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Cortical integration in the visual system of the macaque monkey: large-scale morphological differences in the pyramidal neurons in the occipital, parietal and temporal lobes

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Layer III pyramidal neurons were injected with Lucifer yellow in tangential cortical slices taken from the inferior temporal cortex (area TE) and the superior temporal polysensory (STP) area of the macaque monkey. Basal dendritic field areas of layer III pyramidal neurons in area STP are significantly larger, and their dendritic arborizations more complex, than those of cells in area TE. Moreover, the dendritic fields of layer III pyramidal neurons in both STP and TE are many times larger and more complex than those in areas forming 'lower' stages in cortical visual processing, such as the first (V1), second (V2), fourth (V4) and middle temporal (MT) visual areas. By combining data on spine density with those of Sholl analyses, we were able to estimate the average number of spines in the basal dendritic field of layer III pyramidal neurons in each area. These calculations revealed a 13-fold difference in the number of spines in the basal dendritic field between areas STP and V1 in animals of similar age. The large differences in complexity of the same kind of neuron in different visual areas go against arguments for isopotentiality of different cortical regions and provide a basis that allows pyramidal neurons in temporal areas TE and STP to integrate more inputs than neurons in more caudal visual areas.

Keywords: intracellular injection; extrastriate cortex; temporal lobe; dendritic spines; Lucifer yellow

1. INTRODUCTION

As in other primates, the cortex of the macaque monkey includes a number of visual areas in the occipital, parietal and temporal lobes (e.g. Rosa 1997). Based on their different functional characteristics and connections, it has been suggested that these areas are organized into processing 'streams' (Ungerleider & Mishkin 1982) that reflect, to some extent, a hierarchical organization (for reviews, see Maunsell & Newsome 1987; Weller 1988; Felleman & Van Essen 1991; Gross *et al*. 1993; Graziano & Gross 1997). Both the 'dorsal' and 'ventral' streams originate in the first and second visual areas (V1 and V2), but they involve different areas of the parietal and temporal lobes.

As well as differences in connectivity and response properties, a number of studies have shown marked variation in the morphology of neurons in striate and extrastriate areas (Lund *et al*. 1993; Elston *et al*. 1996; Fujita & Fujita 1996; Elston & Rosa 1997, 1998*a*,*b*,*c*; Peters *et al*. 1997; Jelinek *et al*. 1999). These morphological differences have been implicated in models of surround inhibition (Lund *et al*. 1993) and cortical integration (Amir *et al*. 1993; Elston & Rosa 1997, 1998*a*,*b*). The present study was conducted to determine the morphology of layer III pyramidal neurons in two cortical areas of the temporal lobe, cytoarchitectural area TE and the superior temporal polysensory (STP) area. The response properties and connections of neurons in areas TE and STP suggest that cells in these areas perform sophisticated analyses. Neurons in area TE, a 'high-order' visual area, have exquisite selectivities for object shape, colour and texture, while those in area STP are involved in the integration of inputs from a number of sensory modalities (for reviews, see Perrett *et al*. 1990; Gross *et al*. 1993; Tanaka 1996; Cusick 1997; Yukie 1997). Thus, we were interested in establishing whether these functional differences between temporal areas are paralleled by differences in cell morphology. Moreover, we were interested in comparing the morphology of temporal neurons with those in other visual areas, particularly in view of the persistent belief that neurons in different visual areas are homogenous in their morphology (e.g. Hendry & Calkins 1998).

2. MATERIAL AND METHODS

Tissue was obtained from two adult male macaque monkeys (*Macaca fascicularis*), cases DM4 and MF2 (18 months and 11 years old, respectively). Animals were administered an overdose of barbiturate (sodium pentobarbitone) and perfused with physiological saline, followed by 4% paraformaldehyde (in 0.1 mol $^{-1}$ phosphate buffer). Tissue for cell injection was taken from the rostral third of the ventral bank of the superior temporal sulcus (cytoarchitectural area TEa of Seltzer & Pandya (1978) and TEad(s) of Yukie (1997)) and from the

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Received 22 March 1999 *Accepted* 29 March 1999

