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SPATIAL AND TEMPORAL CONTRAST SENSITIVITY OF NEURONES IN AREAS 17 AND 18 OF THE CAT'S VISUAL CORTEX

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SUMMARY

1. We have examined the spatial and temporal tuning properties of 238 cortical neurones, recorded using conventional techniques from acutely prepared anaesthetized cats. We determined spatial and temporal frequency tuning curves using sinusoidal grating stimuli presented to each neurone's receptive field by a digital computer on a cathode ray tube.

2. We measured tuning curves either by determining response amplitude as a function of spatial or temporal frequency, or by measuring contrast sensitivity (the inverse of the contrast of the grating that just elicited a detectable response). The two measures give very similar tuning curves in all cases.

3. We recorded from 184 neurones in area 17; of these 156 had receptive fields within 5° of the area centralis. The range of preferred spatial frequency for these neurones was 0·3–3 c/deg, and their spatial frequency tuning band widths varied from 0·7 to 3·2 octaves at half-amplitude. The most common band width was roughly 1·3 octaves. Simple and complex cells in area 17 did not differ in their distributions of preferred spatial frequency, although complex cells were, on average, slightly less selective for spatial frequency than simple cells.

4. We recorded from fifty-four neurones from area 18, and performed several experiments in which we recorded from corresponding portions of both area 17 and area 18 in the same electrode penetration. Neurones in area 18 preferred spatial frequencies that were, on average, one third as high as those preferred by area 17 neurones at the same retinal eccentricity. Thus the range of preferred spatial frequency in area eighteen cells having receptive fields within 5 deg of the area centralis was between less than 0·1 and 0·5 c/deg. The distributions of optimum spatial frequency in the two areas were practically non-overlapping at eccentricities as high as 15 deg, the greatest eccentricity we examined. Neurones in area 18 were about as selective for spatial frequency as were neurones in area 17.

5. We determined temporal frequency tuning characteristics for some neurones from each area, using gratings that moved steadily across the screen. Neurones from area 17 all responded well to low temporal frequencies, and less well to higher frequencies (in excess of, usually, 2 or 4 Hz). In contrast, neurones recorded from area 18 sometimes had similar tuning properties, but more commonly showed a

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pronounced reduction in response as the temporal frequency was moved either above or below some optimum value (usually 2–8 Hz).

6. We conclude from these results that areas 17 and 18 act in parallel to process different aspects of the visual information relayed from the retina via the lateral geniculate complex. Some or all of the differences between the areas may be attributable to the predominance of *Y* cell input to area 18 and the predominance of *X* cell input to area 17. The two areas seem reasonable candidates for the 'pattern' (area 17) and 'movement' (area 18) detecting mechanisms whose existence has been inferred from psychophysical experiments in both humans and cats.

INTRODUCTION

There are several areas of the cat's cerebral cortex that receive a direct input from the lateral geniculate nucleus. While in the rhesus monkey area 17 is the only cortical area driven directly from the lateral geniculate nucleus, projections from this structure in the cat extend as well to areas 18, 19 and to the suprasylvian gyrus (Wilson & Cragg, 1967; Garey & Powell, 1967, 1971; Rossignol & Collonier, 1971; Hubel & Wiesel, 1972; Rosenquist, Edwards & Palmer, 1974; LeVay & Gilbert, 1976). In their initial survey of the functional organization of these different areas, Hubel & Wiesel (1962, 1965, 1969) observed several features that led them to suggest that the direct geniculate projections to areas beyond 17 were of secondary importance, and that the properties of neurones in these areas might best be understood in terms of a serial elaboration of visual information relayed by area 17. In recent years, however, it has become clear that at least one of these areas (area 18) may function as a visual processor separate and parallel to area 17. Inactivating area 17, either by making lesions or by cooling, does not substantially alter receptive field properties in area 18 (Dreher & Cottee, 1975; see also Talbot, 1942). The possibility thus exists, in the cat if not in the monkey, that the several visual cortical areas each process a separate subset of the information relayed from the retina by the lateral geniculate nucleus.

In the two preceding papers (Movshon, Thompson & Tolhurst, 1978*a*, *b*) we detailed the receptive field properties of the two cell-types most commonly encountered in area 17. In the course of that study we made measurements of the spatial and temporal frequency tuning characteristics of these neurones, in the hope of resolving a discrepancy between two previous reports (Maffei & Fiorentini, 1973; Ikeda & Wright, 1975*a*, *b*). Maffei & Fiorentini claimed that complex cells in area 17 prefer lower spatial frequencies and are less selective for spatial frequency than simple cells; Ikeda & Wright, on the other hand, found no difference between simple and complex cells in these respects. Rather, they found a separate and orthogonal dichotomy in tuning properties between two groups of cells that they termed 'sustained' and 'transient'; 'sustained' cells prefer high spatial frequencies and are rather selective for spatial frequency, while 'transient' cells prefer lower spatial frequencies and in addition respond poorly to low temporal frequencies. Simple and complex 'sustained' and 'transient' cells may be found.

In the first part of this paper we report our own results on these questions in area 17, which are at variance with both previous reports: we find no difference between simple and complex cells' spatial or temporal tuning properties, nor do we find any

evidence for the existence of Ikeda & Wright's 'transient' cells. In the second part of this paper, we show that these missing 'transient' neurones are located in area 18. We conclude that there are marked and systematic differences in spatial and temporal processing between areas 17 and 18, supporting the notion that they process different aspects of the visual information relayed from the retina. Finally, we attempt to relate the functional differences we observed to what is known of the form and function of the portions of the visual pathway peripheral to the visual cortex.

METHODS

Most of our procedures in these experiments were identical to those detailed in the first paper of this series (Movshon *et al.* 1978*a*); twenty-one of the twenty-five cats were in fact the same animals. Four other cats were used for recordings involving both areas 17 and 18, and were prepared for recording in a slightly different manner that enabled us to visualize the cortex while placing the electrode in such a way that its track traversed both areas 17 and 18 in a single experiment.

A 5 mm square craniotomy was opened between the sagittal suture and Horsley–Clarke co-ordinate L5, centered between H-C A2 and P4; in this region area 18 occupies the bulk of the apical segment of the lateral gyrus (Otsuka & Hassler, 1962; Hubel & Wiesel, 1965). After the electrode in a guide needle had been placed about 1 mm above the cortical surface, the craniotomy was filled with agar gel and covered with dental acrylic. This procedure resulted in excellent recording stability and, in association with intramuscular injections of prednisolone 2·5 mg/kg (Deltastab, Boots) every 24 hr, reduced cortical oedema to a minimum.

The histological procedures we used to reconstruct electrode tracks in these animals were similar to those detailed in the first of these papers (Movshon *et al.* 1978*a*); the cytoarchitectonic border between areas 17 and 18 was determined using the following criteria:

1. The thickness of layer IV is less in area 18 than in area 17;
2. Layer III is thicker in area 18 than in area 17, and contains larger and more prominent pyramidal neurones;
3. The fibre bundles in the deep layers of area 18 are coarser than in area 17, and may be visualized under dark-field illumination of fresh Nissl-stained sections.

