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Cortical heterogeneity: Implications for visual processing and polysensory integration

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Abstract

Recent studies have revealed substantial variation in pyramidal cell structure in different cortical areas. Moreover, cell morphology has been shown to vary in a systematic fashion such that cells in visual association areas are larger and more spinous than those in the primary visual area. Various aspects of these structural differences appear to be important in influencing neuronal function. At the cellular level, differences in the branching patterns in the dendritic arbour may allow for varying degrees of non-linear compartmentalisation. Differences in total dendritic length and spine number may determine the number of inputs integrated by individual cells. Variations in spine density and geometry may affect cooperativity of inputs and shunting inhibition, and the tangential dimension of the dendritic arbours may determine sampling strategies within cortex. At the systems level, regional variation in pyramidal cell structure may determine the degree of recurrent excitation through reentrant circuits influencing the discharge properties of individual neurones and the functional signature of the circuits they compose. The ability of pyramidal neurones in visual areas of the parietal and temporal lobes to integrate large numbers of excitatory inputs may also facilitate cortical binding. Here I summarise what I consider to be among the most salient, and testable, aspects of an inter-relationship between morphological and functional heterogeneity in visual cortex.

Heterogeneity vs. homogeneity of cortical structure

There are two opposing views on cortical organisation: one states that cortical circuitry is similar across all areas/species (Szentagothai, 1975; Creutzfeldt, 1977; Rockel *et al*., 1980; Eccles, 1984; Douglas *et al*., 1989; Kolb & Tees, 1990; Krubitzer, 1995; Hendry & Calkins, 1998), while the other maintains that various aspects of cortical circuitry vary between different cortical areas and species (Brodmann, 1907; von Economo, 1929; Walker, 1940; Colonnier & Rosignol, 1969; Lund *et al*., 1981; Haug, 1987; Morrison *et al*., 1998; Hof *et al*., 1999; Preuss, 2001). The former view attributes areal functional specificity to the source of inputs, while the latter contends that aspects of intrinsic circuitry are also important for generating functional specificity within a given area. The differences in opinion are largely attributable to which cortical areas/regions have been chosen for comparison, what aspects of circuitry were compared, methodologies used, and species studied.

Recent studies have revealed impressive variation in circuitry in different cortical areas at the molecular, cellular and systems levels. At the molecular level, the laminar distribution and density of receptor subunits vary between different cortical areas. At the cellular level, pyramidal neurones show marked interareal differences in their arbour structure. At the systems level, populations of intrinsic axons differ in their arborisation patterns across cortical areas, as does the density and distribution of neurochemically-identified subpopulations of cells (Fig. 1) (see Zilles & Clark, 1997; Morrison *et al*., 1998; Hof *et al*., 1999; Preuss, 2001; Elston & DeFelipe, 2002; Jacobs & Scheible, 2002; Elston, 2003a, b for reviews).

Quantification of regional variations in circuit structure has yielded some surprising results. For example, by developing new methodologies to quantify pyramidal cell structure (Elston & Rosa, 1997; Elston, 2001), we have shown that those in the prefrontal cortex (PFC) of the macaque monkey are, on average, up to 16 times more spinous than those in the primary visual area (V1) (Elston, 2000). Pyramidal cells in human prefrontal cortex are up to 23 times more spinous than those in macaque V1 (cf Elston & Rosa, 1998; Elston *et al*., 2001).

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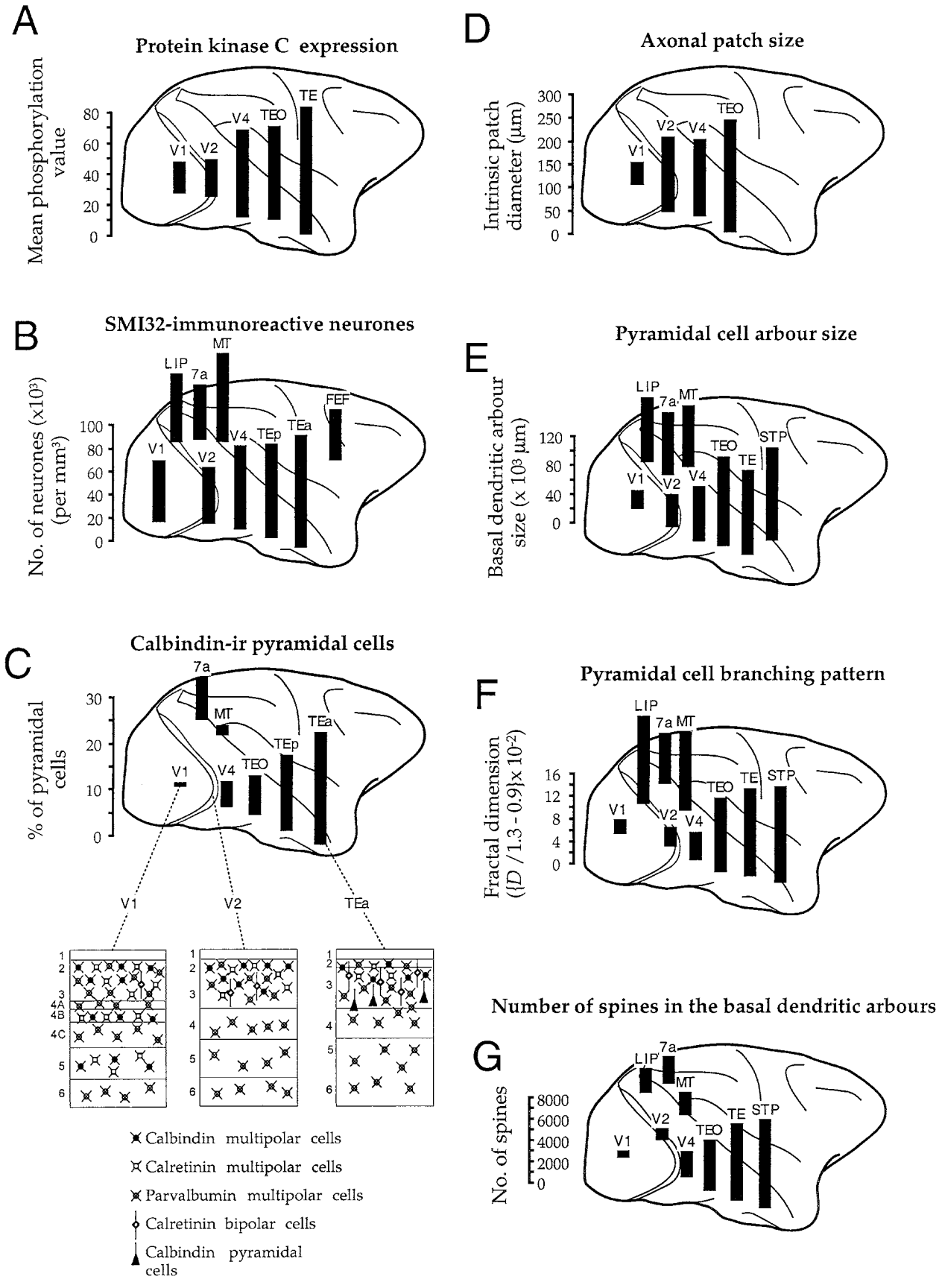

A
Protein kinase C expression
Mean phosphorylation value
80
60
40
20
0
V1
V2
V4
TEO
TE
B
SMI32-immunoreactive neurones
No. of neurones (x10³) (per mm³)
100
80
60
40
20
0
V1
V2
LIP
7a
MT
V4
TEp
TEa
FEF
C
Calbindin-ir pyramidal cells
% of pyramidal cells
30
20
10
0
7a
MT
TEa
TEp
V1
V4
TEO
V1
V2
TEa
1
2
3
4A
4B
4C
5
6
Calbindin multipolar cells
Calretinin multipolar cells
Parvalbumin multipolar cells
Calretinin bipolar cells
Calbindin pyramidal cells
D
Axonal patch size
Intrinsic patch diameter (μm)
300
250
200
150
100
50
0
V1
V2
V4
TEO
E
Pyramidal cell arbour size
Basal dendritic arbour size (x 10³ μm)
120
80
40
0
LIP
7a
MT
TEO
STP
TE
V1
V2
V4
F
Pyramidal cell branching pattern
Fractal dimension ([D /1.3 - 0.9]x 10⁻²)
16
12
8
4
0
LIP
7a
MT
TEO
TE
STP
V1
V2
V4
Number of spines in the basal dendritic arbours
G
No. of spines
8000
6000
4000
2000
0
7a
LIP
MT
TE
STP
V2
TEO
V1
V4

One is left to speculate on the functional significance of these structural differences, particularly in view of the fact that pyramidal cells are the basic neural substrate of the cerebral cortex comprising more that 70% of all neurones. In a bid to explore this issue we have focussed our efforts on the most extensively studied, and best understood, of cortices, the visual cortex. The results of our initial investigations of visual cortex have revealed marked, and systematic, differences in pyramidal cell structure between different cortical areas. For example, pyramidal cells become progressively larger, more branched, and more spinous, with anterior progression through V1, the second visual area (V2), the fourth visual area (V4) and inferotemporal cortex (IT) in the Old World macaque monkey, resulting in a successive doubling in the number of spines in their arbours (Lund *et al*., 1993; Elston & Rosa, 1998; Elston *et al*., 1999a; Jelinek & Elston, 2001; Fig. 2). A similar trend is found in the occipitotemporal cortex of the New World marmoset and owl monkeys (Elston *et al*., 1997, 1999b; Elston & Jelinek, 2001; Elston, 2003c; Fig. 3), suggesting that the trend for an increase in the structural complexity of pyramidal cells with anterior progression through areas of the occipitotemporal cortex is a common organizational principle in primates and was likely to be present in a common ancestor of anthropoids. Here I speculate how these differences in pyramidal cell structure may influence different aspects of visual processing and polysensory integration.

Pyramidal cell structure: Functional implications for the cell

Pyramidal cells constitute the largest group of neurones, and form the majority of interareal connections, in cortex (Feldman, 1984; Jones, 1984; DeFelipe & Fariñas, 1992). Arguably, they are the principal neurones of the cerebral cortex, generating nearly all facilitation (excitation) of cortical origin. They are characterised by many types, but are distinguished by their prominent apical dendrite and basal dendritic arbour.

(A) Excitatory and inhibitory inputs

The function of any cortical neurone is to receive, integrate, and relay, inputs to other cells. The first step in this process, to receive inputs, includes both excitatory and inhibitory synapses. As a relative measure of the number of excitatory inputs received by a given pyramidal neurone, one can count the number of dendritic spines, each of which receives at least one asymmetrical synapse (Colonnier, 1968; Jones, 1968; Peters & Kaiserman-Abramof, 1969), the presynaptic terminals of which have been shown to contain the excitatory neurotransmitter glutamate (DeFelipe *et al*., 1988; Kharazia & Weinberg, 1993). Thus, more spinous pyramidal cells such as those in cytoarchitectonic areas TEO, TE and the superior temporal polysensory area (STP) are likely to receive more excitatory inputs than less spinous cells such as those in V1 (see Elston & DeFelipe, 2002 for a review).

Cortical pyramidal cells also receive inhibitory inputs from interneurones, which contain the transmitter GABA (see Houser *et al*., 1984; Hendry *et al*., 1987; Jones, 1993 for reviews). These cells include a diverse range of morphologies, including double bouquet cells, basket cells, chandelier cells, bipolar cells, neurogliaform cells, and Cajal-Retzius cells which are characterized by different dendritic and axonal arborisation patterns, neurochemical content, and in some cases may have uniquely identifiable post synaptic targets (see DeFelipe & Fariñas, 1992; DeFelipe, 1997; Douglas & Martin, 1998; Somogyi *et al*., 1998 for reviews). For example, chandelier cells form synapses with the axon initial segments of pyramidal cells whereas basket cells form synapses with the soma and proximal dendrites of pyramidal cells. Double bouquet cells project to the apical collateral branches of pyramidal cells and their basal dendrites. The majority of inhibitory inputs to cortical pyramidal cells are located on the dendrites and dendritic spines (Beaulieu, 1985; Beaulieu & Somogyi, 1990; Beaulieu *et al*., 1992; Peters & Harriman, 1992); thus, differences in the arbour structure of pyramidal cells in visual and visual association areas may result in the integration of different numbers of inhibitory inputs within their arbours.

Integration of inputs within the dendritic arbour

Integration within markedly different dendritic arbours may behave according to two different principles,

Fig. 1. Examples of molecular, cellular, and systems specialisations in visually-related cortical areas of the macaque monkey. (A) Mean phosphorylation values of protein kinase C (F1/50 kDa) expressed through all cortical layers (taken from Nelson *et al*., 1987). (B) Density of layer IIII cells immunoreactive for SMI32 (taken from Hof & Morrison, 1995). (C) Number of cells immunoreactive for calbindin which are of the pyramidal type (taken from Kondo *et al*., 1999), and differences in the distribution of cells immunoreactive for calcium binding proteins (taken from DeFelipe *et al*., 1999). (D) Diameter of intrinsic axonal patches in supragranular cortical layers (taken from Lund *et al*., 1993; Fujita & Fujita, 1996). Size (E), fractal dimension of branching patterns (F), and number of spines in the basal dendritic arbour (G), of the basal dendritic arbours of layer III pyramidal cells (taken from Elston & Rosa, 1997, 1998a; Elston *et al*., 1999a; Jelinek & Elston, 2001). Bars are illustrated in relation to area groupings and may not reflect the exact location of the cortical area.