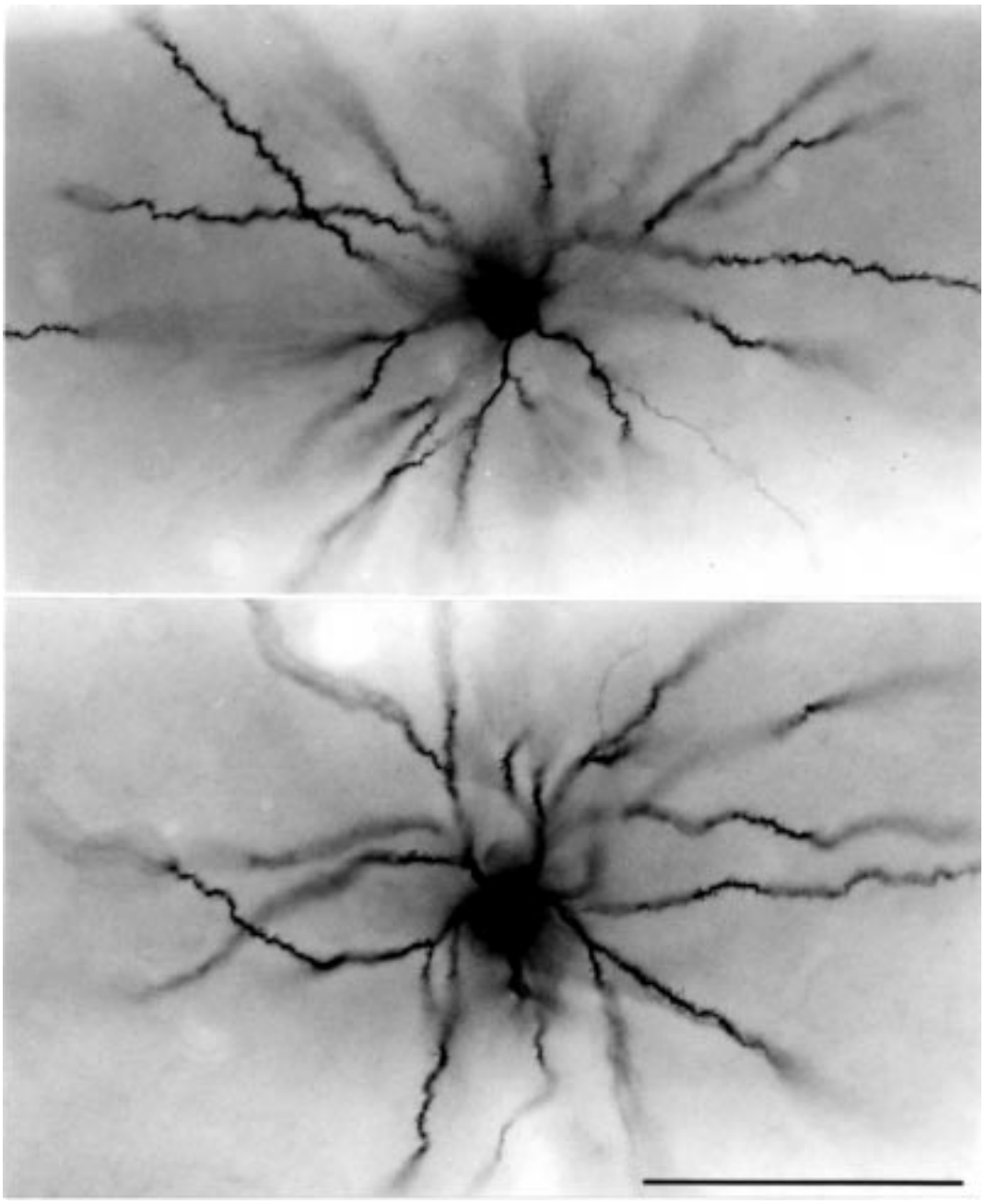

Figure 1. Photomicrographs of layer III pyramidal neurons in area STP that were injected with Lucifer yellow and processed for a light-stable diaminobenzidine reaction product, revealing the cellular anatomy in fine detail. Scale bar, 100 μm.

middle third of the dorsal bank of the superior temporal sulcus (area STP of Bruce *et al.* (1981), rSTP of Hikosaka *et al.* (1988), STPp of Felleman & Van Essen (1991) and TPOr of Cusick *et al.* (1995)).

