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RECEPTIVE FIELD PROPERTIES OF NEURONES IN VISUAL AREA 1 AND VISUAL AREA 2 IN THE BABOON

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Abstract—In order to compare the receptive field properties of cells in the striate area (visual area 1; V1), and the parastriate area (visual area 2; V2), we have recorded from 174 cells in V1 and 112 cells in V2 in five anaesthetized and paralysed baboons (*Papio ursinus*). The receptive fields were mapped to determine their type, size and position in the visual field, and the binocular interaction, if any. Moving and stationary optimally oriented bars were used to distinguish cells with single "on" or "off" subregions and those with more than one such subregion (S and A types) from those with overlapping "on" or "off" subregion (C and B types). The A types had larger receptive fields than S types and C types had larger receptive fields than B types, but as receptive fields increase in size with eccentricity in V1 and even more rapidly in V2, the distinction between large and small receptive fields has to be defined for the different ranges of eccentricity.

In V1 there are more cells with non-oriented receptive fields than in V2. In V1 S cells are found in all cortical layers except layer 5. C cells are absent from layer 4C, but predominate in layer 5. There is a preference for horizontal and vertical orientations in S cells only.

The transition in cell properties from V1 to V2 occurs in two stages. There is a strip extending from the V1–V2 border for up to 6 mm containing the representation of the visual field from $-2°$ ipsilateral to $+2°$ (contralateral) azimuth in which the cell type distribution resembles that of V1 more than that of V2. By contrast, in V2 from 2 to 10° there are very few S cells, many more C cells and over three times as many cells driven only by binocular stimulation, as compared to V1.

We set out to compare the functional properties of neurons in the striate cortex (visual area 1; V1) with those in the adjacent parastriate area (visual area 2; V2). The main input to V1 comes from the lateral geniculate nucleus, and there is only a small input to V2 from the intralaminar zones of the lateral geniculate nucleus[9] and a major input from V1. Differences in the physiological properties of cell types may therefore provide some information on cortical processing. Previous studies of the functional properties of neurones in V2 have produced differing results.[1,20,35,41,42] In particular there is some doubt about the increase in the number of binocular depth cells in V2. According to Hubel and Wiesel,[20] "As one proceeds forward and downward into the lunate sulcus and then up over the buried annectant gyrus, the retinal representation moves out from the midline. At the same time the proportion of binocular depth cells increases to more than 50%." According to Van Essen and Zeki,[38,41] however, the annectant gyrus usually forms part of visual area 3 (V3) rather than V2. We were also interested in the region of V2 immediately adjacent to the V2 border with anatomical peculiarities described by von Economo[12] and called by him OB_{γ}. This region was first shown by Myers[28] to contain the terminations of callosal fibres which are absent from V1 and the rest of V2. Although Poggio and Fischer[35] have made a careful comparison of the properties of binocular cells in V1 and V2, they found little difference in their properties, and did not pay particular attention to the V1–V2 border.

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Abbreviations: H, end zone inhibition; OB, obligate binocular; RF, receptive field; V1, V2, V3, visual areas 1, 2 and 3, respectively.

EXPERIMENTAL PROCEDURES

After induction of anaesthesia with ketamine hydrochloride (Ketalar, Parke–Davis) or phencyclidine hydrochloride (Sernylan; Bio-ceutic Lab), adult baboons (*Papio ursinus*, 2 male, 3 female) were maintained under anaesthesia with alfadolone acetate plus alfaxalone (Althesin; Glaxo) or halothane (Fluothane; ICI), and prepared for electrophysiological recording under sodium pentobarbitone (1–2 mg/kg/h) and a 60:40 mixture of N_2O and O_2. The animals were paralysed by an infusion of tubocurarine and gallamine triethiodide. Temperature was maintained at 38–39°C. Heart rate and blood pressure were monitored and used to indicate when further anaesthetic was required. End-tidal CO_2 was maintained at about 5%. Pupils were dilated with atropine, and afocal contact lenses used to prevent the cornea from drying. Correcting lenses were added to focus the eyes on a tangent screen at 1.14 m. These experiments each lasted at least 5 days and care had to be taken to prevent infection and deterioration of the optics. The eyes were cleaned daily with a hypertonic 1.5% NaCl solution. Antibiotics were given locally to the eye and by intramuscular injection.

A small craniotomy was made over V1 and the dura removed. Single units were isolated by means of glass-

coated tungsten microelectrodes.[26] A plastic cylinder (2 cm dia) was cemented onto the skull and, after lowering the electrode onto the surface of the brain, was filled with agar and sealed with wax. Vertical electrode penetrations were made at between 1 and 6 mm behind the lunate sulcus.

The receptive fields of well isolated units were studied with hand-held slits, edges, bars and gratings. Only if the cell could not be driven with white light was the wavelength changed. Cells were classified according to a scheme developed for the cat[31] and similar to that of Henry.[17] The ability of each eye to drive the cell was determined by alternate stimulation of each eye, and the cell was classified in one of seven ocular dominance groups.[18a] A Risley prism placed in front of the left eye allowed the superimposition of the receptive fields (RFs) in the two eyes. Simultaneous stimulation of the two eyes allowed us to classify neurons: (1) cells showing no difference in the response to monocular or binocular stimulation; (2) facilitated cells, which show moderate or strong facilitation when stimulated binocularly; (3) obligate binocular (OB) cells, which can only be driven by simultaneous stimulation of both eyes, or in which the monocular response was too poor to allow the RF to be plotted; and (4) inhibited cells, which gave a weaker response to binocular than to monocular stimulation.