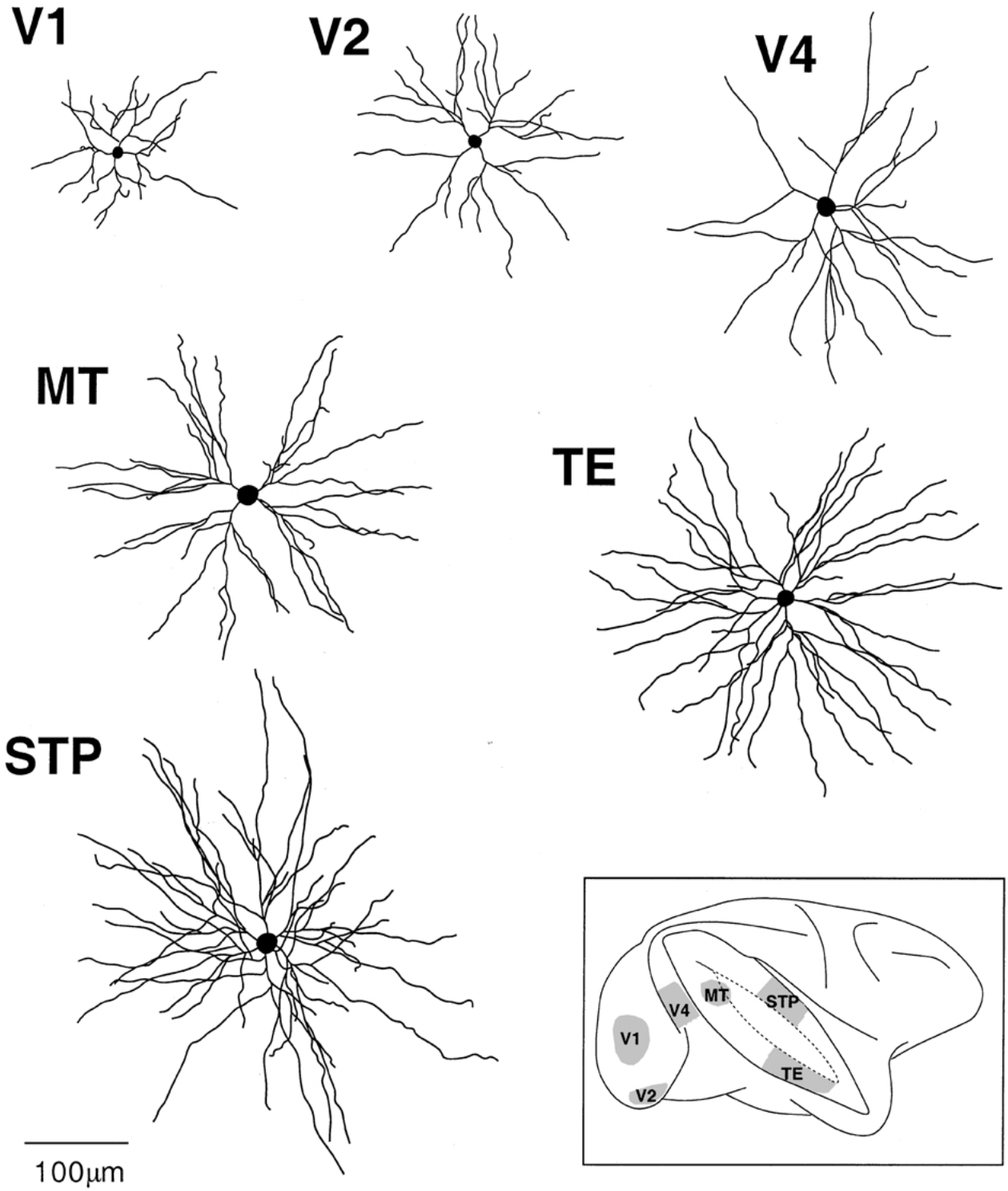


Fig. 2. Drawings of the average sized layer III pyramidal neurone in the primary (V1), second (V2), fourth (V4), and middle temporal (MT) areas as well as cytoarchetectonic area TE and the superior temporal poly sensory area (STP), as seen in the plane of section tangential to the cortical layers. Cells are skeletonized images, spines are not illustrated. Insert shows the parts of the brain from which neurons were sampled (modified from Elston *et al.*, 1999a).

which may act in concert to determine the relation between arbour structure and cellular function. In the first instance the arbour can be considered as a passive receiver of inputs (such as a cable) with summation of input excitatory postsynaptic potentials (EPSP), and propagation to the soma, behaving in a linear manner (Rall, 1959). In the second instance, the arbour itself actively influences the propagation of input EPSPs, resulting in non-linear processing (*e.g.*, Redman & Walmsley, 1983). Mechanisms that determine such

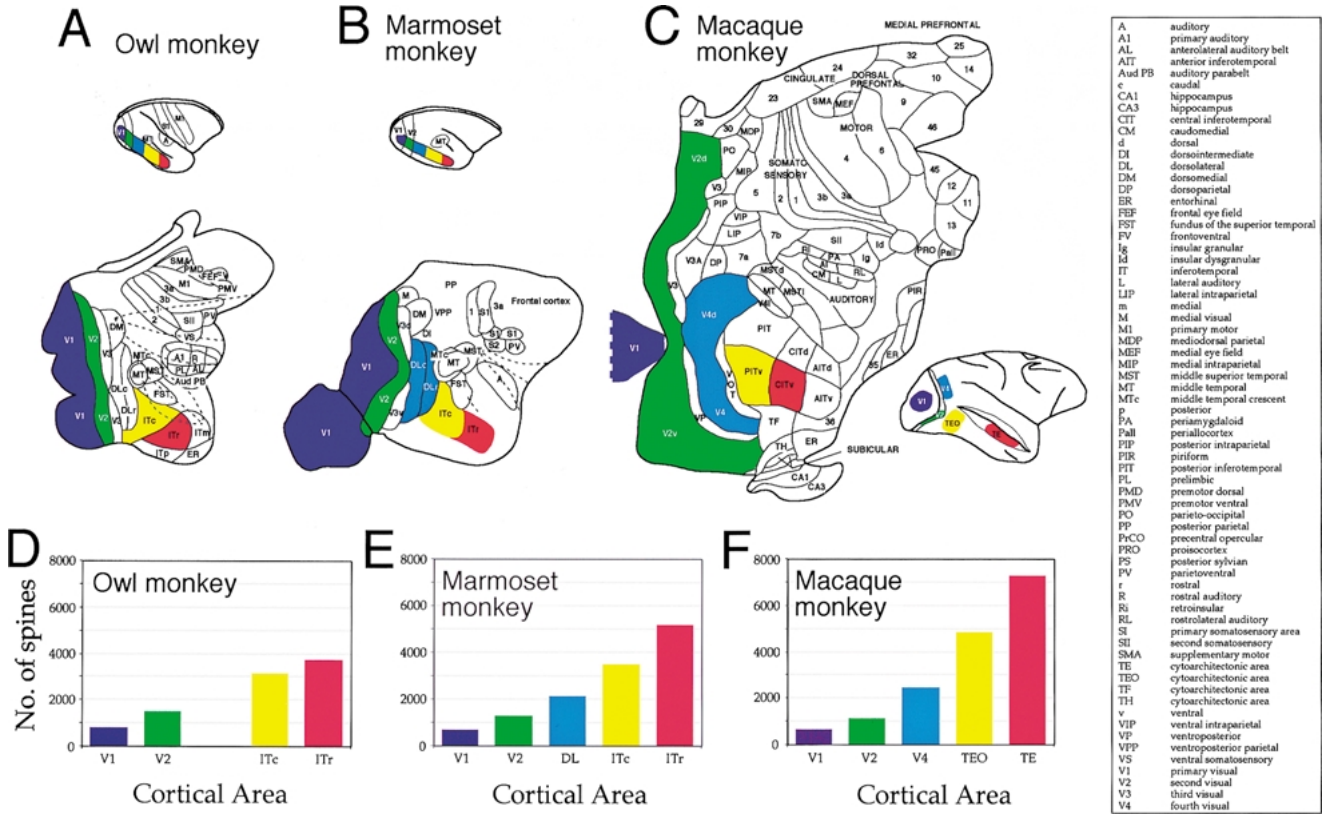


Fig. 3. Illustrations of the brains and schematics of cortical organization in the (A) macaque (B) marmoset and (C) owl monkeys (modified from Kaas, 1984; Felleman & van Essen, 1991; Rosa, 1997; Elston *et al.*, 1999b; Lyon & Kaas, 2001, 2002). Locations in which neurones were injected and the cortical areas included for study are illustrated in colour (purple = V1, green = V2, blue = V4 (DL), yellow = TEO (PIT or ITc), red = TE (CIT or ITr). (E-F) Plots of the total number of spines in the basal dendritic arbour of the "average" layer III pyramidal cells in occipitotemporal cortical areas.

active propagation have been the subject of intense research over the ensuing years.

While the linear models provide an invaluable platform for testing some aspects of neural function, cortical pyramidal neurons are non-linear. As demonstrated originally by Rall (1964), non-linear integration leads to compartmentalisation of processing within dendritic arbours (see Rall *et al.*, 1992; Mainen & Sejnowski, 1996; Segev & Rall, 1998; Koch, 1999; Mel, 1999 for reviews). Thus, inputs to different branches within the arbour may undergo some form of processing within the arbour before input potentials arrive at the soma. Presumably then there may be a greater degree of compartmentalisation in the highly branched arbours of pyramidal cells in areas such as TE and STP as compared to those with less branched arbours in V1. The degree of compartmentalisation may be further determined by the extent to which excitatory inputs are clustered within the dendritic arbour: baseline activity of any given cell varies for a set number of inputs, according to the distribution of the inputs (Mel, 1992, 1993). Moreover, the baseline activity of a given cell increases, for a set number of inputs, with increasing cluster size (see Fig. 8 of Mel, 1993). There is also a greater potential for local vetoing, or shunting inhibition (Koch *et al.*, 1982), of excitatory inputs within the dendritic arbours of highly branched, spinous pyramidal cells due to the potential for a greater number of inhibitory synapses to these processes.

The potential functional significance of non-linear compartmentalisation for specific aspects of visual processing such as direction selectivity and orientation selectivity remains controversial (see Livingstone, 1998; Ferster & Miller, 2000 for reviews). However, dendritic processing has been demonstrated empirically in the retina (Taylor *et al.*, 2000; Taylor & Vaney, 2002; see Vaney & Taylor, 2002 for a review), making it a real possibility in visual cortex. Poirazi and Mel (2000) have also demonstrated that compartmentalisation acts as a mechanism for boosting cellular potential for learning paradigms, aspects of neural function fundamental in visual processing. For example, scaling the size, and/or changing branching patterns, of a cell's dendritic arbour results in a logarithmic increase in the input-output functions in non-linear cells, but only a relatively minor increase in linear cells. Thus, highly branched pyramidal cells in areas such as TE, the superior polysensory area (also known as TPOr) and the frontal eye field (FEF), may have greater input-output

functionality than less branched cells such as those in areas V1 and V2.

Visual circuitry and pyramidal cell structure

(A) TOPOGRAPHIC SAMPLING

Cortical neurones characterised by a smaller dendritic arbour may integrate inputs over a smaller region of cortex than larger cells. In topographically organised visual cortex, this translates to a smaller portion of the sensory map being sampled. Whilst this may at first appear trivial, differences in arbour size, coupled with receptive field map compression, results in more than a 100-fold difference in the region of the visual map sampled by individual cells in V1 and TEO (Elston & Rosa, 1998b). Moreover, there is a linear correlation between the proportion of the visuotopic representation sampled by individual pyramidal cells and their receptive field size[1] in visual areas V1, V2, V4 and TEO (Fig. 4). However, the proportion of the topographic representation sampled by individual pyramidal cells is 1/10 that of their receptive field size. None the less, this difference may be offset, in part, by patterns of intrinsic axon projections. For example, many axons of supragranular pyramidal cells in visual cortex project horizontally forming a lattice of intrinsic axonal patches (Gilbert & Wiesel, 1979, 1983; Rockland & Lund, 1982, 1983; Rockland *et al.*, 1982; Livingstone & Hubel, 1984; Martin & Whitteridge, 1984; Rockland, 1985; Kisvárday *et al.*, 1986; McGuire *et al.*, 1991). As many as 80–95% of the horizontal projection synapses of individual supragranular pyramidal cells are formed with other supragranular pyramidal cells (Kisvárday *et al.*, 1986; McGuire *et al.*, 1991) in reciprocally connected patches (Kisvárday & Eysel, 1992), thus providing an anatomical substrate for the functional similarities of neurones reported between the patches (Mitchison & Crick, 1982; Matsubara *et al.*, 1985; Ts'o *et al.*, 1986; Ts'o & Gilbert, 1988; Gilbert & Wiesel, 1989; Malach *et al.*, 1993; Malonek *et al.*, 1994). As the extent of the patches is reportedly greater in areas such as the fourth visual area (V4) and TEO, as compared to V1 (Lund *et al.*, 1993; Fujita & Fujita, 1996), an even greater portion of the visual map may be sampled by cells in the former cortical areas as compared with those in V1 and V2 (Fig. 5).