The methods of cell injection and morphological analysis have been detailed previously (Elston & Rosa 1997; Elston *et al.* 1997; see also Buhl & Schlote 1987; Einstein 1988; Buhl & Singer 1989). Briefly, 250 μm thick cortical slices cut tangential to the cortical surface were labelled with 4,6 diamidino-2-phenylindole (DAPI, Sigma D9542), which enabled the distinction to be made between the larger, less densely spaced cell bodies of layer III pyramidal cells and the small, densely packed cell bodies of spiny multipolar cells in layer IV (see fig. 2 of Elston & Rosa (1997)). Neurons were injected with Lucifer yellow (Sigma L 0259) by continuous hyperpolarizing current (up to 100 nA). The tissue was processed with an antibody to Lucifer yellow (raised by Dr D. Pow), biotinylated and processed for a light-stable reaction product (3,3′-diaminobenzidine, Sigma D8001; figure 1).

In order to be included in the analysis, neurons had to be of the pyramidal type, had to be completely filled and had to have their complete basal dendritic arbor contained within the section (for details see Elston *et al.* 1996). All neurons with an unambiguous apical dendrite were analysed, including modified pyramidal neurons (e.g. DeFelipe & Fariñas 1992). Neurons were drawn with the aid of a camera lucida, scanned and analysed using standard features of NIH-IMAGE software (NIH Research Services, Bethesda). Sholl (1953) analysis was performed in the tangential plane to study the complexity of dendritic fields at different distances from the cell body (Elston & Rosa 1997). Spine densities were determined by counting the number of spines per 10 μm of dendrite (as seen with a ×100

Zeiss oil-immersion objective) of different layer III pyramidal neurons. Cell bodies were also drawn at this magnification to test for differences between cross-sectional areas and for correlation between cell body and basal dendritic field areas. Statistical comparisons were made using Statview SE software (Abacus Concepts, Berkeley, CA) for the Macintosh.

3. RESULTS

Two hundred and fifty-five neurons were injected in layer III of areas TE and STP of the temporal lobe. One hundred and twenty-seven of these neurons were deemed to be well-filled pyramidal neurons and were the subject of further analyses. Neurons were sampled in areas TE and STP in both cases (for case MF2, area TE $n=29$ and area STP $n=38$, and for case DM4, area TE $n=21$ and area STP $n=39$). The results were consistent in the two cases, revealing that layer III pyramidal cells in area STP have larger basal dendritic fields and branch more profusely than those in area TE. Moreover, cells in areas STP and TE are much larger, more complex and spine dense than those previously studied in visual areas of the macaque monkey.

(a) *Basal dendritic field morphology*

For both cases MF2 and DM4, two-tailed unpaired *t*-tests revealed that neurons in area STP had significantly larger basal dendritic fields than those in area TE ($t_{65}=3.13$, $p<0.05$ and $t_{58}=5.52$, $p<0.05$, respectively; figure 2*a*). Moreover, ANOVAS (two-way repeated measures, 2×10 design) on the results of Sholl (1953) analyses in cases MF2 and DM4, revealed that the number of branches in the basal dendritic fields of layer III pyramidal neurons in area STP was significantly greater than that in area TE ($F_{679}=211.9$ and $p<0.01$, and $F_{601}=46.5$ and $p<0.01$, respectively). Comparison with data from visual areas of the occipital, parietal and temporal lobes (Elston & Rosa 1997, 1998*a*) revealed that layer III neurons in areas TE and STP have much larger basal dendritic fields with many more bifurcations than those in areas V1, V2, MT or V4 (figures 2 and 3). The extent of these differences is made clear by comparing, for example, the neuron with the smallest basal dendritic field in areas STP ($1.09\times10^5\,\mu m^2$) and TE ($0.82\times10^5\,\mu m^2$) with the largest neuron sampled in the corresponding layer in area V1 ($0.51\times10^5\,\mu m^2$).