Eye position was checked with a Fison indirect ophthalmoscope which was used without its 15 D lens to give a direct plot of the edges of the blind spot on a perspex screen. The fovea is not visible in these conditions and its position was derived from that of the blind spot. This allowed an approximate measurement of elevation of the RF to be made, and all the units recorded were between 2 and 6° below the fovea. In each animal the position of the midline of the visual field was calculated from the RFs of about 20 binocularly activated cells.[21,30] Movements of the eye of 0.25° were detectable and the total daily drift was less than 0.5°.

We have concentrated on those properties which can be explored using hand held stimuli.[7,22,31,32,33] These of course do not include velocity characteristics. Moving an edge or a slit through the RF at different orientations defined the limits at which the cell just failed to respond. The angle between these limits is the orientation-tuning range. The preferred orientation bisects that angle. Although strictly this gives a measure of axial selectivity, testing with a stationary stimulus gave similar results and we believe that the response to the moving slit reflects orientation selectivity. The cells showing orientation selectivity were classified as being A, B, S or C cells. When the RF was shown to have discharge regions for moving light and dark edges which had a common spatial location for a given direction of movement the neuron was classified as being a B or a C cell. When B and C cells responded to an optimally oriented light slit of suitable length they revealed an "on–off" region corresponding to the superimposed light and dark edge discharge regions. Cells having single or separate discharge regions for moving light and dark edges were classified as S or A cells. When S and A cells responded to the appropriate flashed light slit they revealed a single or separate "on" and/or "off" areas. The response to flashed and moving stimuli always corresponded in sign, i.e. a dark edge discharge region always gave an "off" response and a light edge discharge region an "on" response, and the superimposition of light and dark edges moving in the same direction an "on–off" response. Moving edges frequently revealed more subregions than did flashed stimuli, confirming that, at least with hand plotting, the use of moving stimuli is more effective for characterizing RFs.[17]

During each penetration, microlesions (1.5 μA electrode negative current for 2–7 s) were made interspersed amongst single unit recordings to permit identification of the laminar position of the recorded units. After the animal had been killed with an overdose of sodium pentobarbitone the brain was fixed, prepared for histological examination and stained with cresyl violet.

RESULTS

We recorded 312 neurones (186 in V1 and 126 in V2) in 19 electrode penetrations in 5 baboons. We recorded only 4 units which we failed to drive with visual stimuli (all in V1). Penetrations were on the lip of the lunate sulcus in area V1 and the electrode was driven vertically through the V1–V2 border into V2 on the posterior bank of the lunate sulcus. In one instance the electrode reentered V1 in the depth of the calcarine fissure.

As penetrations were made orthogonal to the V1–V2 border the azimuth of RF position increased and the elevation decreased as the electrode advanced. In V1, 168 neurons were recorded from the surface of the occipital cortex with RF positions ranging from 0 to 5° azimuth and 14 neurons from the calcarine fissure with a mean eccentricity in the visual field of 17°. These 14 neurons recorded in cortex subserving the peripheral visual field are only considered for RF width and the distribution of RF types within cortical layers. In V2, 126 neurons were recorded with RF positions between 0 and 10° azimuth.

Receptive field dimensions

Receptive field dimensions were found to be smaller in V1 than V2 and in both areas RF width was influenced by eccentricity. The median width of RFs within 5° azimuth was 0.5° in area V1 and 0.96° in V2. The 14 neurons recorded at an eccentricity of 17° in V1 had a median RF width of 0.76° and the 27 neurons recorded between 5 and 10° azimuth in V2 had a median value of 2.57°. These results indicate that, as in the cat,[31] the increase in RF width with eccentricity is much steeper in V2 than in V1.

Receptive field types

Receptive field width enables C and A cells to be distinguished from B and S cells. Narrow fields with non-overlapping subregions correspond to S cells and with overlapping subregions, to B cells (Fig. 1). The narrow RFs give rise to the first major peak in the distribution of RF width (Fig. 1). Broad fields with overlapping subregions correspond to C cells, and with non-overlapping subregions to A cells. As mean RF width increases with eccentricity, the distinction between broad and narrow RFs must be made for each eccentricity class. In V1 at azimuths less than 5°, S and B family cells had RF widths less than 0.8° (median 0.4° for each family). In V2 at azimuths less than +2°, S and B cells had RF widths less than 0.85° (median 0.4° for each family) and at azimuths +2 to +5°, less than 0.9° (median 0.6° in B family). Over 5° azimuth, B family cells had RF widths smaller than 1.5 (median 1.1°). Each of the four cells types can show end-zone inhibition (end-stopped cells; indi-