Other aspects of circuit structure are also likely to influence the receptive field properties of cortical pyramidal neurones. Recently attention has been refocussed on the relationship between receptive field properties of neurones and circuit structure. By using newly developed axon tracing techniques, various authors have demonstrated a correlation between patterns of axonal projections (both intra- and interareal) and receptive field properties of neurones in V1 (see Gilbert, 1993; Lund *et al.*, 1995; Angelucci & Bullier, 2002; Angelucci

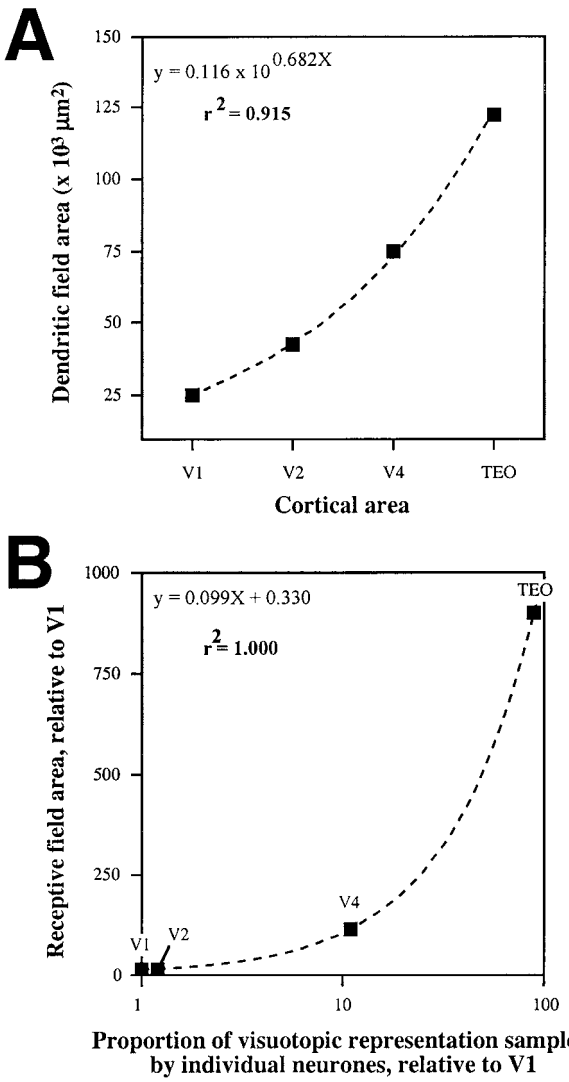


Fig. 4. (A) Graph showing the trend for increasingly larger pyramidal cells in the primary (V1), second (V2), and fourth (V4) visual areas and cytoarchtectonic area TEO of the macaque monkey. (B) Graph showing the linear relationship between the proportion of the visuotopic representation sampled by the average layer III pyramidal neurone in the central 5 degrees of each visual area and their receptive field size (data taken from Elston *et al.*, 1998).

et al., 2002 for reviews). Inhibitory circuitry is also thought to play an important role in shaping neuronal receptive field properties (see Gilbert, 1998; Kaas, 1991; Calford, 2002 for reviews), although the extent to which they may do so is still under investigation (Lund *et al.*, 1993; Angelucci *et al.*, 2002; Wang *et al.*, 2002).

DENDRITIC ARBOURS AND AXON PATCHES

The size of the intrinsic axonal patches that arise from supragranular pyramidal cells is also correlated with the size of their dendritic arbours (Lund *et al.*, 1993; Elston *et al.*, 1999a). Malach (1994) presented evidence

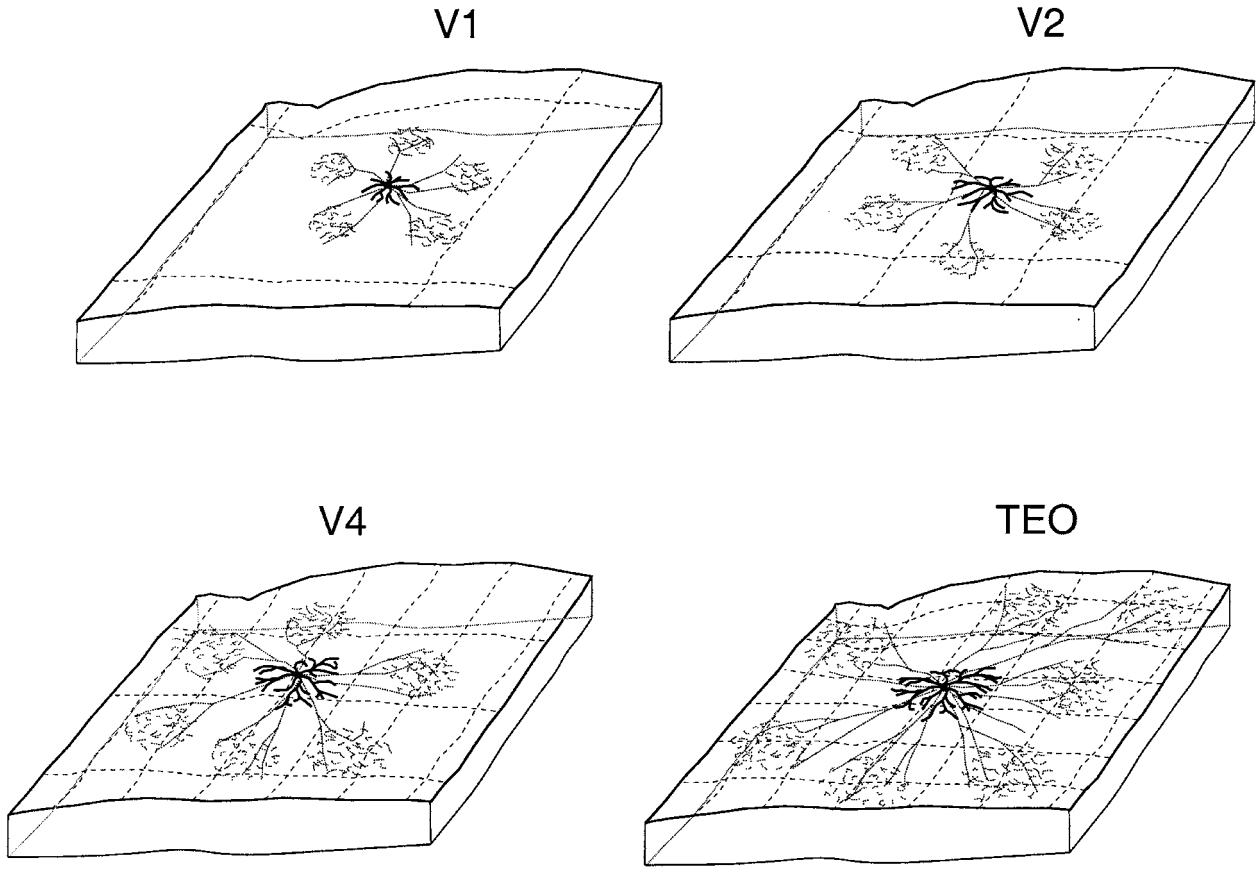


Fig. 5. Schematic of sampling topography of supragranular pyramidal cells in the primary (V1), second (V2) and fourth (V4) visual areas and cytoarchitectonic area TEO. Differences in pyramidal cell arbour size (solid black), intrinsic connectivity (grey hatch), and visuotopic compression (solid dashed lines) result in dramatic differences in the proportion of the topographic map sampled by individual neurones.

to suggest that a correlation in the geometrical relationship of axon modules (*e.g.*, intrinsic patches, corticocortical arborisation, or thalamocortical afferents) and dendritic arbours determine the sampling ratios of neurones. According to this theory, the correlation between intrinsic patches and the basal dendritic arbours of pyramidal cells in supragranular cortex would result in maximal sampling diversity (Fig. 6). Furthermore, the correlation between *interareal* axon arborisation and the dendritic arbours of pyramidal cells further suggests that the geometrical relationship between inputs and pyramidal cells is functionally significant. For example, the size of pyramidal cells in area STP (TPOr) closely approximates the average diameter of projections from prefrontal area 46 (Cusick *et al.*, 1995; Elston *et al.*, 1999b; Elston & Rosa, 2000) and the dimensions of the functional columns (Fujita, 1997; Wang *et al.*, 2000).

However, while columnar axonal arborisations may be a feature of cortical organisation (see Jones, 1981, 1983; Innocenti, 1986; Mountcastle, 1997, 1998 for reviews), not all projections form such arborisations. In many cases, interareal projections form more diffuse arborisation which may, or may not, extend throughout the cortical depth (see Rockland, 1997 for a review). Thus, any particular region in cortex may receive projections from different sources, which are characterised by different arborisation patterns (Fig. 7). Consequently, cells throughout the cortical layers may sample inputs with different transverse and tangential geometrical relationships. Thus, in some cortical areas such as V1 and V2 it may be advantages to maintain distinction between inputs within modules, whereas in other areas, such as those in inferotemporal cortex, different sampling strategies may subserve different functional requirements. These sampling strategies are determined by both the size of axon arborisations, and the dendritic arbour, of their target cells. Regional differences in both of these elements in different cortical visual areas allow a greater diversity and specificity of sampling strategies.

SAMPLING FROM INHIBITORY MODULES

As well as determining the number of inhibitory inputs sampled, the tangential dimensions of pyramidal cell dendritic arbours may influence the number and diversity of cells from which it receives inhibitory projections (Elston *et al.*, 1999c). As certain GABAergic neurones