(b) *Spine density*

Spine densities were calculated for layer III pyramidal neurons sampled in case DM4, an 18-month-old monkey, to allow comparison with previously published data in other visual areas collected from animals of 14–28 months (Elston & Rosa 1997, 1998*a*). This choice was made in view of the well-established decrease in spine density with ageing (e.g. Lund *et al*. 1977). The basal dendrites of layer III pyramidal neurons in areas TE and STP are clearly more spinous than those in other visual areas previously studied (figure 4). The peak spine density in areas STP and TE was of the order of 23 spines per 10 μm of dendrite, at approximately one-third the distance from the soma to the distal tips, much greater than that of neurons in areas V1 (seven spines per 10 μm), V2 (seven spines per 10 μm), MT (eight spines per 10 μm) and V4 (13 spines per 10 μm; figure 2).

(c) *Total number of dendritic spines*

By combining data from the Sholl (1953) analyses and spine densities obtained from the 18-month-old animal, we were able to estimate the number of spines on the basal dendritic field of the 'average' layer III pyramidal neuron in each area. These analyses revealed that layer III pyramidal neurons in area STP had, on average, 8337 spines on their basal dendritic fields, more than the corresponding estimate for area TE (7260 spines). These estimates are considerably higher than those obtained for layer III pyramidal neurons in other visual areas (Elston & Rosa 1997, 1998*a*) such as areas V1 (643; average of the number of spines on the 'average' layer III pyramidal neurons in the blobs and interblobs), V2 (1139), MT (2077) and V4 (2429). It should be noted, however, that these estimates are a best approximation and, therefore, the absolute values should be viewed cautiously as they are most likely to be underestimates. Nonetheless, as a relative measure, these estimations provide a sound indication of differences in the numbers of spines of layer III pyramidal neurons in cortical areas involved in visual processing.

(d) *Somal areas*

We also observed a significant difference in cross-sectional area of cell bodies of layer III pyramidal neurons between areas STP and TE (for case MF2 $t_{65}=2.67$, $p<0.05$, and for case DM4, $t_{58}=3.6$, $p<0.05$). The cell bodies of neurons in area STP tended to be larger than those of neurons in area TE. Moreover, the cross-sectional area of the cell bodies of layer III pyramidal neurons in areas TE and STP tended to be larger than those in other visual areas previously studied in the occipital, parietal and temporal lobes (figure 2*d*; see also Elston & Rosa 1997, 1998*a*).

4. DISCUSSION

The temporal cortex is involved in various aspects of visual function, including object recognition and memory, and the response characteristics of temporal cortex neurons are strongly influenced by behavioural state, including attention (Gross *et al*. 1969, 1972; Desimone & Gross 1979; Desimone *et al*. 1984; Rolls 1992; Miyashita *et al*. 1993*a*,*b*). The present study is restricted to two areas of the temporal cortex, areas TE and STP. Area TE receives its main 'feedforward' projections from areas such as V4 and TEO and projects to, among other targets, memory-related areas of the medial temporal and parahippocampal cortices. Based on connections and response properties, area TE is considered to be a high-order area of the occipitotemporal stream (for reviews see Maunsell & Newsome 1987; Felleman & Van Essen 1991; Gross *et al*. 1993; Tanaka 1996; Yukie 1997). The response properties and connections of neurons in area STP suggest that cells in this area perform analyses based on more diverse sets of inputs: not only do they receive projections from visual areas, they also integrate somatosensory and auditory information (for reviews, see Gross *et al*. 1993; Cusick 1997; Graziano & Gross 1997). Despite differences in opinion on boundaries, function and connectivity of different areas in the superior temporal sulcus, most agree that neurons in these areas are involved in 'global'

