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X AND Y CELLS IN THE LATERAL GENICULATE NUCLEUS OF MACAQUE MONKEYS

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SUMMARY

1. Cells of the lateral geniculate nucleus (l.g.n.) in macaque monkeys were sorted into two functional groups on the basis of spatial summation of visually evoked neural signals.

2. Cells were called X cells if their responses to contrast reversal of fine sine gratings were at the fundamental temporal modulation frequency with null positons one quarter of a cycle away from positions for peak response. Cells were called Y cells if their responses to such stimuli were at twice the modulation frequency and were approximately independent of spatial phase.

3. Ninety-nine percent of the cells in the four dorsal parvocellular layers of the l.g.n. were X cells; about seventy-five percent of the cells in the two ventral magnocellular layers were also X cells. The remainder were Y cells.

4. We confirmed previous findings that magnocellular cells had a shorter latency of response to electrical stimulation of the optic chiasm.

5. Magnocellular cells had much higher contrast sensitivities than did parvocellular cells.

6. Therefore, two distinct classes of X cells exist in the macaque l.g.n.: parvocellular X cells and magnocellular X cells. The great difference in their properties suggests that they have different functions in vision. The Y cells in the magnocellular layers form a third functional group with spatial properties distinctly different from the X cells.

7. We propose that the magnocellular layers of the macaque monkey's l.g.n. may be homologous to the A and A1 layers of the cat's l.g.n.

INTRODUCTION

The sorting of visual cells into separate functional groups has been a continuous theme of visual neurophysiology. In the retina, optic tract, and lateral geniculate nucleus (l.g.n.) of the cat, the X/Y classification has been particularly important (Enroth-Cugell & Robson, 1966; Cleland, Dubin & Levick, 1971; Lennie, 1980*a* among others). The distinct visual properties of different cell types had led to attempts to incorporate physiological discoveries about parallel processing in the cat visual pathway into theories of human visual perception (Tolhurst, 1973; Lennie, 1980*a*, *b*).

Recently, the organization of the macaque monkey's l.g.n. into several layers of cells has been related to the possible anatomical segregation of X and Y cells. The main conclusions of previous investigators were that all cells in the four dorsal parvocellular laminae of the macaque l.g.n. resembled X cells in the cat while cells in the two ventral magnocellular laminae were similar to the cat's Y cells (Dreher, Fukada & Rodieck, 1976; Sherman, Wilson, Kaas & Webb, 1976; Schiller & Malpeli, 1978). These conclusions were mainly based on measurements of afferent conduction velocity and response time course. We have investigated the functional classes of l.g.n. cells in the (cynomolgus) macaque monkey *Macaca fascicularis* by means of measurements of visual spatial summation and visual spatial resolution, methods for assigning cells into the X and Y classes which have been applied previously to the cat's retinal ganglion cells and l.g.n. cells (Hochstein & Shapley, 1976*a*, *b*; So & Shapley, 1979). Our results imply that there is functional segregation in the macaque's l.g.n., but the X cells are not segregated from Y cells.

A preliminary report of this work has been published (Shapley, Kaplan, & Soodak, 1981).

METHODS

Monkeys (*Macaca fascicularis*) were initially anaesthetized with 10 mg/kg ketamine and then given sodium thiamylal (Surital) as needed during preparatory surgery, and then anaesthetized with urethane (20 mg/kg.h) I.V. during the experiment. Muscle paralysis was produced by infusion of gallamine triethiodide (5 mg/kg.h). Blood pressure, expired carbon dioxide, electrocardiogram, and body temperature were monitored and kept within the physiological range.

Phenylephrine hydrochloride (10%) and atropine sulphate (1%) were applied to the eyes. The corneas were protected with clear plastic contact lenses. The dilated pupil was about 6 mm in diameter. For work on foveal units an artificial pupil might be required, but in our experiments on parafoveal and peripheral cells the physiological optics were sufficiently good without one. Control experiments with a 3 mm diameter pupil showed very little improvement in spatial resolution of the cells. Preliminary refraction was performed with an ophthalmoscope, but the exact refractive correction was determined by optimizing the spatial resolution of parafoveal cells with corrective lenses. The optic disks and foveas were mapped on a tangent screen onto which the receptive field positions of single cells were later also mapped.

The stimuli were produced with a raster display on the face of a cathode ray tube (c.r.t.) monitor (Tektronix 606 or 608). Drifting and contrast reversal gratings were generated with electronic circuitry which has been described (Shapley & Rossetto, 1976). The visual stimulus can be represented formally as

contrast reversal:
$$L(x, t) = L_0 + L_1 \sin(2\pi kx + \phi) \cdot M(t). \quad (1a)$$

drift:
$$L(x, t) = L_0 + L_1 \sin(2\pi(kx - ft)). \quad (1b)$$

In these equations L_0 is the mean luminance, L_1/L_0 is the contrast (or depth of modulation), k is spatial frequency, x is position in degrees, ϕ is spatial phase, $M(t)$ is the temporal modulation signal, usually a sinusoid or square wave and f is the temporal rate of drift in Hz. The mean luminance was constant throughout an experiment and was in the range from 20 to 60 cd/m^2. The luminance and contrast were calibrated with a Spectra Brightness Spot Meter. The Tektronix 606 we used had a P31 (yellow-green) phosphor and was 8 by 10 cm. The Tektronix 608 had a P4 (white) phosphor and was 10 by 12 cm. Similar results were obtained with both. The c.r.t. was located approximately 57 cm from the monkey. A front surface mirror reflected the image of the c.r.t. screen onto the receptive field of the cell under study. Stimulation was monocular.

The lateral geniculate nucleus was located stereotaxically with the central sulcus as a surface landmark. Extracellular single unit recording was performed with glass micropipettes. On about half of the penetrations the pipettes were filled with a saturated solution of Fast Green dye in 0·9%

saline. On the other half of the penetrations, saline-filled pipettes were used. A negative capacitance bridge preamplifier was used. Nerve impulses were led to an oscilloscope and an audio monitor and to a comparator circuit. The comparator converted the impulses to standard pulses which were used for averaging and analysis by a digital computer (PDP 11/45).

