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THE RELATIONSHIP OF RECEPTIVE FIELD PROPERTIES TO THE DENDRITIC SHAPE OF NEURONES IN THE CAT STRIATE CORTEX

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SUMMARY

1. In this study, we examined the hypothesis that some features of the receptive fields of cortical neurones are determined by the extent to which their dendrites can sample from different parts of the visual field representation on the cortex. In particular, the orientation selectivity and size of the receptive fields of cortical neurones were examined for their relationship to the tangential organization of the dendrites of cortical neurones.

2. Single neurones in the visual cortex of anaesthetized and paralysed cats were physiologically characterized and injected intracellularly with horseradish peroxidase (HRP). In some cases it was possible to identify whether the neurones received direct (monosynaptic) or indirect (polysynaptic) input from afferents of the lateral geniculate nucleus. The dendritic arborizations of the HRP-filled cells, sampled from all layers, were reconstructed in three dimensions with computer assistance, and rotated to give the tangential or surface view.

3. The bias in the tangential arrangement of the dendrites was determined by calculating the mean vector angle for the distribution of the dendrites of each cell. This bias was related to the orientation selectivity of the neurones. There was no consistent relationship between orientation selectivity and the tangential bias of the dendritic tree.

4. The width of the receptive fields was compared to the equivalent 'width' of the tangential extent of the dendrites. There was no significant relationship between the two widths.

5. The tangential arrangement of the dendritic field does not appear to be important in determining the orientation selectivity or the size of the receptive fields of neurones in the cat visual cortex. The former feature of the receptive fields may be determined by inhibitory processes, while the extent and number of the afferents providing input to a single neurone may determine the latter property.

INTRODUCTION

One of the most striking features of the response properties of single neurones in the striate visual cortex of the cat is their selectivity for the orientation of the stimulus (Hubel & Wiesel, 1959, 1962). Several models have been proposed to account

for this selectivity, but one of the most simple is that of Colonnier (1964). He proposed that because the visual field is projected onto an essentially two-dimensional surface in the striate cortex (Bilge, Bingle, Seneviratne & Whitteridge, 1967), a cortical cell could selectively sample afferents that are excited from a particular line of points in the visual field, by elongation of its dendrites in the appropriate tangential dimension. Consequently, only a bar or edge of appropriate orientation would maximally stimulate the cortical cell.

This idea, that one role of dendritic morphology is to allow a selective sampling of particular afferents, has been explored most thoroughly in the retina. There is now evidence showing a good correlation between the size of the receptive field centre of a ganglion cell and its dendritic field size (Peichl & Wässle, 1981, 1983), presumably because a larger dendritic field can sample afferents from a larger region of retina. More recently, it has been shown that the receptive fields of ganglion cells themselves are weakly biased to different orientations (Hammond, 1974; Levick & Thibos, 1982), and that these biases correlate with biases in the arrangement of ganglion cell dendrites (Leventhal & Schall, 1983). Thus, cells with receptive fields biased towards the horizontal would have a dendritic tree which is elongated along the horizontal dimension in the retina, allowing the dendrites to sample the appropriate bipolar cell input.

In the cortex the relation of receptive field size and orientation selectivity to the size and the tangential organization of the dendritic tree is much more difficult to study because regions of known physiology cannot be easily related to cells of known morphology. Nevertheless, two studies (Coleman, Flood, Whitehead & Emerson, 1981; Tieman & Hirsch, 1982) have now attempted to test Colonnier's (1964) hypothesis experimentally. This has been done by exposing kittens to horizontally or vertically arranged stripes during development in order to bias the cortical neurones to a particular orientation tuning (Blakemore & Cooper, 1970, Hirsch & Spinelli, 1970). Neurones in the striate cortex were then stained by the Golgi method and the orientation of the dendrites of a sample of neurones was examined and compared to neurones from the same region in normally reared cats. All these experiments showed that selective rearing had an effect on some neurones, but the interpretation of the results is difficult. Coleman *et al.* (1981) found a rearrangement in the dendritic structure of neurones from the selectively reared animals that agreed with Colonnier's proposal. Tieman & Hirsch (1982) on the other hand, found that the only neurones showing any change had biases in their dendritic orientation completely orthogonal to that predicted on Colonnier's hypothesis.

