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; Colonner & 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 32 times more spinous than those in macaque V1 (cf Elston & Rosa, 1998; Elston et al., 2001).
A. Protein kinase C expression

B. SM132-immunoreactive neurones

C. Calbindin-ir pyramidal cells

D. Axonal patch size

E. Pyramidal cell arbour size

F. Pyramidal cell branching pattern

G. Number of spines in the basal dendritic arbours