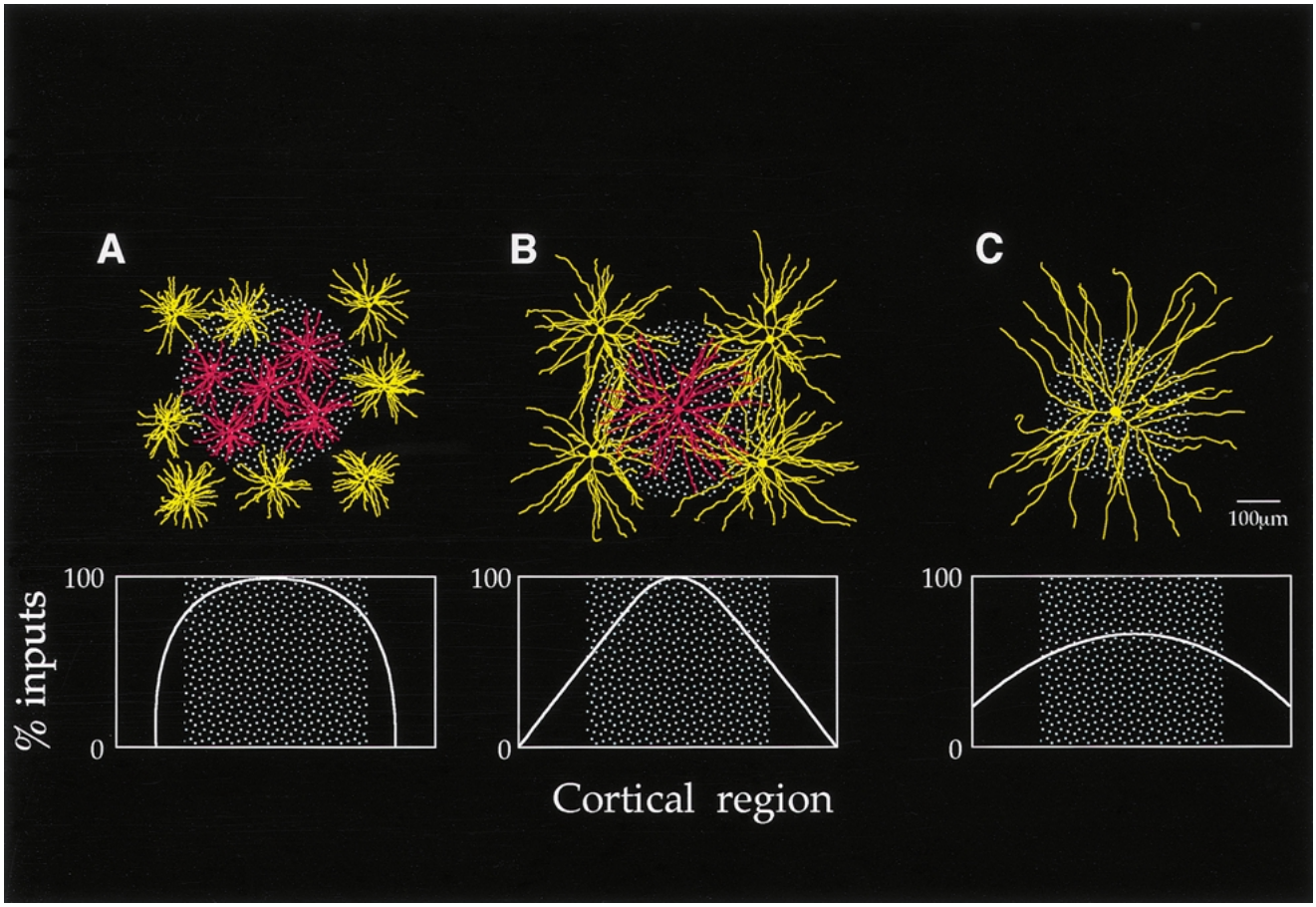
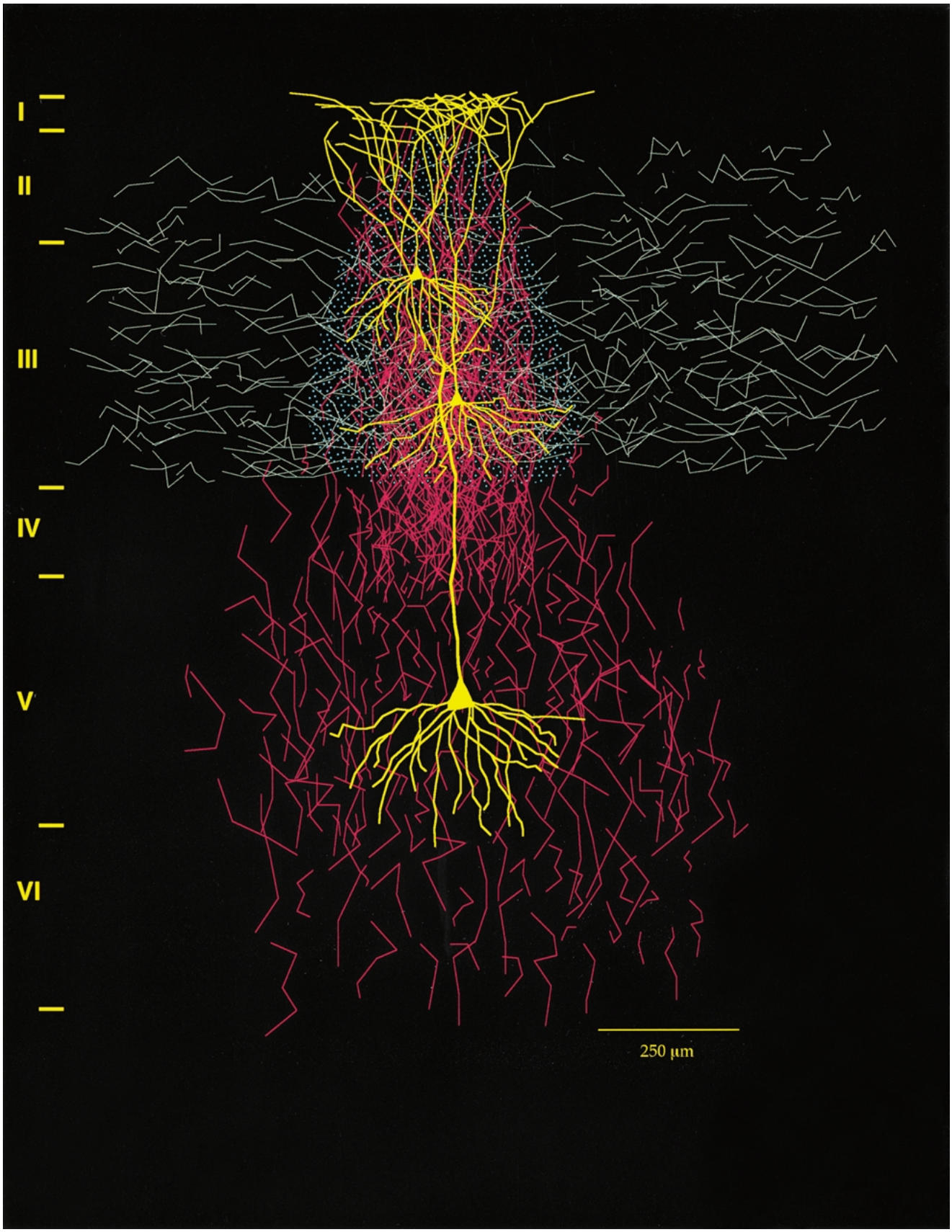


Fig. 6. Schematic depicting three possible sampling strategies between pyramidal cell basal dendritic arbours and modular axonal arborisation. If the dendritic arbours are smaller than the axon patches there is a large population of cells that potentially sample the same set of inputs (A). Maximum connectivity may be achieved if the basal dendritic arbours are the same size as the axon modules (B). If the pyramidal cell dendritic arbour is larger than the axon modules it is likely that no cell samples inputs from a single modules (C). Modified from Malach (1994).

primarily form local projections throughout cortex (Somogyi *et al*., 1981, 1983; DeFelipe & Jones, 1985), pyramidal cells with larger dendritic arbours may be able to integrate from a greater number, and diversity, of interneurones than those with smaller arbours (Fig. 8). Moreover, as the proportion of subpopulations of GABAergic neurones, such as those containing the calcium binding proteins parvalbumin, calbindin and calretinin differ amongst cortical areas (Kritzer *et al*., 1992; Kritzer & Goldman-Rakic, 1995; DeFelipe *et al*., 1999; Kondo *et al*., 1999; Elston & González-Albo, 2003), the proportion of these subtypes sampled by pyramidal cells in different cortical areas is also likely to vary. For example, a progressive increase in the size of the dendritic arbours of pyramidal cells through areas V1, V2, V4 (DL), TEO (ITc) and TE (ITr), coupled with a trend for a decrease in the density of calbindin immunoreactive neurones, potentiall results in a greater convergence of

Fig. 7. Schematic showing possible sampling strategies of pyramidal cells located in different layers throughout the cortical depth in cortical area TE of the macaque temporal lobe. Three pyramidal cells are illustrated, those in layers III and V have basal dendritic arbours of approximately the same tangential size, with an average diameter of the order of 400 μm (cf Elston *et al*., 1999a; Elston & Rosa, 2000), being larger than those in layer II (unpublished observations). Feedforward projections from area TEO (red lines) form an arborisation that extends throughout the cortical layers, with a focal core in layers III and IV (200–380 μm in the mediolateral direction) with more diffuse terminals in the other layers (Saleem *et al*., 1993). Projections from area 46v to the rostral portion of TEa form a dense core in layer III, extending into layer II (blue stipple) (Rempel-Clower & Barbas, 2000). Intrinsic projections originating from supragranular pyramidal neurones arborise over a relatively expansive region (Fujita & Fujita, 1996). Overlap of diverse sets of inputs to any given area results in multiple potential sampling strategies for cells in the different cortical layers. This "cross-column" connectivity may influence the functional signatures of both neuronal and circuits (see Kaas, 1982 for a review).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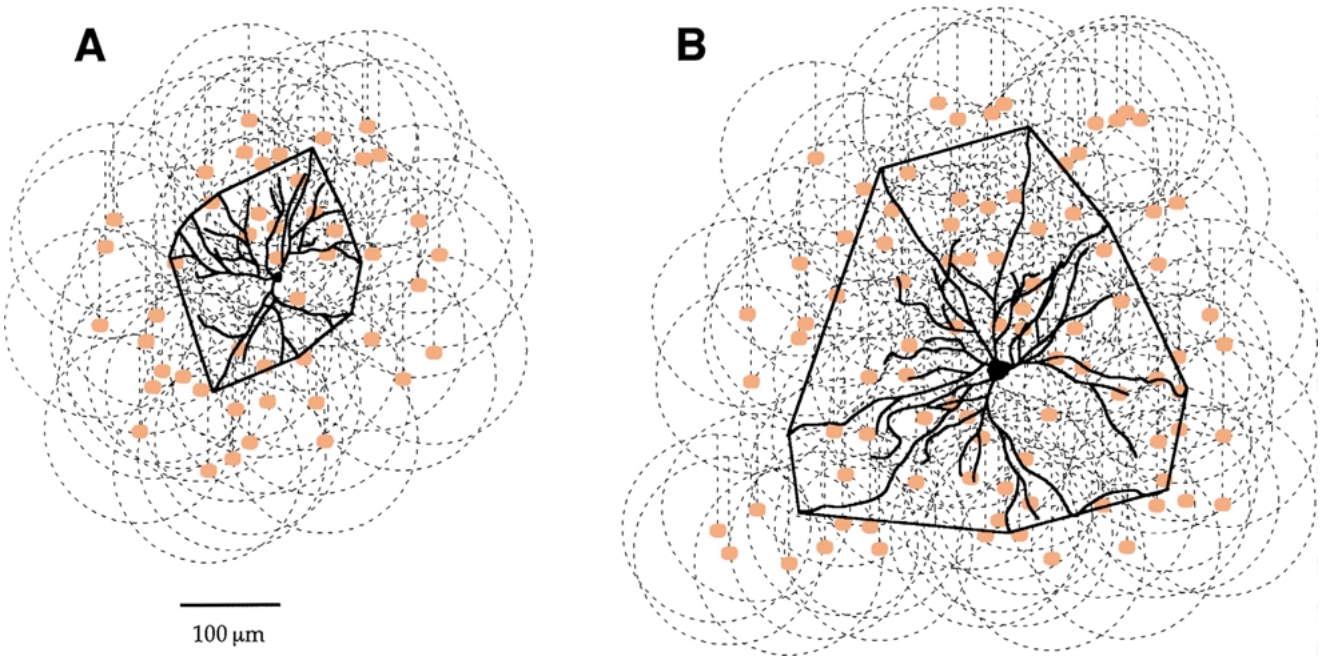

Fig. 8. Schematic showing the relationship between the basal dendritic arbours of pyramidal cells (solid black) and the number of inhibitory neurones contained within (grey). A pyramidal cell characterised by a relatively small basal dendritic arbour (A) potentially receives inputs from a smaller number/diversity of interneurones than a larger cell (B). Putative axonal arbours of inhibitory interneurones are pictured as dashed grey circles (modified from Elston *et al*., 1999d).

inhibitory inputs to pyramidal neurones in the more anterior visual areas.

On the relationship between cell morphology and function visual/ polysensory areas

Neurones involved in different aspects of visual processing may be characterized by different discharge properties, which are reportedly fundamental to their functional requirements. For example, cells in visual areas in inferotemporal cortex are characterised by sustained tonic activity whereas those in V1 are characterized by phasic discharge properties (Ashford & Fuster, 1985; Miller *et al*., 1993; Sobotka & Ringo, 1993; Lueschow *et al*., 1994; Nakamura & Kubota, 1995). The sustained activity of IT neurons is thought to enable these neurones/circuits to "hold" a memory whereas the phasic activity of V1 cells does not (see Fuster, 2000; Miller & Cohen, 2001; Elston, 2003a for reviews). It is not difficult to conceptualise how the structure of these neurons may be instrumental in determining their differing discharge properties. For example, pyramidal cells in V1 are relatively small, have relatively small horizontal axon projections, integrate relatively few excitatory inputs and are located in within a relatively large visuotopic map. Thus, the (relative lack of intrinsic) complexity of their connectivity offers advantages for high fidelity sampling of the visual scene by integrating relatively few inputs over a restricted region of the visual map. Pyramidal cells in IT, on the other hand, are relatively large, have relatively expansive horizontal axon projections, integrate a large number of excitatory inputs and are located in within a relatively small visuotopic map.[2] The high degree of connectivity between the larger, more branched and more spinous pyramidal cells in IT cortex imparts a degree of complexity in cortical circuitry more suited to sustaining neural activity through reentrant input (see following section on Distributed Systems). Pyramidal cell structure may also influence other aspects of visual processing. For example, differences in their complexity of the branching structure of pyramidal cells in different cortical areas may influence their potential to compartmentalise aspects of visual processing. More specifically, encoding of global and fine information (Sagase *et al*., 1999) and tolerance to changing stimuli (Hikosaka, 1999) reported for cells in IT may also be influenced by the spatio-temporal characteristics of the propagation of potentials throughout their dendritic trees. The large spinous dendritic trees of cells in STP may be instrumental in their ability to process stimuli of more than one sensory modality (Perrett *et al*., 1984; Hikosaka *et al*., 1988) by allowing temporal/spatial distinction between inputs. Differences in pyramidal cell structure may also be important in determining the diametrically opposed response characteristics of cortical circuitry in the occipital and temporal lobes (*i.e.*, long term potentiation in TE cells, but long term depression in V1 cells, following tetanic stimulation of the soma: Murayama *et al*., 1997). Stepanyants and colleagues (2002) have also

demonstrated that differences in the number of excitatory inputs integrated by pyramidal cells in different cortical areas may endow them with different structural plasticity.

Whilst these claims remain speculative, it is worth considering the scope of the morphological differences of pyramidal cells between different cortical areas, and relating them to previous studies that have correlated morphology and function in pyramidal cells in different layers of a single cortical area (*e.g.*, Calvin & Sypert, 1976; Deschenes *et al.*, 1979; Gilbert & Wiesel, 1979; Hamada *et al.*, 1981; Chagnac-Amitai *et al.*, 1990; Mason & Larkman, 1990; de la Peña & Geijo-Barrientos, 1996). In many instances, these studies conclude that the morphologically determined functional differences are attributable to the large apical dendrites of cells studied in infragranular cells as compared to those in supragranular layers. However, whilst the apical dendrites of pyramidal cells may provide a conduit for mixing of inputs (Sawatari & Callaway, 1996), the relative differences in the number of spines on pyramidal cells in the different laminae of any given cortical area may be small by comparison to *interareal* differences for neurones in the same layer. For example, no study has reported that infragranular cells have as many as 13-fold more spines, or dendritic arbours 6 times larger, than supragranular cells: differentials that exist for *interareal* comparisons of layer III pyramidal cells involved in visual processing (Elston *et al.*, 1999a). Instead, relative comparisons between layer III and layer V pyramidal cells show considerably smaller differences (Larkman, 1991; Elston, 2001).