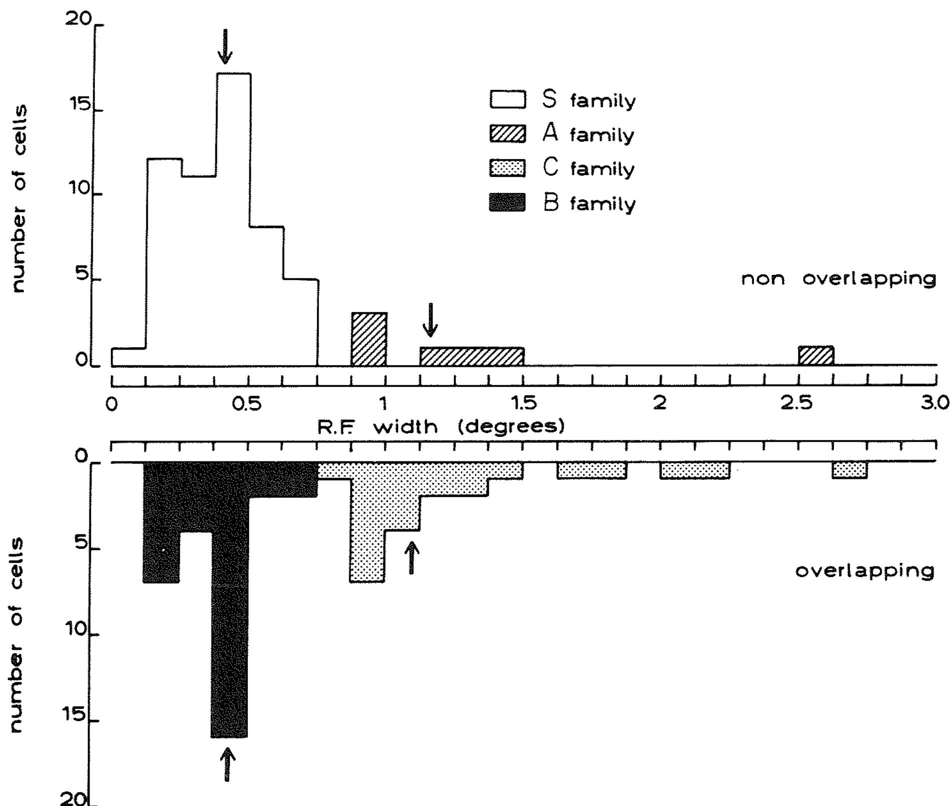

Fig. 1. Histograms of widths of RFs with non-overlapping "on" and "off" subregions (above) and overlapping "on" and "off" subregions (below) in V1. Arrows refer to median RF width values. S family cells 0.39°; A family cells, 1.12°; B family cells, 0.4°; C family cells 1.1°.

cated by prefix "H"). Although end-zone inhibition can vary in efficiency between 40 and 100%, it has been shown that end-stopped members of S and C families constitute distinct cell classes.[22] Consideration of RF width, using the same criteria as for cells with orientated RFs, also enabled the cells with non-orientated RFs to be divided into two groups, large and small non-orientated RFs. Most (80%) cells with small non-orientated RFs had either "on" or "off" centre fields. The cells with large non-orientated RFs were composed of equal numbers of either "on" or "off", or "on–off" centre responses.

Those cells which could not be driven with slits, bars, gratings or spots of white light were stimulated with different wavelengths using interference filters and slits or coloured cards. No attempt was made to determine the optimal colour stimuli for these cells, and it is probable that some of the cells which responded to slits or bars of white light would have responded better to appropriate "coloured" light. Our "colour" driven cells are the residue which could not be driven by anything except colour. They have been labelled wavelength-specific cells, but are not discussed further. A few cells in V2 could only be driven by moving or stationary gratings.

The S family cells were the major cell group in V1 where they comprised 34% of classified cells (Table 1). These were followed by cells with non-orientated RFs (20%) and B cells (19%). In V2 the most commonly encountered cell group were C family cells which comprised 44%, followed by B family cells (19%) and S family cells (18%). In contrast to V1, cells with non-orientated RFs were rarely encountered in V2 where they accounted for only 2% of the cells. S cells were composed of either one subregion (S_1 cells) or more than one subregion (S_2 cells), as revealed with either stationary and/or moving stimuli. Both types of S cells were found in V1 and V2, although in both areas more than twice as many S_1 than S_2 cells were found. Twice as many S_1 cells responded to onset of light as to offset of light. In V1 the S_1 "on" and "off" cells tend to be segregated; in 6 out of 19 penetrations, groups of 3–8 S_1 cells were encountered and this grouping of S_1 cell types appeared as strict as the ocular dominance grouping. When cells with non-orientated RFs were recorded they showed a strong tendency to give the same response to onset or offset of light as the adjacent S_1 cells.

Receptor field types were not found to be evenly distributed within V2. Tabulating cell types in V2 according to azimuth shows that within 2° of the vertical meridian the proportion of cell types is very different from those recorded between 2 and 10° (Table 1). In V2, S family cells were largely restricted

Table 1. Numbers and proportions of cell types

	V1	V2 < 2°	V2 > 2°	V2 (total)
Undrivable	4			0
Unclassified	8			15
Classified	174	64	48	112
Wavelength specific	11 (7)	1 (1.5)	1 (2)	2 (1.8)
Non-orientated	35 (20)	3 (4.6)		3 (2.7)
Grating cell	0	4 (6.2)		4 (3,6)
S cells	60 (34.5)	18 (28)	3 (6.2)	21 (18.7)
B cells	34 (19.5)	12 (18.7)	10 (20.8)	22 (19.6)
C cells	26 (15)	18 (28)	32 (66.6)	50 (44.6)
A cells	7 (4)	8 (12.5)	2 (4.1)	10 (8.9)

Figures in brackets are percentages.

to within the first 2° azimuth, where they constitute 28% of cells encountered, whereas at azimuths between 2° and 5°, they constitute only 6.2% and no S family cells were found at azimuths greater than 5°. The proximal strip of V2 had cells with RFs very similar to V1. Nearly all the S cells and also the non-orientated cells encountered in V2 were found in this strip and as in V1, C cells were relatively less numerous compared to regions further from the V1–V2 border: at distances of 6-10 mm from the V1–V2 border cell proportions were radically different and C cells constituted 66% of all cells encountered.

Laminar distribution of cell types

In V1, S family cells were found in all layers except layer 5 (Fig. 2). S family cells were most frequently encountered in supragranular layers where they constituted nearly two thirds of the cells. In layer 4, S family cells constituted one third of the neurons encountered and it is worth noting that the majority were HS cells. B cells were found principally in layers 3, 4 and 5. In the infragranular layers there were found to be twice as many B cells in layer 5 as in layer 6. C family cells were found predominantly in layers 4B and 5 and to a lesser extent in 2 and 6, and were absent from layer 4C. A cells were found predominantly in layer 4B where they constituted 20% of the cells encountered. Cells with small non-orientated RFs were found in all cortical layers except layer 5 and were most frequently encountered in layer 4C where they constituted over 40% of the cells. Cells with large non-orientated RFs were restricted to the infragranular layers and were most commonly found in layer 5 where they constituted 40% of the cells. End-stopped cells were found to be restricted to supragranular layers and layer 4 and constituted 28% of the cells recorded in these layers.

