A Study of Pyramidal Cell Structure in the Cingulate Cortex of the Macaque Monkey with Comparative Notes on Inferotemporal and Primary Visual Cortex

Recent studies have revealed a marked degree of variation in the pyramidal cell phenotype in visual, somatosensory, motor and prefrontal cortical areas in the brain of different primates, which are believed to subserve specialized cortical function. In the present study we carried out comparisons of dendritic structure of layer III pyramidal cells in the anterior and posterior cingular cortex and compared their structure with those sampled from inferotemporal cortex (IT) and the primary visual area (V1) in macaque monkeys. Cells were injected with Lucifer Yellow in flat-mounted cortical slices, and processed for a light-stable DAB reaction product. Size, branching pattern, and spine density of basal dendritic arbors was determined, and somal areas measured. We found that pyramidal cells in anterior cingular cortex were more branched and more spiny than those in posterior cingular cortex, and cells in both anterior and posterior cingular were considerably larger, more branched, and more spiny than those in area V1. These data show that pyramidal cell structure differs between posterior dysgranular and anterior granular cingular cortex, and that pyramidal neurons in cingular cortex have different structure to those in many other cortical areas. These results provide further evidence for a parallel between structural and functional specialization in cortex.

Keywords: association, cognition, dendritic spine, emotion, intracellular injection, Lucifer Yellow, Sholl

Introduction

The mammalian cerebral cortex is composed of many different areas, some of which, such as the primary sensory areas, are widely believed to have been present in ancestral mammals, whereas others, such as sensory association and granular prefrontal areas, are thought to have evolved more recently (for reviews, see Preuss, 2000; Allman et al., 2001; Kaas and Collins, 2001; Northcutt, 2002; Kaas and Preuss, 2003; Elston, 2003a). Various theories exist for how new cortical areas may have evolved (e.g. Sanides, 1970; MacLean, 1989; Gould, 2002). Most of these theories assume that expansion of cortex allowed the evolution of more sophisticated, and/or cognate, processing. Many believe that this expansion occurred through the addition of more of the same basic repeated unit of cortex (Crair and Schloetter, 1977; Mountcastle, 1978; Szentagothai, 1978; Rockland, 2002). Granular prefrontal cortex (gPFC) in higher primates, which has undergone dramatic expansion (Brodman, 1913; for a translation, see Elston and Garvy, 2004), is composed of highly branched and spiny pyramidal cells: macaque prefrontal pyramidal cells have, on average, over 16 times more dendritic spines than those in its V1 and those in human prefrontal cortex have 23 times more spines than those in macaque V1 (Elston, 2000; Elston et al., 2001). As each dendritic spine receives at least one excitatory input (for reviews, see Harris, 1999; Elston and DeFelipe, 2002), regional differences in the number of spines in the dendritic arbours of neurons suggest that they integrate different numbers of inputs. It has been argued that regional specializations in pyramidal cell structure reflect fundamental differences in patterns in cortical circuitry, which shape its functional abilities (for reviews, see Elston, 2002, 2003a; Jacobs and Scheibel, 2002). Here we focus on pyramidal cell structure in anterior and posterior cingular areas of the macaque monkey in a bid to gather more information regarding the underlying trends that result in specialization of the pyramidal cell phenotype and how they relate to cortical function.

Materials and Methods

Methods of perfusion, slice preparation, cell injection, classification, morphological and statistical analysis have been detailed in previous studies (Buhl and Schlote, 1987; Elston et al., 1997). Two male Macaca fascicularis (four and a half years old) and a single male M. mulatta (unknown age) were used in the present study. The animals were deeply anaesthetized with sodium pentobarbitol, perfused intracardially with physiological saline, followed by a solution of 4% paraformaldehyde in 0.1 mol/l phosphate buffer (pH 7.2). The protocol for these experiments was in accordance with those endorsed by the NIH (publication No. 86-23, revised 1985) and was approved by the University of Queensland and RIKEN Animal Ethics Committees.