The basic experiment we performed was measurement of the spatial phase dependence of the response to a grating undergoing contrast reversal as described by equation (1*a*). The visual

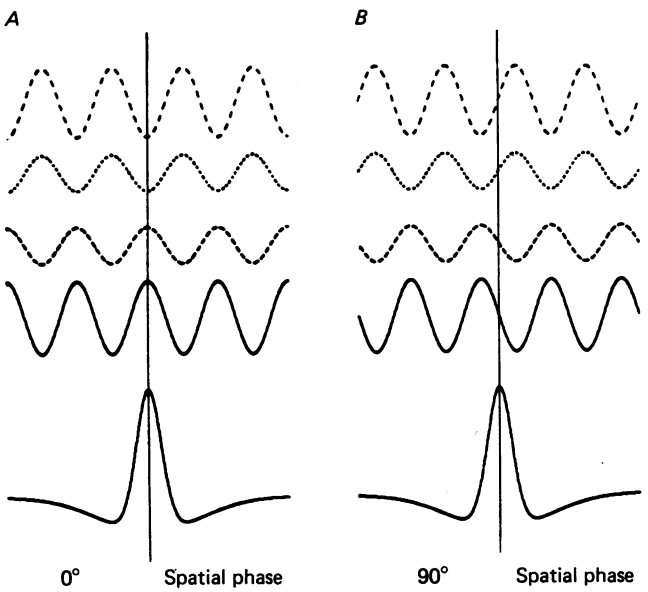

Fig. 1. Contrast reversal of grating patterns at two spatial phases. The curves at the top of each side of the Figure represent the one-dimensional luminance profile of the grating at four instants of time. The luminance profile of the stimulus in space is a sinusoid. Its amplitude is modulated by a slow sinusoidal temporal modulation signal ($M(t)$ in eqn. 1*a*). The continuous curve is the luminance profile of the grating at the crest of the temporal modulation signal. The coarsely dashed (– – –) curve is the luminance profile at the trough of the temporal modulation signal. The finely dashed curves (- - - and · · ·) are stimulus luminance profiles at intermediate values of the temporal modulation signal. The continuous curve below the stimulus represents the sensitivity profile of a typical centre-surround visual neurone in the retina or l.g.n. The vertical line represents the mid-point of the receptive field. In the stimulus situation on the left hand side, denoted 0° spatial phase, the crest of the spatial sinusoid is lined up with the peak of the sensitivity profile. In the stimulus condition on the right, denoted 90° spatial phase, a zero-crossing of the grating is lined up with the peak of the sensitivity profile.

stimulus is illustrated in Fig. 1. The grating was first positioned to produce a maximal response as in Fig. 1*A*. Then, it was moved to a new location 90° away in spatial phase as in Fig. 1*B*. Were the neural pathway leading up to the neurones we were studying linear, then if the response were maximal in position *A*, it would be zero in position *B*.

Quantitative study of response time course, spatial resolution, contrast sensitivity, and spatial phase responsivity was performed as follows. The computer produced the stimulus modulation signal $M(t)$ (in the case of contrast reversal) or produced the drifting grating pattern, averaged the responses and calculated the fundamental response component, the Fourier component in the response which was at the same temporal frequency as the input frequency.

Electrical stimulation of the optic chiasm was done routinely with a pair of stainless steel

electrodes insulated with Teflon except at the tips. The optic chiasm was usually found at Horsley–Clarke co-ordinates A18 L0·5 about 25 mm below the surface of the cortex.

The position of the recording electrode was reconstructed from dye marks and lesions left at the top and bottom and at some crucial places along an electrode track through the l.g.n. Lesions or dye marks were left by passing 20 μA anodal current through the pipette for 5 min. At the end of the experiment the monkey was killed with an overdose of barbiturate and then immediately perfused with 0·9 % saline followed by 10 % formaldehyde in saline. After suitable fixation, coronal sections were cut on a freezing microtome and stained with Cresyl Violet to allow reconstruction of tracks (see Figs. 2, 3, 4).

RESULTS

Parvocellular X cells

We classified cells by studying their responses to contrast reversal of a sinusoidal grating pattern. The properties we used to identify X cells were (1) response at the modulation frequency of the contrast reversal and (2) grating positions for a null response separated by 90° in spatial phase from positions for a peak response. Both of these properties are what one would expect from the response of a single linear receptive field mechanism to stimulation by contrast reversal of a grating pattern (cf. Hochstein & Shapley, 1976*a*; Shapley & Gordon, 1978).

The spatial phase dependence of a parvocellular X cell is illustrated in Fig. 2. The cell was stimulated by a 2·5 c/deg sine grating which was undergoing contrast-reversal with a sinusoidal time course at a rate of 4 Hz. One of the averaged responses displayed in Fig. 2 was elicited by the grating at a spatial phase denoted 0° for the position of maximal response. At a spatial phase 90°away from this (or one quarter of a spatial period, equivalent to 0·1° of visual angle for a 2·5 c/deg grating) the cell produced no modulated response to grating contrast reversal. Thus, an X cell's response is highly dependent on spatial phase.

The time course of the response of parvocellular X cells to contrast reversal is also typified by the results in Fig. 2. One can show that if the neural transductions from photoreceptors to retinal ganglion cells to geniculate cells were all linear for modulations of the stimulus around its steady-state level, then the time course of the averaged response ought to be sinusoidal at the temporal modulation frequency of the stimulus. In fact, the response of the parvocellular X cell in Fig. 2 was dominated by the fundamental temporal modulation frequency at 0° spatial phase, and a null point was seen at 90° spatial phase. The amplitude of the response at the fundamental modulation frequency was 23·9 impulses/s. There was some harmonic distortion at 0° spatial phase: an amplitude of 4·5 impulses/s for the second harmonic and 5·9 impulses/s for the third harmonic. At 90° spatial phase the amplitudes of fundamental, second harmonic, and third harmonic were 1·0, 1·0, and 0·9 impulses/s respectively. The variability in response amplitude in this cell was approximately two impulses/s so that the responses at 90° were in the noise.

Strictly speaking, the identification of a cell as an X cell on the basis of linear summation requires more than a strong dependence on spatial phase and response at the modulation frequency. It is known that Y cells, in the cat retina and lateral geniculate nucleus, have a strong spatial phase dependence and respond primarily at the fundamental modulation frequency *if a sine grating of low spatial frequency is used* (Hochstein & Shapley, 1976*a*, *b*; So & Shapley, 1979). It is crucial to test spatial

phase dependence over a range of spatial frequencies and especially at high spatial frequencies for the cell. For parvocellular X cells the strong spatial phase dependence (with peaks and nulls), and the dominance of the response by the fundamental modulation frequency, persisted as spatial frequency was increased up to the highest value to which the cell responded. This indicates that the smallest neural summing

