(R & G) units. Both units were less sensitive than those of Fig. 7, but their curves were otherwise similar.

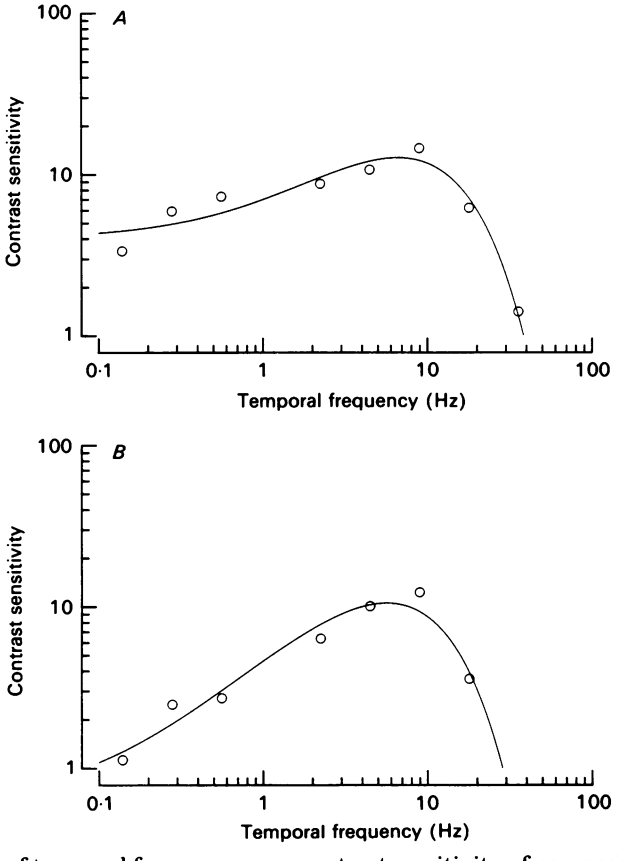

Fig. 7. Effect of temporal frequency upon contrast sensitivity of parvocellular units. Cells were excited by gratings of optimum spatial frequency (determined at 5·2 Hz) moving at different rates. Parameters of best-fitting solutions to eqn. (6) are, for cells of *A* and *B* respectively: $S_1 = 517, 143$; $S_2 = 513, 143$; $k_1 = 0{\cdot}128, 0{\cdot}157$; $k_2 = 0{\cdot}135, 0{\cdot}192$.

Spatio-temporal interactions. If centre and surround have different temporal properties then the form of the spatial contrast sensitivity curve will depend upon the temporal frequency used in its measurement. We expect the effect of temporal frequency to be most noticeable at low spatial frequencies, to which centre and surround are both most sensitive. For forty-two cells (including two B–(R & G) units) spatial contrast sensitivities were measured at four temporal frequencies (0·65, 2·6, 10·4 and 20·8 Hz) that spanned the range over which parvocellular units responded. Results from two units (Fig. 8) show that, as well as controlling the position of the contrast sensitivity curve on the ordinate, changes in temporal frequency alter its

