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Research Report

Spinogenesis and pruning in the primary auditory cortex of the macaque monkey (*Macaca fascicularis*): An intracellular injection study of layer III pyramidal cells

Guy N. Elston[a,*], *Tsuguhisa Okamoto*[b], *Tomofumi Oga*[b], *Dimity Dornan*[c,d], *Ichiro Fujita*[b]

[a]*Centre for Cognitive Neuroscience, 60 Duke Rd, Doonan, Sunshine Coast, Queensland, 4562, Australia*
[b]*Graduate School of Frontier Biosciences, Osaka University, Machikaneyama 1-3, Toyonaka, Osaka 560-8531, Japan*
[c]*I HEAR Innovation Research Centre, Brisbane, Queensland, Australia*
[d]*Hear and Say Centre, Brisbane, Queensland, Australia*

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ABSTRACT

Recently we demonstrated that neocortical pyramidal cells in visual, visual association and prefrontal cortex of the macaque monkey are characterised by different growth, branching, spinogenesis and pruning during development. Some neurons, such as those in the primary visual area, prune more spines than they grow following sensory onset, while others such as those in area TE grow more than they prune. To what extent these different neuronal growth profiles may vary among cortical areas remains to be determined. To better comprehend the nature and extent of these regional differences in pyramidal cell growth profiles we expanded the bases for comparison by studying neurons in the primary auditory cortex (A1). We found that pyramidal cells in A1 continue to grow their basal dendritic trees beyond the peak period of spinogenesis ($3^1/_2$ months) up until at least 7 months of age. Likewise, the most prolific branching patterns were observed in the dendritic trees of pyramidal cells at 7 months of age. These data reveal that the basal dendritic trees of cells in A1 continue to grow for a much longer period, and attain almost double the number of spines, as compared with those in V1. Such differences in the growth profiles of neocortical pyramidal cells among cortical areas may influence therapeutic outcomes when applying new technologies such as neurotrophic delivery devices or stem cell therapy.

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1. Introduction

The basal dendritic trees of pyramidal cells, which comprise more than 70% of all cortical neurons (DeFelipe and Fariñas, 1992), grow in size, extend and retract branches, and grow and prune spines at different rates among cortical areas in the macaque monkey. For example, the dendritic trees of pyramidal cells in the primary visual area (V1) are at their biggest at birth, and then decrease in size by 40% during the first $3^1/_2$ months of postnatal development (Elston et al., 2009a). Pyramidal cells in inferotemporal association cortex continue to grow from birth to adulthood, doubling in size during this time (Elston et al., 2009b). Pyramidal cells in the granular prefrontal cortex also continue to grow from birth to adulthood (Elston et al., 2009a; Travis et al., 2005). These data suggest that, while the peak in exuberant connections may

* Corresponding author.
E-mail address: guyelston@yahoo.com (G.N. Elston).

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occur relatively early in postnatal development in the macaque (approximately $3^1/_2$ months (Rakic and Kornack, 2001)), neurons continue to refine their connections over an extended period of time. The magnitude of this refinement in connectivity and the period over which it occurs vary considerably in different parts of the cerebral cortex.

However, pyramidal cell development has only been quantified systematically in a handful of cortical areas, less than one tenth of the total number of areas reported in the cortical mantle (see (Felleman and Van Essen, 1991; Kaas, 2005; Northcutt, 2002) for reviews of cortical organization). Here we focus our attention on the primary auditory cortex (A1). A1, like V1, is a primary sensory area; however, unlike V1, A1 receives sensory inputs *in utero*, which have been demonstrated to be essential for the normal development of auditory processing (Mody, 2003; Vouloumanous and Werker, 2007). Thus, it might be reasonable to assume that cortical circuits mature more rapidly in A1 as compared with V1. However, surgical implantation of prosthetic cochlea has been remarkably successful in young children up to ages of 3–4 (Sharma and Dorman, 2006), suggesting that circuit refinement in auditory cortex may occur over an extended period. The present investigation was designed to probe these opposing possibilities.

2. Results

One hundred and seven pyramidal cells injected in layer III of A1 were included for analyses as they had an unambiguous apical dendrite, had their complete basal dendritic trees contained within the section, and were well filled (Table 1). These data are presented and compared with those obtained from one hundred and twenty-five cells from V1 in the right hemisphere of the same animals (Elston et al., 2009a,b) to allow comparisons of the developmental profiles of cells in these two primary sensory areas. Over 14,000 individual dendritic spines in A1 were drawn and tallied.