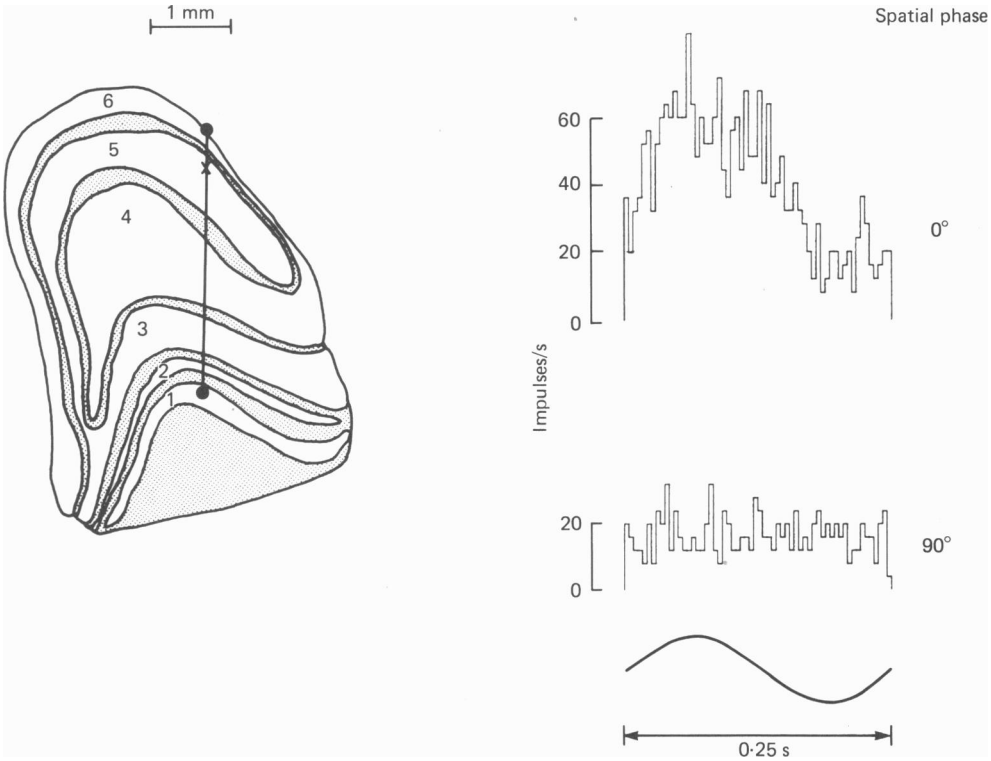

Fig. 2. Localization and identification of a parvocellular X cell. On the left side of the Figure is a tracing from the l.g.n. of *M. fascicularis*. A single electrode track is represented by the continuous line terminated by ●, which represent positions of electrolytic lesions. From the micrometer readings of the micromanipulator used to advance the electrode, we deduced that this neurone was at the position marked with an X along the electrode track. Thus it was a parvocellular neurone in the parvocellular layer 5 which receives input from the eye ipsilateral to the l.g.n. That the cell was X-like was deduced from its response to a sine grating as a function of spatial phase, represented on the right hand side of the Figure. In this case the grating was 2·5 c/deg in spatial frequency, 0·32 contrast, and was modulated by a 4 Hz sinusoid. The temporal modulation signal is represented at the bottom of the right hand column.

area within the receptive field, presumably the receptive field centre, is part of a linear receptive field mechanism in X cells of the monkey's geniculate.

The cell in Fig. 2 was assigned to parvocellular layer 5 by reconstruction of the track of the electrode through the lateral geniculate nucleus, also illustrated in Fig. 2. The positions of the electrode at the bottom and at the top of the track were marked by electrolytic lesions.

Magnocellular X cells

Most of the cells encountered in the magnocellular layers were identified as X cells based on the criteria of linear spatial summation described above. A typical example is illustrated in Fig. 3 from a cell assigned to magnocellular layer 2. The visual stimulus was a sine grating undergoing contrast reversal with a sinusoidal time course. The spatial phase dependence of the cell's response is indicated in the Figure. The

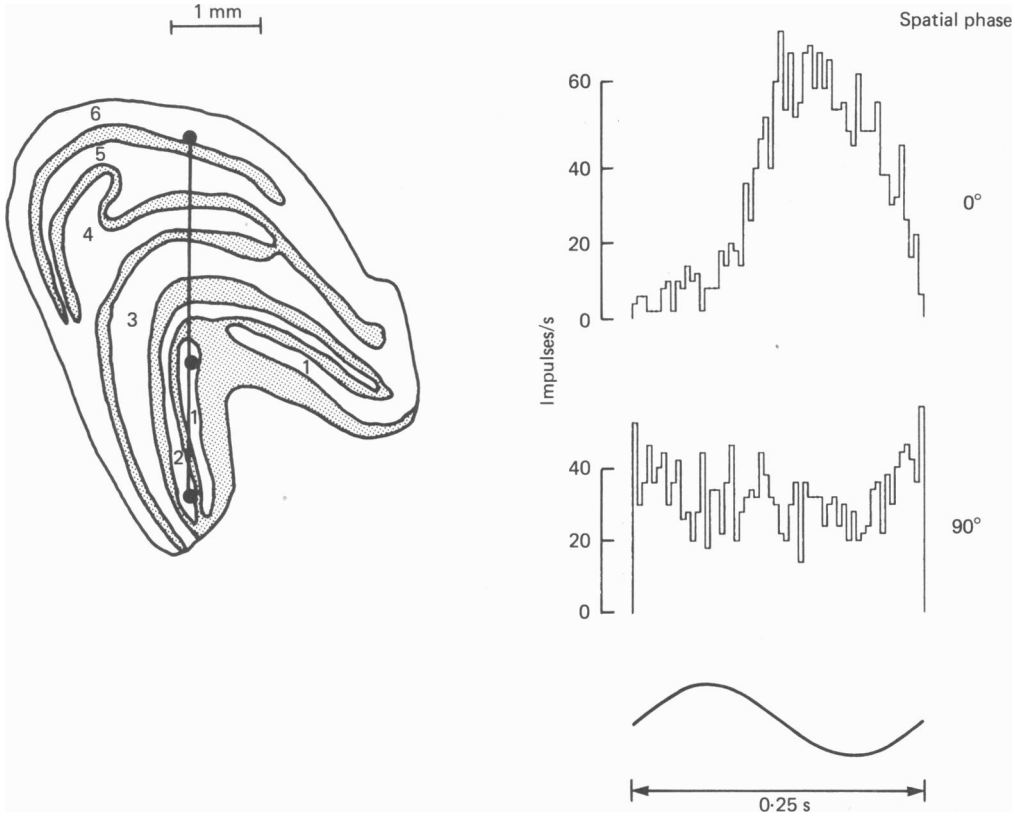

Fig. 3. Localization and identification of a magnocellular X cell. This cell was located at the bottom of the electrode track sketched on the left side of the Figure. Positions along the track were marked by ionophoresis of Fast Green dye. The cell was located at the position of the green dot at the bottom of the track, in magnocellular layer 2. It was identified as an X cell on the basis of its responses to grating contrast reversal at different spatial phases as indicated on the right hand side of the Figure. The spatial frequency was 1·5 c/deg, temporal frequency 4 Hz, contrast 0·5.

amplitude of response at the fundamental frequency was 31 impulses/s at 0° spatial phase which was a position of peak sensitivity of the cell for the grating. One quarter of a spatial cycle away, or at 90° spatial phase, the amplitude of the cell's fundamental response was only 5 impulses/s. The fundamental response was predominant at all positions which were effective in producing a modulated response. This behaviour is characteristic of a cell driven by a single linear receptive field mechanism. Such linear

behaviour was present at all spatial frequencies used, for this cell and the other magnocellular X cells.