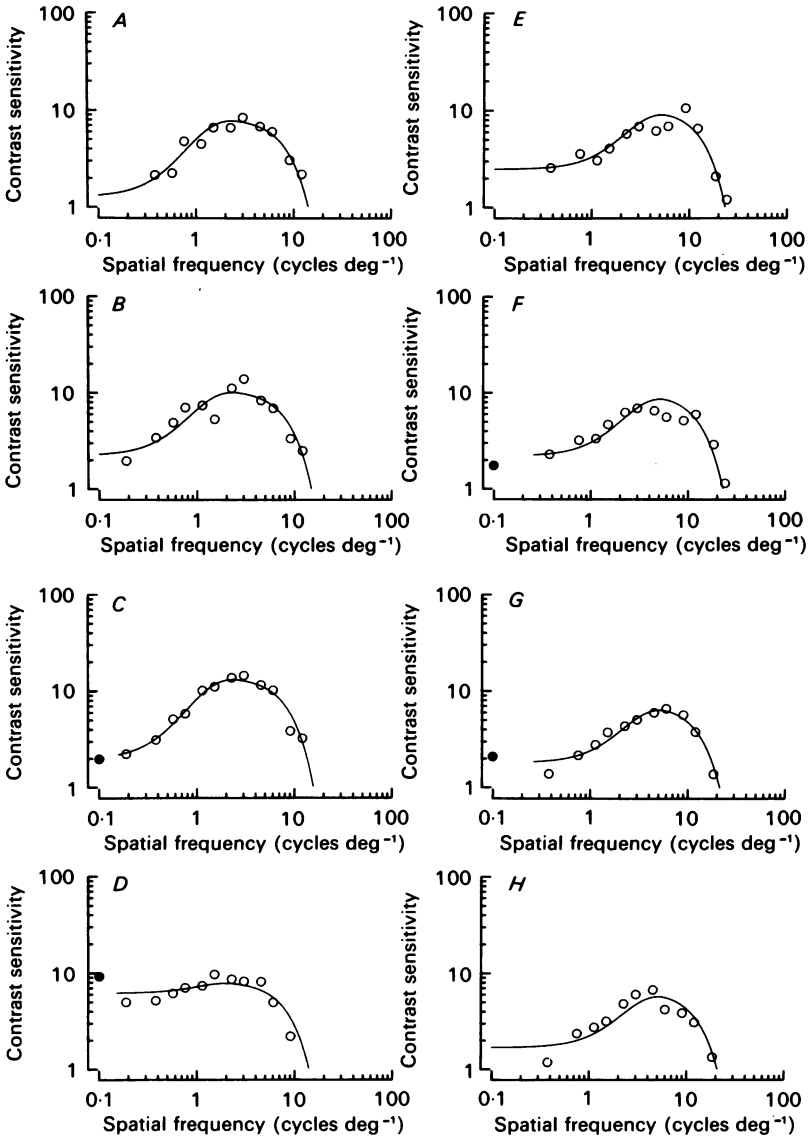

Fig. 8. Spatial contrast sensitivity functions obtained at different temporal frequencies, for one type I cell (*A*, *B*, *C* and *D*) and one type III cell (*E*, *F*, *G* and *H*). Threshold measurements at the four temporal frequencies (0·65, 2·6, 10·4 and 20·8 Hz) were made concurrently in a single experimental run. Smooth curves are best-fitting solutions to eqn. 1, constrained by the requirement that r_c and r_s be constant for each cell. Filled circles on the ordinates mark sensitivities to modulation of a spatially uniform field.

shape. Similar spatio-temporal interactions are seen in the cat's retinal ganglion cells (Derrington & Lennie, 1982; Enroth-Cugell *et al.* 1983), and for X cells can be rather well explained by supposing that the signal from the surround is delayed by a fixed amount relative to that from the centre (Enroth-Cugell *et al.* 1983). The effects of

temporal frequency on the shape of the spatial contrast sensitivity curves obtained in the present experiments could not be described adequately by a model in which the signal from the surround is delayed by a fixed amount; the smooth curves in Fig. 8 are solutions to eqn. (1), constrained to ensure that, for each cell, r_c and r_s were held constant.

Laminar distribution of cells. Table 2 shows the laminar distribution of on- and off-centre units in the thirteen animals used in the present experiments. There is a preponderance of on-centre units in laminae 5 and 6, but not in laminae 3 and 4. The

TABLE 2. Laminar distribution of cell types

Lamina	On-centre	Off-centre
6	55	35
5	63	38
4	28	31
3	21	19

difference between the distributions in the two pairs of laminae is highly significant (χ^2 11·2, $P < 0{\cdot}005$). Our observations agree with those of Wiesel & Hubel (1966), though we found a much less extreme segregation of cells than did Schiller & Malpeli (1978), who used electrodes that recorded the activity of several units at once. In their work, on-centre units were substantially confined to laminae 5 and 6 and off-centre units to laminae 3 and 4. We found many more units driven by B cones in laminae 5 and 6 than in laminae 3 and 4, though no significance should be attached to this since many more cells were studied in the two most dorsal layers, and in one animal we deliberately sought units that were driven by B cones.

Magnocellular layers

All units isolated in the magnocellular layers had receptive fields with centre–surround organization. In eighty-seven of these there was no apparent chromatic opponency, so they were called type III cells (Wiesel & Hubel, 1966). The remaining eighteen were on-centre units with a surround that was rather more sensitive than the centre to long wave-lengths. Following Wiesel & Hubel (1966) we call these type IV. We were unable to distinguish type III from type IV units by any of the measures described below.