The cytoarchitectonic border between the two areas coincides with that determined functionally by mapping the reversal of polarity of the visual field representation at the vertical meridian (Talbot & Marshall, 1941; Hubel & Wiesel, 1965; Tusa, Palmer & Rosenquist, 1978).

Localization of the position of a particular neurone was made with respect to electrolytic lesions made retrospectively as the electrode was withdrawn at the end of the penetration; we were unable to make lesions at each recording site because of the fragility of our microelectrodes, and some small errors in the localization of units recorded in the upper cortical layers early in the penetration may have resulted due to distortion of the brain during the experiment.

Our methods for presenting visual stimuli and analysing neuronal responses were identical to those detailed previously, save only that in order to effectively stimulate the large receptive fields of neurones in area 18 we moved the display screen to a distance of 57 cm from the animal, where it subtended $20 \times 25°$ at the cat's eye. Measurements made on area 17 neurones under these conditions were not different from those obtained earlier using a screen subtending $10 \times 12·5°$.

Stimuli. A sinusoidal grating is a pattern of light and dark bars whose luminance profile in a direction orthogonal to the bars is a sine wave; in our experiments, its orientation was fixed at the optimum stimulus orientation for the receptive field under study. The gating's *spatial frequency* is the number of cycles of the sine wave that subtend one degree of visual angle, its *contrast* is the difference between the luminances of the brightest and dimmest portions of the display divided by twice their sum. All the gratings in this study were moved at a constant angular velocity in a direction orthogonal to the bars. The rate of movement is given in terms of *temporal frequency*, the number of cycles of the grating that pass a given point on the screen in 1 sec. This is also the frequency with which the luminance of each point on the screen is varied sinusoidally (see Appendix to Movshon *et al.* 1978*a* for a more formal discussion).

When we determined only spatial frequency tuning for a given neurone, all the gratings moved at the same temporal frequency, which resulted in an inverse relationship between their angular velocity (in deg/sec) and their spatial frequency (in c/deg). In some cases we made measurements of both spatial and temporal frequency tuning by determining responses or sensitivity to gratings of several spatial frequencies, each moving at several temporal frequencies; in other cases, we measured temporal frequency tuning for gratings whose spatial frequency was fixed at the neurone's optimum; these procedures give identical results, in view of the independence of the spatial and temporal tuning characteristics of cortical neurones (Tolhurst & Movshon, 1975).

RESULTS

We made measurements of spatial frequency tuning on 184 neurones from area 17 and fifty-four neurones from area 18. The majority of neurones had receptive fields within 5 deg of the area centralis, although we undertook several experiments to examine spatial frequency tuning at eccentricities up to 15 deg in both areas.

The measurement of tuning characteristics

We used two different methods to assess spatial frequency tuning in single cortical neurones. Usually we determined each neurone's *contrast sensitivity* to moving sinusoidal gratings of several different spatial frequencies; the experimenter adjusted the contrast of the grating until he judged that its presence just noticeably altered the neurone's resting activity; the difference produced by the grating could be either a repetitive modulation of the neurone's firing rate in synchrony with the passage of the grating's bars across the receptive field, or an increase in the neurone's mean firing rate without detectable modulation (see Movshon *et al.* 1978*a*, *b*). Less commonly, we determined the neurone's *average response amplitude* to the different gratings, each of the same suprathreshold contrast (usually 0·25 or 0·5), and determined how this amplitude depended on spatial frequency. In thirty-four cases we obtained both response and sensitivity measurements on the same neurone; Fig. 1 presents some representative comparisons between results obtained using the two measures.

In each part of the Figure, the filled symbols indicate how contrast sensitivity depended on spatial frequency, while the open symbols show how response amplitude depended on this parameter. Two measures of response amplitude are presented: open circles represent the net increase in firing rate produced by the grating, while open squares represent the depth of modulation of the response about the mean level, at the frequency with which the grating was moved. The three curves for neurones *A* and *B* have been arbitrarily shifted vertically to facilitate comparison, but the logarithmic scale applies equally to each curve. For a simple cell from area 17 (Fig. 1*A*) the three sets of data were similar in shape; both the optimum spatial frequency and the range of effective frequencies were similar in all three determinations. For a complex cell from area 17, on the other hand, there were differences in tuning according to the measure used (Fig. 1*B*). Complex cells usually respond to low spatial frequencies with a modulated discharge, while at higher frequencies their discharge is not greatly modulated by the stimulus (Movshon *et al.* 1978*b*). In Fig. 1*B* this is reflected in the fact that the curve plotting modulated response (open squares) peaks at a lower spatial frequency than the other two; these other measures are, however, well correlated.

Fig. 1*C* shows an interesting phenomenon which we occasionally observed, and which was evident only in measurements of spatial tuning made using response methods: when the spatial frequency of the grating differed from the optimum for this cell (an area 17 complex cell) by more than one and a half octaves, the neurone's response was a *decrease* in firing rate below resting level; the neurone thus possessed inhibitory sidebands in the frequency domain (see Tolhurst, 1972; Maffei & Fiorentini, 1976). Most neurones in the visual cortex lack maintained discharge, which may explain the rarity with which we observed this effect.

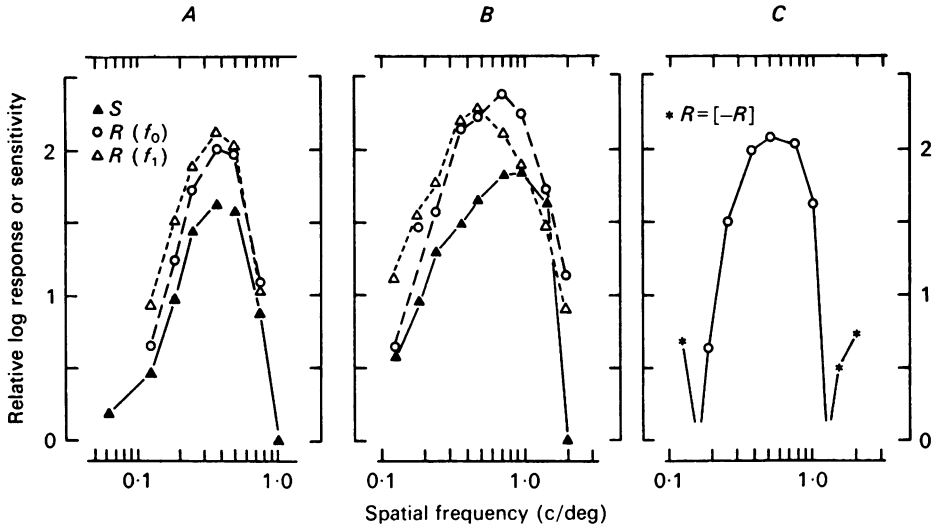

Fig. 1. Response amplitude (open symbols) and sensitivity (filled triangles) of three neurones to sinusoidal gratings drifting across their receptive fields. The response to a grating of contrast 0·5 could be measured as an increase in mean firing rate (circles) or depth of modulation in synchrony with the bars of the grating (open triangles). The stars in *C* show a *decrease* in mean firing rate. The ordinate is log response amplitude or log sensitivity. The curves in *A* and *B* have been shifted on the ordinate to facilitate comparison. *A* is data for a simple cell; *B* and *C* are data for two complex cells.