Magnocellular Y cells

Not all l.g.n. neurones in the magnocellular layers were X-like in terms of spatial summation. Approximately one quarter of the magnocellular cells resembled Y cells in the cat retina and l.g.n. The primary characteristic we have used to identify Y

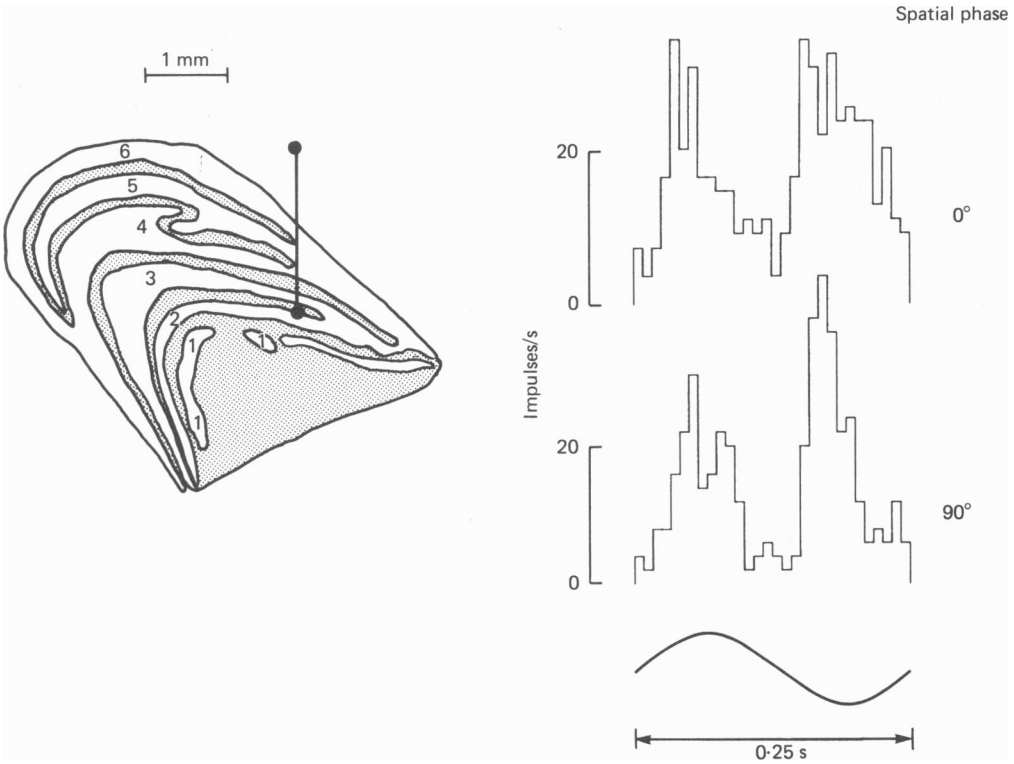

Fig. 4. Localization and identification of a magnocellular Y cell. The cell was located at the bottom of the electrode track sketched on the left side of the Figure. The lower of the two dye marks was left at the position at which the cell was recorded, clearly in layer 2. When the spatial frequency of a contrast reversal grating was increased, the response of the cell was as shown on the right, mainly at twice the modulation frequency and more or less independent of spatial phase. The spatial frequency of the grating was 1·6 c/deg, the temporal frequency was 4 Hz, and the contrast was 0·18. The cell was an off-centre Y cell with fundamental spatial resolution of 0·8 c/deg and second harmonic spatial resolution of 3·3 c/deg.

cells in the cat is the non-linear behaviour these cells exhibit in response to contrast reversal of fine grating patterns (Hochstein & Shapley, 1976*a*; So & Shapley, 1979). Cat Y cells respond to such patterns predominantly at twice the modulation frequency; the frequency doubled response of the Y cells does not change as the spatial phase of the grating is varied. Such behaviour is also shown by cells in the monkey's geniculate which we have identified as Y cells. An example is given in

Fig. 4. One can see that the cell's responses were dominated by a component at twice the frequency of stimulus modulation. This frequency doubled response was the same at several spatial phases, two of which (separated by 90°) are shown in the Figure. This cell produced responses at the temporal modulation frequency and at twice the modulation frequency for spatial frequencies below 0·8 c/deg. Between 0·8 c/deg and its spatial resolution limit of 3·3 c/deg, the cell produced only or mainly frequency doubled responses.

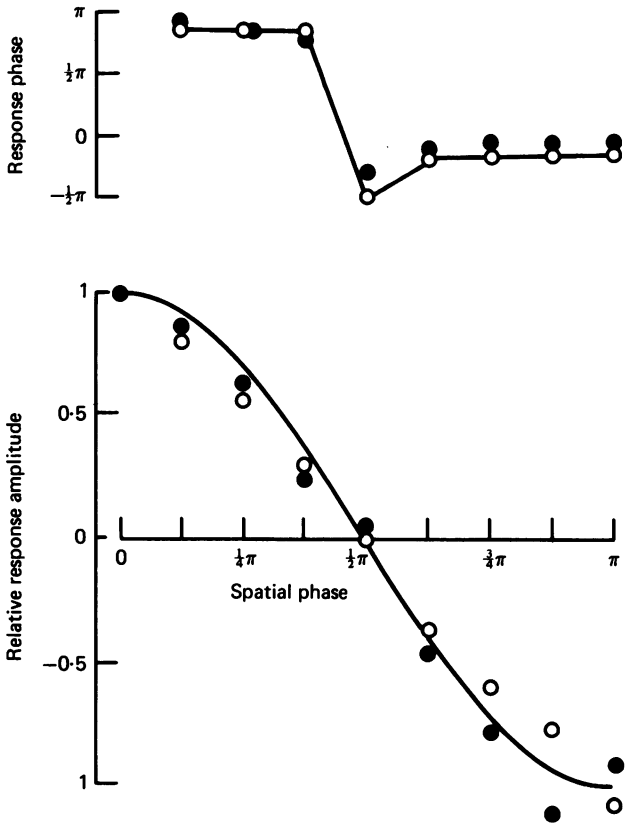

Fig. 5. Fundamental Fourier components of responses to grating contrast reversal are plotted *vs.* spatial phase. The contrast of the stimulus was 0·35; the temporal modulation frequency was 4 Hz; the spatial frequency was 2 c/deg. Results from two parvocellular X cells are shown. The continuous curve in the lower panel is a one half cycle of a best fit sinusoid. Straight lines were drawn through the response phase plots. Amplitude and phase from one cell are represented by filled circles, from the other cell by open circles.