Linearity of spatial summation. The test developed by Hochstein & Shapley (1976) was applied routinely to magnocellular units.

The unit in Fig. 9*A* shows the behaviour expected of a cell with linear spatial summation: the amplitude of the fundamental component of the response F_1 to a stationary grating whose contrast was modulated sinusoidally in time is a sinusoidal function of the spatial position of the grating. The second harmonic component of the response F_2 is small and varies in size with the fundamental, suggesting that it occurs only as a distortion product. This pattern of response, which is exactly like that obtained from parvocellular units, does not depend upon the spatial frequency of the grating.

Fig. 9*B* shows the responses of another type III neurone that was encountered just above the cell whose responses are shown in Fig. 9*A*. The fundamental

component of response varies sinusoidally with spatial phase (as in Fig. 9*A*), but the second harmonic response is large, and does not change with spatial phase. In cells like this the frequency-doubled component is seen most clearly when the spatial frequency or spatial phase is such that the grating elicits a small response at the fundamental temporal frequency, so, to ensure that non-linearities in spatial

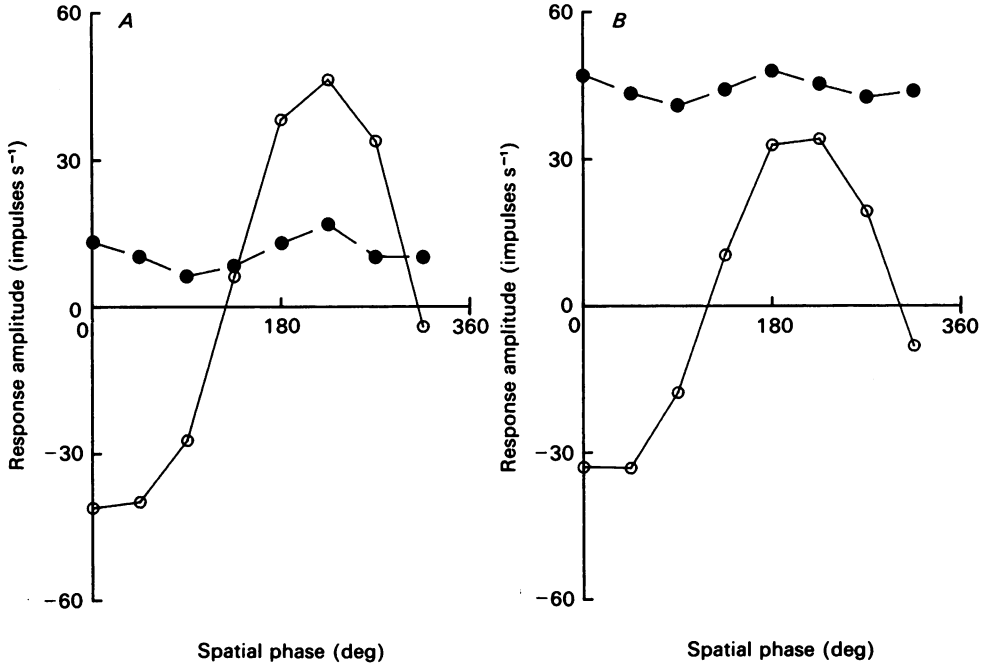

Fig. 9. Linearity of spatial summation in magnocellular units. Open circles show how the amplitude of the fundamental Fourier component of discharge varied with the spatial phase of the grating whose contrast was modulated at a temporaral frequency of 5·2 Hz. Responses are shown with negative amplitude when the phase differed by more than 90 deg from the phase of the peak response. Filled circles show the corresponding variation in the amplitude of the second harmonic (10·4 Hz) component of response. *A*, unit showing linear spatial summation; *B*, unit showing substantially non-linear summation.

summation were reliably detected, the test was always made using a spatial frequency 1·5–2 times the optimum for the cell.

The histogram in Fig. 2*B* shows, for magnocellular units, the distribution of the ratio of amplitudes F_2:F_1 (peak F_1, mean F_2) obtained using a grating of high spatial frequency. The distribution of the index of non-linearity is clearly not the same as the distribution for parvocellular neurones (Fig. 2*A*), but there is no suggestion that a distinct subgroup exists that has pronounced non-linearities of spatial summation; indeed Fig. 2 shows that such units are quite rare.