We extracted two parameters from each spatial frequency tuning curve we measured: the *optimum spatial frequency* (that frequency to which the cell responded most vigorously or was most sensitive) and the *spatial tuning band width*, the ratio between the highest and lowest frequencies to which the cell was at least half as sensitive or responsive as it was to its optimum frequency, expressed in octaves. Fig. 2 presents a comparison between sensitivity and response determinations of these two parameters for the thirty-four cells on which we obtained both sets of data.

Fig. 2*A* compares the estimates of optimum spatial frequency obtained by the two methods; apart from a slight (but significant) tendency for the response measurements to estimate higher optimum frequencies for neurones selective to frequencies over 1 c/deg, the two methods appear to yield very similar results. Fig. 2*B* reveals that the band width estimates obtained in the two methods are also well correlated, although perhaps not as strikingly as the estimates of optimum spatial frequency.

In view of the good agreement between the two methods, we have pooled data obtained in either fashion for the analysis below.

Spatial frequency tuning of neurones in area 17

We classified the 184 neurones from area 17 as simple or complex according to standard criteria (Hubel & Wiesel, 1962). We encountered a few other units with different receptive field properties (non-oriented, hypercomplex or direction-selective)

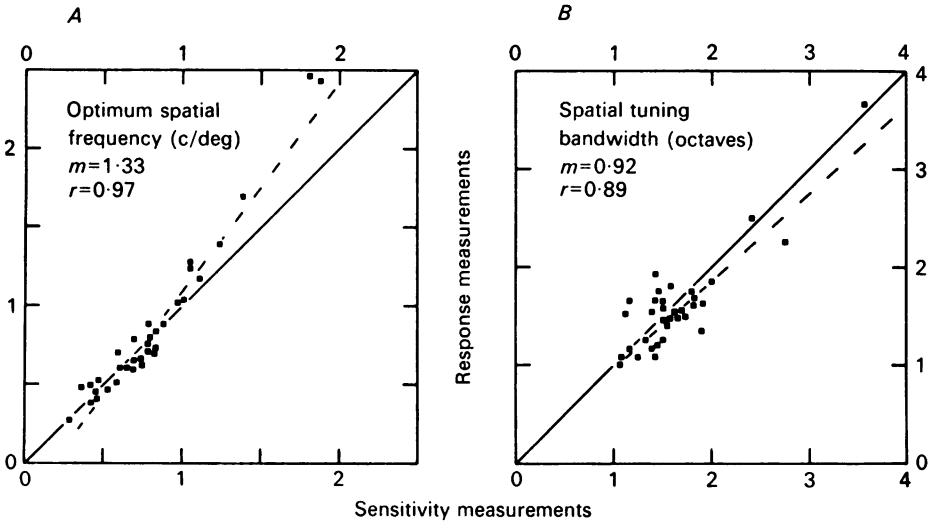

Fig. 2. Graphs comparing the optimal spatial frequency (c/deg) and band width (octaves) for thirty-four cells in which spatial tuning was examined by determining contrast sensitivity (abscissa) and by measuring response amplitude to gratings of fixed contrast (ordinate). The continuous line in each graph has a slope of 1·0; the dashed line is the least-squares regression line drawn through the data points.

but we have excluded them from our analysis. We encountered no cell that was unresponsive to moving gratings, and we noticed no overall difference in the vigour with which cells responded to gratings as opposed to bars or edges. Some cells of both types responded very briskly to gratings, while others were clearly more responsive to bars or edges of similar contrast. In general there was no sign we could detect that cortical cells generally 'prefer' bars to gratings, or gratings to bars.

All simple and complex cells in area 17 were selective for the spatial frequency of sinusoidal gratings, having a definite preference for a narrow range of spatial frequency and giving reduced responses to higher or lower frequencies. In general, the spatial frequency tuning curves we obtained were similar to those that have been presented elsewhere (Cooper & Robson, 1968; Maffei & Fiorentini, 1973; Ikeda & Wright, 1975*a*). Fig. 3 summarizes our data on the distributions of optimum frequency and spatial tuning band width for 149 neurones from area 17 whose receptive fields lay within 5 deg of the area centralis. The distributions of optimum spatial frequency for simple and complex cells are indistinguishable, ranging in this sample between 0·3 and 3 c/deg. Our measurements of band width revealed a small but systematic

difference between the two cell-types: simple cells are, on average, slightly more narrowly tuned than complex cells (simple cells: mean 1·45 octaves, S.D. = 0·37; complex cells: mean 1·59 octaves, S.D. = 0·40; $t = 1{\cdot}26$, $P < 0{\cdot}2$). In the first paper of this series (Movshon *et al.* 1978*a*) we showed that simple cells may be divided into two groups, linear and non-linear, on the basis of their spatial summing properties. This division is, however, not reflected in these neurones' spatial tuning properties: linear and non-linear simple cells have statistically indistinguishable distributions of optimum spatial frequency (linear cells, mean = 0·77 c/deg; non-linear cells, mean = 0·74 c/deg).

For both simple and complex cells, and for both parameters, our measurements were sufficiently reliable to permit us to say that the great part of the scatter in the distributions shown in Fig. 3 is due to genuine differences from neurone to neurone