Almost all Y cells were found in the magnocellular laminae. An example is shown in Fig. 4. The lower green mark on the track was left near the site of recording of the Y cell whose responses are presented in the Figure. Therefore, the cell was in layer 2, the dorsal magnocellular layer. In one case we recorded a Y cell in a parvocellular layer. This cell was like magno-Y cells in its receptive field properties.

There were very few non-visual cells encountered in the monkey's l.g.n. All the visual cells could be sorted into either the X or the Y class. Thus, we did not see any cells in the l.g.n. which resembled the non-concentric types of retinal ganglion cells

reported by De Monasterio (1978), which presumably project to mid-brain visual centres (Rodieck, 1979).

Spatial phase dependence

X cells. To illustrate the similarity between X cells in monkey and cat, we offer the measurements of spatial phase responsivity in Fig. 5. In most cells we only determined that the peak and null were 90° apart in spatial phase. However, in seven

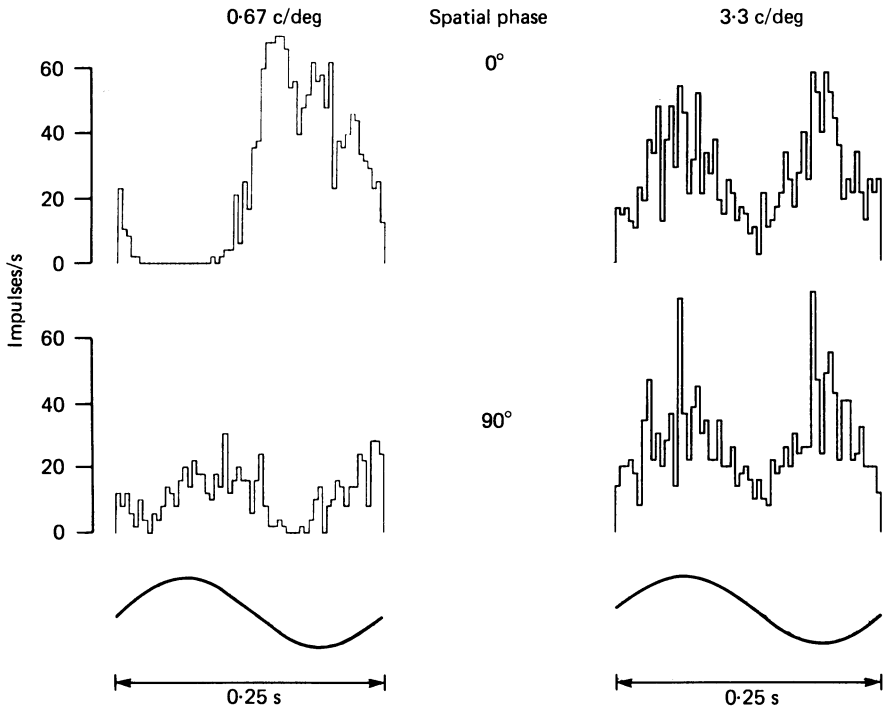

Fig. 6. Spatial frequency dependence of non-linear and linear response components in a Y cell. Averaged responses are shown for two spatial phases at two spatial frequencies. At 0·67 c/deg the main response component at 0° spatial phase was at the same temporal frequency as the modulation signal, represented below the histograms by the continuous sine-wave curve. At 90° spatial phase at 0·67 c/deg the fundamental response disappeared to reveal a small but significant frequency-doubled (second harmonic) component. At 3·3 c/deg the second harmonic component was the only response component present, and it was independent of spatial phase. These experiments were done with 0·25 contrast and 4 Hz temporal frequency of modulation.

parvocellular X cells and five magnocellular cells we made more extensive measurements of the spatial phase dependence. In these cells we averaged the response to grating contrast reversal at spatial phases separated by either 45 or 22·5° spatial phase. The spatial phases of the stimuli extended from one half period to a full period of the grating. The variation in response phase and amplitude for two parvocellular X cells is shown in Fig. 5. There were two major features of the X cells' dependence on spatial phase. The response amplitude was approximately a sinusoidal

function of spatial phase, as can be seen in the lower graph of Fig. 5. Furthermore, the response phase was approximately constant on either side of the null position (designated 90° spatial phase) and jumped by almost precisely π radians (one half cycle) as the stimulus grating was moved from one side of the null to the other. This is exactly what one would expect from a neurone which receives input from a single, linear receptive field mechanism. Note that the response phases at the null position were unreliable because they are estimated from very small neural responses which are probably in the noise.

Y cells. The spatial phase dependence of Y cells also reveals similarities between monkey and cat. Fig. 6 shows one aspect of this similarity, the emergence of a spatial-phase-insensitive response as spatial frequency is increased. On the left side of the Figure are two averaged responses to contrast reversal of a coarse grating of spatial frequency 0·67 c/deg. At 0° spatial phase the response was very large and was dominated by a fundamental component. This can be seen by observing that there was only one major response peak per cycle of contrast reversal. Fourier analysis of the response confirmed this intuitive observation. At 90° in spatial phase, again at 0·67 c/deg, the fundamental response was gone but a small second harmonic response became apparent; there were two response peaks per cycle. When the spatial frequency of the stimulus grating was increased to 3·3 c/deg, the averaged responses looked very similar at spatial phases separated by 90°, as can be seen on the right side of Fig. 6. Both responses were dominated by a frequency-doubled, second harmonic component (compare with Fig. 4). This kind of linkage of spatial phase dependence with spatial frequency is just what one observes in Y cells from the cat optic tract and l.g.n. (Hochstein & Shapley, 1976*a*, *b*; So & Shapley, 1979).

An explanation for the duplex behaviour of Y cells in terms of a receptive field model has been offered previously (Hochstein & Shapley, 1976*b*). The essence of the model is that in the Y cell's receptive field there must be many dispersed subunits which only excite the cell after their signals have passed through a non-linear transducer like a threshold or a rectifier. This array of 'non-linear subunits' appears to be arranged in parallel with a conventional, linear receptive field centre and surround (Hochstein & Shapley, 1976*b*; Victor & Shapley, 1979). This explains why Y cells appear most non-linear in response to gratings of high spatial frequency, gratings which are too fine to be resolved by the Y cell's large linear centre but are still resolvable by the cell's non-linear subunits.

Proportions of X and Y cells in different layers

There was a definite difference in the proportions of cells with X and Y receptive field properties between the parvocellular and magnocellular layers of *M. fascicularis*. In twelve monkeys we isolated 262 X and Y cells which we could assign to specific geniculate layers on the basis of histological reconstruction of tracks. Of these cells, 185 were in the parvocellular laminae and 77 were assigned to magnocellular layers. The proportions of X and Y cells in the geniculate layers are displayed in Fig. 7. More than 99% of our sample of parvocellular neurones were X-like. Only one out of 185 was a definite Y cell. In the magnocellular laminae there were both X and Y cells. The ratio of X to Y cells was approximately 3:1 in both magnocellular layers.