Spatial contrast sensitivity. Fig. 10 shows contrast sensitivity functions obtained from a linearly summating cell and one that showed non-linear summation. Both units have substantially higher peak contrast sensitivity than had been encountered in any

parvocellular unit, but do not differ appreciably from one another. In a sample of 105 we encountered only 6 units that showed clearly non-linear summation, and these could not be distinguished by their contrast sensitivity curves. (Magnocellular units were typically 5–10 times more sensitive than parvocellular units.)

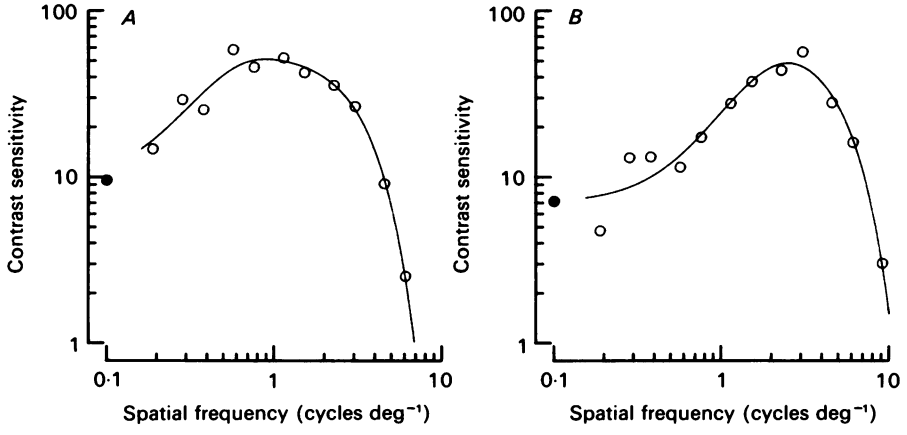

Fig. 10. Spatial contrast sensitivity functions obtained from magnocellular units, using gratings moving at 5·2 Hz. Filled circles on the ordinates mark sensitivities to modulation of a spatially uniform field. *A*, unit that showed linear spatial summation; *B*, unit that showed substantially non-linear spatial summation.

The smooth curves drawn through the points in Fig. 10 are the best-fitting solutions to eqn. (1), which for these units provides an acceptable description of the observations. The fits of eqn. (1) were generally less good for magnocellular units than for parvocellular ones. Parameter r_c (the characteristic radius of the centre) is in Fig. 6*C* and *D* plotted against eccentricity for all magnocellular units whose receptive field positions are known. (For one animal, in which several magnocellular units were studied, the record of receptive field positions is lost.) At all eccentricities where both groups are represented r_c of the magnocellular receptive field is substantially larger than r_c of the parvocellular one only for units driven from ipsilateral retina.

The high contrast sensitivity of magnocellular units was not due to some peculiarity of the relationship between stimulus contrast and response amplitude: Fig. 11 shows this relationship for two units. The smooth curves drawn through the points are best-fitting solutions to eqn. (4). Values of K and c_0 are much smaller than those for parvocellular units, which reflects the fact that responses of magnocellular units saturate for much lower contrasts. However, the relationship between stimulus contrast and response amplitude was linear over a substantial range that included the criterion. As stimulus contrast was progressively increased, the phase of the response advanced by between 30 and 40 deg, possibly reflecting the operation of a 'contrast gain control' (Shapley & Victor, 1978).

Sensitivity to temporal frequency. For most magnocellular units contrast sensitivity to gratings of optimum spatial frequency was measured at several temporal

frequencies. Sensitivities of two units (one linear, the other non-linear) are shown in Fig. 12. Magnocellular units were most sensitive when temporal frequency was between 10 and 20 Hz, and were progressively less sensitive at higher or lower temporal frequencies. The smooth curves drawn through the points are best-fitting solutions to eqn. (6); parameters are given in the caption to the Figure. The curves