Tissue was taken from the caudal region of the cingulate gyrus (corresponding to Brodmann’s area 23), the rostral portion of the cingulate gyrus (corresponding to Brodmann’s area 24), the rostral third of the ventral bank of the superior temporal sulcus (IT); cytotoxicl architectural area TEa of Seltzer and Pandya, 1978; TEad(s) of Yukie, 1997; PIT of
that were only partially filled. Neurons were drawn with the aid of identification of individual dendritic spines (Fig. 2). In addition, we were revealed using 3,3'-diaminobenzidine (DAB; 1:200 in 0.1 mol/l phosphate buffer; Amersham RPN1051). Labelling solution for 2 h) followed by a biotin- -horseradish-peroxidase complex biotinylated secondary antibody (Amersham RPN 1004; 1:200 in stock 0.1 mol/l phosphate buffer]. Anti-LY was detected by a species-specific albumin (Sigma A3425), 1% Triton X-100 (BDH 30632), 5% sucrose in the tissue was processed with an antibody to Lucifer Yellow (LY), tips and the dendritic spines were easily visible. Following cell injection until the individual dendrites of each cell could be traced to abrupt distal layers). [Here we use the terminology of Hassler (1966) in preference to that of Brodmann (1909; translated by Garey, 1994) for reasons outlined in Elston and Rosa (1997) and Casagrande and Kaas (1994)]. In the case of posterior dysgranular cingulate cortex, we calculated from our own preparations, and previous studies (e.g. Figure 3 of Nimchinsky et al., 1996), that the base of layer III is located approximately half way between the cortical surface and the white matter, corresponding to our third successive 250 μm tangential section.

Neurons were injected with a continuous current (up to 1000 nA) until the individual dendrites of each cell could be traced to abrupt distal tips and the dendritic spines were easily visible. Following cell injection the tissue was processed with an antibody to Lucifer Yellow (LY), at a concentration of 1:400 000 in stock solution [2% bovine serum albumin (Sigma A3425), 1% Triton X-100 (BDHI 30632), 5% sucrose in 0.1 mol/l phosphate buffer]. Anti-LY was detected by a species-specific biotinylated secondary antibody (Amersham RPN 1004; 1:200 in stock solution for 2 h) followed by a biotin-horseradish-peroxidase complex (1:200 in 0.1 mol/l phosphate buffer; Amersham RPN1051). Labelling was revealed using 3,3'-diaminobenzidine (DAB; 1:200 in 0.1 mol/l phosphate buffer; Sigma D 80001) as the chromogen. This method allowed reconstruction of cell morphology in fine detail, including the identification of individual dendritic spines (Fig. 2). In addition, we were able to determine which cells were completely filled and exclude those that were only partially filled. Neurons were drawn with the aid of a camera lucida attached to a Zeiss Axioplan microscope (40× objective). The size of the basal dendritic arbours was determined by calculating the area contained within a polygon that joined the outermost distal tips of the dendritic arbour (using features of NIH image software; NIH Research Services, Bethesda, MD; see Elston and Rosa, 1997). Branching patterns were determined by Sholl analyses (Sholl, 1953), using a 25 μm incremental increase in the radii of successive concentric circles. Spines were drawn at high power (100× oil immersion objective) and were counted as a function of distance from the cell body to the distal tips of the dendrites. The density of spines was determined per 10 μm dendritic segment (e.g. Eayrs and Goodhead, 1959). All spine types, including sessile and pedunculate (Jones and Powell, 1969), were included in the spine counts but no distinction was made between them. Correction factors used in other studies when quantifying spines (e.g. Feldman, 1984) were not used in the present study as the DAB reaction product is more transparent than the Golgi precipitate, allowing the visualization of spines that issue from the underside of dendrites. All spine data were obtained from a single case (MF2) in which we sampled the greatest number of cells. Cell bodies were drawn with the aid of a Zeiss 100× oil-immersion lens and their areas determined by tracing the outermost perimeter, whilst changing focal plane, and using standard features of NIH Image. Statistical analysis was performed using SPSS (SPSS Inc., Chicago, IL).

Results

Fifty-six layer III pyramidal cells in anterior cingulate and 64 layer III pyramidal cells in posterior cingulate were compared with 67 layer III pyramidal cells in IT and 53 cells in V1 sampled from the same hemispheres of two M. fascicularis monkeys. An additional 39 cells were sampled from anterior cingulate and 53 from posterior cingulate cortex from a single M. mulatta monkey. Only cells that had an unambiguous apical dendrite, had their complete basal dendritic arbours contained within the section and were well filled were included for analysis. Data are presented as individual cases.

Pyramidal Neurons in M. fascicularis

Basal Dendritic Arbour Size

The size of the basal dendritic arbours of pyramidal cells in anterior cingulate were larger (>50%) than those in posterior cingulate (Table 1; Figs 3 and 4). Moreover, cells in both anterior and posterior cingulate were larger than those in IT and V1 (Table 1; Figs 3 and 4). A one way analysis of variance (ANOVA) revealed significant differences (P < 0.001) in the sizes of the basal dendritic arbours of pyramidal cells these four cortical areas in both MF1 [F(3,103) = 115.1] and MF2 [F(3,129) = 117.2]. Post hoc Scheffe tests revealed significant differences (P < 0.05) in the size of the basal dendritic arbours of layer III pyramidal cells between cingulate (anterior and posterior) cortex and both IT and V1 in both cases MF1 and MF2.

