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Research Report

Comparative analysis of neurogenesis between the core and shell regions of auditory areas in the chick (*Gallus gallus domesticus*)

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ABSTRACT

Early embryogenesis can reflect constituting organizations and evolutionary origins of brain areas. To determine whether a clear core-versus-shell distinction of neurogenesis that occurs from the auditory midbrain to the telencephalon in the reptile also appears in the bird, a single dose of [3H]-thymidine was injected into chick (*Gallus gallus domesticus*) eggs at some successive embryonic days (E) (from E3 to E10). Towards the end of hatching, [3H]-thymidine labeling was examined, and the results were as follows: 1) Neuronal generation in the nucleus intercollicularis (ICo) (shell region) began at E3, whereas neurogenesis began at E4 in the nucleus mesencephalicus lateralis pars dorsalis (MLd) (core region); 2) Neurogenesis initiated at E3 in the nucleus ovoidalis (Ov) shell, but initiated at E4 in the rostral Ov core. In the medial or caudal Ov core, the percentage of heavily-labeled neurons with [3H]-thymidine was significantly lower at E3 age group than that in the Ov shell; 3) In field L1 and L3, two flanking regions of the primary telencephalic auditory area (field L2a), neurogenesis started at E5, but started at E6 in field L2a. These data indicate that the onset of embryogenesis began earlier in the auditory shell areas than in the core areas from the midbrain to the telencephalon. These findings provide insight into the organization of auditory nuclei and their evolution in amniotes.

1. Introduction

Amniote auditory nuclei in the mesencephalon and diencephalon comprise two parts, the 'internal core' and the 'external shell', which differ in cytoarchitecture, physiology, neurochemistry and physiological function. Generally, the 'internal core' is compactly organized with relatively large cells, whereas the 'external shell' is diffusely organized with small cells (reptiles: Browner et al., 1981; birds: Karten, 1967, 1968; Durand et al., 1992; Zeng et al., 2004; Wild et al., 1993; mammals: Aitkin and Webster, 1972; Morest and Oliver, 1984; Faye-Lund and Osen, 1985; Huffman and Henson, 1990; Jones, 1998). Neurons in core regions respond rapidly and vigorously to auditory stimuli in frequency- and intensity-topographical manners. In contrast, neurons in shell regions respond relatively slowly to auditory stimuli without topographical organization (reptiles: Khachunts, 1982; Khachunts and Belekhova, 1986; birds: Durand et al., 1992; Cheng and Havens, 1993; mammals: Syka et al.,

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2000). Various neurotransmitters, neuromodulators and other neuroactive substances, including serotonin (5-HT), enkephalin (ENK), substance P (SP), calcitonin gene-related peptide and calbindin (CB)/ parvalbumin (PV), are richly distributed throughout shell regions, but are almost absent in core regions (reptiles: Brauth and Reiner, 1991; Belekhova et al., 2002; Zeng et al., 2007b; birds: Martinez-Vargas et al., 1976; Reubi and Jessell, 1978; Blähser and Dubois, 1980; De Lanerolle et al., 1981; Erichsen et al., 1991; Durand et al., 1993; Puelles et al., 1994; mammals: Cuello and Kanazawa, 1978; Fallon and Leslie, 1986; Nakagawa et al., 1995; Peruzzi and Dut, 2004). Additionally, the core and shell regions are located in two distinct neural pathways. The core regions are connected in an orderly manner to form a neural pathway with topographical organization, exclusively devoted to auditory relay or perception, whereas the shell regions are broadly connected with various brain areas (in or outside of the auditory system) to form diffuse neural pathways with non-topographical organization, involved in auditory