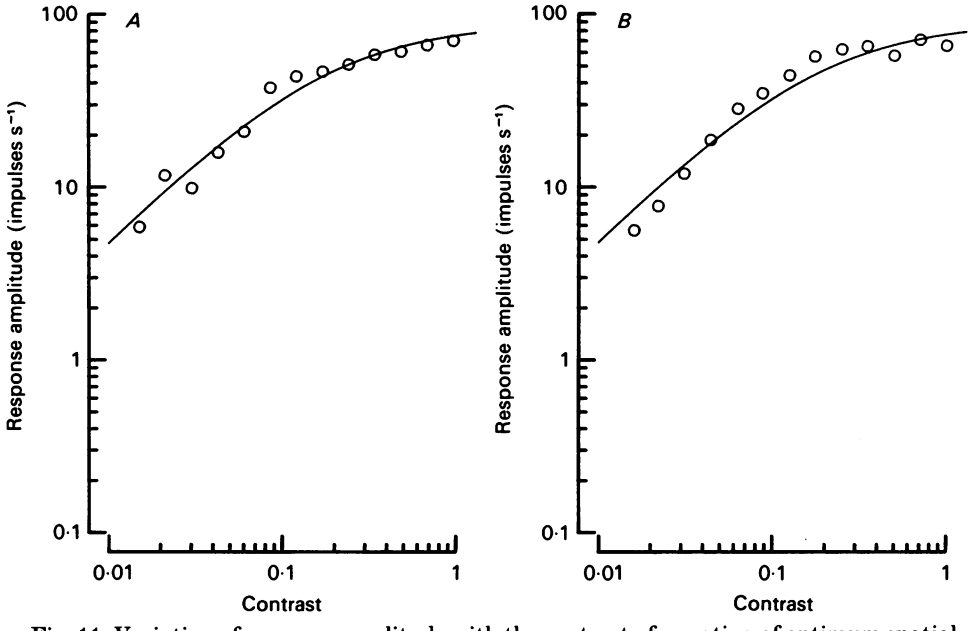

Fig. 11. Variation of response amplitude with the contrast of a grating of optimum spatial frequency, moving at 5·2 Hz. Histograms from which the amplitudes were measured contained responses to 90 cycles of the stimulus. Smooth curves drawn through the points are best-fitting solutions to eqn. (4).

differ from those of parvocellular units in having peak sensitivities that occur at higher temporal frequencies, and low-frequency limbs that have steeper slopes. These differences are reflected principally in the time constant (k_1) of the excitatory process. Our observations are consistent with the finding of Dreher, Fukada & Rodieck (1976) and Schiller & Malpeli (1978) that magnocellular units give more transient responses to step changes in illumination.

Spatio-temporal interactions. Spatial contrast sensitivity curves for two units, obtained using four different temporal frequencies, are shown in Fig. 13. As was the case for parvocellular units, temporal frequency controls the peak sensitivity and also the shape of the function. The smooth curves in Fig. 13 are the best-fitting solutions to eqn. (1), obtained with r_c and r_s constrained to be constant for each cell. As for parvocellular units, the changes in the shapes of the curves brought about by variations in temporal frequency could not be explained by supposing only that the surround signal is delayed by a fixed amount more than the centre signal.