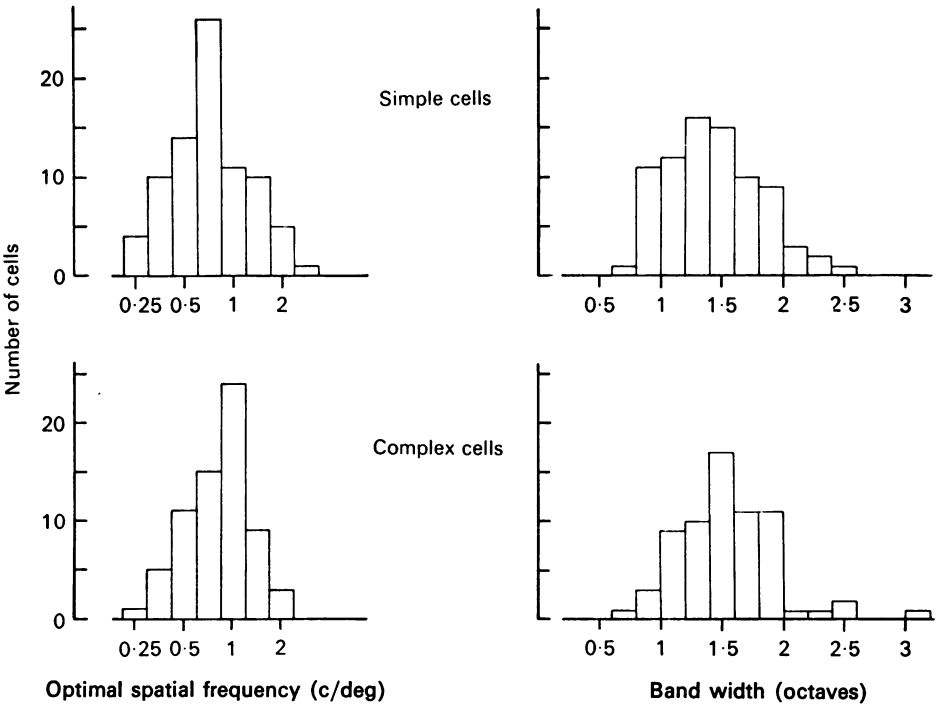

Fig. 3. The optimal spatial frequencies and band widths of the spatial tuning curves for eighty-one simple cells and sixty-eight complex cells, whose receptive fields lay within 5° of the area centralis. The mean optimal frequency for simple cells was 0·86 c/deg (S.D. 0·48); for complex cells, the mean optimum was 0·93 c/deg (S.D. 0·38). $t = 0{\cdot}9$ (not significantly different).

in optimum spatial frequency and spatial tuning band width. We often repeated measurements of spatial tuning at intervals up to 16 hr and never observed substantial changes in either parameter. Thus different cortical neurones, like retinal ganglion cells, have different characteristic spatial frequencies (Enroth-Cugell & Robson, 1966). Unlike ganglion cells, different cortical neurones differ considerably in their spatial frequency selectivity; a possible reason for this variation was discussed by Robson (1975).

Our data support Ikeda & Wright's (1975*a*) conclusion that simple and complex cells do not differ greatly in their spatial tuning properties; they appear to refute the contrary claim of Maffei & Fiorentini (1973). However, Ikeda & Wright (1975*a*) reported a much wider range of both preferred frequency and frequency selectivity in their population than we observed. They distinguished a class of cell, comprising about half their recorded sample, which they called 'transient' and which included both simple and complex cells, preferring spatial frequencies between 0·1 and 0·5 c/deg and having particular temporal tuning properties. Inspection of our data (Fig. 3) reveals that this range of optimum spatial frequencies was poorly represented in our sample, and we sought the reason for this discrepancy in area 18.

Comparison of spatial frequency tuning in areas 17 and 18

Ikeda & Wright (1975*a*) reported that examples of their 'transient' class were much more common in the representation of the retinal periphery than they were in the central representation. The method by which they chose to sample the periphery (placing electrodes on the dorsal convexity of the anterior portion of the lateral gyrus) led us to suspect that they might have inadvertently sampled many of their neurones from area 18; if true, this might account for the discrepancy between their results and our own with respect to area 17. Moreover, neurones in area 18 have larger receptive fields than do area 17 neurones (Hubel & Wiesel, 1965), and might therefore be expected to prefer lower spatial frequencies. We thus undertook several experiments designed to sample from both areas in a single electrode penetration. This approach has the important advantage that the neurones in both areas would have receptive fields lying in the same region of visual space, ruling out differences in retinal eccentricity as an explanation for any differences. Moreover, any major differences between the two areas should reveal themselves by a more or less abrupt change in properties as the 17/18 border is traversed by the electrode, which may be referred back to a histological reconstruction of the track of the electrode penetration.

Figure 4 illustrates the results of one such experiment, in which the electrode passed down the lateral bank of the lateral gyrus near H-C P5, passing through the superficial layers of the cortex (Fig. 4*A*). The neurones encountered during the first 2 mm of this penetration were typical of those we had previously encountered in area 17. They had small receptive fields and responded most vigorously to lines moving at slow to moderate velocities. As may be seen from Fig. 4*C*, most neurones in this region preferred spatial frequencies in excess of 0·5 c/deg; 7 of the 11 neurones preferred frequencies above 1 c/deg.

At electrode depths between 2 and 2·5 mm we had difficulty in isolating neurones, but the next neurones we encountered were notably different from those analysed earlier. The neurones could still generally be classified as simple or complex, but their receptive fields were three to twenty times larger in area than those encountered earlier. Most of these neurones had a marked preference for moderate or high rates of stimulus movement; rapidly moving objects were also very effective in driving the unresolved background activity. These general properties are characteristic of area 18 (Hubel & Wiesel, 1965; Riva Sanseverino, Galletti & Maioli, 1973, 1974; Orban, Callens & Colle, 1975; Tretter, Cynader & Singer, 1975; Dreher & Cottee, 1975). The differences in receptive field properties between the two portions of the