2.1. *Dendritic tree size*

The basal dendritic trees of pyramidal cells in A1 at 2 days of age ($59.38 \times 10^3 \pm 9.47 \times 10^3$ μm^2, mean ± standard deviation) were smaller than those observed at $3^1/_2$ months of age ($69.16 \times 10^3 \pm 11.04 \times 10^3$ μm^2), which were, in turn, smaller than those observed at 7 months of age ($84.91 \times 10^3 \pm 13.20 \times 10^3$ μm^2) (Fig. 1A). Those in the adult ($4^1/_2$ years old) were the smallest of all ($50.55 \times 10^3 \pm 7.98 \times 10^3$ μm^2). The dendritic trees of cells in the adult were less than 60% the size of those observed at

Table 1 – Vital statistics of the animals used in the present study and number of layer III pyramidal cells sampled from the primary auditory (A1) and primary visual (V1) areas that were included for analyses.

Age	Animal	Gender	Body weight (kg)	Number of cells	
				A1	V1 [a]
2D	CI9	male	0.35	21	25
3.5M	CI10	male	0.56	26	29
7M	CI8	male	0.70	27	34
4.5Y	CI12	male	2.74	33	37
Total				107	125

[a] Data sampled from references 14 and 15.

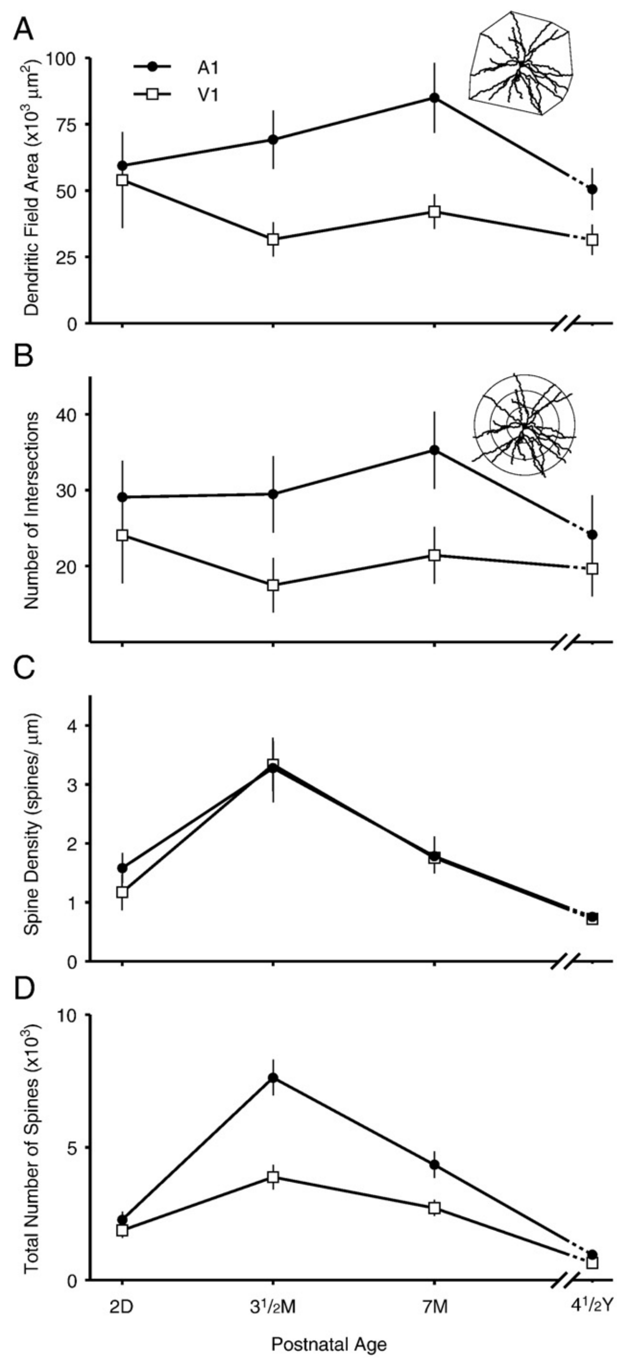

Fig. 1 – Plots of the (A) size of, (B) number of branch points in, (C) the peak spine density along and (D) total number of spines in the basal dendritic trees of layer III pyramidal neurons in the primary auditory cortex (A1) and primary visual cortex (V1). Data were sampled from animals 2 days old (2D), $3^1/_2$ months old ($3^1/_2$M), 7 months old (7M), and $4^1/_2$ years old ($4^1/_2$Y). Error bars = standard deviation.

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