In V2, 61 cells could be confidently attributed to a cortical layer (Fig. 2). V2 differed notably from VI in that in the former S and A cells were confined to infragranular layers. In V1 there was a significant absence of C cells from layer 4C, whereas in V2 layer 4 showed one of the highest proportions of C cells.

Orientation selectivity

Orientation selectivity appeared to be a more general feature in V2 than in V1. Whereas almost all the cells in V2 would only respond to visual stimuli over a limited range of orientations, in V1 20% were not selective to orientation (i.e. cells with non-orientated

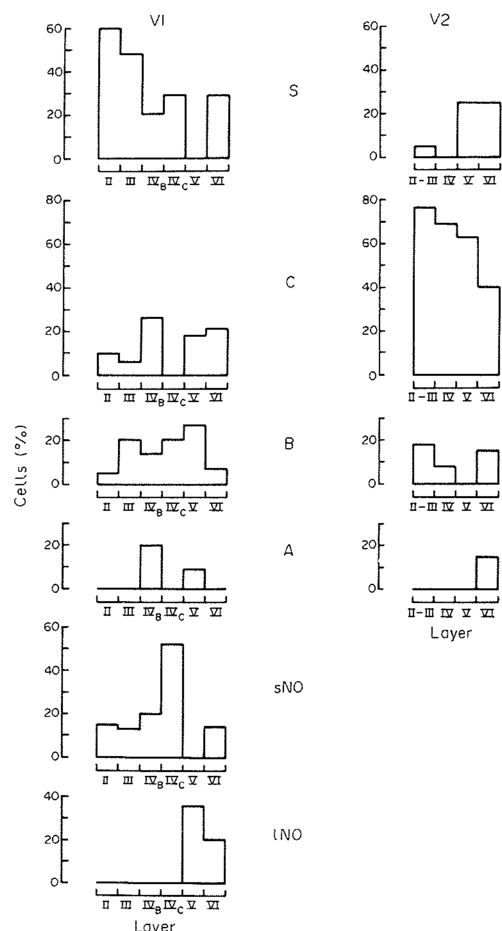

Fig. 2. Laminar distribution of RF type. Percentages are calculated on the number of cells of a given type per lamina. lNO, sNO, cells with large and small-orientated RFs.

Table 2. Width of orientation tuning

	Median	n	Interquartile range	Median azimuth (< 2°)	Median azimuth (> 2°)
VI					
S	41°	59	25–78		
B	54°	29	25–70		
C	92°	22	59–151		
A	57°	8	34–80		
V2					
S	42°	21	24–63	42	
B	42°	22	28–60	49	38
C	60°	49	39–77	76	56
A	48°	10	33–64	46	

RFs). If, however, the cells with non-orientated RFs of VI are excluded, then the overall selectivity for orientation, as measured by the median value of tuning width, appeared very similar in the two areas (up to 2° azimuth median orientation tuning: V2 = 49°; V1 = 54°).

The orientation tuning of each RF type was characteristically different. This can be seen in Table 2 where in both areas S cells were found to have the narrowest orientation tuning range (VI = 41°; V2 = 42°) and C cells the widest (V1 = 92°; V2 = 60°). The similarity in orientation-tuning range for each RF type in the two areas is clear if RFs with azimuths less than 2° are considered in V2. At azimuths of more than 2° there is a tightening of the orientation-tuning range for the C cells. It might well be that the drop off in the proportion of S cells, the most tightly tuned cells at these eccentricities, and the tightening in the orientation tuning of the C cells (azimuth less than 2°:76°; azimuth more than 2°:56°), are related phenomena. The result of these two changes is that the overall selectivity for orientation remains very similar.

Preferred orientations were not uniformly distributed in either V1 or V2 (Fig. 3). In V2 there was a marked bias for neurons to prefer vertically orientated stimuli, particularly obvious amongst OB neurons, since only 1 out of 33 such cells had an orientation preference within 30° of the horizontal. When compared to the overall population of V2 neurons the absence of horizontally orientated OB cells was significant (χ^2; $P \ll 0.01$). The bias for vertical orientation was found at both large and small azimuths, and was more pronounced amongst S cells than all the other cell types.

The preference of V1 neurons for orientations around the horizontal and vertical can be made more obvious by plotting preferred orientation with respect to the principal meridian (Fig. 4). The meridional anisotropy in V1 was not found in all cortical layers. Significantly fewer (4/19 cells) orientated cells in layer 4 had a preferred orientation within 15° of a principal meridian compared to cells outside layer 4(24/44 cells).

The meridional anisotropy is significant for S cells (Fig. 4). The possibility that the anisotropy is due to sampling more horizontal or vertical orientation columns is unlikely, because this effect is found only in one cell type and is absent in V2. HS and C cells do not show a preference for horizontal and vertical orientations (Fig. 4). The differences in orientation preferences between S and HS cells and between B and C cells are statistically significant, which supports their functional distinction.

Binocular interactions

Simultaneous binocular stimulation could give responses which were weaker or stronger than the monocular response (Table 3). Excitatory interaction gave cells which could be stimulated through either eye, but which showed a much stronger response when both eyes were stimulated (facilitated cells), or produced OB cells. The proportion of facilitated cells was very similar in the two areas, but 33% of the cells tested in V2 were OB, as against 9% in V1. The proportion of cells showing inhibitory interaction was around 10% in both areas. It is remarkable that the proportion of OB cells in V2 is not appreciably increased in the strip adjoining the V1–V2 border where −2 to +2° of the visual field is represented (see Fig. 8). At azimuths from +2 to 10°, 46% of cells were OB (Fig. 5).