There are many problems with these studies, not the least being that the cortical physiology was abnormal, the orientation tuning of any individual Golgi-stained neurone was unknown, and the entire dendritic arbor of the cells were not reconstructed. The problems of sampling are also severe in these studies, because of the well-known vagaries of the Golgi method and because even after selective rearing many cells remain whose orientation selectivity is not biased towards the orientation of the stripes used.

In contrast to the above studies, we have adopted a direct approach to this problem. We have recorded from single cells, determined their orientation selectivity, injected them intracellularly with horseradish peroxidase (HRP), reconstructed them

three dimensionally, and related the tangential arrangement of their dendrites to their physiological orientation selectivity. Where possible we have also determined the serial position of the cell in the cortex, i.e. whether the cell is driven directly (monosynaptically) or indirectly (polysynaptically) by the afferents of the lateral geniculate nucleus (l.g.n.), using electrical stimulation methods (Bullier & Henry, 1979; Martin & Whitteridge, 1981, 1982).

An analogous problem is that of the relationship between the size of the receptive field and the tangential extent of the dendrites. Gilbert & Wiesel (1979), using similar methods, have reported that cells with larger dendritic fields have larger receptive fields in area 17 of the cat, but no quantitative data were given. We have been able to study quantitatively the relationship between receptive field size and dendritic field size in the course of this investigation. Our results show that there is no clear correlation between the receptive field orientation and dendritic orientation, nor between receptive field size and the dendritic field size.

METHODS

Determining the orientation selectivity of the cell

Preparations for recording from the cats (1·8–3·0 kg mean weight) and injecting the cells with HRP has been described elsewhere (Martin & Whitteridge, 1981, 1984; Martin, Somogyi & Whitteridge, 1983). The cats were anaesthetized with Althesin (0·3 ml/kg . h) for the duration of the experiment. Blood pressure, heart rate, temperature and end-tidal CO_2 were continuously monitored. Most cells were recorded in the crown of the precentral gyrus between Horsley–Clarke coordinates P3–P6. This sample had fields located within 5 deg of the vertical meridian and 5–10 deg below the horizon. Quantitative plotting of the receptive fields was not feasible given the time required. Thus, a standard protocol was used to hand plot the receptive fields using hand-held bars and edges. The range of orientations to which the cell would respond was plotted on a tangent screen and the optimum orientation was taken to be the line bisecting the orientation range. While this method does not take into account possible asymmetries in the orientation tuning (Hammond & Andrews, 1978; Henry, Bishop & Dreher, 1974*a*; Henry, Bishop, Tupper & Dreher, 1973; Henry, Dreher & Bishop, 1974*b*), quantitative assessments of orientation tuning curves indicate that most curves can be as well fitted by a Gaussian curve as by an inverted V (Henry *et al.* 1973, 1974*a*,*b*; Sherk & Stryker, 1976), and that the preferred orientation determined by hand plotting is usually indistinguishable from the orientation at the centre of the orientation range that has been determined quantitatively (Blasdel, Mitchell, Muir & Pettigrew, 1977; Orban & Kennedy, 1981; Wilson & Sherman, 1976). Asymmetries in the orientation tuning, if present in our cells, were too small to be detected using hand plotting. The preferred orientation of the receptive fields mapped through the dominant eye was used, or that of the contralateral eye if the cell responded equally well through both eyes. The orientation difference between the receptive fields mapped through each eye was usually within 10 deg.

Histological procedures

The relevant block of cortex was cut out in stereotaxic planes and cut in coronal sections, 100 μm thick, on an Oxford vibratome, and reacted for HRP using the *p*-phenylene/*p*-catechol methods with heavy metal intensification (Hanker, Yates, Metz & Rustioni, 1977; Adams, 1981; Perry & Linden, 1982). The sections were mounted on gelatinized slides, blotted and air dried before counter-staining in Cresyl Violet, dehydrating, clearing in xylene and applying a cover-slip. Using this procedure, the shrinkage in the *X*-axis (mediolateral axis) and *Y*-axis (dorsoventral axis) is negligible, presumably because the section is stuck down, but the shrinkage in the *Z*-axis (anteroposterior axis) is considerable, as much as 80%. The shrinkage in the *Z*-axis was measured by computer-rotating each section by 90 deg to give the side view. The mean distance between the cut ends of the HRP-filled processes emerging at the two surfaces of the section could then be measured. The focusing program used to determine the *Z* coordinate of the cut ends was accurate

to 1 μm (Houchin, 1981), and most cut ends lay within a single plane of section. Thus, the shrinkage for individual each section could be corrected appropriately.