Rarely one can record single units from the S laminae, the two most ventral cell

layers of the macaque l.g.n. (Kaas, Huerta, Weber & Harting, 1978). Our sample included two such cells, each of which was marked with a green dot so that the assignment to the S1 lamina was certain. One of these cells was an X cell and one was a Y cell. Their receptive field properties resembled those of magnocellular cells.

We have also studied the spectral sensitivity of cells in the macaque's l.g.n. to determine the correlation between colour and pattern sensitivity. Results of this work will be reported elsewhere.

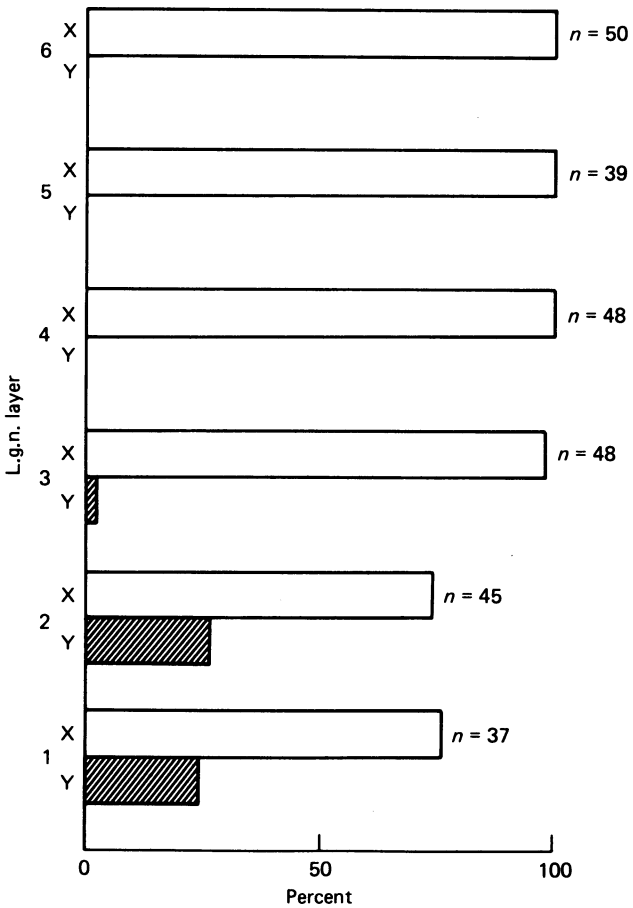

Fig. 7. X and Y percentages by layer in the l.g.n. of *M. fascicularis*. X cells are represented by open bars, Y cells by shaded bars. The sample size is given to the right of the bars.

Spatial resolution

The synchronous, fundamental response of lateral geniculate neurones to a drifting sine grating becomes progressively weaker as the spatial frequency is increased until the response finally disappears into the noise. We call the spatial frequency at which the response disappears the *fundamental spatial resolution* of the neurone. The fundamental spatial resolution depends on the contrast of the drifting grating. In the experiments reported here we measured the fundamental spatial resolution with a

grating of 0·8 contrast produced on a c.r.t. screen. The drift rate was 4–8 Hz; the drift rate was kept contant in temporal frequency as the spatial frequency was varied. Control experiments established that the temporal frequency responses of the geniculate neurone were relatively flat over the range of drift rates used. The temporal frequency of the drifting grating was kept constant, as in previous studies (Enroth–

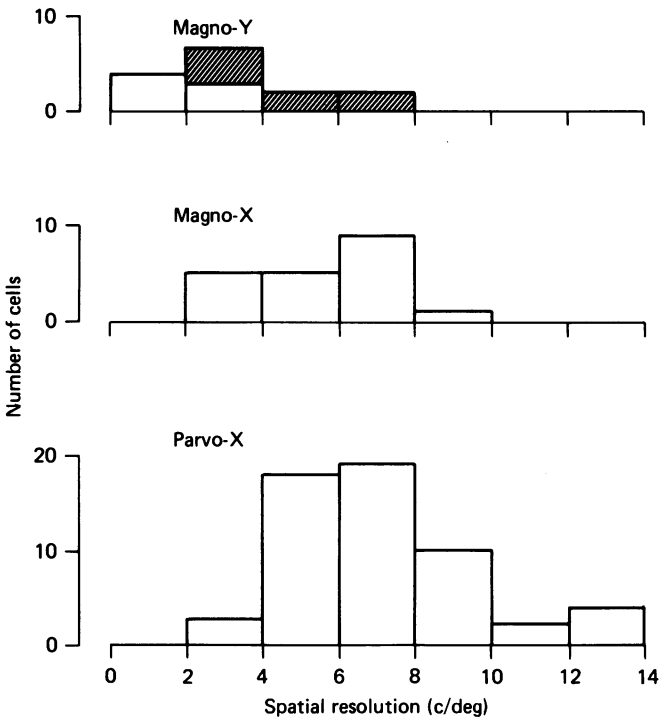

Fig. 8. Spatial resolution distributions of parvo-X, magno-X and magno-Y cells. The spatial resoluton of fundamental responses (see text) are indicated by open bars. The spatial resolution of second harmonic responses of Y cells are indicated by the shaded bars. Positions of the cells' receptive fields were from 3–10° from the fovea.

Cugell & Robson, 1966; So & Shapley, 1979), because the measurement of spatial resolution was performed subjectively by the experimenter who listened for a modulated neural response on an audio monitor. Criterion changes of the experimenter with temporal frequency lead to inaccuracy in the determination of spatial resolution if temporal frequency is not fixed.

The distribution of the fundamental spatial resolution is displayed in Fig. 8. The cells in this graph were located from 3 to 10° from the fovea. Our electrode tracks generally were aimed to record from all six layers of the l.g.n. so that we did not sample from the foveal representation. Cells more peripheral than 10° were excluded from the histograms. While spatial resolution continually decreases away from the fovea, it is a relatively flat function of retinal eccentricity from 3 to 10° (cf. Blakemore & Vital-Durand, 1979). The average values of spatial resolution of this sample are as

follows: parvocellular X, 8·0 c/deg (fifty-nine cells); magnocellular X, 5·7 c/deg (twenty cells); magnocellular Y, 2·2 c/deg (seven cells).