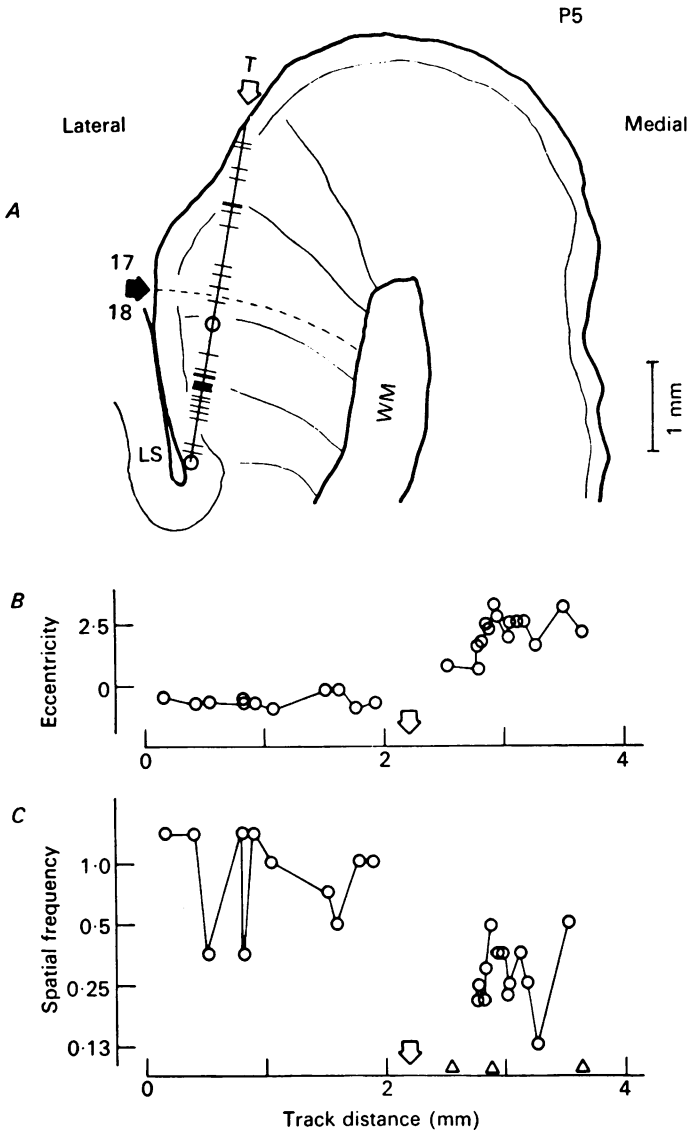

Fig. 4. Reconstruction of an electrode penetration passing through the cytoarchitectonically defined border between areas 17 and 18. *A*, the arrow labelled T points to the electrode track, beginning near the crest of the gyrus and ending in the lateral sulcus (LS). Each short line crossing the electrode track represents the position of a neurone whose spatial tuning was examined. The two circles on the track are the sites of electrolytic lesions. The cytoarchitectonic border is indicated by the filled arrow and the dashed line. The inner border of layer 1 is indicated by the thin line running roughly parallel to the cortical surface. The thin lines radiating from the white matter (WM) show the orientation of fascicles of neurones. *B*, the distance of each neurone's receptive field from the vertical meridian (deg of visual angle) is plotted against the position of that neurone in the electrode track (mm from entry into the cortex). The arrow pointing to the abscissa shows the site of an electrolytic lesion. *C*, the optimal spatial frequency (c/deg) is plotted for each neurone against its position in the electrode track. The three neurones represented by triangles had no low spatial frequency cut and hence no optimum. The arrow again shows the site of the electrolytic lesion.

penetration were reflected in the neurones' spatial frequency preferences (Fig. 4*C*): all the neurones we encountered more than 2·5 mm into the cortex had optimum spatial frequencies below 0·5 c/deg; indeed three neurones showed no obvious decline in sensitivity as spatial frequency was reduced down to 0·03 c/deg.

Fig. 4*B* plots the distance of each receptive field from the vertical meridian of the visual field. Although there was little change in eccentricity during the first 2 mm of the penetration (probably due to the relatively high magnification factor in the central representation in area 17: Talbot & Marshall, 1941; Tusa *et al.* 1978), beyond 2·5 mm there was a clear trend for the receptive fields to move along the horizontal meridian away from the centre of the visual field. An extrapolation of this trend suggests that the border between area 17 and 18 was traversed during the region between 2 and 2·5 mm in which we were unable to isolate neurones. At the end of the experiment we withdrew the electrode and made a lesion at a depth of 2·25 mm; the position of this lesion is indicated on the tracing in Fig. 4*A*; it lies less than 0·25 mm from the cytoarchitectonically defined border between the two areas.

The penetration illustrated in Fig. 4 was restricted to the upper layers of the cortex; Fig. 5 shows a similar reconstruction of another penetration which traversed all the cellular layers of both areas 17 and 18 except layer VI. This penetration was placed near H-C A3; in this region the border between the two areas lies on the medial side of the lateral gyrus, and the region of the visual field about 5 deg below the horizontal meridian is represented (Otsuka & Hassler, 1962; Hubel & Wiesel, 1965; Tusa *et al.* 1978). For the first 2 mm of this penetration the neurones and background activity behaved similarly to that described above for area 18; most of the neurones preferred spatial frequencies of 0·25 c/deg or less. In the next 1·5 mm, only three neurones were recorded; two of these had properties similar to those encountered earlier in the penetration; the third had properties reminiscent of area 17. Inspection of the receptive field eccentricities (Fig. 5*B*) suggests that the border between the two areas lay in this region; and a lesion placed there lies very close to the cytoarchitectonic border (lesion a, Fig. 5*A*). Beyond this region we encountered only cells typical of area 17, having small receptive fields and preferring spatial frequencies between 0·4 and 1·3 c/deg.

These results are typical of those we have obtained in several micro-electrode penetrations that sampled from both cortical areas: neurones in area 17 had a preference (on average) for spatial frequencies about three times (or 1·5 octaves) higher than those in area 18. Despite this clear trend, we felt it important to ensure that uneven sampling across the visual field did not account for these differences, optimum spatial frequencies would certainly be expected to decline with retinal eccentricity. We therefore performed several other recording experiments designed to cover a reasonable range of eccentricity in both areas. We also took care to sample as evenly as possibly from the different layers of the cortex; Gilbert (1977) has reported laminar variations in receptive field size in area 17, and similar variations may well occur in area 18. Our final results are summarized in Figs. 6 and 7.

Fig. 6 plots the optimum spatial frequencies of 238 cortical neurones, 184 from area 17 (filled symbols) and fifty-four from area 18 (open symbols), as a function of receptive field eccentricity. It is clear that within the range we examined (out to

approximately 15 deg) there is little or no overlap in the distributions of optimal spatial frequency in the two areas. Indeed, even considering the whole range of eccentricities tested, the *lowest* preferred frequency we found in area 17 was 0·25 c/deg, while the *highest* in area 18 was only 0·5 c/deg. By comparison, the total range of preferred frequencies in both areas, even neglecting neurones lacking low spatial frequency attenuation, was over 30:1. In both areas, at least in the representation

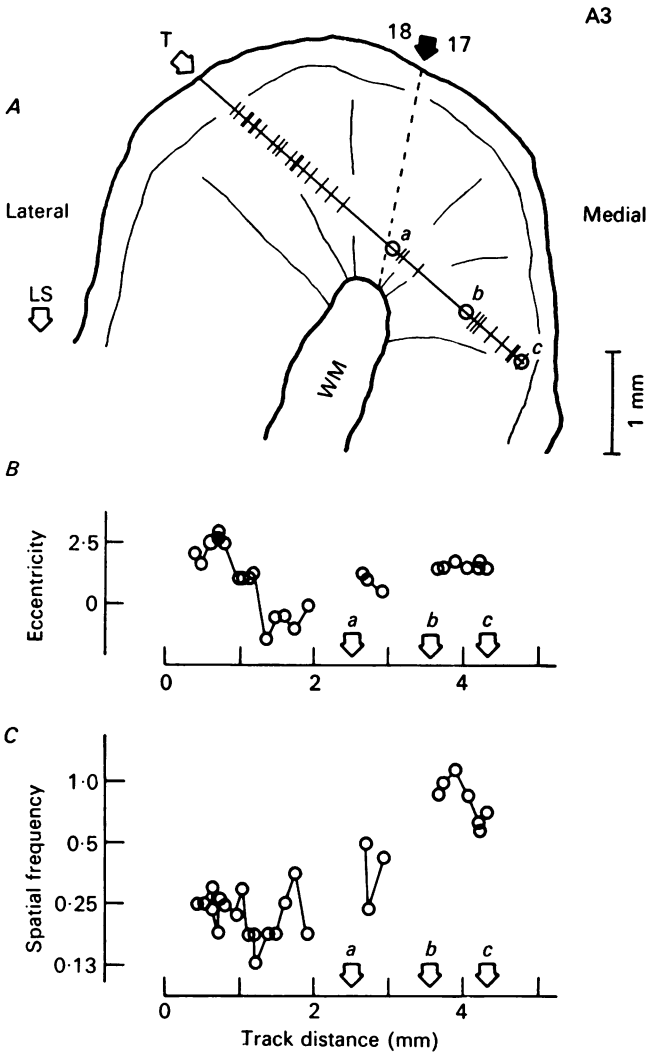

Fig. 5. Reconstruction of a second electrode penetration. Conventions as for Fig. 5. Three electrolytic lesions (*a*, *b*, *c*) were made. Their sites are shown in *A* as circles, in *B* and *C* as lettered arrows.

of the central 5 deg or so, the range of preferred frequencies seems roughly constant at each eccentricity (a five- to tenfold range in each area), while the average optimum frequency declines smoothly with increasing eccentricity. This decline is by a factor of roughly three in the 10 deg nearest the area centralis, which agrees well with the

2·5-fold decrease in cortical magnification factor in area 17 reported over this range of eccentricity by Tusa *et al.* (1978).