Reconstruction

A total of twenty-four cells was studied. Neurones were sampled randomly from all layers and included spiny stellate cells, pyramidal cells, and cells with smooth dendrites. For comparison, this sample includes cells driven monosynaptically or polysynaptically by afferents of the l.g.n. Each cell was reconstructed at a magnification of 1000 × using the modified Joyce–Loeb Magiscan of Dr A. G. Brown. This machine was programmed for the task by Dr J. Houchin, for whose help we are most grateful. The entire reconstructed cell was then computer-rotated to give a tangential view. For pyramidal cells, the apical dendrite was assumed to be radially aligned and orthogonal to the cortical surface. These cells were rotated until the apical dendrite was viewed end-on. For spiny stellate cells and cells with smooth dendrites, the regular palisades of counterstained cells, and the radially aligned blood vessels were used as references to achieve a similarly rotated view.

Analysis of dendritic bias

In the case of non-pyramidal cells, the entire dendritic tree was used for analysis, but for pyramidal cells only the basal dendrites were used for the analysis to allow comparison with another study (Tieman & Hirsch, 1982). In the event the results were unaffected by this step because similar biases were obtained with or without including the apical dendrites. This is probably because the apical dendrites of most of the pyramidal cells used in our sample contributed only one to three branches *versus* the thirty to fifty branches of the basal dendritic tree. The tangential views of the dendrites were analysed in two ways. First, the angle between the mediolateral axis of the cell and the dendritic tips, with the cell body as origin was determined. Since in our situation angles 180 deg apart are equivalent, the data were treated as for axial data as described in Batschelet (1981). The mean vector angle was computed, assuming a vector length of 1 for the distance between the cell body and dendritic tips. A program was written to make the analysis less time consuming. This enabled the data to be collected and analysed using a digital bit pad interfaced with a RML 380Z microcomputer. We are grateful to Dr V. H. Perry for the use of this facility.

In the second analysis the same standard method of computing the vector angle was used, but the length of each dendrite was also taken into account. This was done by placing a series of concentric rings, spaced at 50 μm with the cell body as centre, over the dendrites and computing the angle between each point of intersection of the rings and the dendrites, and the mediolateral axis of the cell. A vector length of 1 was assigned for each angular measurement. The longer the dendrite, the more intersection points, and the more weight it was given in the mean vector angle. This latter method was similar to that used by Tieman & Hirsch (1982) and Leventhal & Schall (1983), and when applied to their examples gave very similar results. Although for some cells this method gave a different mean vector angle to that derived from the dendritic tips (see Fig. 1), both methods gave an essentially similar end-result. No attempt was made to assess whether the mean vector angle was significantly different from that expected by chance because the data points collected along one dendrite cannot be considered as independent observations for statistical purposes (see Leventhal & Schall, 1983).

Relating dendritic bias to orientation bias

The visual field is mapped in two dimensions over the surface of the striate cortex (Bilge *et al.* 1967; Whitteridge, 1973). The representation of the vertical meridian was taken as the reference line for orientating the receptive field relative to the cortical surface. In these experiments only four shallow penetrations were made in each hemisphere on average, so the precise alignment of the vertical meridian could not be determined. However, the data from eight cats whose visual cortex had been extensively mapped (Donaldson & Whitteridge, 1977, and D. Whitteridge, unpublished observations) were used to obtain a mean value for the alignment of the vertical meridian for the region within 4 mm anterior to the representation of the area centralis. This angle was $13{\cdot}6 \pm 2{\cdot}9$ deg (mean $\pm$S.E. of mean) to the mid line of the skull, running from posterolateral to anteromedial. Since the rotation of the cell also gave the surface view of the dendritic fields, both the receptive field and the dendritic field orientation could be plotted on the same coordinate system, as shown in Fig. 1 and the relationship between the two parameters could be established for each cell.

Relating the dendritic field size to the receptive field size

The method shown in Fig. 1 also enabled the relationship of receptive field size and dendritic field size to be assessed. Using hand plotting, the receptive field width is the only reliable measurement of receptive field dimension because the length of the receptive field depends on the summation properties of the cell. Both flashed and moving stimuli were used to plot the fields, but for some cells the response to flashed stimuli was weak or absent (Hubel & Wiesel, 1962). Therefore, the width measurement was taken from the receptive field plotted using light and/or dark moving edges. To get an equivalent dimension for the dendrites, in effect the dendritic field 'width', we have taken the span of the dendrites orthogonal to the line of optimum orientation, as shown in Fig. 1.