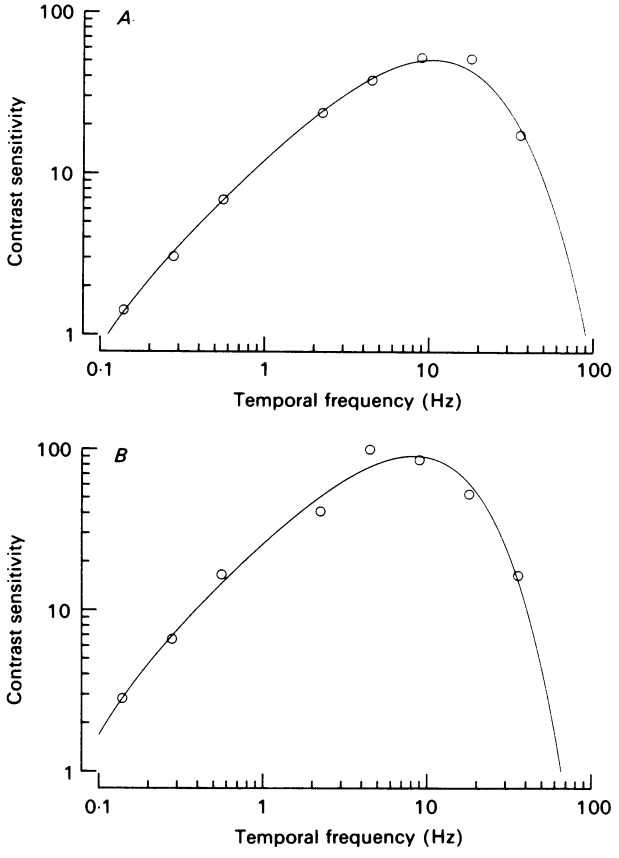

Fig. 12. Temporal contrast sensitivity functions for two magnocellular units, measured with gratings of optimum spatial frequency (detrmined at 5·2 Hz). Parameters of best-fitting solutions to eqn. (6) are, for cells of *A* and *B* respectively: $S_1 = 137, 508$; $S_2 = 138, 509$; $k_1 = 0{\cdot}54, 0{\cdot}095$; $k_2 = 0{\cdot}156, 0{\cdot}155$.

DISCUSSION

Distinctive classes of parvocellular units

Achromatic gratings reveal no difference between receptive fields of type I and type III units. Even by the use of chromatic patterns it has sometimes been hard to draw the distinction first made by Wiesel & Hubel (1966). Padmos & van Norren (1975) showed the existence of 'concealed' type I units whose chromatic opponency could only be revealed by chromatic adaptation, and subsequent studies (e.g. De Monasterio, Gouras & Tolhurst, 1975; Dreher *et al.* 1976) have corroborated this observation. Our results are consistent with the position (which is more thoroughly developed in the following paper) that cells of types I and III are continuously distributed on a dimension of R–G chromatic opponency.

Type II units that receive inputs from B cones were recognized as a separate class by Wiesel & Hubel (1966), and subsequent work has upheld their distinctiveness.