Visual processing in heterogeneous cortex

(A) WITHIN HIERARCHIES

Whilst most cortical areas are highly interconnected, it is widely accepted that visual processing in the primate occurs in two pathways which stream through the primary (V1) and second (V2) visual areas to cortical areas of the parietal and temporal lobes (Ungerleider & Mishkin, 1982). The ventral stream (directed to the temporal lobe) reportedly contains neurones that are primarily involved in processing for object recognition, while the dorsal processing stream (directed primarily to the parietal lobe) contains neurones responsive primarily to motion detection and visuomotor control. Furthermore, it is suggested that these pathways are arranged into quasi hierarchies, and that encoded visual information is "feedforward" through these streams by supragranular pyramidal neurones (see Weller, 1988; Felleman & Van Essen, 1991; Gross *et al.*, 1993; Rockland, 1997 for reviews). According to this theory the major retinal input to visual areas in temporal and parietal cortex of monkey flows through the occipital lobe, and that incoming information is processed in the occipital lobe before being fed forward to higher areas (see Garey *et al.*, 1991; Casagrande & Kaas, 1994 for reviews). For example, neurones in early stages of the two pathways, such as those in V1 and V2, are not responsive to presentation of complex visual scenes *per se*. Instead, they are highly tuned for specific stimuli within the visual scene such as orientation and direction selectivity, luminance contrast, and spectral opponency (Livingstone & Hubel, 1984; Hubel & Livingstone, 1987; Roe & Ts'o, 1997; Conway *et al.*, 2002). Neurones in higher visual areas in temporal and parietal cortex differ in that they are responsive to stimuli such as complex two- and three-dimensional objects and to visuomotor co-ordination (Gross & Bender, 1969; Yin & Mountcastle, 1977; Perrett *et al.*, 1984; Motter *et al.*, 1987). What then is the potential implication of heterogeneity in cortical circuitry in different processing pathways?

According to the hierarchical model, the flow of encoded visual information through a series of different cortical areas, and processing within these areas, allows neurones (as integral parts of neural networks) to ultimately decipher complex visual scenes. The nature of the projection patterns of, and inputs sampled by, supragranular pyramidal neurones provide a route for the rapid interpretation of a visual stimulus, and its integration with other sensory modalities. For example, the majority of pyramidal neurones in V1 that stream to the dorsal and ventral streams are found in the supragranular layers (Seltzer & Pandya, 1978; Rockland & Pandya, 1979; Shipp & Zeki, 1989a, b; Elston & Rosa, 1998b) and their axons arborise mainly in layer IV but also extend into layer III (Rockland, 1989; Rockland & Virga, 1990). A similar pattern is seen for feedforward projections originating from other cortical areas of the two processing streams (de Lima *et al.*, 1990; Rockland, 1992, 1995; Vogt Weisenhorn *et al.*, 1995; Elston & Rosa, 1999a), although variation in this pattern has been reported in association cortex (Saleem *et al.*, 1993; see Rockland, 1997 for a review). The majority of the feedforward projections form asymmetrical synapses onto the spines and shafts of dendrites of neurones in layers III and IV (Johnson & Burkhalter, 1996; Anderson *et al.*, 1998). Thus, the projections originate from supragranular cells and may synapse directly, or via layer IV cells, with feedforward projection cells in the next cortical area. Such a rapid transmission route may be important for motion detection, rapid motor response, and recognition of specific stimuli in "real" time.

Furthermore, feedforward axon projections to progressively more rostral extrastriate visual areas are generally more divergent than those to more caudal visual areas (Rockland, 1989, 1995; Saleem *et al.*, 1993). For example, V1 > V2 projections are less divergent than those from V2 > V4 and V2 > V4 projections are less divergent than those from TEO > TE. In parallel, the extent of the lateral intrinsic connections of pyramidal cells becomes more expansive through V1, V2, V4, TEO

and TE. Thus, the diverging feedforward projection, coupled with the progressively more expansive intrinsic connections, may result in a form of "converging divergence": the divergent feedforward projections increasing the extent of visuotopic connectivity through cortical areas, the intrinsic connections acting in concert to insure the integration of larger portion of the visuotopic representation by populations of cells (see Fig. 5).

WITHIN DISTRIBUTED SYSTEMS

Various converging lines of research suggest that visual processing is more complex than the proposed serial hierarchical schemes. For example, inactivation of V1 doesn't result in complete blindness, the response latencies of neurones in different cortical areas and the pattern of their corticocortical projections don't necessarily comply with the proposed hierarchical schemes, and imaging studies reveal that large ensembles of neurones in different hierarchical levels may be activated during a particular task (see Kaas, 1986; Cowey & Stoerig, 1991; Bullier *et al*., 1994; Schiller, 1996; Rockland, 1997; Lennie, 1998 for reviews). An alternative, and more flexible, theory is that cortical processing occurs within distributed systems (Mountcastle, 1978, 1995), which have been defined by the following criteria:

- Action may be initiated at any of a number of nodal loci
- Signal flow through such a system may follow any of a number of different paths
- They are not hierarchical, although some subsystems may have hierarchical properties
- Local lesions may degrade, but not completely eliminate, function
- Recovery after a lesion is dynamic, and does not necessarily require reorganisation of circuitry
- The system is re-entrant, and their nodes are influenced by both externally induced, and internally generated, signals

Understanding the possible functional advantages conferred by regional specialization in cortical circuitry within distributed systems is perhaps more difficult to conceptualise than in cortical hierarchies. As a starting point it is important to note that, according to the above definition, hierarchies may be incorporated within distributed systems. Thus, any functional advantage identified within a hierarchical structure may apply to some aspects of distributed processing although this is not necessarily the case (see Elston & Rockland, 2002). Within the wider context of a distributed system, regional differences in the structure of pyramidal cells (and the circuits they form) may influence patterns of interareal connectivity and thus the potential for recurrent excitation through reentrant circuits. This logic is merely an extension of that used previously when relating cell structure with neural function; however, instead of discussing individual neurones we consider cortical circuits (composed of neurones) and instead of discussing individual cortical areas we consider cortical regions (comprised of cortical areas). Thus, simultaneous activation of cortical areas during a particular task (see Friston, 2001 for a review) not only depends on the patterns of connectivity between cortical areas, but also the degree of connectivity: the degree of connectivity being conferred by both the number of axon projections/boutons and the number of inputs that can be received by target neurones. Clearly more quantitative data are needed on the patterns of connectivity between neurones in different cortical areas. However, what is presently known of variation in the number of spines in the dendritic arbours of pyramidal cells in different cortical areas, and their consistency in different primate species, raise some interesting possibilities for visual function. For example, the sampling capabilities of highly spinous pyramidal cells found in visual areas of the parietal and temporal lobes may serve to maintain topographic and/or temporal coherence (binding) in visual processing by integrating diverse sets of inputs from many cortical areas (see Singer & Gray, 1995; Llinás & Paré, 1996 for reviews). Moreover, the differences in circuit complexity in different brain regions such as V1 and inferotemporal cortex, for example, may also be instrumental in determining the potential for recurrent stimulation of neurones through reentrant input, which is widely believed to influence their discharge properties (see Fuster, 1985, 2000; Miller & Cohen, 2001 for reviews). These differences in discharge properties of populations of neurones are thought to be fundamental in memory processing: the sustained tonic discharge properties of neurones such as those in IT underpining their ability to "hold" a memory. It is perhaps not surprising then that neurones in prefrontal cortex,[3] which are capable of holding a memory despite interference from distractors, are even more branched and more spinous than those in IT (Elston, 2000; Elston *et al*., 2001; Jacobs *et al*., 2002).

That regional variation in pyramidal cell structure is important in determining the functional capabilities of distributed systems is further strengthened when we consider the evolution of cortical functions such as visual processing. The thirty or so visual areas found in higher primates are believed to have evolved through cortical expansion, with only a few having been present in ancestral mammals (see Kaas, 1987, 1989a, b, 1995; Northcutt & Kaas, 1995; Krubitzer, 2000 for reviews on the evolution of visual cortex). This expansion was widely believed to occur through cortical folding and the addition of more of the same basic repeated unit of cortex, or canonical circuit. However, expansion of cortex through the addition of more of the same cortical circuit results in decreased connectivity between

cortical areas (Ringo, 1991). The resulting decrease in connectivity would ultimately lead to fragmentation of processing. Alternatively, expansion of cortex through the addition of more complex circuitry (composed of neurones that have the potential to integrate larger numbers of inputs) may allow specialisation through cortical expansion without fragmentation in function. Support for this idea can be found in visual, somatosensory, motor and prefrontal cortex (Lund *et al*., 1993; Elston *et al*., 2001; Jacobs *et al*., 2001; Elston & Rockland, 2002; Elston, 2003d), where expansion of cortex has occurred through the addition of pyramidal cells of increasing structural complexity (see Elston 2003b for a review). Based on these converging data it is not unreasonable to conclude that regional specialisation in pyramidal cell structure within distributed system potentially leads to a richness of diversity of, and functional cohesiveness in, cortical function not attainable in cortex composed of the same basic repeated circuit. How regional specializations in pyramidal cell (and circuit) structure act in concert with subcortical and interhemispheric connections, as well as top-down modulation, in visual processing remain challenges for future studies.

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Notes

1. Here receptive field size refers to the classical receptive field size as determined by using high-contrast stimuli.
2. Area TEO is reported to be topographically organized, albeit loosely (Boussaoud *et al*., 1991).
3. Pyramidal cells in the prefrontal cortex of humans and macaque monkeys are more spinous than those in inferotemporal cortex, whereas in owl monkeys and marmoset monkeys this appears no to be the case (see Elston, 2003b for a review).

References

ANDERSON, J. C., BINZEGGER, T., MARTIN, K. A. C. & ROCKLAND, K. S. (1998) The connection from cortical area V1 to V5: A light and electron microscopic study. *Journal of Neuroscience* **18**, 10525–10540.

ANGELUCCI, A., LEVITT, J. B., WALTON, E. J., HUPE, J. M., BULLIER, J. & LUND, J. S. (2002) Circuits for local and global signal integration in primary visual cortex. *Journal of Neuroscience* **22**, 8633–8646.

ANGELUCCI, A., LEVITT, J. B. & LUND, J. S. (2002) Anatomical origins of the classical receptive field and modulatory surround field of single neurons in macaque visual cortical area V1. In *Prog. Brain. Res.* (edited by AZMITIA, E., DEFELIPE, J., JONES, E. G., RAKIC, P. & RIBAK, C. E.) pp. 371–388. Amsterdam: Elsevier.

ASHFORD, J. W. & FUSTER, J. M. (1985) Occipital and inferotemporal responses to visual signals in the monkey. *Experimental Neurology* **90**, 444–446.

BEAULIEU, C. & SOMOGYI, P. (1990) Targets and quantitative distribution of GABAergic synapses in the visual cortex of the cat. *European Journal of Neuroscience* **2**, 296–303.

BEAULIEU, C., KISVÁRDAY, Z., SOMOGYI, P., CYNADER, M. & COWEY, A. (1992) Quantitative distribution of GABA-immunopositive and -immunonegative neurons and synapses in the monkey striate cortex (area 17). *Cerebral Cortex* **2**, 295–309.

BEAULIEU, C. & COLONNIER, M. (1985) A laminar analysis of the number of round-asymmetrical and flat-symmetrical synapses on spines, dendritic trunks, and cell bodies in area 17 of the cat. *Journal of Comparative Neurology* **231**, 180–189.

BOUSSAOUD, D., DESIMONE, R. & UNGERLEIDER, L. G. (1991) Visual topography of area TEO in the macaque. *Journal of Comparative Neurology* **306**, 554–575.

BRODMANN, K. (1907) Beiträge zur histologischen lokalisation der großhirnrinde. *Journal of Psychology and Neurology* **6**, 1–16.

BULLIER, J., GIRARD, P. & SALIN, P. A. (1994) The role of area 17 in the transfer of information to extrastriate visual cortex. In *Cerebral Cortex* Vol. 10, *Primary Visual Cortex in Primates* (edited by PETERS, A. & ROCKLAND, K. S.) pp. 301–331. New York: Plenum.

CALFORD, M. B. (2002) Dynamic representational plasticity in sensory cortex. *Neuroscience* **111**, 709–738.

CALVIN, W. H. & SYPERT, G. W. (1976) Fast and slow tract pyramidal neurons: An intracellular analysis of their contrasting firing properties in the cat. *Journal of Neurophysiology* **39**, 420–434.

CASAGRANDE, V. A. & KAAS, J. H. (1994) The afferent, intrinsic and efferent connections of primary visual cortex in primates. In *Cerebral Cortex* Vol. 10, *Primary Visual Cortex in Primates* (edited by PETERS, A. & ROCKLAND, K. S.) pp. 201–259. New York: Plenum.