Branching Patterns of the Basal Dendritic Arbours

Pyramidal cells in anterior cingulate had more branches in their basal dendritic arbours than those in posterior cingulate (Fig. 5). In addition, pyramidal cells in both anterior and posterior cingulate had more branches than those in IT and V1 (Fig. 5; Table 2). Analysis of variance revealed these differences to be significant [P < 0.001; MF1, intercept F(1,118) = 2558, cortical area F(3,118) = 99.16; MF2, intercept F(1,131) = 2826, cortical area F(3,131) = 98.63]. Post hoc Scheffe tests revealed that, in both MF1 and MF2 monkeys, cells in anterior cingulate were significantly more branched than those in IT. In addition, those

Figure 1. Schematic showing the regions of cortex from which tissue was sampled. Tissue was taken from the caudal region of the cingulate gyrus (Post Cing), the rostral region of the cingulate gyrus (Ant Cing), the rostral third of the ventral bank of the superior temporal sulcus (IT; cytoarchitectural area T[6] of Seltzer and Pandya, 1978; T[6a]l of Yukie, 1997; FIT of Fellman and Van Essen, 1991) and the occipital operculum (V1, or area 17 of Brodmann). In the case of cingulate cortex, neurons were injected as close to incisions made and the anterior and posterior extremities of the corpus callosum (dashed lines) as possible.
in both anterior and posterior cingulate were significantly more branched than those in V1 ($P < 0.05$).

**Spine Densities of the Basal Dendrites**

In order to determine possible differences in the density and distribution of dendritic spines we drew and tallied $>16,000$ spines from 20 horizontally projecting basal dendrites of different neurons in each cortical area. From Figure 6 it is clear that the density of spines varied markedly for pyramidal cells in the different areas. Pyramidal cells in anterior cingulate had higher average peak spine density than those in posterior cingulate (Fig. 6; Table 3). The average peak spine density of cells in IT was similar to that reported in our previous studies (Elston and Rosa, 1997, 1998), being considerably lower than that in the other cortical areas (Fig. 6; Table 3). A repeated measures ANOVA (cortical area $\times$ distance from soma $\times$ spine density), revealed a significant difference in the distribution of spines [intercept $F(1.76) = 1463$, cortical area $F(3.76) = 93.3$; $P < 0.001$]. Post hoc Scheffe tests revealed all between area comparisons to be significantly different ($P < 0.05$), except that between area 24 and IT. By combining data from the Sholl analyses with that of spine densities we were able to determine an estimate for the total number of dendritic spines in the basal dendritic arbour of

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**Figure 2.** Photomicrographs of layer III pyramidal cells injected with Lucifer Yellow and processed for a DAB (3,3'-diaminobenzidine) reaction product. (A–D) Low power micrographs illustrating the gross structure of individually injected cells in inferotemporal (A, B), and anterior (C) and posterior (D) cingulate cortex. Higher power photomicrographs of the proximal dendrites of cells in anterior (E) and posterior (F) cingulate cortex and inferotemporal cortex (G, H) reveal differences in the diameter of the basal dendrites and the density of dendritic spines. Scale bars = 200 µm (A–D) and 50 µm (E–H).
the ‘average’ pyramidal neuron in each area (see Elston, 2001). The ‘average’ neuron in anterior cingulate had considerably more spines in its basal dendritic arbour than that in posterior cingulate (6825 and 4357 spines, respectively). The ‘average’ cell in IT had 6170 spines, whereas that in V1 had 855 spines in its basal dendritic arbour.

**Somal Areas**

Cell bodies were drawn in the plane tangential to the cortical surface, and plotted in Figure 7. In contrast to the size of the basal dendritic arbour, the somata of cells in layer III of anterior cingulate were, on average, smaller than those in posterior cingulate (Table 4). In addition, somata in both regions of the cingulate cortex were larger than those in IT and V1 (Table 4). Statistical analysis of the size of the cell bodies revealed significant differences between anterior and posterior cingulate areas [repeated measures ANOVAs: MF1, F(3,106) = 53.0, MF2, F(3,132) = 128, P < 0.001] and these cells were significantly different to those in IT and V1 (P < 0.05).