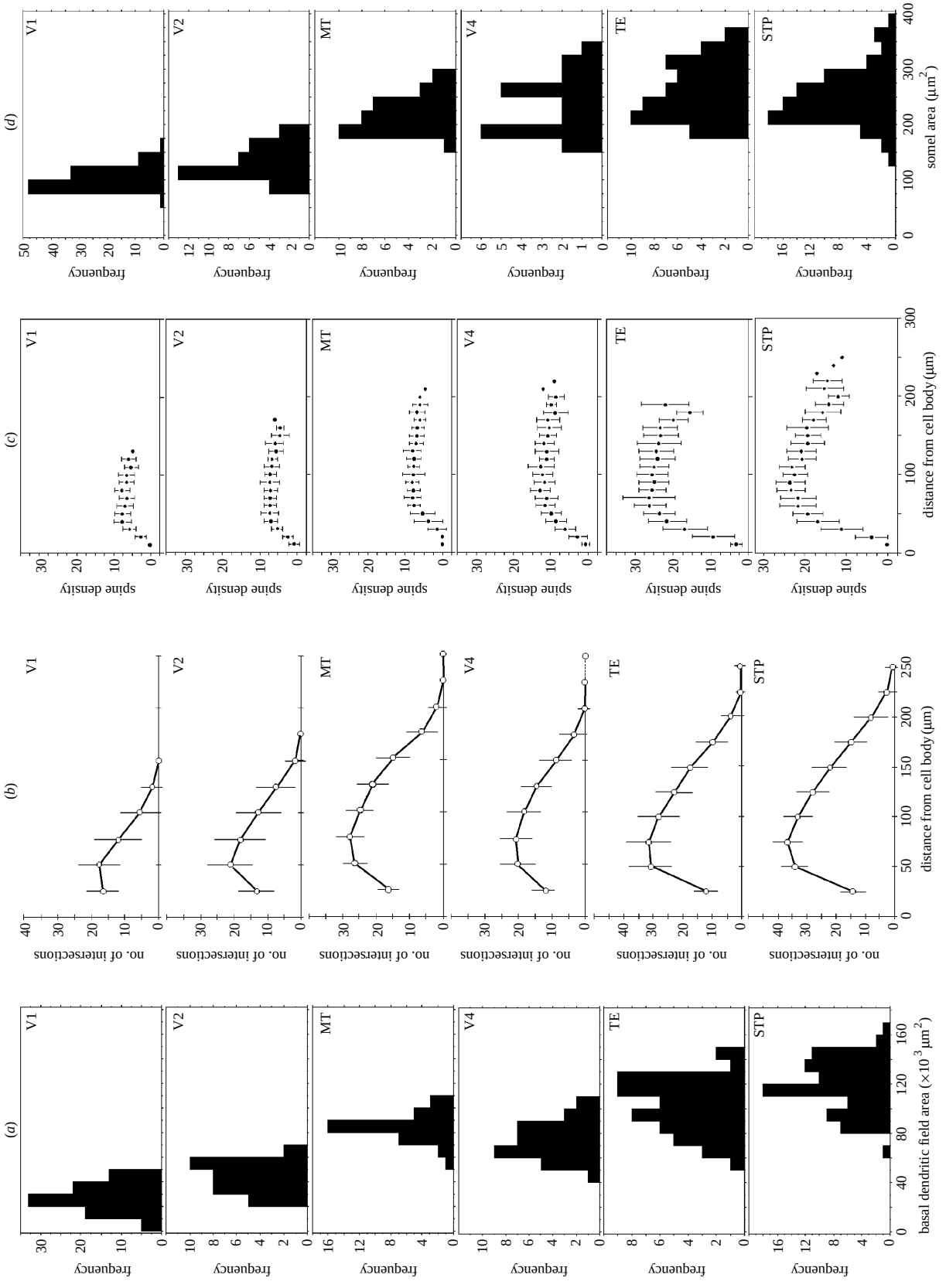

Figure 2. Graphs of (*a*) basal dendritic field areas, (*b*) Sholl (1953) analyses, (*c*) spine densities, and (*d*) somal areas for neurons in areas V1, V2, MT, V4, TE and STP. Data for area V1 represent cells found in the blobs of the middle and upper layer III of Hassler (1966). Values illustrated for areas TE and STP represent a combined data set for both animals studied, except in the case of spine densities (*c*) which were determined (per 10 μm of dendrite) in an 18-month-old animal. Note that layer III pyramidal neurons in areas TE and STP have larger basal dendritic fields (*a*) which have more branches (*b*) and greater spine density (*c*) than those in areas V1, V2, MT and V4. The degree of variation in the size of their cell bodies (*d*) is less marked amongst visual areas of the parietal and temporal lobes, as compared to areas V1 and V2. Error bars are standard deviations.