The spatial resolution of the non-linear response of Y cells was higher than that of the fundamental response (Fig. 8). This was measured by increasing the spatial frequency of a grating, which was being reversed in contrast, until the frequency

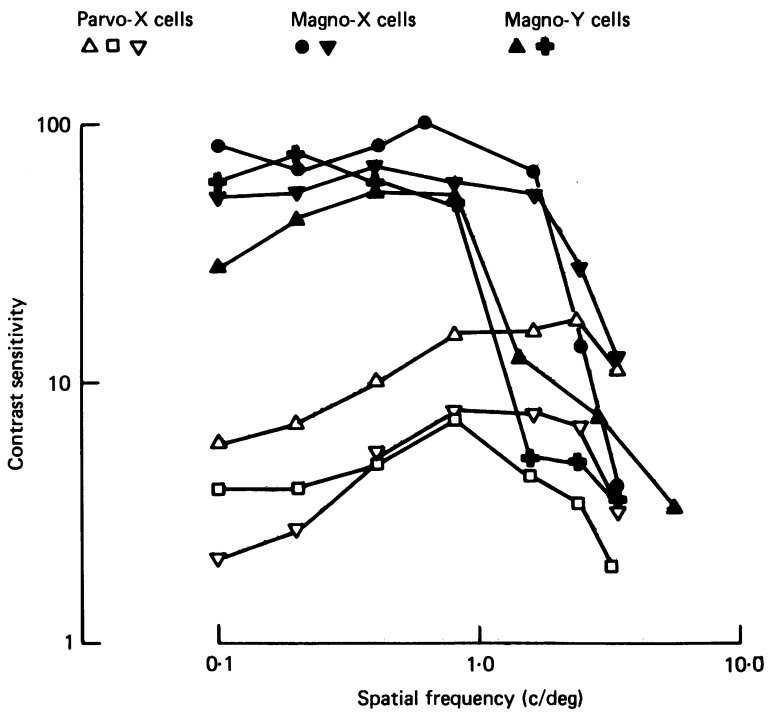

Fig. 9. Contrast sensitivity functions of monkey l.g.n. neurones. The filled symbols are from magnocellular neurones; the open symbols are from parvocellular neurones. Contrast sensitivity was the reciprocal of the contrast required to give a response with a fundamental Fourier amplitude of 5 impulses/s. Temporal modulation frequency was 2·5–3 Hz. The parvo-cell which is indicated by the upright triangles (△) was among the most sensitive parvocellular neurones. More typical results are represented by the other two parvocellular X cells.

doubled response of the Y cell finally disappeared. The average spatial resolution of the second harmonic, non-linear response in seven Y cells was 4·9 c/deg which is close to the fundamental spatial resolution of magnocellular X cells.

Contrast sensitivity

One of the factors which determines spatial resolution is the contrast sensitivity, which is defined as the reciprocal of the contrast required to evoke a criterion response. Cells with small receptive fields but low sensitivity may have the same spatial resolution as cells with larger fields and higher sensitivity. This reasoning led us to compare the contrast sensitivities of parvocellular and magnocellular neurones.

Magnocellular cells all have much higher contrast sensitivity than parvocellular

cells. This point is illustrated in Fig. 9 which shows contrast sensitivity curves for seven typical cells: three parvocellular neurones, two magnocellular X cells and two magnocellular Y cells. The stimuli were sine gratings drifting at a rate of 2·5–3 Hz. The response *vs.* contrast was measured at two or three contrasts for each of seven spatial frequencies. The reciprocal of the contrast required to elicit an amplitude of

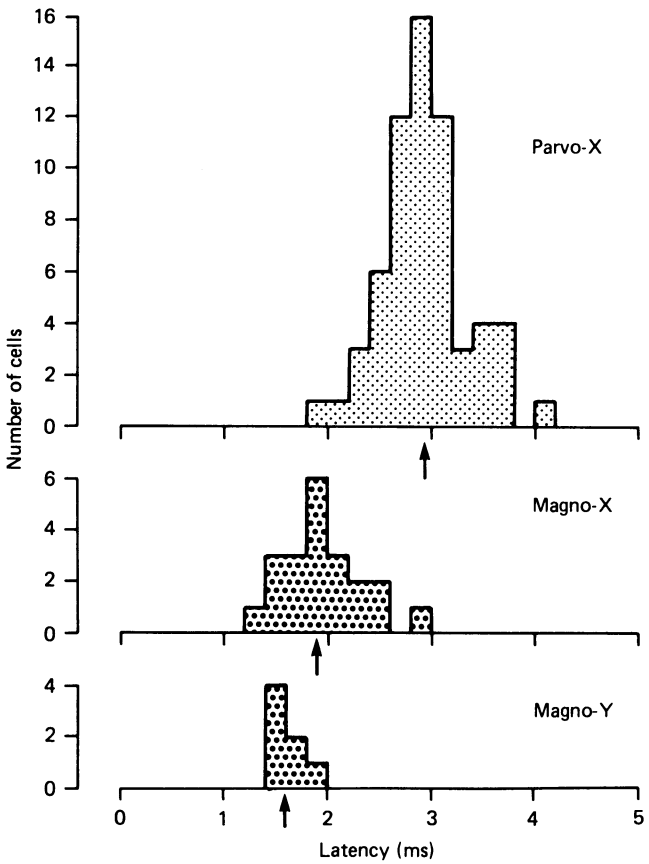

Fig. 10. Latency distributions to stimulation of the optic chiasm. Neurone spikes were elicited by repetitive electrical stimulation of the optic chiasm. Current pulses were 50 μs in duration and were delivered by a constant current source. Latency measurements were taken at suprathreshold current values. Latency was measured from the start of the stimulus pulse to the peak of the nerve impulse. There was typically some variability in latency, so three to five spike latencies were averaged. In the Figure, the arrows below each latency distribution indicate the average latency for that distribution.

response of 5 impulses/s was taken to be the contrast sensitivity. For each cell we characterized its contrast sensitivity by the peak of a contrast sensitivity curve like those shown in Fig. 9. The average of these peak contrast sensitivities for seventeen parvocellular cells was 11 ± 3. The average peak contrast sensitivity for ten magnocellular cells was 82 ± 20. The magnocellular cells are comparable in contrast sensitivity to cells in the A and A1 layers of the l.g.n. of the cat which also have moderately high sensitivity for contrast. Similar results have been obtained by

P. Lennie & A. M. Derrington (personal communication). Sperling, Crawford & Espinoza (1978) have also obtained results consistent with ours in awake, behaving monkeys.

Latency to electrical stimulation

Another way to study parallel processing in the visual pathway is to measure the speed of impulse conduction of the optic nerve and optic tract axons. In the cat the axons of the X and Y retinal ganglion cells have characteristically different conduction velocities, the Y cells having the fastest axons in the tract and the X cells

TABLE 1. Cell types in monkey l.g.n.

	Parvo-X	Magno-X	Magno-Y
Spatial summation	Linear	Linear	Non-linear
Chiasm latency	Long	Short	Short
Spatial resolution (Fundamental)	High	Medium to high	Low
Spatial resolution (2nd Harmonic)	—	—	Medium to high
Colour	Opponent Concealed opponent	Non-opponent Type IV	Non-opponent —
Contrast sensitivity	Low	High	High

having intermediate conduction velocities (Cleland *et al.* 1971; Hoffmann, Stone & Sherman, 1972; So & Shapley, 1979). Previous investigations have suggested similar correlations in the macaque (Dreher *et al.* 1976) between receptive field properties and conduction velocity but have not addressed the specific question of whether linear and non-linear summation are correlated with medium and fast conduction velocity respectively.