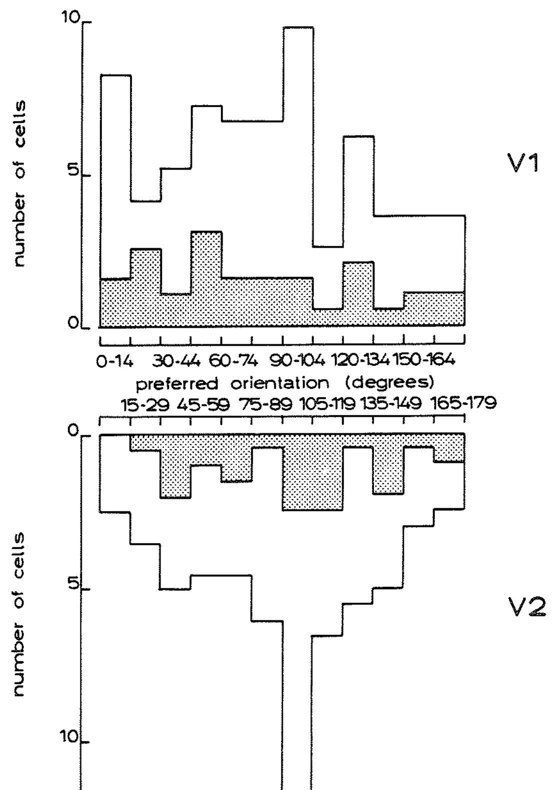

Fig. 3. Histogram of preferred orientations of V1 (upper) and V2 (lower). (V1 n = 131; V2 n = 120.) Shading, end-stopped cells. Horizontal is 0–180°.

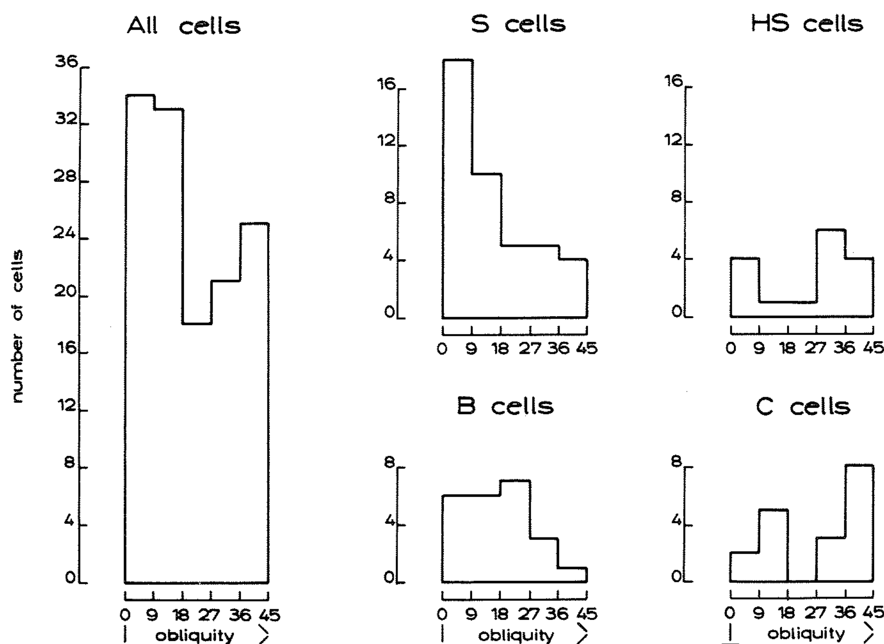

Fig. 4. Histograms of preferred orientations of V1 cells subserving central vision (1–7°). Obliquity indicates preferred orientation relative to horizontal or vertical. ($n = 131$:S cells, $n = 42$; HS cells, $n = 17$; B cells, $n = 21$; C cells, $n = 18$.)

In both areas the type of binocular interaction displayed by a cell was found to be related to its ocular dominance. Seventy-four percent of cells displaying binocular facilitation showed "balanced" ocular dominance (ocular dominance groups 3–5; see ref. 35), while 88% of cells with binocular inhibitory interaction showed "unbalanced" ocular dominance (ocular dominance groups 1, 2, 6 and 7). Ocular balance was found to vary amongst different RF types (Fig. 6). In V1, the highest proportions of unbalanced cells were found amongst S (66%) and B (61%) family cells, and cells with small non-orientated RFs (73%). Only 30% of C cells and 13% of cells with non-orientated RFs were unbalanced. Visual area 2 resembled V1 in that the highest proportions of unbalanced cells were also found amongst S (50%) and B (59%) family cells, and the smallest proportion amongst C cells (3%).

The precision with which the RFs in the two eyes had to be superimposed to obtain a modified binocular response differed for excitatory and inhibitory interactions. Excitatory interactions were more tightly tuned than inhibitory interactions, and on the whole V1 neurons were more tightly tuned than V2 neurons.