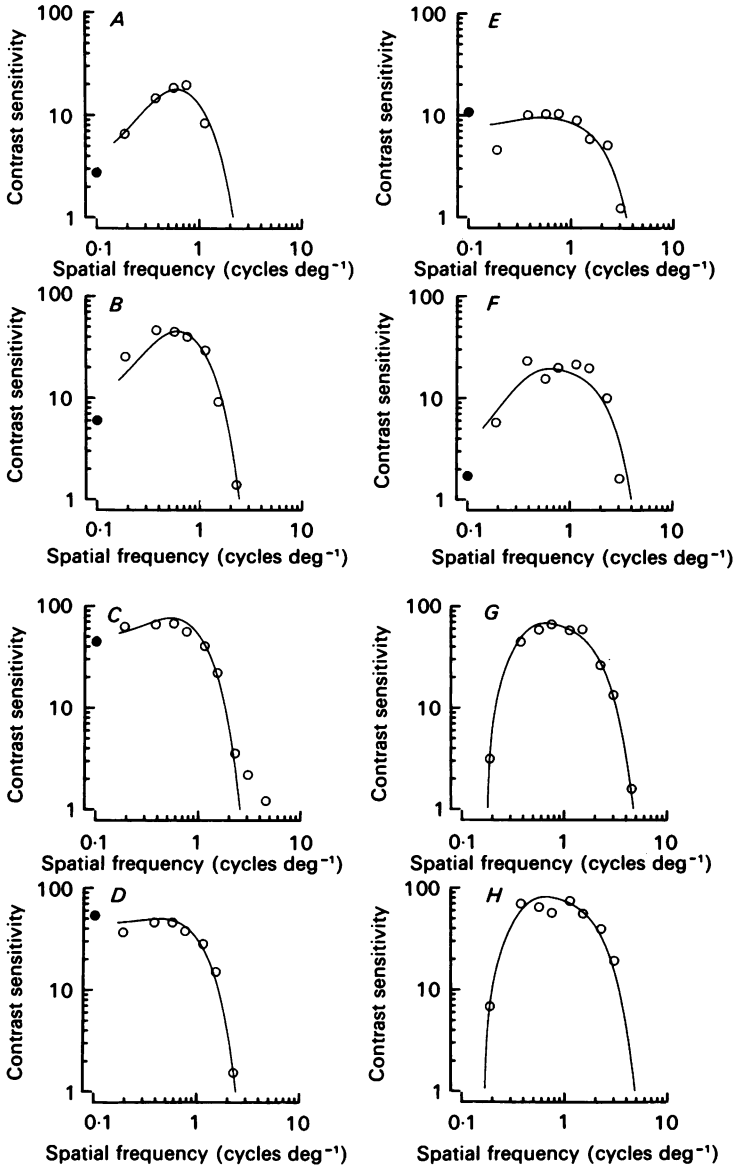

Fig. 13. Effect of temporal frequency upon spatial contrast sensitivities of two magnocellular cells. Different panels show contrast sensitivity curves obtained at 0·65 Hz (*A* and *E*), 2·6 Hz (*B* and *F*), 10·4 Hz (*C* and *G*) and 20·8 Hz (*D* and *H*). For each cell the measurements at all four temporal frequencies were made concurrently in a single experimental run. Smooth curves drawn through the points are best-fitting solutions to eqn. (1), constrained by the requirement that for each cell r_c and r_s remain constant. Filled circles on the ordinates mark sensitivities to modulation of spatially uniform fields.

However, it is not clear that 'type II' units that receive opposed inputs from R and G cones (a group identified only very tentatively by Wiesel & Hubel) can usefully be distinguished from the type I/type III units discussed above. Our measurements of spatial contrast sensitivity show a continuous variation in the degree to which contrast sensitivity falls from its peak as spatial frequency is lowered, and for that reason we do not wish to draw a qualitative distinction.

In summary, our observations encourage the view (for which we argue further in the following paper) that parvocellular units can be divided into only two distinct types: one has a spatially and chromatically opponent receptive field (type I) and is driven only by R and G cones. From cell to cell there is considerable variation in both the spatial and chromatic antagonism. The second type of cell receives inputs from B cones opposed to some combination of inputs from R and G cones, and the antagonistic mechanisms are more nearly spatially co-extensive.

Distinctive classes of magnocellular unit

Wiesel & Hubel (1966) recognized two types of unit in the magnocellular layers: a spatially but not chromatically opponent type III cell and a type IV cell that always had an on-centre receptive field with a strong (very large) surround that was relatively more sensitive to long than to short wave-lengths. Although we studied examples of both types of unit, they were not distinguished by their behaviours when stimulated by achromatic gratings, and we have no grounds to treat them as distinctive classes. The observations of De Monasterio & Schein (1980) and those described in the companion paper (Derrington *et al.* 1984), bolster this conclusion.

Within the magnocellular layers a relatively small number of units show pronounced non-linearities of spatial summation. Our observations on this point confirm those of Kaplan & Shapley (1982), although they do not clearly point to a dichotomy. A convenient index of non-linearity, introduced by Hochstein & Shapley (1976) for the classification of ganglion cells in cat, is the ratio of amplitudes of second harmonic to fundamental response. The distribution of this statistic for magnocellular units (Fig. 2*B*) is unimodal. Kaplan & Shapley (1982) found that their non-linear magnocellular units had poorer spatial resolution than their linearly summating ones, though in our observations this is not the case. In both our work and that of Kaplan & Shapley (1982) the sample sizes were small (we found only six units that showed pronounced non-linearities of spatial summation), and eccentricities of receptive fields are not always known precisely, so there may be no real disagreement.

Receptive field size and distribution

The smallest receptive fields of parvocellular units in the central fovea can resolve over 40 cycles deg^{-1} (Fig. 3), a performance that matches that of the behaving monkey. The characteristic radius of units with this resolving power is of the order of 2·6 μm at the retina, about the diameter of the inner segment of a single foveal cone, but it is most unlikely that the dimensions of cones limit the resolving power of foveal ganglion cells. Optical factors are probably much more important (Campbell & Gubisch, 1966).

We encountered no magnocellular units with receptive fields in the central fovea, and there are good grounds for believing that they are relatively rare. First, Ogden

& Miller (1966) showed that the compound action potential recorded from the temporal margin of the optic disk contained only one mode that represented the activity of slow-conducting fibres, while records obtained from the nasal, inferior and superior margins of the disk contained a second mode that represented the activity of fast-conducting fibres. Secondly, Perry & Cowey (1984) show that in retinae in which virtually all ganglion cells are filled with horseradish peroxidase, the most likely substrate of input to magnocellular laminae (Pα, or A type of Leventhal, Rodieck & Dreher, 1981) is relatively rarer in the foveal region. Thirdly, the magnocellular layers occupy a much larger fraction of the anterior part of the l.g.n. (which represents the peripheral visual field) than they do the posterior part (which represents the fovea), with the result that the ratio of parvocellular to magnocellular neurones may be 10 times greater in the fovea than in the far periphery (Connolly & Van Essen, 1984).