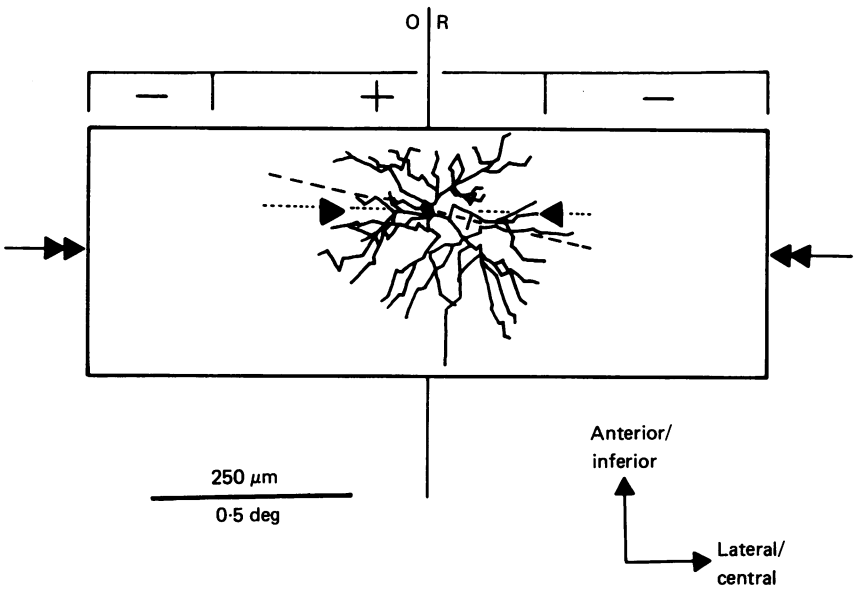

Fig. 1. The surface projection of the dendrites of a spiny stellate cell of layer 4 and its receptive field (rectangle). The receptive field width is indicated by the double arrows, the receptive field axis of orientation by the lines (OR) at the middle of the receptive field, and the extent of the receptive field's 'on' and 'off' subfields by the brackets enclosing + and − signs respectively. The 'width' of the dendritic field is indicated by the arrowheads. The bias calculated from the position of the dendritic tips is shown by the dotted line across the dendritic field; the dashed line indicates the dendritic bias when the length of the dendrites are taken into consideration (see Methods). The axes indicate the anterior and lateral directions on the cortical surface of the brain, and the inferior and the central (i.e. towards the vertical meridian) regions of the visual field projection on the cortical surface.

RESULTS

The sample of twenty-four cells included three cells with B-type receptive fields, five with C-type fields, fifteen with S-type fields and one cell with a non-orientated receptive field. The morphological type of cell, its laminar position, and serial position (where possible to determine) in the cortex are shown in Fig. 2. Also shown are the orientation preference of the cell (dotted line) and the mean vector for the dendrites (unbroken line), determined for the dendritic tips. It can be seen that there is no obvious relationship between the orientation biases for cells in any of the cortical

layers. It should also be noted that one cell with a non-orientated receptive field had a biased dendritic field. Both the sample of cells driven monosynaptically by l.g.n. afferents and the sample of those driven polysynaptically, had a wide range of differences between the dendritic orientation and the receptive field orientation (range for monosynaptically driven cells: 20–134 deg; range for polysynaptically driven cells: 20–126 deg).