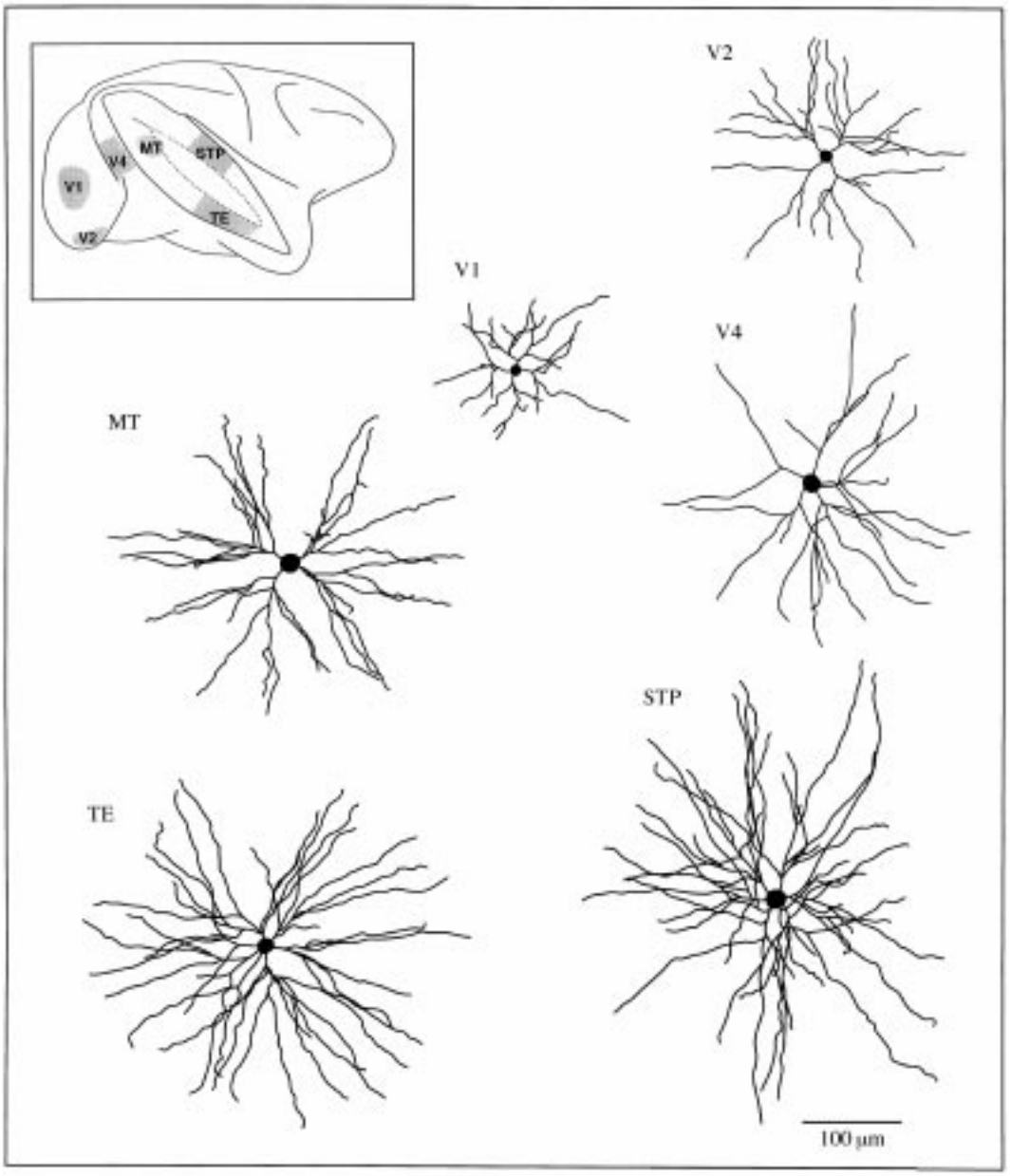

Figure 3. Drawings of layer III pyramidal neurons in visual areas V1, V2, MT, V4, TE and STP, as seen in the plane of section tangential to the cortical layers. Illustrated cells were selected for having a basal dendritic field area close to the mean for each visual area. Even in this small selection of cells it can be seen that there are differences in the number of bifurcations in the basal dendritic fields of cells in the different areas. Statistical analyses of the results of Sholl (1953) analyses for the entire sample of cells in each area revealed these differences to be significant. Cells are skeletonized images and spines are not illustrated. The insert shows the parts of the brain from which blocks of tissue were excised.

visual analyses, as opposed to local feature extraction, and are strongly influenced by the animal's behavioural state, including attention.

Conventional wisdom based on cytoarchitectural studies using the Nissl stain has assumed that neurons in different extrastriate areas are similar in their morphologies and the differences in their neuronal response properties have largely been attributed to different patterns of connections (Zeki 1978). However, recent studies have revealed large-scale variation in cell morphology between different cortical areas involved in visual processing (Lund *et al.* 1993; Elston *et al.* 1996; Elston & Rosa 1997, 1998*a*,*b*,*c*; Peters *et al*. 1997; Jelinek *et al*. 1999). The present results reveal marked variation in the morphology of neurons in visual areas of the superior temporal sulcus. For example, the 'average' layer III pyramidal neuron in area STP has fourfold more spines on its basal dendritic field than that in area MT and 3.2-fold more spines than that in cytoarchitectural area 7a (see Elston & Rosa 1997; figure 3). Furthermore, the basal dendritic fields of layer III pyramidal neurons in area TE have, on average, 1.5 times the number of spines found in those of cells in area TEO, another temporal area involved in the object recognition pathway (see Elston & Rosa 1998*a*). Indeed, comparison of the present data with those obtained in our previous studies of neurons in visual areas of the occipital lobe reveals that pyramidal cell morphology varies to an even greater extent than previously reported. For example, the basal dendritic fields of layer III pyramidal neurons in area