The different centre sizes of magnocellular receptive fields in ipsilateral and contralateral eyes probably reflect the difference between the dendritic field diameters of ipsilaterally and contralaterally projecting ganglion cells of the Pα type (Perry, Oehler & Cowey, 1984). The much greater thickness of lamina 1 (contralateral) than lamina 2 (ipsilateral) presumably reflects the fact that to achieve the same coverage of the retina with cells that have smaller receptive fields the visual system requires more of them. At any one eccentricity the centres of receptive fields of magnocellular units were, on average, 1·6 times larger than those of parvocellular units, but this ratio disguises the fact that the disparity between centre sizes of the two classes of unit is much greater for those driven by the ipsilateral eye than for those driven by the contralateral eye. Since many factors operate to impair the resolution of units with small receptive fields, we believe that the best estimates of the centre diameters of parvocellular units are those from the lower margins of the distributions in Fig. 6*A* and *B*. If one compares these diameters with the mean diameters of receptive fields of magnocellular units (Fig. 6*C* and *D*) the ratio grows to about 3; comfortingly close to the ratio of dendritic field diameters of the Pα and Pβ types of ganglion cells.

Sensitivity of parvocellular neurones

One striking feature of our results was the low sensitivity of parvocellular units. Since this observation has been made by others in both awake monkey (Sperling, Crawford & Espinoza, 1978) and animals anaesthetized with urethane (Kaplan & Shapley, 1982) or barbiturate with nitrous oxide (Hicks, Lee & Vidyasagar, 1983), and since in our work insensitive parvocellular neurones were encountered in the same penetrations as sensitive magnocellular ones, we are confident that the low contrast sensitivity is not the result of pathology or anaesthesia.

One reason for low sensitivity is the small size of the receptive field centre. Consider a receptive field centre of area A (deg^2) excited by illumination I (quanta s^{-1} deg^{-2}). If we assume all quanta are effectively absorbed then for reasonable levels of illumination the quantum catch has an approximately Gaussian distribution about a mean of AI with a variance AI, so a detectable change in the catch will be proportional to $(AI)^{0.5}$. If we now consider units with receptive fields of different sizes we find that the quantum catch grows with A but the noise as $A^{0.5}$, so the signal-to-noise ratio improves as $A^{0.5}$, and therefore as the radius of the receptive field. This is clearly

not the only reason for the difference between the sensitivities of the two classes of cell, for the ratio of sensitivities is considerably greater than the ratio of centre radii (r_c).

Contribution to psychophysically measured sensitivities

Our observations suggest that magnocellular units cannot support the high visual acuities found in and near the fovea; for that we require parvocellular units, most of which have chromatically opponent receptive fields. The question of interest is whether we need magnocellular units to account for the high contrast sensitivities found near the peak of the contrast sensitivity curve. Since we have reason to believe that the foveal region is poorly represented in the magnocellular layers, it is instructive to consider whether the form and the position of the (psychophysical) contrast sensitivity curve could be based on the signals from parvocellular units alone.

In most psychophysical measurements of spatial contrast sensitivity the gratings are extended in both space and time, so that the detectability of patterns depends upon the sensitivity of individual mechanisms and upon probability summation in space and time. When the attempt is made to control probability summation across space by using small patches of grating containing a constant number of cycles at each spatial frequency, contrast sensitivity in the fovea is higher than outside it, for all spatial frequencies, and the peak contrast sensitivity (at high luminance) falls to about 40 (Robson & Graham, 1981). In rather different experiments (again undertaken at high luminance) Watson, Barlow & Robson (1983) found that the most efficiently detected patch of grating had a spatial frequency of 6 cycles deg^{-1} and, at threshold, a contrast of 69. Moreover, in both these experiments the threshold value includes probability summation over space, and whatever algebraic summation occurs for signals from mechanisms with overlapping receptive fields. When one takes account of differences in threshold criterion, a single magnocellular unit seems to be slightly more sensitive than any detector inferred from psychophysical experiments, while a parvocellular unit is perhaps one-third as sensitive; a gap that could be removed by probability summation across as few as ten units.

A. Parker kindly commented on the manuscript. This work was supported by grants from the Medical Research Council (979500) and the National Eye Institute (EY 04440) to P.L. A.M.D. held a Beit Memorial Fellowship.

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