**Pyramidal Neurons in M. mulatta**

In agreement with our findings in M. fasicularis, we found that the basal dendritic arbours of pyramidal cells in anterior cingulate of M. mulatta were larger than those in posterior cingulate (Fig. 8; Table 1). A Mann–Whitney U-test revealed the difference to be significant (P < 0.001; kurtosis = 0.39, skew = 0.753). Moreover, we found that pyramidal cells in anterior cingulate of M. mulatta had more dendritic branches than those in posterior cingulate (Fig. 8; Table 3). A repeated measures ANOVA revealed the difference to be significant [P < 0.001; intercept F(1,111) = 24.72, cortical area F(1,111) = 29.8; P < 0.05]. As in M. fasicularis, we found that the size of the somata in anterior cingulate of M. mulatta were, on average, smaller than those in posterior cingulate (Fig. 8; Table 4). However, an unpaired t-test revealed no significant difference between the two groups [t(90) = 1.27; P = 0.2075; kurtosis = 0.0397, skew = 0.432].

**Discussion**

In the present study we found that pyramidal cells within the cingulate cortex in both M. fasicularis and M. mulatta differed in structure, those in anterior cingulate being larger and more branched and more spinous than those in posterior cingulate. Moreover, cells in anterior cingulate, but not posterior cingulate, are more spinous than those in IT. Pyramidal cells in both anterior and posterior cingulate cortex, as well as those in IT cortex, are considerably larger, more branched and more spinous than those in V1. Comparison of these data across seven different macaque monkeys reveals that the interindividual differences in pyramidal cell structure for any given cortical area.
area are relatively small compared with the interareal differences reported in each animal (Table 5; for a discussion, see Elston et al., 1999b; Elston and Rockland, 2002). These data show that the size, branching complexity and spine density of the basal dendritic arbors of pyramidal neurons, differs between cytoarchitectonically distinct regions of cingulate cortex, and that these cells show markedly different structure to those in many other cortical areas.

**Structure and Function in Cingulate Cortex**

A study of the literature reveals little agreement regarding functions performed in anterior and posterior cingulate cortex. Various authors have attributed higher cognitive and emotional functions to the anterior cingulate cortex and vegetative functions to posterior cingulate cortex (Goldman-Rakic, 2000; Passingham, 2000; Allman et al., 2001) whereas others have claimed the reverse (e.g. Baleydier and Mauguiere, 1980). Indeed, there are many differences in opinion regarding the evolution and function of cingulate cortex (for reviews, see Sanides, 1970; Baleydier and Mauguiere, 1980; MacLean, 1989; Allman et al., 2001). In a recent series of studies in which cortical activity was recorded in awake behaving monkeys by fMRI, Dreher and colleagues revealed that anterior cingulate, unlike posterior cingulate, is often co-activated with granular prefrontal cortex (gPFC) during cognitive tasks (Dreher and Berman, 2002; Dreher and Grafman, 2003). Our results show

**Figure 4.** Frequency histograms of the size of the basal dendritic arbours of layer III pyramidal neurons in anterior and posterior cingulate cortex (Ant Cing and Post Cing, respectively), inferotemporal cortex (IT) and primary visual area (V1) of M. fascicularis (cases MF1 and MF2).
that the size, branching pattern and spine density along the dendrites of the pyramidal cells in anterior cingulate is considerably higher than that in posterior cingulate cortex. Moreover, pyramidal cell structure in anterior cingulate cortex more closely approximates that seen for cells sampled from gPFC of the same hemisphere, than do those in posterior cingulate (unpublished observations).

As reviewed elsewhere, these different aspects of pyramidal cell microanatomy may influence different aspects of cellular, and systems, function (Segev and Rall, 1998; Koch, 1999; Mel, 1999; Spruston et al., 1999; Häusser et al., 2000; Segev et al., 2001; Elston, 2002, 2003a; Häusser and Mel, 2003). Briefly, the size of the arbour influences sampling geometry: the relationship between the size of the dendritic arbour and the arborization pattern of axons from which they sample inputs determines the degree of convergence/divergence (Malach, 1994). The branching structure influences the potential for compartmentalization of processing within the arbours of pyramidal cells, which reportedly endows more branched cells with greater functional capability (Poirazi and Mel, 2000). The branching structure and spine density influence the total number of putative excitatory inputs sampled by cells. That pyramidal cells in anterior cingulate cortex have more complex

![Graph of the branching patterns of the basal dendritic arbours of layer III pyramidal neurons in anterior and posterior cingulate cortex (Ant Cing and Post Cing, respectively), inferotemporal cortex (IT) and primary visual area (V1) of M. fasicularis (cases MF1 and MF2).](image1)

![Frequency histograms of the size of the somata of layer III pyramidal neurons in anterior and posterior cingulate cortex (Ant Cing and Post Cing, respectively), inferotemporal cortex (IT) and primary visual area (V1) of M. fasicularis (cases MF1 and MF2).](image2)

Table 2

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Data are averaged for all neurons in each cortical area (mean ± SEM). The peak dendritic branching complexity is highlighted in bold; n is the same as for Table 1.