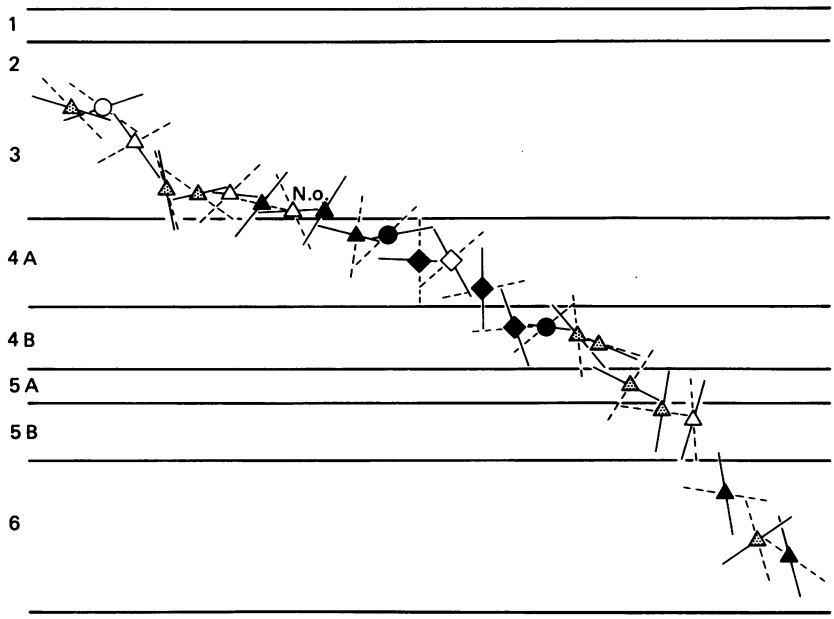

Fig. 2. The laminar location of the different cells used for this analysis. Triangles, pyramidal cells; diamonds, spiny stellate cells; circles, cells with smooth dendrites. Filled symbols indicate that the cells received direct (monosynaptic) input from l.g.n. afferents; unfilled symbols indicate that the cells receive indirect (polysynaptic) input from l.g.n. afferents; dotted symbols indicate cells whose serial position could not be determined. The dashed lines across the symbols indicate the receptive field orientation and the continuous lines indicate the dendritic bias calculated from the tips. The angles are plotted as shown in Fig. 1. The cell with a non-oriented receptive field is marked N.o. and has a biased dendritic field.

Fig. 3 shows the relationship of the mean vector angle for the dendrites, taking into account the length of the dendrite, and the receptive field orientation. Here circular symmetry has been eliminated because angles 180 deg apart are equivalent for our purposes. As for the dendritic bias calculated from the position of the dendritic tips, shown in Fig. 2, there is no obvious relationship between the dendritic bias and the receptive field orientation.

Although Figs. 2 and 3 clearly indicate that there is not the direct relationship between the dendritic orientation and the receptive field orientation hypothesized by Colonnier (1964), it is possible that some other relationship exists, e.g. that the dendrites are orientated orthogonal to the receptive field orientation, as suggested by Tieman & Hirsch (1982). This aspect was investigated by examining the

distribution of the differences between the receptive field orientation and dendritic orientation for each cell (Fig. 4). Here there is a tendency, at least for the biases calculated from the dendritic tips (Fig. 4*A*), for cells to have dissimilar dendritic and receptive field orientations. The differences between the dendritic orientation and the

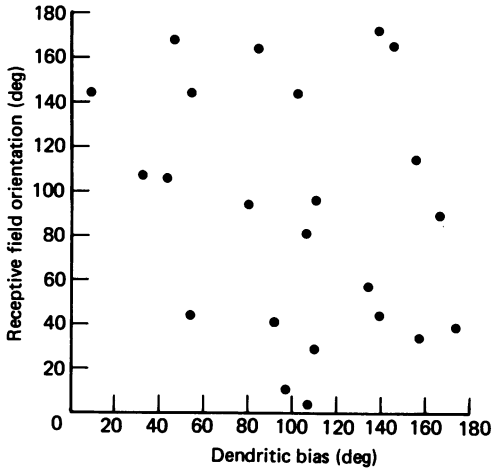

Fig. 3. The relationship of the preferred receptive field orientation and the dendritic bias of the cell. In this case the length of the dendrite was taken into account as explained in the Methods. The angles were measured as shown in Fig. 1.

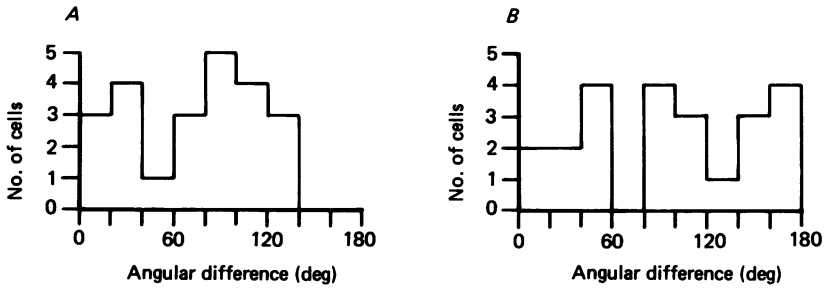

Fig. 4. The distribution of the angular difference between the orientation of the receptive field and the mean vector angle for the dendrites. *A*, distribution obtained when the mean vector angle was calculated from the dendritic tip position. *B*, distribution obtained when the length of the dendrites was taken into account in calculating the mean vector angle.