CHAGNAC-AMITAI, Y., LUHMANN, H. J. & PRINCE, D. A. (1990) Burst generating and regular spiking layer V pyramidal neurons of rat neocortex have different morphological features. *Journal of Comparative Neurology* **296**, 598–613.

COLONNIER, M. (1968) Synaptic patterns on different cell types in the different laminae of the cat visual cortex. *Brain Research* **9**, 268–287.

COLONNIER, M. & ROSIGNOL, S. (1969) Heterogeneity of the cerebral cortex. In *Basic Mechanisms of the Epilepsies* (edited by JASPER, H., WARD, A. & POPE, A.) pp. 29–40. Boston: Little Brown.

CONWAY, B. R., HUBEL, D. H. & LIVINGSTONE, M. S. (2002) Color contrast in macaque V1. *Cerebral Cortex* **12**, 915–925.

COWEY, A. & STOERIG, P. (1991) The neurobiology of blindsight. *Trends in Neuroscience* **14**, 140–145.

CREUTZFELDT, O. D. (1977) Generality of the functional structure of the neocortex. *Naturwissenschaften* **64**, 507–517.

CUSICK, C. G., SELTZER, B., COLA, M. & GRIGGS, E. (1995) Chemoarchitectonics and corticocortical terminations within the superior temporal sulcus of the rhesus monkey: Evidence for subdivisions of superior temporal polysensory cortex. *Journal of Comparative Neurology* **360**, 513–535.

DE LA PEÑA, E. & GEIJO-BARRIENTOS, E. (1996) Laminar localization, morphology, and physiological properties of pyramidal neurons that have low-threshold calcium current in the guinea pig medial frontal cortex. *Journal of Neuroscience* **16**, 5301–5311.

DE LIMA, A. D., VOIGT, T. & MORRISON, J. H. (1990) Morphology of the cells within the inferior temporal gyrus that project to the prefrontal cortex in the macaque monkey. *Journal of Comparative Neurology* **296**, 159–172.

DEFELIPE, J. (1997) Types of neurons, synaptic connections and chemical characteristics of cells immunoreactive for calbindin-D28K, parvalbumin and calretinin in the neocortex. *Journal of Chemical Neuroanatomy* **14**, 1–19.

DEFELIPE, J. & FARIÑAS, I. (1992) The pyramidal neuron of the cerebral cortex: Morphological and chemical characteristics of the synaptic inputs. *Progress in Neurobiology* **39**, 563–607.

DEFELIPE, J. & JONES, E. G. (1985) Vertical organization of γ-aminobutyric acid- accumulating intrinsic neuronal systems in monkey cerebral cortex. *Journal of Neuroscience* **5**, 3246–3260.

DEFELIPE, J., CONTI, F., VAN EYCK, S. L. & MANZONI, T. (1988) Demonstration of glutamate-positive axon terminals forming asymmetric synapses in cat neocortex. *Brain Research* **455**, 162–165.

DEFELIPE, J., DEL RÍO, M. R., GONZÁLEZ-ALBO, M. C. & ELSTON, G. N. (1999) Distribution and patterns of connectivity of interneurons containing calbindin, calretinin and parvalbumin in visual areas of the occipital and temporal lobes of the macaque monkey. *Journal of Comparative Neurology* **412**, 515–526.

DESCHENES, M., LABELLE, A. & LANDRY, P. (1979) Morphological characterization of slow and fast pyramidal tract cells in the cat. *Brain Research* **178**, 251–274.

DOUGLAS, R. J., MARTIN, K. A. C. & WHITTERIDGE, D. (1989) A canonical microcircuit for neocortex. *Neural Computation* **1**, 480–488.

DOUGLAS, R. J. & MARTIN, K. A. C. (1998) The synaptic organization of the brain. In *Neocortex* (edited by SHEPHERD, G. M.) pp. 735–769. New York: Oxford University Press.

ECCLES, J. C. (1984) The cerebral neocortex: A theory of its operation. In *Cerebral Cortex* Vol. 1, *Cellular Components of the Cerebral Cortex* (edited by PETERS, A. & JONES, E. G.) pp. 1–32. New York: Plenum.

ELSTON, G. N. (2000) Pyramidal cells of the frontal lobe: All the more spinous to think with. *Journal of Neuroscience* **20**, RC95(1–4).

ELSTON, G. N. (2001) Interlaminar differences in the pyramidal cell phenotype in cortical areas 7m and STP of the macaque monkey. *Experimental Brain Research* **138**, 141–152.

ELSTON, G. N. (2003a) Comparative studies of pyramidal neurons in visual cortex of monkeys. In *The Primate Visual System* (edited by KAAS, J. H. & COLLINS, C.) pp. 365–385. Boca Raton: CRC.

ELSTON, G. N. (2003b) Cortex, cognition and the cell: New insights into the pyramidal cell and prefrontal function. Cerebral Cortex.

ELSTON, G. N. (2003c) Pyramidal cell heterogeneity in the visual cortex of the nocturnal New World owl monkey (*Aotus trivirgatus*). *Neuroscience* **117**, 213–219.

ELSTON, G. N. (2003d) The pyramidal neuron in occipital, temporal and prefrontal cortex of the owl monkey (*Aotus trivirgatus*): Regional specializatoin in cell structure. *European Journal of Neuroscience* **17**, 1313–1318.

ELSTON, G. N. & DEFELIPE, J. (2002) Spine distribution in neocortical pyramidal cells: A common organizational principle. In *Progress in Brain Research* (edited by AZMITIA, E. C., DEFELIPE, J., JONES, E. G., RAKIC, P. & RIBAK, C. E.) pp. 109–133. Amsterdam: Elsevier.

ELSTON, G. N. & GONZÁLEZ-ALBO, M. C. (2003) Density and distribution of parvalbumin-, calbindin-, and calretinin-immunoreactive neurons in the prefrontal cortex of the owl monkey (*Aotus trivirgatus*): A quantitative comparison with sensory and motor cortical areas. *Brain, Behavior and Evolution*, in press.

ELSTON, G. N. & JELINEK, H. F. (2001) Dendritic branching patterns of pyramidal cells in the visual cortex of the New World marmoset monkey, with comparative notes on the Old World macaque monkey. *Fractals* **9**, 297–303.

ELSTON, G. N. & ROCKLAND, K. (2002) The pyramidal cell in sensory-motor cortex of the macaque monkey: Phenotypic variation. *Cerebral Cortex* **12**, 1071–1078.

ELSTON, G. N. & ROSA, M. G. P. (1997) The occipitoparietal pathway of the macaque monkey: Comparison of pyramidal cell morphology in layer III of functionally related cortical visual areas. *Cerebral Cortex* **7**, 432–452.

ELSTON, G. N. & ROSA, M. G. P. (1998a) Complex dendritic fields of pyramidal cells in the frontal eye field of the macaque monkey: Comparison with parietal areas 7a and LIP. *NeuroReport* **9**, 127–131.

ELSTON, G. N. & ROSA, M. G. P. (1998b) Morphological variation of layer III pyramidal neurones in the occipitotemporal pathway of the macaque monkey visual cortex. *Cerebral Cortex* **8**, 278–294.

ELSTON, G. N. & ROSA, M. G. P. (2000) Pyramidal cells, patches, and cortical columns: A comparative study of infragranular neurons in TEO, TE, and the superior temporal polysensory area of the macaque monkey. *Journal of Neuroscience* **20**, RC117 (1–5).

ELSTON, G. N., BENAVIDES-PICCIONE, R. & DEFELIPE, J. (2001) The pyramidal cell in cognition: A comparative study in human and monkey. *Journal of Neuroscience* **21**, RC163(1–5)

ELSTON, G. N., DEFELIPE, J., ARELLANO, J. I., GONZÁLEZ-ALBO, M. C. & ROSA, M. G. P. (1999c) Variation in the spatial relationship between parvalbumin immunoreactive interneurones and pyramidal neurones in rat somatosensory cortex. *NeuroReport* **10**, 2975–2979.

ELSTON, G. N., ROSA, M. G. P. & CALFORD, M. B. (1996) Comparison of dendritic fields of layer III pyramidal neurones in striate and extrastriate visual areas

of the marmoset: A Lucifer Yellow intracellular injection study. *Cerebral Cortex* **6**, 807–813.

ELSTON, G. N., TWEEDALE, R. & ROSA, M. G. P. (1999a) Cortical integration in the visual system of the macaque monkey: Large scale morphological differences of pyramidal neurones in the occipital, parietal and temporal lobes. *Proceedings of the Royal Society Series B* **266**, 1367–1374.

ELSTON, G. N., TWEEDALE, R. & ROSA, M. G. P. (1999b) Cellular heterogeneity in cerebral cortex. A study of the morphology of pyramidal neurones in visual areas of the marmoset monkey. *Journal of Comparative Neurology* **415**, 33–51.

FELDMAN, D. (1984) Morphology of the neocortical pyramidal neuron. In *Cerebral Cortex* Vol. 1, *Cellular Components of the Cerebral Cortex* (edited by PETERS, A. & JONES, E. G.) pp. 123–200. New York: Plenum.

FELLEMAN, D. J. & VAN ESSEN, D. C. (1991) Distributed hierarchical processing in primate cerebral cortex. *Cerebral Cortex* **1**, 1–47.

FERSTER, D. & MILLER, K. D. (2000) Neural mechanisms of orientation selectivity in the visual cortex. *Annual Review of Neuroscience* **23**, 441–71.

FRISTON, K. J. (2001) Brain function, nonlinear coupling, and neuronal transients. *Neuroscientist* **7**, 406–418.

FUJITA, I. (1997) The inferior temporal cortex; columns and horizontal axons. In *The Association Cortex, Structure and Function* (edited by SAKATA, H., MIKAMI, A. & FUSTER, J.) pp. 247–258. Amsterdam: Harwood Academic Publishers.

FUJITA, I. & FUJITA, T. (1996) Intrinsic connections in the macaque inferior temporal cortex. *Journal of Comparative Neurology* **368**, 467–486.

FUSTER, J. M. (2000) Cortical dynamics of memory. *International Journal of Psychophysiology* **35**, 155–164.

GAREY, L. J., DREHER, B. & ROBINSON, S. R. (1991) The organization of the visual thalamus. In *Neuroanatomy of the Visual Pathways and their Development* (edited by DREHER, B. & ROBINSON, S. R.) pp. 176–234. London: MacMillan Press.

GILBERT, C. D. (1993) Circuitry, architecture, and functional dynamics of visual cortex. *Cerebral Cortex* **3**, 373–386.

GILBERT, C. D. (1998) Adult cortical dynamics. *Physiological Reviews* **78**, 467–485.

GILBERT, C. D. & WIESEL, T. N. (1979) Morphology and intracortical projections of functionally characterised neurones in the cat visual cortex. *Nature* **280**, 120–125.

GILBERT, C. D. & WIESEL, T. N. (1983) Clustered intrinsic connections in cat visual cortex. *Journal of Neuroscience* **3**, 1116–1133.

GILBERT, C. D. & WIESEL, T. N. (1989) Columnar specificity of intrinsic horizontal and corticocortical connections in the cat visual cortex. *Journal of Neuroscience* **9**, 2432–2442.

GROSS, C. G. & BENDER, D. B. (1969) Visual receptive fields of neurones in inferotemporal cortex of the monkey. *Science* **166**, 1303–1306.

GROSS, C. G., RODMAN, H. R., GOCHIN, P. M. & COLOMBO, M. W. (1993) Inferior temporal cortex as a pattern recognition device. In *Computational Learning and Recognition: Proceedings of the 3rd NEC Research Symposium* (edited by BAUM, E.) pp. 44–73. Philadelphia: Society for Industrial and Applied Mathematics.

HAMADA, I., SAKAI, M. & KUBOTA, K. (1981) Morphological differences between fast and slow pyramidal tract neurons in the monkey motor cortex as revealed by intracellular injections of horseradish peroxidase by pressure. *Neuroscience Letters* **22**, 233–238.

HAUG, H. (1987). Brain sizes, surfaces, and neuronal sizes of the cortex cerebri: A stereological investigation of man and his variability and a comparison with some mammals (primates, whales, marsupials, insectivores and one elephant). *American Journal of Anatomy* **180**, 126–142.

HENDRY, S. H. C. & CALKINS, D. J. (1998) Neuronal chemistry and functional organization in the primate visual system. *Trends in Neuroscience* **21**, 344–349.

HENDRY, S. H. C., SCHWARK, H. D., JONES, E. G. & YAN, J. (1987) Numbers and proportions of GABA-immunoreactive neurons in different areas of monkey cerebral cortex. *Journal of Neuroscience* **7**, 1503–1519.

HIKOSAKA, K. (1999) Tolerance of responses to visual patterns in neurons of the posterior inferotemporal cortex in the macaque against changing stimulus size and orientation, and deleting patterns. *Behavioural Brain Research* **100**, 67–76.

HIKOSAKA, K., IWAI, E., SAITO, H. & TANAKA, K. (1988) Polysensory properties of neurones in the anterior bank of the caudal superior temporal sulcus of the macaque monkey. *Journal of Neurophysiology* **60**, 1615–1637.