We also examined other parameters of the tuning curves of these neurones, and Fig. 7 summarizes our data on the optimum spatial frequencies and spatial tuning band widths of all 238 neurones recorded in the cortex. As may be seen, the major difference in tuning properties between the two areas seems to be in the distribution of optimum frequency; neglecting the four neurones from area 18 that lacked low frequency attenuation within the range of our measurements, and which consequently may not meaningfully be assigned a 'band width', the distributions of spatial tuning band width are very similar in the two areas (the mean band width for area 18

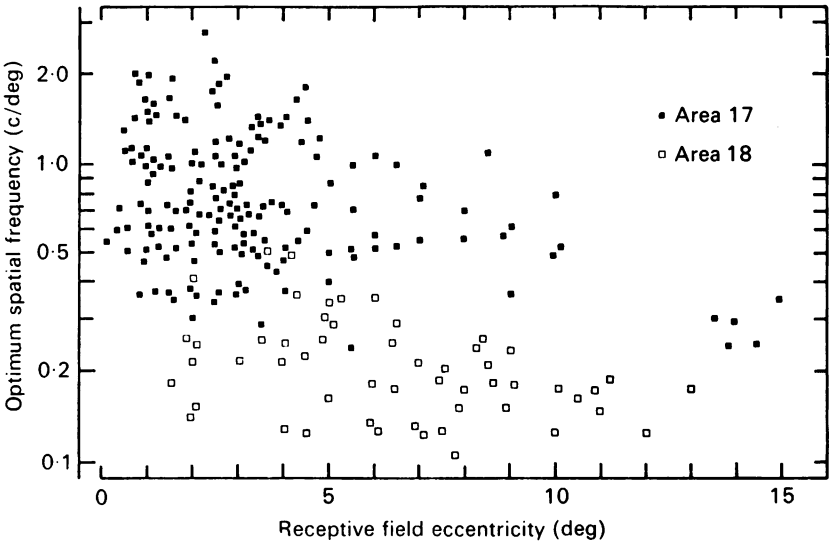

Fig. 6. The optimal spatial frequency (c/deg) for 238 neurones is plotted against the eccentricity (deg of visual angle). Note that, in this Figure, eccentricity is the radial distance from the area centralis. Neurones recorded in area 17 are represented by filled symbols; neurones recorded in area 18 are represented by open symbols. Excluded from this Figure are four neurones recorded in area 18 which had no low spatial frequency decline in sensitivity.

neurones was 1·49 octaves; that for area 17 neurones was 1·50 octaves). Thus the spatial frequency tuning curves of area 18 neurones, plotted logarithmically, closely resemble those of area 17 neurones save that they are translated down the frequency axis by about 1·5 octaves. Measurements such as 'visual acuity' (the highest frequency to which a neurone responds: Maffei & Fiorentini, 1973) or the highest frequency to which a cell is half as sensitive or responsive as it is to the optimum frequency give an equally clear distinction between the two areas. Neurones in area 17 occasionally resolved frequencies as high as 7 c/deg, while no neurone in our sample from area 18 responded to spatial frequencies above 1·5 c/deg.

Temporal frequency tuning of neurones in area 17 and 18

It is generally agreed that neurones in area 18 have a preference for higher angular velocities of stimulus movement than do area 17 cells, when bars or edges are used as stimuli (Riva Sanseverino *et al.* 1973; Orban *et al.* 1975; Movshon, 1975; Dreher & Cottee, 1975; Tretter *et al.* 1975). Since the angular velocity of a grating's movement is inversely related to its spatial frequency when temporal frequency is held constant, we might expect a roughly threefold difference in preferred velocity between the two areas simply because of the difference in optimum spatial frequency described

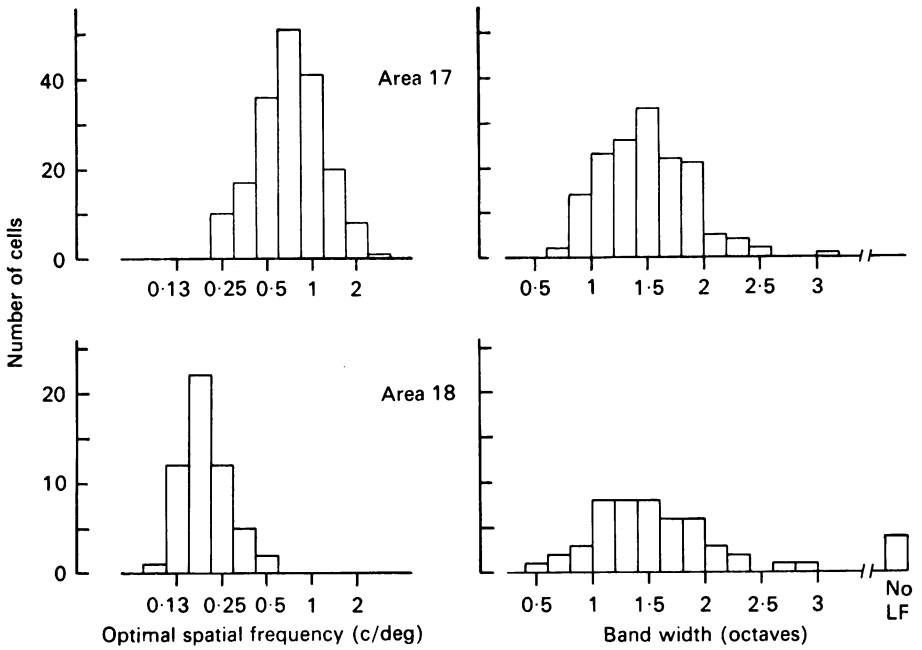

Fig. 7. Comparison of the optimal spatial frequencies and the band widths of spatial tuning curves for 184 neurones recorded in area 17 and fifty-four neurones recorded in area 18. All the neurones from Fig. 6 are represented, irrespective of their eccentricity. The four neurones recorded in area 18 which had no low spatial frequency decline in sensitivity are excluded from the lower left histogram; they are included in the lower right as 'no lf' (i.e. no low frequency cut).

above. Another factor that could, of course, produce a difference would be a genuine difference in the temporal frequency tuning characteristics between the two areas. We examined neuronal responses and sensitivity to gratings moving at different temporal frequencies in order to establish whether the difference in velocity tuning between areas 17 and 18 was solely attributable to spatial factors, or whether there also existed temporal differences between the two areas.