receptive field orientation for each cell were also plotted on probability paper (Cassie, 1954), and gave an approximately straight line, indicating that the samples were normally distributed. Similar means and standard deviations (S.D.) of the differences were obtained for both methods of assessing the dendritic orientation. (Dendritic tip method: mean = 73 deg; S.D. = 43, and method taking the length of dendrite into account: mean = 70 deg; S.D. = 41). Cells that were monosynaptically driven had similar distributions to those that were driven polysynaptically via l.g.n. afferents. Although there is a tendency for the dendritic orientation to be aligned obliquely to the receptive field orientation, the wide range of the distribution, reflected in the large

standard deviations and seen in Fig. 4, indicates that there is no consistent relationship between the two parameters.

Although we have treated all biases as if they were of equal significance, some cells had a more distinctly bipolar arrangement of their dendrites than other cells. Leventhal & Schall (1983) have discussed the problems of assessing whether a bias

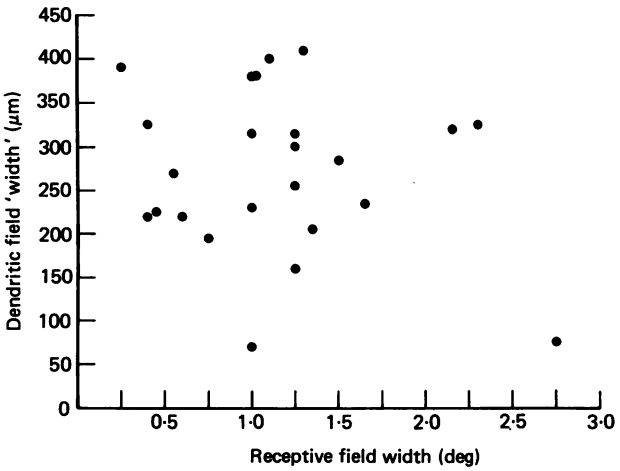

Fig. 5. The relationship of the width of the receptive field and the 'width' of the dendritic field. The widths were measured as shown in Fig. 1. A mean value for the dendritic width was used for the non-oriented cell.

is significantly different from a random one using these methods. On the basis of their analysis of the dendritic fields of retinal ganglion cells they have concluded that when the orientation bias (i.e. the length of the mean vector) is greater than 0·1 then the dendritic field can be said to be orientation biased. Applying their criteria to our data, sixteen of the twenty-four cells had an orientation bias. These cells were not restricted to one cell type or particular layers, and when plotted on their own, gave the same net result as shown for all twenty-four.

A less widely scattered distribution of points was obtained when the width of the receptive field was plotted against the dendritic 'width' (Fig. 5). A linear regression analysis gave a regression coefficient of $-0{\cdot}18$, indicating that the relationship is not significant.

DISCUSSION

Both the orientation selectivity and the receptive field size of the cell bore no clear relationship to the tangential organization or size of the dendritic field. Thus, Colonnier's hypothesis about the generation of orientation selectivity does not hold for the cells we have examined in the normal cat. Although our sample is small, these results do not encourage us to look for more subtle relationships using yet more sophisticated techniques on a larger number of cells.

Similarly, the relationship between the size of the receptive field and the tangential

extent of the dendritic tree is weak. This failure to confirm the observations of Gilbert & Wiesel (1979) may be due to differences in the method of assessing the receptive field size. Gilbert (1977) has previously used length and area as a measure of size. Because the length summation properties of cells varies enormously, the length measurements are best assessed using quantitative methods, which we have not used. It remains possible that using quantitative methods, a length, or areal measurement would give a better correlation with dendritic field size. However, our lack of correlation for one dimension suggests that other factors are more important in determining the receptive field size.