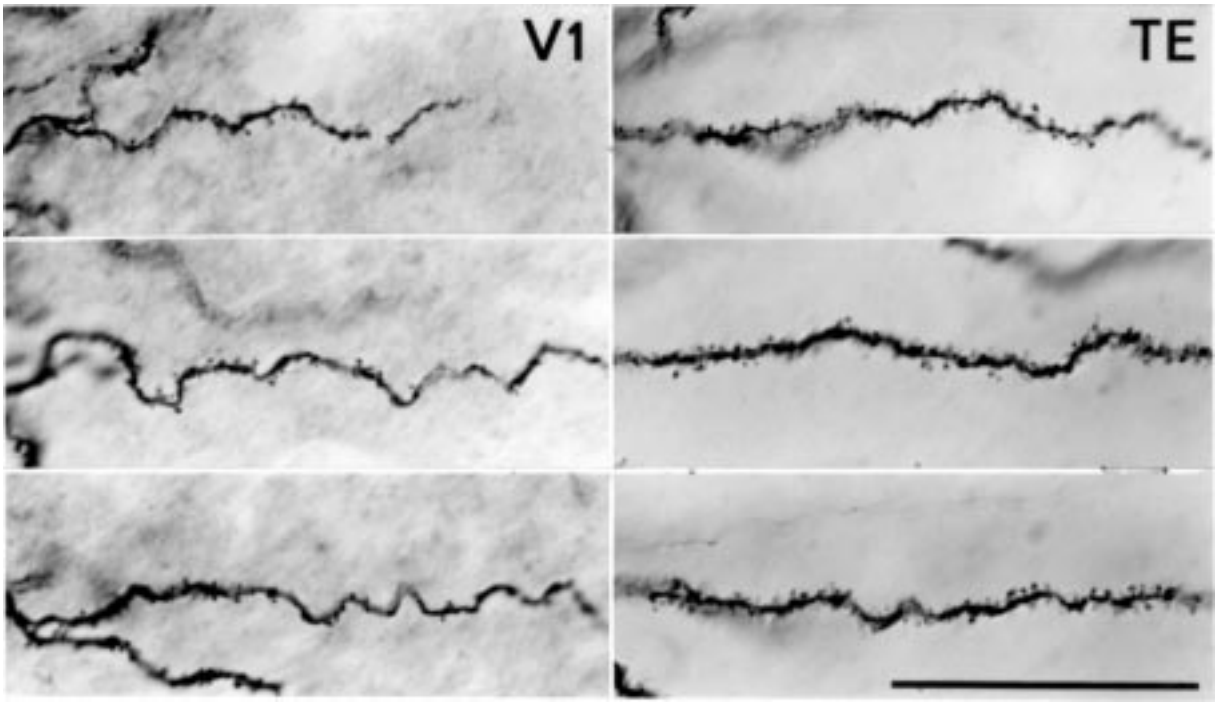

Figure 4. High-power photomicrographs of horizontally projecting basal dendrites of layer III pyramidal neurons in areas V1 (left column) and TE (right column). In all examples the cell body is located to the left and the distal tips of the dendrites to the right. Scale bar, 50 μm.

STP cover, on average, an area more than six times that of neurons in area V1 and have, on average, four times more branches. The differences in the size and complexity of the basal dendritic fields, in conjunction with differences in the spine density, result in spectacular differences in the total number of dendritic spines in the basal dendritic field of the 'average' neuron in the different visual areas (e.g. 13 times more spines in the basal dendritic fields of area STP cells as compared with area V1).

Following Gray's (1959) hallmark discovery that synapses could be divided into two morphological types, various groups have shown that dendritic spines are the principal site for asymmetrical synapses in the neocortex (e.g. Jones & Powell 1969), the presynaptic terminals of which have since been shown to contain the excitatory transmitter glutamate (DeFelipe *et al.* 1988; Kharazia & Weinberg 1993). Moreover, although variation has been reported, it is generally accepted that, in the visual cortex, each cortical dendritic spine receives one excitatory input and models of cortical processing make this assumption (e.g. DeFelipe 1997). The variation in the total number of basal dendritic spines of layer III pyramidal neurons in different cortical visual areas, in conjunction with the difference in the extent of intrinsic connectivity (Amir *et al.* 1993; Lund *et al.* 1993; Fujita & Fujita 1996) and the number of sources of corticocortical inputs (e.g. Felleman & Van Essen 1991), suggest that the number and diversity of excitatory inputs which can be integrated by single neurons differs markedly between areas. Recent observations which revealed a marked increase in the density of supragranular glutamate (GluR2/3) receptor subunits with rostral progression through visual areas of the occipitotemporal pathway (Xu *et al.* 1997) support this idea. Furthermore, the majority of GABAergic inhibitory inputs in the sensory cortex are found on dendrites and dendritic spines (Beaulieu & Colonnier 1985; Beaulieu & Somogyi 1990; Beaulieu *et al.* 1992). Therefore, differences in the total dendritic length and number of dendritic spines of layer III pyramidal neurons in the different cortical areas would most likely result in the integration of different numbers of inhibitory inputs. The greater number and diversity of inputs to neurons in areas TE and STP may be important for the generation of complex stimulus selectivities and the context dependency reported for cells in these areas (e.g. Perrett *et al.* 1982, 1985*a*,*b*, 1990; Desimone *et al.* 1984; Mistlin & Perrett 1990; Desimone 1991; Hietanen & Perrett 1993; Oram *et al.* 1993; Oram & Perrett 1996; Baker *et al.* 1998).

We would like to thank Dr David Vaney for generously allowing us access to his laboratory, Dr Soumya Ghosh for providing some of the tissue samples and Dr David Pow for providing his superb antibody to Lucifer yellow. Supported by project grants 961144 and 971113 from the National Health and Medical Research Council of Australia.

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