Table 3. Binocular interaction

	V1 ($n = 76$)	V2 ($n = 95$)
Obligate binocular	9%	33%
Facilitatory	33%	37%
Inhibitory	11%	9%
No interaction	47%	20%

It is likely that hand-plotting overestimates the range of disparities over which a neuron will show a binocular interaction. Retinal disparities were found

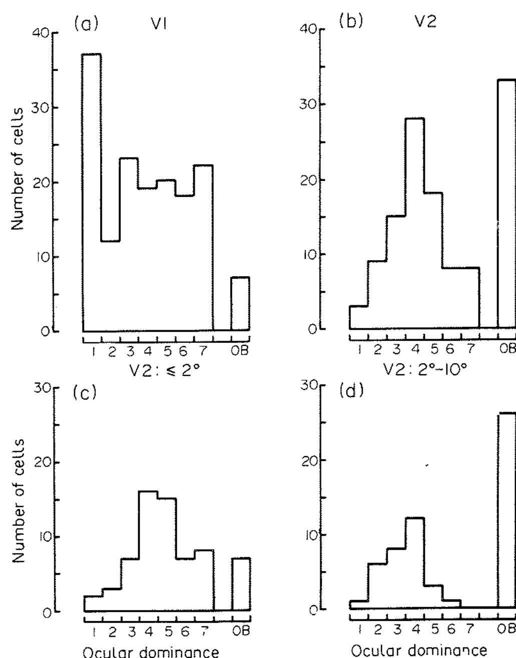

Fig. 5. Ocular dominance distribution. (a) V1; azimuth less than 5°, $n = 158$. (b) V2; azimuth less than 10°, $n = 112$. (c) V2; azimuth less than 2°, $n = 65$. (d) V2; azimuth more than 2°, $n = 57$. OB, obligate binocular cells.

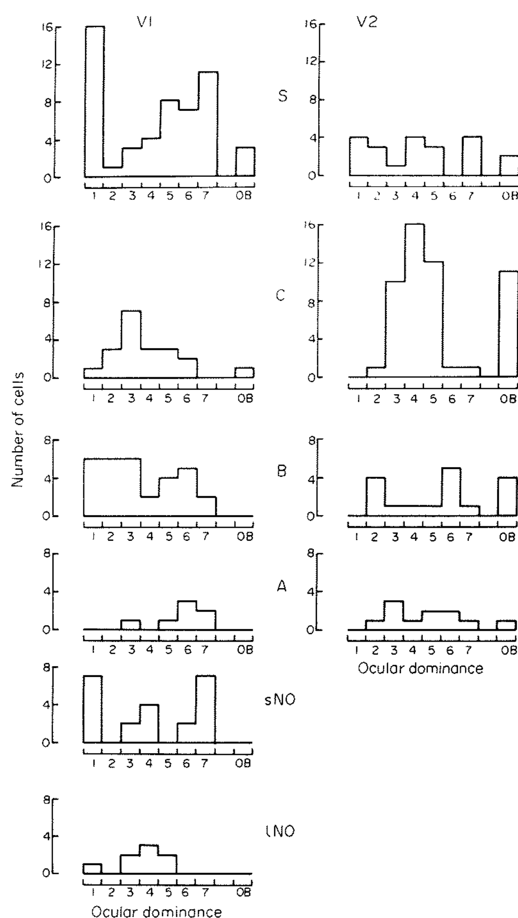

Fig. 6. Ocular dominance for RF types in V1 and V2. (V1) S family cells, $n = 38$; B family cells, $n = 20$; C family cells, $n = 15$; cells with small non-orientated RFs (sNO), $n = 22$; cells with large non-orientated RFs (lNO) $n = 8$. (V2) S family cells $n = 21$; A family cells, $n = 10$; B family cells, $n = 16$; C family cells, $n = 30$; OB, obligate binocular cells.

in both visual areas and ranged between -2 and $+2°$. In V1, 12% of these cells had disparities greater than 1°, and in V2, 33% had disparities greater than 1°.

The V1–V2 border

The extent of the visual field represented in V1 and V2 of a given hemisphere was not limited to the contralateral hemifield. In both areas the representation of the midline was at some distance from the 17–18 border. Examples of electrode tracks made in one hemisphere of a baboon are shown in Fig. 7. Track 2, which was entirely within V1, starts off in cortex subserving the ipsilateral field, and terminates on the representation of the vertical meridian at approximately 4 mm from the 17–18 border. The extent of V2 subserving the ipsilateral visual field is very much narrower in this example and is explored by track 4. In this track the vertical meridian representation in V2 is at a maximum of 1 mm from the 17–18 border. In the tracks shown in this section the proximal 2° strip of V2 is only partially explored. Typically the only S cell in V2 was recorded in track 4 at an azimuth of 0.4°. Further down this track, when the electrode was exploring V2 at azimuths in excess of 2°, only C and B family cells were recorded (Fig. 8).

The width of the -2 to $+2°$ proximal strip in V2 is shown to be approximately 6 mm in Fig. 7. However it must be emphasized that the width of this strip varied during different penetrations. Further experiments are needed to investigate whether this change in width of the -2 to $+2°$ strip in V2 is uniquely related to recording distance from the foveal representation (i.e. magnification factors) or if there are local non-homogeneities within V2.

DISCUSSION

Receptive field types

In this study we confirmed an earlier observation that cortical neurons, when judged qualitatively, appear often to give a poor response to a flashed light. The use of moving edges for the classification of neurons has repeatedly been shown to reveal large proportions of S cells in V1 (in ref. 36, 35%; in ref. 8, 44%; in this study, 35%). This contrasts with earlier studies which largely relied on flashed stimuli and found between 5 and 10%.[10,16,19,34] However, some differences in the proportion of S and simple cells reported are not surprising since the two categories overlap but do not coincide. In the original definition of simple cells[18] they had to have separate subregions. Those S_2 cells which respond to flashed stimuli would be equivalent to simple cells, and in fact they occur in similar proportions. However S_1 cells have only one excitatory area which can be "on" or "off", and they would be grouped with complex cells in Hubel and Wiesel's classification scheme.[18a] An added reason for including S_1 cells in the S family is that it has been shown that simple cells can have subliminal discharge regions for stationary stimuli[11,15] as well as for moving edges.[3]