Fig. 10 shows frequency histograms of conduction latency for parvocellular X, magnocellular X, and magnocellular Y cells excited by a brief electrical shock to the optic chiasm. The average latency of each distribution is indicated by the arrow beneath the appropriate horizontal axis. Clearly, the latency of the parvocellular X cells is longer than that of either type of magnocellular neurone. The magnocellular X cells have a slightly longer latency than the magnocellular Y cells on average, though the difference is not significant because of the variance of the magnocellular X distribution. Also there is considerable overlap between the parvocellular X and magnocellular X conduction latencies between 2 and 3 ms. It is worth noting anecdotally that the one verified parvocellular Y cell mentioned earlier had a long latency characteristic of parvocellular neurones. Also, the two cells recorded from lamina S1 had short conduction latencies similar to those of magnocellular cells.

A summary of the major results reported in this paper is presented in Table 1.

DISCUSSION

Functional implications

Our results imply that the parvocellular cells are not homologous to the X cells in the A and A1 layers of the cat's l.g.n. Rather, the cells of the magnocellular layers,

both X and Y, seem to be homologous to the achromatic X and Y cells of high contrast sensitivity found in the cat's A and A1 layers.

The behavioural contrast sensitivity of macaque monkeys is comparable to that of humans (DeValois, Morgan & Snodderly, 1974). This finding and our results on the contrast sensitivities of single cells in the macaque's l.g.n. have the following implications: the magnocellular cells are likely to be the neural pathway for contrast vision near threshold because the parvocellular cells are inactive until almost ten times the behavioural threshold. This implication is likely to be applicable to man as well as monkey.

The function of the parvocellular neurones seems mainly to be the front end for the cortical analysis of coloured patterns. The parvocellular cells also may play a role in the analysis of pattern contrast. Although their peak contrast sensitivities are too low to account for the peak of behavioural contrast sensitivity at intermediate spatial frequency, their contrast sensitivity at high spatial frequency may be sufficient to account for psychophysical sensitivity there. Moreover, parvocellular cells definitely can give brisk responses to patterns of luminance contrast if the contrast is high enough. Perhaps the parvocellular cells may be used to extend the dynamic range of the visual system to higher contrasts.

The monkey's magnocellular cells resemble the X and Y cells of the A and A1 layers of the cat's l.g.n. in their visual function. Therefore, previous speculation about the functions of X and Y cells in the cat might apply to magnocellular cells of the monkey (cf. among others, Levick, 1975; Robson, 1975; Lennie, 1980*a*). Thus, the magnocellular X cells may be important for analysing form and detail while the magnocellular Y cells may respond more to large objects and movement. The non-linear input to a Y cell allows it to respond to fine patterns but only in a way which enables the cell to signal that a fine pattern is present somewhere in its field but does not enable the cell to signal where the pattern is located. Thus, Y cells could act to gate the cortical analysis of fine patterns by their increased impulse activity when patterns are present in their receptive fields (Lennie, 1980*a*).

Comparison with previous work

By using spatial summation and spatial resolution as tools for investigating neurones in the monkey's lateral geniculate, we have found that there are many X cells in the magnocellular layers as well as Y cells which are very similar in visual function to Y cells in the cat. Results consistent with ours have also been obtained by P. Lennie & A. M. Derrington (personal communication) who worked with cynomolgus monkeys, and Blakemore & Vital-Durand (1981) who worked with Cebus monkeys. Also Lee, Creutzfeldt, & Elepfandt (1979) have pointed out similarities, in the response to moving stimuli, of monkey magnocellular neurones and cells from the A and A1 layers of the cat's l.g.n., in agreement with the homology we have proposed above.

Our conclusions about the monkey's geniculate nucleus are different from those of previous workers who concluded that there was complete segregation of X and Y cells in the monkey l.g.n. (Dreher *et al.* 1976; Sherman *et al.* 1976; Schiller & Malpeli, 1978). The different conclusions rest on differences in how one identifies cells as X or Y. Those who concluded that all magnocellular cells were Y-like did so mainly

because of the cells' short latency to electrical stimulation of the optic chiasm and because of the transient time courses of the cells' responses to steps of illumination. In the cat l.g.n. there is a correlation between latency (to electrical stimulation of the chiasm) and the linear and non-linear summation properties we have used to identify X and Y cells (So & Shapley, 1979). However, even in the cat the correlation is not perfect and there are many examples of 'slow' Y cells and 'fast' X cells. In the monkey we have found that three quarters of the short latency cells in the magnocellular layers are X like in terms of visual spatial summation and spatial resolution.

It is difficult to use response time course as an identifying characteristic of X and Y cells. It may be particularly complicated in comparing the colour-opponent parvocellular cells with the broad-band magnocellular cells in the monkey unless care is taken to test the response time courses of all the cells with stimuli which are exactly the same in size or spatial frequency, wave-length distribution, contrast, and background. Some magnocellular cells we studied gave quite sustained responses to monochromatic light (cf. Wiesel & Hubel, 1966). Parvocellular cells produced transient responses to stimuli with a broad wave-length distribution or to stimuli near their neutral points (Marrocco, 1976). Using Wiener analysis, Gielen (1980) has found that parvocellular and magnocellular cells have similar dynamics of response to achromatic stimuli.

It has been suggested that the use of a null test to identify cells as X or Y necessarily results in dichotomy, i.e. those cells with a null (X) and those cells with no null position (Y) (Rodieck, 1979). However, our method for identifying X and Y cells is not based simply on a null test but on an investigation of the spatial phase and spatial frequency dependence of a visual neurone's response to contrast reversal of sine gratings. As first pointed out by Movshon, Thompson & Tolhurst (1978), there are many possible outcomes to such an investigation, not just two. Some of these possible outcomes, besides X and Y cells, have in fact been found in vertebrate retinas. For example, some 'on-off' ganglion cells in the frog retina produce frequency doubled respones which have a null (Gordon & Shapley, 1978). Some ganglion cells in the eel's retina have a linear component in their response which does not have a strong spatial phase dependence, with no null (Shapley & Gordon, 1978). X and Y spatial phase and spatial frequency dependencies are only two of the many possible results and it is not trivial to find them.

Developmental and functional homologies

Our proposal about the homology between cells in the A layers of the cat and magnocellular layers of the monkey is consistent with recent work on the sequence of development in the mammalian lateral geniculate nucleus. Rakic (1977) has shown that the magnocellular cells are the first to be generated in the monkey's l.g.n., based on his results with thymidine labelling. Recently, Shatz (1981) has reported that the cells of the A and A1 layers are the first cells to be generated in the cat's l.g.n. Thus, the cells which we have found to be most sensitive to contrast are born earliest in development. This supports the idea that the anatomical segregation has functional significance.

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