HOF, P. R. & MORRISON, J. H. (1995) Neurofilament protein defines regional patterns of cortical organization in the macaque monkey visual system: A quantitative immunohistochemical analysis. *Journal of Comparative Neurology* **352**, 161–186.

HOF, P. R., GLEZER, I. I., CONDÉ, F., FLAGG, R. A., RUBIN, M. B., NIMCHINSKY, E. A. & VOGT WIESENHORN, D. M. (1999) Cellular distribution of the calcium-binding proteins parvalbumin, calbindin and calretinin in the neocortex of mammals: Phylogenetic and developmental patterns. *Journal of Chemical Neuroanatomy* **16**, 77–116.

HOUSER, C. R., VAUGHN, J. E., HENDRY, S. H. C., JONES, E. G. & PETERS, A. (1984) GABA neurons in cerebral cortex. In *Cerebral Cortex* Vol. 2, *Functional Properties of Cortical Cells* (edited by JONES, E. G. & PETERS, A.) pp. 63–89. New York: Plenum.

HUBEL, D. H. & LIVINGSTONE, M. S. (1987) Segregation of form, color, and stereopsis in primate area 18. *Journal of Neuroscience* **7**, 3378–3415.

INNOCENTI, G. M. (1986) General organization of callosal connections in the cerebral cortex. In *Cerebral Cortex* Vol. 5, *Sensory-Motor Areas and Aspects of Cortical Connectivity* (edited by JONES, E. G. & PETERS, A.) pp. 291–353. New York: Plenum.

JACOBS, B. & SCHEIBEL, A. B. (2002) Regional dendritic variation in primate cortical pyramidal cells. In *Cortical Areas: Unity and Diversity* (edited by SCHÜZ, A. & MILLER, R.) pp. 111–131. London: Taylor and Francis.

JACOBS, B., SCHALL, M., PRATHER, M., KAPLER, L., DRISCOLL, L., BACA, S., JACOBS, J., FORD, K., WAINWRIGHT, M. & TREML, M. (2001) Regional

dendritic and spine variation in human cerebral cortex: A quantitative study. *Cerebral Cortex* **11**, 558–571.

JELINEK, H. F. & ELSTON, G. N. (2001) Pyramidal neurones in macaque visual cortex: Interareal phenotypic variation of dendritic branching patterns. *Fractals* **9**, 287–295.

JOHNSON, R. R. & BURKHALTER, A. (1996) Microcircuitry of forward and feedback connections within rat visual cortex. *Journal of Comparative Neurology* **368**, 383–398.

JONES, E. G. (1968) An electron microscopic study of the terminations of afferent fiber systems onto the somatic sensory cortex of the cat. *Journal of Anatomy* **103**, 595–597.

JONES, E. G. (1981) Anatomy of cerebral cortex: Columnar input–output organization. In *The Cerebral Cortex* (edited by SCHMITT, F. O., WORDEN, F. G., ADELMAN, G. & DENNIS, M.) pp. 199–235. Cambridge, MA: MIT Press.

JONES, E. G. (1983) The columnar basis of cortical circuitry. In *The Clinical Neurosciences* (edited by WILLIS, W. D.) pp. 357–383. New York: Churchill Livingstone.

JONES, E. G. (1984) Laminar distribution of cortical efferent cells. In *Cerebral Cortex* Vol. 1, *Cellular Components of the Cerebral Cortex* (edited by PETERS, A. & JONES, E. G.) pp. 521–553. New York: Plenum.

JONES, E. G. (1993) GABAergic neurons and their role in cortical plasticity in primates. *Cerebral Cortex* **3**, 361–372.

KAAS, J. H. (1982) The segregation of function in the nervous system: Why do sensory systems have so many subdivisions? In *Contributions to Sensory Physiology* (edited by NEFF, W. P.) pp. 201–240. New York: Academic Press.

KAAS, J. H. (1984) The organization of sensory and motor cortex in owl monkeys. In *Aotus: The Owl Monkey* (edited by BAER, J. F., WELLER, R. E. & KAKOMA, I.) pp. 331–351. Orlando: Academic Press.

KAAS, J. H. (1986) The structural basis for information processing in the primate visual system. In *Visual Neuroscience* (edited by PETTIGREW, J. P., SANDERSON, K. J. & LEVICK, W. R.) pp. 315–339. Cambridge, UK: Cambridge University Press.

KAAS, J. H. (1987) The organization of neocortex in mammals: Implications for theories of brain function. *Annual Reviews in Psychology* **38**, 129–151.

KAAS, J. H. (1989a) The evolution of complex sensory systems in mammals. *Journal of Experimental Biology* **146**, 165–176.

KAAS, J. H. (1989b) Why does the brain have so many visual areas? *Journal of Cognitive Neuroscience* **1**, 121–135.

KAAS, J. H. (1991) Plasticity of sensory and motor maps in adult mammals. *Annual Reviews of Neuroscience* **14**, 137–167.

KAAS, J. H. (1995) The evolution of isocortex. *Brain Behavior and Evolution* **46**, 187–196.

KHARAZIA, V. N., WEINBERG, R. J. (1993) Glutamate in terminals of the thalamocortical fibers in rat somatic sensory cortex. *Neuroscience Letters* **157**, 162–166.

KISVÁRDAY, Z. F. & EYSEL, U. T. (1992) Cellular organization of reciprocal patchy networks in layer III of cat visual cortex (area 17). *Neuroscience* **46**, 275–286.

KISVÁRDAY, Z. F., BEAULIEU, C. & EYSEL, U. T. (1993) Network of GABAergic large basket cells in cat visual cortex (area 18): Implications for lateral disinhibition. *Journal of Comparative Neurology* **327**, 398–415.

KISVÁRDAY, Z. F., MARTIN, K. A. C., FREUND, T. F., MAGLOCZKY, Z., WHITTERIDGE, D. & SOMOGYI, P. (1986) Synaptic targets of HRP-filled layer III pyramidal cells in the cat striate cortex. *Experimental Brain Research* **64**, 541–552.

KOCH, C. (1999) *Biophysics of Computation. Information Processing in Single Neurons*. New York: Oxford University Press.

KOCH, C., POGGIO, T. & TORRE, V. (1982) Retinal ganglion cells: A functional interpretation of dendritic morphology. *Philosophical Transactions of the Royal Society of London Series B* **298**, 227–264.

KOLB, B. & TEES, R. C. (1990) The rat as a model of cortical function. In *The Cerebral Cortex of the Rat* (edited by KOLB, B. & TEES, R. C.) pp. 3–17. Cambridge, MA: MIT Press.

KONDO, H. T., TANAKA, K., HASHIKAWA, T. & JONES, E. G. (1999) Neurochemical gradients along monkey sensory cortical pathways: Calbindin-immunoreactive pyramidal neurons in layers II and III. *European Journal of Neuroscience* **11**, 4197–4203.

KRITZER, M. & GOLDMAN-RAKIC, P. S. (1995) Intrinsic circuit organization of the major layers and sublayers of the dorsolateral prefrontal cortex in monkeys. *Journal of Comparative Neurology* **359**, 131–143.

KRITZER, M., COWEY, A. & SOMOGYI, P. (1992) Patterns of inter- and intralaminar GABAergic connections distinguish striate (V1) and extrastriate (V2, V4) visual cortices and their functionally specialized subdivisions in the rhesus monkeys. *Journal of Neuroscience* **12**, 4545–4564.

KRUBITZER, L. A. (1995) The organization of neocortex in mammals: Are species differences really so different? *Trends in Neuroscience* **18**, 408–417.

KRUBITZER, L. A. (2000) How does evolution build a complex brain. In *Evolutionary Developmental Biology of the Cerebral Cortex* (edited by BOCK G. R. & CARDEN, G.) pp. 206–226. Chichester: Wiley.

LARKMAN, A. U. (1991) Dendritic morphology of pyramidal neurones in the visual cortex of the rat: III. Spine distributions. *Journal of Comparative Neurology* **306**, 332–343.

LENNIE, P. (1998) Single units and visual cortical organization. *Perception* **27**, 889–935.

LIVINGSTONE, M. S. (1998) Mechanisms of direction selectivity in macaque V1. *Neuron* **20**, 509–526.

LIVINGSTONE, M. S. & HUBEL, D. H. (1984) Anatomy and physiology of a color system in the primate visual cortex. *Journal of Neuroscience* **4**, 309–356.

LLINÁS, R. & PARÉ, D. (1996) The brain as a closed system modulated by the senses. In *The Mind Brain Continuum* (edited by LLINÁS, R. & CHURCHLAND, P. S.) pp. 1–18. Cambridge, MA: MIT Press.

LUESCHOW, A., MILLER, E. K. & DESIMONE, R. (1994) Inferior temporal mechanisms for invariant object recognition. *Cerebral Cortex* **4**, 523–531.

LUND, J. S., YOSHIOKA, T. & LEVITT, J. B. (1993) Comparison of intrinsic connectivity in different areas of macaque monkey cerebral cortex. *Cerebral Cortex* **3**, 148–162.

LUND, J. S., WU, Q., HADINGHAM, P. T., LEVITT, J. B. (1995) Cells and circuits contributing to functional

properties in area V1 of macaque monkey cerebral cortex: Bases for neuroanatomically realistic models. *Journal of Anatomy* **187**, 563–581.

LUND, J. S., HENDRICKSON, A. E., OGREN, M. P. & TOBIN, E. A. (1981) Anatomical organization of primate visual cortex area VII. *Journal of Comparative Neurology* **202**, 19–45.

LYON, D. C. & KAAS, J. H. (2001) Connectional and architectonic evidence for dorsal and ventral V3, and dorsomedial area in marmoset monkeys. *Journal of Neuroscience* **21**, 249–261.

LYON, D. C. & KAAS, J. H. (2002) Evidence from connectional for both dorsal and ventral subdivisions of V3 in three species of monkeys. *Journal of Comparative Neurology* **449**, 281–297.

MAINEN, Z. F. & SEJNOWSKI, T. J. (1996) Influence of dendritic structure on firing pattern in model neocortical neurons. *Nature* **382**, 363–366.

MALACH, R. (1994) Cortical columns as devices for maximizing neuronal diversity. *Trends in Neuroscience* **17**, 101–104.

MALACH, R., AMIR, Y., HAREL, M. & GRINVALD, A. (1993) Relationship between intrinsic connections and functional architecture revealed by optical imaging and *in vivo* targeted biocytin injections in primate striate cortex. *Proceedings of the National Academy of Science USA* **90**, 10469–10473.

MALONEK, D., TOOTELL, R. B. H. & GRINVALD, A. (1994) Optical imaging reveals the functional architecture of neurons processing shape and motion in owl monkey area MT. *Proceedings of the Royal Society Series B* **258**, 109–119.

MARTIN, K. A. C. & WHITTERIDGE, D. (1984) Form, function and intracortical projections of spiny neurones in the striate visual cortex of the cat. *Journal of Physiology (London)* **353**, 463–504.

MASON, A. & LARKMAN, A. U. (1990) Correlations between morphology and electrophysiology of pyramidal neurons in slices of rat visual cortex. II. Electrophysiology. *Journal of Neuroscience* **10**, 1415–1428.

MATSUBARA, J., CYNADER, M., SWINDALE, N. V. & STRYKER, M. P. (1985) Intrinsic projections within visual cortex: Evidence for orientation-specific local connections. *Proceedings of the National Academy of Science USA* **82**, 935–939.

MCGUIRE, B. A., GILBERT, C. D., RIVLIN, P. K. & WIESEL, T. N. (1991) Targets of horizontal connections in macaque primary visual cortex. *Journal of Comparative Neurology* **305**, 370–392.

MEL, B. (1992) NMDA-based pattern discrimination in a modelled cortical neuron. *Neural Computation* **4**, 502–517.

MEL, B. (1993) Synaptic integration in an excitable dendritic tree. *Journal of Neurophysiology* **70**, 1086–1101.

MEL, B. (1999) Why have dendrites? A computational perspective. In *Dendrites* (edited by STUART, G., SPRUSTON, N. & HÄUSSER, M.) pp. 271–289. New York: Oxford University Press.

MILLER, E. K., COHEN, J. D. (2001) An integrative theory of prefrontal cortex. *Annual Review of Neuroscience* **24**, 167–202.

MILLER, E. K., LI, L. & DESIMONE, R. (1993) Activity of neurons in anterior inferior temporal cortex during a short-term memory task. *Journal of Neuroscience* **13**, 1460–1478.

MITCHISON, G. & CRICK, F. H. C. (1982) Long axons within the striate cortex: Their distribution, orientation and patterns of connection. *Proceedings of the National Academy of Science USA* **79**, 3661–3665.

MORRISON, J. H., HOF, P. R. & HUNTLEY, G. W. (1998) Neurochemical organization of the primate visual cortex. In *Handbook of Chemical Neuroanatomy* (edited by BLOOM, F. F., BJÖRKLUND, A. & HÖKFELT, T.) pp. 299–433. Amsterdam: Elsevier.

MOTTER, B. C., STEINMETZ, M. A., DUFFY, C. J. & MOUNTCASTLE, V. B. (1987) Functional properties of parietal visual neurons: Mechanisms of directionality along a single axis. *Journal of Neuroscience* **7**, 154–176.