A definite advantage in the classification scheme we have used is that it reveals functional differences in the orientation and ocular dominance domain. S and B cells have tighter orientation tuning than do C and A cells. The use of quantitative techniques has shown in the cat that these cell groups also differ with respect to their level of spontaneous activity and their velocity characteristics.[32,33] S cells have the narrowest orientation tuning and are also the only cells to show a meridional anisotropy in V1. End-stopped cells recorded in the same region did not show this effect, which provides further evidence that end-stopped cells constitute a distinct cell type.[22]

Comparison with the cat

The principal difference in the receptive field types seen in the cat and in the monkey is that in the cat

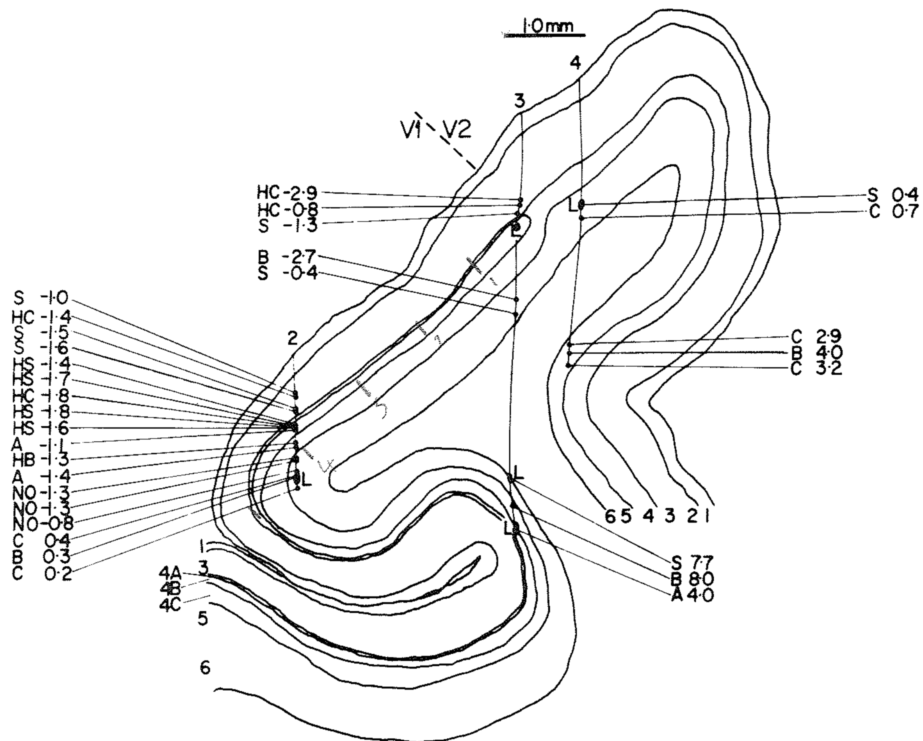

Fig. 7. Parasaggital section through the occipital cortex to show histological reconstruction of electrode tracks in V1 and V2 and position of recorded neurons. Figures refer to azimuth in degrees; negative values indicate ipsilateral fields. L, microlesion; NO, cells with non-orientated RFs. Other abbreviations as in text. Posterior to left, posterior wall of the lunate sulcus to the right. The small sulcus to the left is an inconstant one which can be called the superior lateral occipital sulcus.

there is no difference in the receptive field types in V1 and V2, whereas in the monkey V1 and V2 are very different. In the monkey there are in V1 four principal RF types, S, B, C and non-orientated, but in V2 beyond azimuth +2°, there are only C and B cells. The S cell which is common to V1 and V2 of the cat and V1 of the monkey seems to be characteristic of primary cortex. The cell with non-orientated RFs as a major cell type seems to be restricted to V1 of the monkey.

Laminar distribution of receptive field types

In V1 our results confirm that in layer 4C where the principal geniculate afferents terminate, there is a large proportion of cells with non-orientated RFs.[8,11,19,36] Certain workers have taken the similarity of the non-orientated RFs of some cells to those of cells in the lateral geniculate as an indication that these are first order neurons,[10,19] although Bullier and Henry[8] found cells with non-orientated RFs that did not appear to have monosynaptic input. Cells with non-orientated RFs have been found in layers 2 and 3, and in the blobs where the afferents of the lateral geniculate nucleus terminate.[23,24] Our results also show cells with non-orientated RFs in infragranular layers confirming the finding of others.[11,24] Previous reports on laminar distribution of S cells show them to peak in the granular layers[8,36] in the same way as do simple cells.[19] We found that S family cells were most numerous in the upper layers and, in contrast to Bullier and Henry's[8] finding, absent in layer 5. Layer 5 has been shown to contain those cells which project down to the superior colliculus.[14,25] The corticotectal cells identified by Findlay *et al.*[14] were 80% C cells and 20% cells with non-orientated RFs. This profile for corticotectal cells would correspond to the cell types we identified in layer 5. Our finding of an absence of C family cells in layers 4C and 2 is in agreement with previous results,[8,36] and with the small proportion of complex cells found in the lower part

	V1	V1/V2	V2
	+5° — 0° — −2°	−2° — 0° — +2°	+2° — +10°
S	38%	26%	5·2%
C	16·4%	26%	56%
OB	4·4%	11%	45·6%
	n=158	n=65	n=57

Fig. 8. Schematic representation of the border region between V1 and V2, showing the main changes in the receptive field types and binocular properties of cells as one proceeds from V1 to V2.

of layer 4.[19] We found that end-stopped cells were absent in those layers which provide a feedback to subcortical structures.[36] End-stopped cells were frequently found in layer 4 where they accounted for nearly a third of the cells, so it is possible that they could receive a direct thalamic input.

In V2 the small numbers of cells that we were able to assign to laminae appeared to be distributed very differently from those in V1. In contrast to V1, S and A family cells, where found, were in layer 5 and not in layer 4. C family cells were found in all layers including the superficial layers. In contrast to V1, end-stopped cells were found in all layers including 5 and 6.