Fig. 8 shows temporal frequency tuning curves, determined in each case by measuring contrast sensitivity to gratings of the optimum spatial frequency as a function of drift rate, for twelve typical cortical neurones, six from area 17 and six from area 18. The curves have been arbitrarily shifted along the ordinate to facilitate comparison. The six cells from area 17 had tuning characteristics representative of

those that we have encountered there (see also Tolhurst & Movshon, 1975). They responded well to gratings moving less rapidly than 2 or 4 Hz, and progressively less well to faster movement. No neurone in our sample from area 17 showed a substantial decline in sensitivity as temporal frequency was reduced, at least down to 0·5 or 1 Hz. Most neurones from area 18, on the other hand, had a marked preference for moderate rates of movement (2–8 Hz), and responded poorly to either higher or lower rates (e.g. three lower curves on right in Fig. 8). While three neurones in area 18 had temporal properties similar to those observed in area 17 (three upper right-hand curves in Fig. 8), the majority of neurones from area 18 had typically 'band pass'

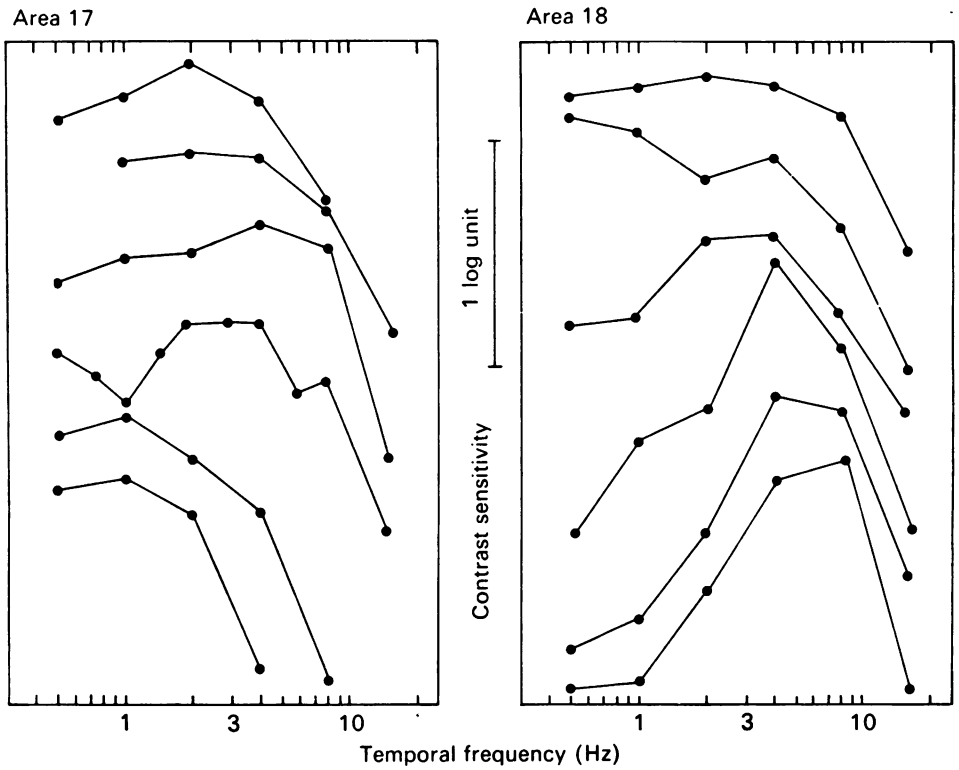

Fig. 8. Contrast sensitivity as a function of the temporal frequency of a moving sinusoidal grating of the neurone's preferred spatial frequency. The left-hand graph shows data for six representative neurones recorded in area 17. The three upper curves in the right-hand graph show data for the three neurones recorded in area 18 which most resembled those of area 17 neurones. The three lower curves are more representative of our findings in area 18. The curves have been shifted on the ordinate to facilitate comparison.

rather than 'low pass' temporal tuning curves, although there was little over-all difference in the highest temporal frequencies that were effective in driving cells in the two areas.

Thus the preferences for high rates of stimulus movement observed in area 18 may be attributable to a combination of the spatial and temporal differences we have observed.

DISCUSSION

Our results confirm, with modifications, the suggestion of Ikeda & Wright (1975*a*, *b*) that there exist in the cat's visual cortex two classes of neurone that may be distinguished on the basis of their spatial and temporal tuning properties. One class, Ikeda & Wright's 'sustained' cells, prefer relatively high spatial frequencies and respond well to low and moderate temporal frequencies; we found these neurones in area 17. The other group, called by Ikeda & Wright 'transient', prefer relatively low spatial frequencies and respond best to moderate temporal frequencies; we found these neurones in area 18. The property used by Ikeda & Wright to distinguish these two groups of cells (the time course of a neurone's response to stationary flashed stimuli) proved rather unreliable as a discriminative test in our hands. This may be due to the tendency of 'sustained' neurones to appear 'transient' if the stimulus is not carefully optimized or if the animal's level of anaesthesia is too deep (Ikeda & Wright, 1974, 1975*a*; Tolhurst & Movshon, 1975). Other neuronal properties, such as their spatial and temporal tuning characteristics, seem to be more reliable measures and we have used them here.

Afferent connexions to the visual cortex

There are three classes of ganglion cell in the cat's retina. X cells sum light-evoked influences linearly across their receptive fields and have axons of moderate conduction velocity; Y cells show non-linear spatial summation and have rapidly conducting axons; and W cells have heterogeneous spatial properties but all have slowly conducting axons (Enroth-Cugell & Robson, 1966; Cleland, Dubin & Levick, 1971; Stone & Hoffman, 1972; Cleland & Levick, 1974*a*, *b*; Stone & Fukuda, 1974; Fukuda & Stone, 1974). All three types of cell project to the visual cortex by way of relay cells in the geniculate complex that have receptive field properties and axonal conduction velocities similar to those of their 'parent' ganglion cells (Cleland *et al.* 1971; Hoffman, Stone & Sherman, 1972; Wilson & Stone, 1975; Cleland, Levick, Morstyn & Wagner, 1976). All three types of cell appear to project to area 17 from the laminar portion of the lateral geniculate nucleus, but area 18 appears to receive input only from Y and W cells, many of which are located in the ventral layers of the dorsal lateral geniculate nucleus and also in the medial interlaminar nucleus (Rosenquist *et al.* 1974; Gilbert & Kelly, 1975; LeVay & Ferster, 1977; Hollander & Vanegas, 1977; Garey & Blakemore, 1977). Moreover, Stone & Dreher (1973) reported that most Y cells of the lateral geniculate nucleus have bifurcating axons that project both to area 17 and to area 18.