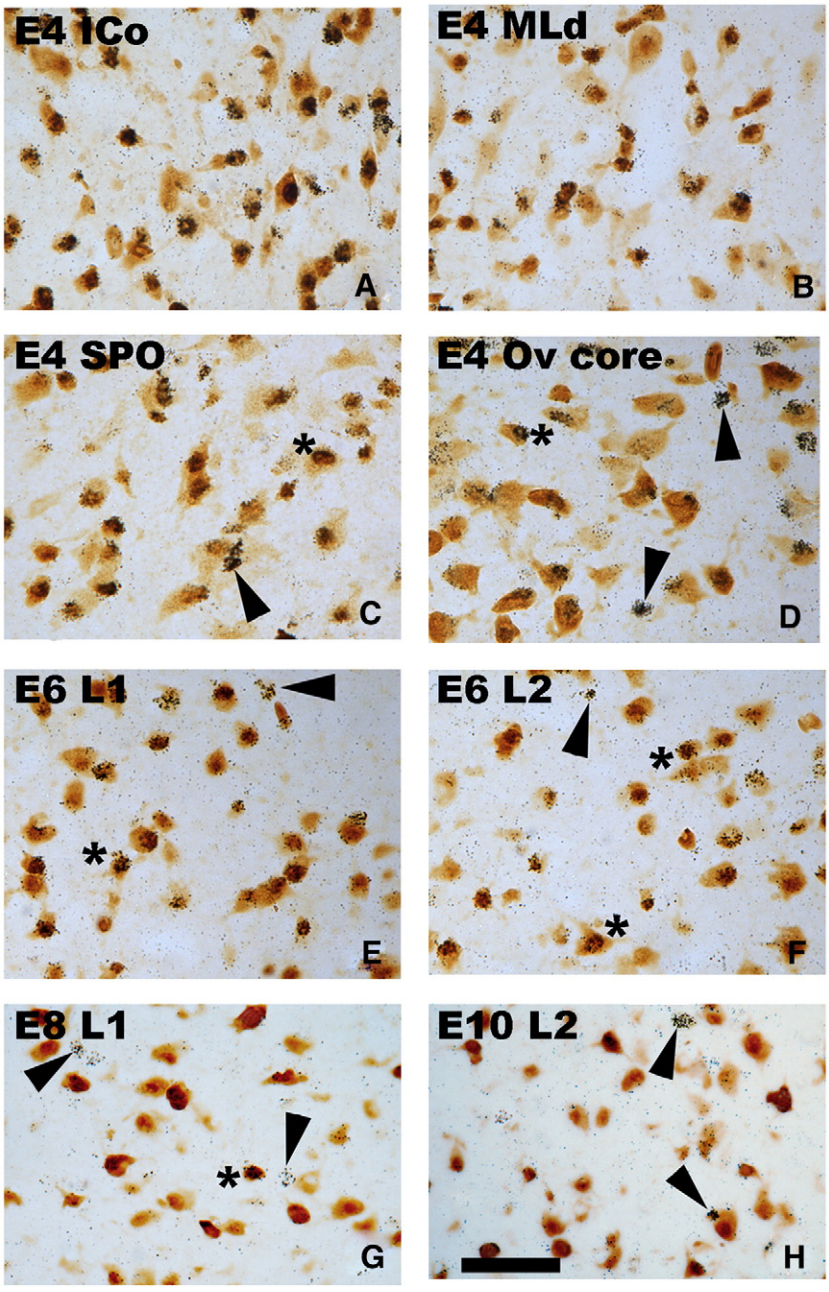

Fig. 1 – Cells labeled by [^{3}H]-thymidine and the neuronal specific marker NeuN in the chick (*G. domesticus*). A and B: Labeled cells in the nucleus intercollicularis (ICo)(A), and in the nucleus mesencephalicus lateralis pars dorsalis (MLd) at embryonic day (E) 4 age group(B). C and D: Labeled cells in the nucleus semilunaris parovoidalis (SPO)(C), and in the nucleus ovoidalis (Ov) core at E4 age group (D). E and F: Labeled cells in the telencephalic auditory areas, the field L1 (E) and L2 (F) at E6 age group. G and H: Labeled cells in the field L1 (G) at E8 age group and L2 (H) at E10 age group. Note that no double-labeled cells appear in figure H. Some cells labeled only by [^{3}H]-thymidine are marked by arrowheads, and some double-labeled by [^{3}H]-thymidine and NeuN antiserum are marked with asterisks. Scale bar represents 50 μm for A–H.