Binocular interaction

The detection of horizontal disparity in the retinal image in the two eyes has been proposed as the neurophysiological basis of binocular depth discrimination.[2,21] Binocular interaction and depth sensitivity in V1 and V2 subserving the central 2° of the visual field has been investigated in awake behaving monkeys by Poggio and Fischer.[35] By examining the response profile to changes in depth these authors were able to distinguish two types of depth sensitive cells, depth-tuned cells (56%) and far and near cells (23%). The former had a symmetrical response profile for a point at a given depth whilst the latter had asymmetrical response profiles around the plane of fixation. Tuned cells showed binocular facilitation or inhibition to stimuli presented at distances from the fixation point corresponding to binocular disparities of 0.2° and were tuned over a range of disparities of about 0.2°. Our range of optimal disparities were much larger than this. This could be because we were more peripheral in the visual field.

The question of whether both V1 and V2 in the monkey mediate stereoscopic depth perception has also been approached by Hubel and Wiesel in a study using an anaesthetized and paralysed preparation.[20] Whereas Poggio and Fischer[35] found binocular interaction and horizontal disparities in both visual areas including a small proportion of OB cells, Hubel and Wiesel found that OB cells were restricted to cortex lying anterior to V1. The difference between these two studies might be partially explained by their having sampled different cortical regions. In their study in the awake monkey, Poggio and Fischer extensively sampled V1 and V2 subserving visual space out to 2° from the vertical meridian and reported OB cells in both areas but in small proportions. The region of V2 that they sampled corresponds to the strip of V2 lying along the vertical meridian where we found similar proportions of OB cells to that in V1. Hubel and Wiesel reported finding no OB cells in V1 but showed that 43% of the cells in undefined visual cortex in front of the V1–V2 border showed this property. As they proceeded away from the representation of the vertical meridian the proportion of OB cells increased to more than 50%. We did not find that there was a gradual increase in the number of OB cells within V2 some distance from the vertical meridian but rather there appeared to be a sharp increase in the proportion of OB cells at about 6 mm from the V1–V2 border, corresponding to +2° azimuth.

The finding that there are three times as many OB cells in V2 as there are in V1, and that V2 shows a wider range of optimal disparities, could imply differences between these two areas in integrating input from the two eyes and therefore in stereopsis. This conclusion is supported by differences of preferred orientations between the two areas. In V2 the majority of cells including the S cells have their preferred orientation aligned to the vertical whereas V1 has orientation preferences on the horizontal as well as the vertical. This is to be expected if V2 has a greater commitment to detecting horizontal disparities. The bias of OB cells for vertical orientations compared to the overall population of cells in V2 emphasizes their role in signalling horizontal disparity and confirms Hubel and Wiesel's finding of few OB cells with preferred orientations within 15° of the horizontal.[20]

The V1–V2 border

The first few mm of V1 and V2 adjacent to the V1–V2 border contains a representation of the ipsilateral field going out to 2° (Fig. 8). Although we did not record the RF position of a sufficiently large number of neurons, it would seem that cortex immediately adjacent to this region of ipsilateral representation has a similar magnification factor.[40]

There are two possible anatomical arrangements which can give rise to the ipsilateral representation, the interhemispheric projection to the V1–V2 border from its contralateral homologue[28] and the strip at the nasal temporal division of the retina that projects to both hemispheres.[37] However, there is evidence that the terminations in layer 4 of the projection from the contralateral hemisphere via the corpus callosum are restricted to V2 (Kennedy and Bullier, unpublished observation, cf. ref. 14a). This would suggest that callosal connections can contribute to the ipsilateral representation in V2 but that partial decussation is required for the ipsilateral representation in V1.

The physiological properties of the cells in V1 with RFs in the ipsilateral visual field appear to be very similar to those in the contralateral field at azimuths out to +5°. In V2, however, the presence of S cells, the low proportions of OB cells and the wider orientation tuning of cells distinguished the −2° to +2° azimuth class from the +2 to +10° azimuth class. There is evidence that the physiological strip of cortex defined in this study corresponds to the juxtastriate area 18 of Myers[28] where callosal afferents terminate. In the present study the physiologically defined region of V2 which had distinctive RF properties extended about 6 mm from the anterior limit of

V1 and has been shown to correspond to that region of V2 which has contralateral projections to the homologous region (Kennedy and Bullier, unpublished observation). This strip of cortex in V2 with distinct RF properties and subserving the visual field from −2 to +2° azimuth is notable in that it is represented in both hemispheres. The outcome of a dual representation, one in each hemisphere, is that the volume of cortex subserving these central 2° is at least twice that for more peripheral fields. It could be that the greater number of neurons available permits V2 at these eccentricities to elaborate small fields (S and B family) similar to those found in V1.

It has been suggested that stereopsis across the midline could be dependent on callosal connections[5,6,27] though Bishop has argued that partial decussation rather than callosal connections would be the anatomical basis for fine stereopsis on the vertical meridian.[4] In either case the tuned excitatory and inhibitory responses observed by Poggio and Fischer could well constitute the neurophysiological basis for fine stereopsis on the vertical meridian. The most suitable RF to fulfill this role of binocular interaction is the S or simple cell because of its sharp width activity profile[3,21,22,29] and its inhibitory sidebands.[13,22] Our results indicate that S cells are found in V2 along the vertical meridian. The small number of OB cells in this region (this study, refs. 20, 35) further demarcate this strip of V2. As one moves further out in V2 there is a decrease in magnification factor and an increase in OB neurons which might correspond to a change in emphasis from fine to coarse stereopsis. Such an explanation of the specialization of area V2 lying adjacent to V1 does not exclude a role in linking the two visual hemifields across the vertical meridian.[20,39]

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