We can, then, seek an explanation for the difference between areas 17 and 18 in the absence of an X cell projection to area 18. Y cells' receptive field centres are, on average, three times the diameter of X cells' receptive field centres; all other things being equal, Y cells might be expected to prefer spatial frequencies about one third as high as X cells do. But, the receptive fields of retinal Y cells are organized differently from those of X cells: in addition to a large centre-surround receptive field that can be described as a 'linear' portion, the receptive field additionally contains non-linear 'subunits', each smaller than the main receptive field. These subunits permit the Y cell to respond, non-linearly, to spatial frequencies higher than a simple receptive field map would predict (Hochstein & Shapley, 1976*a*, *b*); indeed, in the

retina, the highest spatial frequencies detected by Y cells may not be very different from those detected by X cells (Enroth-Cugell & Robson, 1966; R. M. Shapley, personal communication). Recordings in the lateral geniculate nucleus do, however, suggest that X and Y cells there do differ in their spatial frequency tuning, with Y cells preferring lower spatial frequencies than *X* cells (A. M. Derrington & A. F. Fuchs, in preparation; see also Ikeda & Wright, 1976).

This correspondence is suggestive, and Stone and Dreher (1973) claimed that a given lateral geniculate nucleus Y cell projects to both areas 17 and 18; it is therefore surprising that there are virtually no cells in area 17 whose properties resemble those of area 18 cells. It is possible, of course, that the Y cells subserve different functional roles in area 17 (where they are only a fraction of the afferent relay) and in area 18 (where they may be the dominant component). But the observation that the functional synaptic organization of the geniculate input to areas 17 and 18 is very similar makes this notion less attractive (Singer, Tretter & Cynader, 1975; Tretter, Cynader & Singer, 1975). Other factors may also contribute to the properties of area 18 cells: LeVay & Ferster (1977) have claimed that the neurones projecting to area 18 from the laminar lateral geniculate nucleus are in fact different from those projecting to area 17. Moreover, the medial interlaminar nucleus sends a substantial projection of Y cells to area 18 and does not project to area 17 (Rosenquist *et al.* 1974; Mason, 1975; LeVay & Ferster, 1977; Hollander & Vanegas, 1977). Thus the difference between areas 17 and 18 may be in part attributable to a lack of an X cell projection to area 18, and in part to a group of Y cells in the lateral geniculate nucleus that project only to area 18 and not to area 17. It is also possible that differences in the details of W cell projections to the two areas could be a factor, but little is known of the properties of W cells in the lateral geniculate nucleus, or of the functional significance of their projection to the visual cortex.

Serial and parallel processing in the visual cortex

In their original papers on areas 17 and 18, Hubel & Wiesel (1962, 1965) speculated that both within area 17 and between areas 17 and 18 there might be a serially organized elaboration of visual information. The simple cells in area 17 were held to receive the bulk of the direct input from the lateral geniculate nucleus, and to relay this information first within area 17 to complex cells, and thence to the complex and hypercomplex cells of area 18.

Area 17. An alternative theory was proposed by Stone (1972) to account for the properties of neurones in area 17. He suggested that simple and complex cells did not represent sequential stages in the visual process, but rather the separate and parallel terminations of the X and Y cell systems, respectively. There is a certain amount of evidence in favour of this idea: simple and complex cells may both be activated monosynaptically from the lateral geniculate nucleus (Hoffman & Stone, 1971; Stone & Dreher, 1973; Singer *et al.* 1975), and some complex cells respond to stimuli that do not excite simple cells (Movshon, 1975; Hammond & MacKay, 1975).

On the basis of the data we reported in this and the preceding papers, it seems reasonable that, as proposed by Stone, most simple cells in area 17 are driven solely by X cells from the lateral geniculate nucleus. Most simple cells, like X cells, show linear spatial summation (Movshon *et al.* 1978*a*). Since it is difficult to conceive of

a reasonable mechanism by which the non-linear component of the Y cell receptive field might be removed, it seems probable that X cells drive these simple cells. Moreover, even if it were possible to 'linearize' a Y cell in this way, the linear component of a Y cell receptive field would prefer spatial frequencies more than one octave lower than we actually observed in simple cells in area 17 (Hochstein & Shapley, 1976*a*; see also Enroth-Cugell & Robson, 1966). The minority of simple cells from area 17 that show non-linear spatial summation are more reasonable candidates for Y cell input, but these cells did not differ from the linear variety in their spatial tuning properties, nor was the 'linear' portion of their response elicited exclusively by frequencies below 0·3 c/deg. We think that these cells are also driven ultimately by X cells, and that their non-linear behaviour results from their cortical connectivity rather than non-linear afferents.

It is more difficult to come to a clear conclusion about complex cells, probably because this group is rather heterogeneous in its spatial properties. Some complex cell behaviour is certainly consistent with Hubel & Wiesel's hierarchical model (Movshon, 1975; Movshon *et al.* 1978*b*). For one thing, simple and complex cells respond to identical ranges of spatial frequency. That complex cells summate in a non-linear manner could indicate either that they in some way combine only the non-linear components of Y cell receptive fields, or that they combine the outputs of linear X and/or simple cells in a non-linear manner (Movshon *et al.* 1978*b*). The corticotectal complex cells in area 17 seem to receive predominantly Y cell input (Hoffmann, 1973; Palmer & Rosenquist, 1974), but they constitute fewer than 5% of the neurones. We feel that it is premature to speculate on the source of the input to other complex cells, although we should note the possibility that Y cell afferents contribute little to the properties of neurones in area 17, and that complex cells there might often be driven predominantly by X cell input from the lateral geniculate nucleus, or relayed via simple cells in area 17.

Area 17 and area 18. Our results clearly show that areas 17 and 18 process different aspects of the information relayed from the retina by the lateral geniculate nucleus. This fact, combined with the relative immunity of area 18 neurones to disruption of their input from area 17 (Dreher & Cottee, 1975), suggests that the original notion of these areas as part of a serial chain is inadequate. It is tempting to speculate that the properties of area 18 neurones reflect principally the influence of Y cells of the lateral geniculate nucleus, whose large receptive fields and transient responses to flashed stimuli coincide neatly with the spatial and temporal properties we noted in area 18.

A functional dichotomy in the visual cortex?

It is striking to note the parallel between the differences we found between areas 17 and 18 and the differences between two classes of detection mechanism whose existence has been inferred from psychophysical experiments in man (Keesey, 1972; Tolhurst, 1973; Kulikowski & Tolhurst, 1973) and in cat (Blake & Camisa, 1977). This notion, of 'pattern' detectors responding preferentially to high spatial frequencies and low temporal frequencies, and 'movement' detectors preferring low spatial frequencies and insensitive to low temporal frequencies, fits well with our data on the spatiotemporal tuning properties of cortical neurones. Area 17 might be

identifiable with the 'pattern' mechanism, while area 18 could be the 'movement' mechanism. Moreover, Blake & Camisa's experiments suggest that the 'crossover' from one mechanism to the other should take place in the region just above 0·4 c/deg; this is precisely the range in which we would expect area 18's influence to give way to area 17's.

Anatomical differences in cortical organization among species make it unlikely that the cat's area 18 is homologous with our own (in rhesus monkey and, presumably, in man, area 17 is the only cortical area directly driven from the lateral geniculate nucleus). It seems, however, that a clear *functional* homology exists, wherever the neurones that underlie it may lie in the human visual cortex.

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