MOUNTCASTLE, V. B. (1978) An organizing principle for general cortical function: The unit module and the distributed system. In *The Mindful Brain* (edited by SCHMITT, F. O.) pp. 7–50. Cambridge: MIT Press.

MOUNTCASTLE, V. B. (1995) The evolution of ideas concerning the function of neocortex. *Cerebral Cortex* **5**, 289–295.

MOUNTCASTLE, V. B. (1997) The columnar organization of the neocortex. *Brain* **120**, 701–722.

MOUNTCASTLE, V. B. (1998) *The Cerebral Cortex*. Cambridge: Harvard University Press.

MURAYAMA, Y., FUJITA, I. & KATO, M. (1997) Contrasting forms of synaptic plasticity in monkey inferotemporal and primary visual cortices. *NeuroReport* **8**, 1503–1508.

NAKAMURA, K. & KUBOTA, K. (1995) Mnemonic firing of neurons in the monkey temporal pole during a visual recognition memory task. *Journal of Neurophysiology* **74**, 162–178.

NELSON, R. B., FRIEDMAN, D. P., O'NEILL, J. B., MISHKIN, M. & ROUTTENBERG, A. (1987) Gradients of protein kinase C substrate phosphorylation in primate visual system in visual memory storage areas. *Brain Research* **416**, 387–392.

NORTHCUTT, R. G. & KAAS, J. H. (1995) The emergence and evolution of the mammalain neocortex. *Trends in Neuroscience* **18**, 373–379.

PERRETT, D. I., SMITH, P. A. J., POTTER, D. D., MISTLIN, A. J., HEAD, A. S., MILNER, A. D. & JEEVES, M. A. (1984) Neurons responsive to faces in the temporal cortex: Studies of functional organization, sensitivity to identity and relation to perception. *Human Neurobiology* **3**, 197–208.

PETERS, A. & KAISERMAN-ABRAMOF, I. A. (1969) The small pyramidal neuron of the rat cerebral cortex. The synapses upon dendritic spines. *Zeitschrift für Zellforschung* **100**, 487–586.

PETERS, A. & HARRIMAN, K. M. (1992) Different kinds of axon terminals forming symmetric synapses with the cell bodies and initial axon segments of layer II/III pyramidal cells. III. Origins and frequency of occurence of the terminals. *Journal of Neurocytology* **21**, 679–692.

POIRAZI, P. & MEL, B. (2001) Impact of active dendrites and structural plasticity on the storage capacity of neural tissue. *Neuron* **29**, 779–796.

PREUSS, T. M. (2001) The discovery of cerebral diversity: An unwelcome scientific revolution. In *Evolutionary Anatomy*

of the Primate Cerebral Cortex (edited by FALK, D. & GIBSON, K. R.) pp. 138–164. Cambridge, UK: Cambridge University Press.

RALL, W. (1959) Branching dendritic trees and motorneuron membrane resistivity. *Experimental Neurology* **1**, 491–527.

RALL, W. (1964) Theoretical significance of dendritic tree for input-output relation. In *Neural Theory and Modeling* (edited by REISS, R. F.) pp. 73–97. Stanford: Stanford University Press.

RALL, W., BURKE, R. E., HOLMES, W. R., JACK, J. J. B., REDMAN, S. R. & SEGEV, I. (1992) Matching dendritic neuron models to experimental data. *Physiological Reviews* **72**, 159–186.

REDMAN, S. & WALMSLEY, B. (1983) The time course of synaptic potentials evoked in cat spinal motoneurones at identified group Ia synapses. *Journal of Physiology* **343**, 117–133.

REMPEL-CLOWER, N. L. & BARBAS, H. (2000) The laminar pattern of connections between prefrontal and anterior temporal corticies in the rhesus monkey is related to cortical structure and function. *Cerebral Cortex* **10**, 851–865.

RINGO, J. L. (1991) Neuronal interconnection as a function of brain size. *Brain, Behavior and Evolution* **38**, 1–6.

ROCKEL, A. J., HIORNS, R. W. & POWELL, T. P. S. (1980) The basic uniformity in structure of the neocortex. *Brain* **103**, 221–244.

ROCKLAND, K. S. (1985) A reticular pattern of intrinsic connections in primate area V2 (area 18). *Journal of Comparative Neurology* **235**, 467–478.

ROCKLAND, K. S. (1989) Bistratified distribution of terminal arbors of individual axons projecting from area V1 to middle temporal area (MT) in the macaque monkey. *Visual Neuroscience* **3**, 155–170.

ROCKLAND, K. S. (1992) Configuration, in serial reconstruction, of individual axons projecting from area V2 to V4 in the macaque monkey. *Cerebral Cortex* **2**, 353–374.

ROCKLAND, K. S. (1995) Morphology of individual axons projecting from area V2 to MT in the macaque. *Journal of Comparative Neurology* **355**, 15–26.

ROCKLAND, K. S. (1997) Elements of cortical architecture: Hierarchy revisited. In *Cerebral Cortex* Vol. 12, *Extrastriate Cortex in Primates* (edited by ROCKLAND, K., KAAS, J. H. & PETERS, A.) pp. 243–293. New York: Plenum.

ROCKLAND, K. S. & PANDYA, D. N. (1979) Laminar origins and terminations of cortical connections of the occipital lobe in the rhesus monkey. *Brain Research* **179**, 3–20.

ROCKLAND, K. S. & LUND, J. S. (1982) Widespread periodic intrinsic connections in the tree shrew visual cortex. *Science* **215**, 1532–1534.

ROCKLAND, K. S. & LUND, J. S. (1983) Intrinsic laminar lattice connections in primate visual cortex. *Journal of Comparative Neurology* **216**, 303–318.

ROCKLAND, K. S. & VIRGA, A. (1990) Organization of individual cortical axons projecting from area V1 (area 17) to V2 (area 18) in the macaque monkey. *Visual Neurscience* **4**, 11–28.

ROCKLAND, K. S., LUND, J. S. & HUMPHREY, A. L. (1982) Anatomical banding of intrinsic connections in striate cortex of tree shrews (*Tupaia glis*). *Journal of Comparative Neurology* **209**, 41–58.

ROE, A. & TS'O, D. Y. (1997) The functional architecture of area V2 in the macaque monkey: Physiology, topography and connectivity. In *Cerebral Cortex* Vol. 12, *Extrastriate Cortex in Primates* (edited by ROCKLAND, K., KAAS, J. H. & PETERS, A.) pp. 295–333. New York: Plenum.

ROSA, M. G. P. (1997) Visuotopic organization of primate extrastriate cortex. In *Cerebral Cortex* Vol. 12, *Extrastriate Cortex in Primates* (edited by ROCKLAND, K., KAAS, J. H. & PETERS, A.) pp. 127–204. New York: Plenum.

SAGASE, Y., YAMANE, S., UENO, S. & KAWANO, K. (1999) Global and fine information coded by single neurons in the temporal visual cortex. *Nature* **400**, 869–873.

SALEEM, K. S., TANAKA, K. & ROCKLAND, K. S. (1993) Specific and columnar projection from area TEO to area TE in the macaque inferotemporal cortex. *Cerebral Cortex* **3**, 454–464.

SAWATARI, A. & CALLAWAY, E. M. (1996) Convergence of magno- and parvocellular pathways in layer 4b of macaque primary visual cortex. *Nature* **380**, 442–446.

SCHILLER, P. H. (1996) On the specificity of neurons in visual areas. *Behavioural Brain Research*, **76**, 21–35.

SEGEV, I. & RALL, W. (1998) Excitable dendrites and spines: Earlier theoretical insights elucidate recent direct observations. *Trends in Neuroscience* **21**, 453–460.

SELTZER, B. & PANDYA, D. N. (1978) Afferent cortical connections of the superior temporal sulcus and surrounding cortex in the rhesus monkey. *Brain Research* **149**, 1–24.

SINGER, W. & GRAY, C. M. (1995) Visual feature integration and the temporal correlation hypothesis. *Annual Reviews in Neuroscience* **18**, 555–586.

SHIPP, S. & ZEKI, S. (1989a) The organization of connections between area V5 and V2 in macaque monkey visual cortex. *European Journal of Neuroscience* **1**, 333–354.

SHIPP, S. & ZEKI, S. (1989b) The organization of connections between areas V5 and V1 in macaque monkey visual cortex. *European Journal of Neuroscience* **1**, 309–332.

SOBOTKA, S. & RINGO, J. L. (1993) Investigation of long term recognition and association memory in unit responses from inferotemporal cortex. *Experimental Brain Research* **96**, 28–38.

SOMOGYI, P., COWEY, A., HALÁSZ, N. & FREUND, T. F. (1981) Vertical organization of neurones accumulating ^{3}H-GABA in visual cortex of rhesus monkey. *Nature* **294**, 761–763.

SOMOGYI, P., TAMAS, G., LUJAN, R. & BUHL, E. H. (1998) Salient features of synaptic organisation in the cerebral cortex. *Brain Research Reviews* **26**, 113–135.

SOMOGYI, P., COWEY, A., KISVÁRDAY, Z. F., FREUND, T. F. & SZENTÁGOTHAI, J. (1983) Retrograde transport of γ-amino[^{3}H]butyric acid reveals specific interlaminar connections in the striate cortex of monkey. *Proceedings of the National Academy of Science USA* **80**, 2385–2389.

STEPANYANTS, A., HOF, P. R. & CHKLOVSKII, D. B. (2002) Geometry and structural plasticity of synaptic connectivity. *Neuron* **34**, 275–288.

SZENTÁGOTHAI, J. (1975) The "module-concept" in cerebral cortex architecture. *Brain Research* **95**, 475–496.

TANAKA, K., KOYAMA, T. & MIKAMI, A. (1999) Neurons in the temporal cortex change their preferred

direction of motion dependant on shape. *NeuroReport* **10**, 393–397.

TAYLOR, W. R. & VANEY, D. I. (2002) Diverse synaptic mechanisms generate direction selectivity in the rabbit retina. *Journal of Neuroscience* **22**, 7712–7720.

TAYLOR, W. R., HE, S., LEVICK, W. R., VANEY, D. I. (2000) Dendritic computation of direction selectivity by retinal ganglion cells. *Science* **289**, 2347–2350.

TS'O, D. Y. & GILBERT, C. D. (1988) The organization of chromatic and spatial interactions in the primate striate cortex. *Journal of Neuroscience* **8**, 1712–1727.

TS'O, D. Y., GILBERT, C. D. & WIESEL, T. N. (1986) Relationships between horizontal interactions and functional architecture in the cat striate cortex as revealed by cross-correlation analysis. *Journal of Neuroscience* **6**, 1160–1170.

UNGERLEIDER, L. G. & MISHKIN, M. (1982) Two cortical systems. In *Analysis of Visual Behavior* (edited by INGLE, D. J., GOODALE, M. A. & MANSFIELD, R. J. W.) pp. 549–586. Cambridge, MA: MIT Press.

VAN ESSEN, D. C., NEWSOME, W. T., MAUNSELL, J. H. R. & BIXBY, J. L. (1986) The projections from striate cortex (V1) to areas V2 and V3 in the macaque monkey: Asymmetries, areal bounderies, and patchy connections. *Journal of Comparative Neurology* **244**, 451–480.

VANEY, D. I. & TAYLOR, W. R. (2002) Direction selectivity in the retina. *Current Opinion in Neurobiology* **12**, 405–410.

VOGT WEISENHORN, D. M., ILLING, R.-B. & SPATZ, W. B. (1995) Morphology and connections of neurons in area 17 projecting to the extrastriate areas MT and 19DM and to the superior colliculus in the monkey *Callithrix jacchus*. *Journal of Comparative Neurology* **362**, 233–255.

VON ECONOMO, C. (1929) *The Cytoarchitectonics of the Human Cerebral Cortex*. Oxford: Humphrey Milford.

WALKER, A. E. (1940) A cytoarchitectural study of the prefrontal areas of the macaque monkey. *Journal of Comparative Neurology* **73**, 59–86.

WANG, Y., FUJITA, I. & MURAYAMA, Y. (2000) Neuronal mechanisms of selectivity for object features revealed by blocking inhibition in inferotemporal cortex. *Nature Neuroscience* **3**, 807–813.

WANG, Y., FUJITA, I., TAMURA, H. & MURAYAMA, Y. (2002) Contribution of GABAergic inhibition to receptive field structures of monkey inferior temporal neurons. *Cerebral Cortex* **12**, 62–74.

WELLER, R. E. (1988) Two cortical visual systems in Old World and New World primates. In *Progress in Brain Research* (edited by HICKS, T. P. & BENEDEK, G.) pp. 293–306. Amsterdam: Elsevier.

YIN, T. C. & MOUNTCASTLE, V. B. (1977) Visual input to the visuomotor mechanisms of the monkey's parietal lobe. *Science* **197**, 1381–1383.

ZILLES, K. & CLARKE, S. (1997) Architecture, connectivity, and transmitter receptors of human extrastriate visual cortex. In *Cerebral Cortex* Vol. 12, *Extrastriate Cortex in Primates* (edited by ROCKLAND, K., KAAS, J. H. & PETERS, A.) pp. 673–742. New York: Plenum.