Quantitative *versus* qualitative methods are not an issue in the orientation relationships, and we cannot easily account for the results found by Coleman *et al.* (1981) and Tieman & Hirsch (1982) after selective rearing. It is unclear why Coleman *et al.* (1981) find a change in accord with Colonnier's hypothesis while Tieman & Hirsch (1982) find an elongation of dendrites orthogonal to the direction predicted. There is a further discrepancy between the two sets of results because Coleman *et al.* (1981) find an effect on layer 4 spiny stellate cells, while Tieman & Hirsch (1982) find that the effect is restricted to the layer 3 pyramidal cells and does not occur in the spiny stellate cells of layer 4.

Tieman & Hirsch (1982) have carefully pointed out that the changes in dendritic shape seen in their selectively reared animals may be unrelated to the generation of orientated fields. Although our results also indicate that there may be a weak tendency for the receptive fields to be orientated obliquely to the dendritic orientation, the range of differences of the orientations is so large that even in our small sample virtually every relationship can be found. Thus, on the basis of our data, a number of quite arbitrary assumptions would have to be made if one were to hypothesize that receptive field orientation is dependent on the dendritic field orientation.

In studies like those of Coleman *et al.* (1981) and Tieman & Hirsch (1982), one is faced with a severe sampling problem, because one cannot be sure that the Golgi method stains similar populations of cells in normal and selectively reared animals. Even within the population of Golgi-stained cells, particular cells were selected (Coleman *et al.* 1981; Tieman & Hirsch, 1982). Coleman *et al.* (1981) state that the cells used in their analysis were incomplete, whereas Tieman & Hirsch (1982), selected cells for which the basal dendritic tree appeared complete in one 125 μm thick section. As can be seen in our Figs 1 and 5, and from HRP-filled cells (Gilbert & Wiesel, 1979, 1983; Martin & Whitteridge, 1984), most dendritic fields are larger than 125 μm in all dimensions. This would mean that Tieman & Hirsch (1982) must have selected a very special sample of cells. Tieman & Hirsch (1982) report that cells from the selectively reared animals have fewer dendritic branches than those in normal animals. The cells they show from selectively reared animals have an average of 20 % fewer branch tips than our normal HRP-filled cells. This difference may not be entirely due to the rearing because one cannot be sure that all dendritic branches become impregnated with the Golgi precipitate.

A further issue relates to the shape of the receptive field itself. Colonnier (1964) had assumed that receptive fields were always elongated along the axis of best orientation. For many cells this is not so, particularly for the cells in layers 3 and 4 that often have receptive fields that are square, or elongated orthogonally to the

axis of preferred orientation (Spinelli & Barrett, 1969; Gilbert, 1977) when assessed quantitatively. Thus, it remains possible that the orientations of the particular Golgi-stained cells selected by Tieman & Hirsch (1982) were, in effect, following Colonnier's principle as far as their dimensions were concerned. One then still has the problem of how the orientation selectivity is set up in cells where the long axis of the receptive field is orthogonal to the preferred orientation. The most likely mechanism has been suggested by physiological studies showing that much of the orientation selectivity of cells is determined by inhibitory processes (Henry *et al.* 1974*b*; Sillito, 1975, 1979; Sillito, Kemp, Milson & Berardi, 1980; Tsumoto, Eckart & Creutzfeldt, 1979). These inhibitory mechanisms would reduce the need for a highly precise pattern of excitatory inputs to produce orientation selectivity.

The simplest explanation for our result, showing that the orientation of the receptive field is not consistently aligned with the orientation of the dendrites, is that the size of individual terminal arborizations of both l.g.n. cells and cortical cells is so much greater than that of the size of the dendritic fields of cortical cells (Ferster & Le Vay, 1978; Gilbert & Wiesel, 1979, 1983; Martin & Whitteridge, 1984). Any single afferent could then, in theory, contact any cell within its terminal field, regardless of the orientation bias of the dendrites. If particular afferents converge on particular cells, and our results do not rule this out, such selectivity of innervation must be determined by some mechanism other than selective elongation of particular dendrites.

Our failure to find a significant relationship between the size of the dendritic field and the size of the receptive field may also be accounted for on the basis of widely arborizing afferents, both from the l.g.n. and from other cortical cells. Single cells in the cortex can have intracortical axons which extend up to 5 mm in the anteroposterior and mediolateral dimensions (Gilbert & Wiesel, 1983; Martin & Whitteridge, 1984) and the tangential spread of the dendrites of a single cell are insignificant in comparison. Differences in the size of the dendritic field may be more related to the role of the particular cell and the number of afferent paths which synapse on the cell.

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