Cerebral Cortex January 2005, V 15 N 1
structure than those in posterior cingulate cortex but less complex structure than those in granular prefrontal cortex (cf. Elston, 2000) suggests that patterns of intrinsic connectivity and, hence, the functional capabilities, of circuitry in the anterior cingulate is intermediate between the posterior cingulate and gPFC.

Specialization in Pyramidal Cell Structure in Cingulate Cortex

The present data confirm and extend previous findings of regional variation in pyramidal cell structure in primate cingulate cortex (Nimchinsky et al., 1996, 1997). Moreover, direct comparison of layer III pyramidal cells sampled in cingulate cortex with those sampled in V1 of the same hemisphere revealed that those in anterior cingulate are, on average, at least eight times more spinous than those in V1. Comparison of the present data with those of previous studies reveals that layer III pyramidal cells in cingulate (both anterior and posterior) are characterized by more complex structure than those in primary somatosensory and auditory areas (cf. Elston and Rockland, 2002; Elston et al., 2002). In addition, layer III pyramidal cells in cingulate cortex are more spinous than those in many association areas. For example, they are more branched and more spinous than those in the lateral intraparietal area (LIP), cytoarchitectonic area 7a and the fourth visual area (cf. Elston

Figure 7. Graph of the spine density along the basal dendritic arbours of 20 horizontally projecting basal dendrites of different layer III pyramidal neurons in anterior and posterior cingulate cortex (Ant Cing and Post Cing, respectively), inferotemporal cortex (IT) and primary visual area (V1) of M. fascicularis.
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Data are averaged over 20 randomly selected dendrites of different neurons in each cortical area (mean ± SEM).
Table 4
Size of the cell bodies of layer III pyramidal cells in anterior and posterior cingulate cortex (Ant Cing and Post Cing, respectively), inferotemporal cortex (IT) and the primary visual area (V1) [mean ± SD (n)]

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<td>219.6 ± 7.36 (31)</td>
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<td>295.0 ± 6.65 (28)</td>
<td>366.4 ± 10.7 (38)</td>
<td>239.3 ± 4.44 (36)</td>
<td>146.6 ± 5.40 (31)</td>
</tr>
<tr>
<td>RS1</td>
<td>217.3 ± 8.66 (39)</td>
<td>235.5 ± 10.5 (53)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 5
Summary of animals in which data has been sampled from anterior and posterior cingulate cortex (AC and PC, respectively), inferotemporal cortex (IT) and the primary visual area (V1)

<table>
<thead>
<tr>
<th>Animal</th>
<th>Cortical areas</th>
<th>Age</th>
<th>Sex</th>
<th>No. of cells</th>
</tr>
</thead>
<tbody>
<tr>
<td>DM4</td>
<td>IT*</td>
<td>18 months</td>
<td>Male</td>
<td>21</td>
</tr>
<tr>
<td>RM12</td>
<td>V1*</td>
<td>28 months</td>
<td>Male</td>
<td>143</td>
</tr>
<tr>
<td>RM13</td>
<td>V1*</td>
<td>20 months</td>
<td>Male</td>
<td>26</td>
</tr>
<tr>
<td>RS1d</td>
<td>PC, AC</td>
<td>Unknown</td>
<td>Male</td>
<td>92</td>
</tr>
<tr>
<td>m1fl</td>
<td>IT*</td>
<td>11 years</td>
<td>Male</td>
<td>29</td>
</tr>
<tr>
<td>MF1</td>
<td>PC, AC, IT, V1</td>
<td>4½ years</td>
<td>Male</td>
<td>107</td>
</tr>
<tr>
<td>MF2</td>
<td>PC, AC, IT, V1</td>
<td>4½ years</td>
<td>Male</td>
<td>133</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td></td>
<td></td>
<td>551</td>
</tr>
</tbody>
</table>

Notes
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References