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Research Report

Calbindin D-28K and parvalbumin expression in embryonic chick hippocampus is enhanced by prenatal auditory stimulation

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ABSTRACT

Calcium-binding proteins (CaBPs) buffer excess of cytosolic Ca^{2+}, which accompanies neuronal activity following external stimuli. Prenatal auditory stimulation by species-specific sound and music influences early maturation of the auditory pathway and the behavioral responses in chicks. In this study, we determined the volume, total number of neurons, proportion of calbindin D-28K and parvalbumin-positive neurons along with their levels of expression in the developing chick hippocampus following prenatal auditory stimulation. Fertilized eggs of domestic chicks were exposed to sounds of either species-specific calls or sitar music at 65 dB for 15 min/h round the clock from embryonic day (E) 10 until hatching. Hippocampi of developmental stages (E12, E16 and E20) were examined. With an increase in embryonic age during normal development, the hippocampus showed an increase in its volume, total number of neurons as well as in the neuron proportions and levels of expression of calbindin D-28K and parvalbumin. A significant increase of volume at E20 was noted only in the music-stimulated group compared to that of their age-matched control ($p<0.05$). On the other hand, both auditory-stimulated groups showed a significant increase in the proportion of immunopositive neurons and the levels of expression of calbindin D-28K and parvalbumin as compared to the control at all developmental stages studied ($p<0.003$). The increase in proportions of CaBP neurons during development and in the sound-enriched groups suggests an activity-dependent increase in Ca^{2+} influx. The enhanced expression of CaBPs may help in cell survival by preventing excitotoxic death of neurons during development and may also be involved in long-term potentiation.

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1. Introduction

Calcium-binding proteins (CaBPs), namely calbindin-D-28K (CALB) and parvalbumin (PV) are abundant neuron-specific proteins distributed in a distinct population of neurons of the central and peripheral nervous systems of mammals, birds and other species. Although their functions in the neurons are not fully understood, they are considered to buffer a stimulated rise in intracellular free Ca^{2+}. CaBPs are also used as neuroanatomical markers (Celio, 1990; Braun, 1990; Rogers and Resibois, 1992). CALB and PV sequester the excess of Ca^{2+} during development and activity-dependent synaptic plasticity. CaBPs alter the duration of action potentials, promote neuronal bursting activity and protect neurons against the damaging effect of excessive Ca^{2+} influx (Baimbridge et al., 1992). During development, CaBPs generally appear with the

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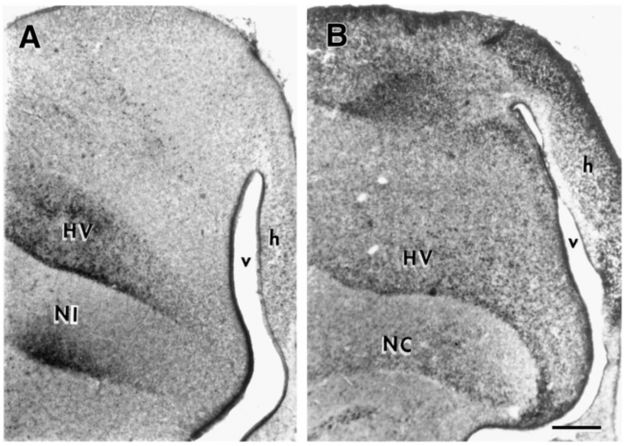

Fig. 1 – Photomicrographs of chick forebrain at E16 show the distribution of (A) calbindin and (B) parvalbumin immunoreactivity. HV—ventral hyperpallium, h—hippocampus, NI—intermediate nidopallium, NC—caudal nidopallium, v—lateral ventricle. Scale bar—200 μm.

initiation of differentiation, functional maturation or at the time of neuronal connectivity (Hendrickson et al., 1991). A local increase in intracellular Ca^{2+} in the postsynaptic spine initiates long-lasting activity-dependent enhancement in synaptic strength (Nicoll et al., 1989). A role for PV in short-term synaptic plasticity is demonstrated in paired-pulse recordings of connected interneuron Purkinje cells of mice (Caillard et al., 2000).

External environment influences the brain in all living organisms. Maternal care influences the glutamate receptor expression and neuronal survival in rat hippocampus (Bredy et al., 2003, 2004). Brief as well as long maternal deprivation decreases the density of CALB and PV neurons in the paraventricular region of rat (Giachino et al., 2007). Significant structural change such as an increase in the number and segmental length of the dendrites of pyramidal neurons of the visual cortex is observed in rats following postnatal environmental enrichment (Venable et al., 1989). Changes in the expression of a large number of genes in the cerebral cortex in response to enrichment training in mice are also reported (Rampon et al., 2000). Using auditory enrichment, Engineer et al. (2004) demonstrated remodeling and improved auditory processing in the adult rat auditory cortex, which were, however, transient. Experiments conducted by Dmitrieva and Gottlieb (1994) showed the importance of perinatal auditory stimulation in the development and maintenance of species-typical perceptual preference by devocalization of mallard and wood ducklings. Also, prenatal auditory stimulation modifies the development of species-specific auditory perception (Lickliter and Stoumbos, 1992). Prenatal sound stimulation increases the volume, neuronal area, total number of neurons and glia as well as expression of synaptic and c-fos proteins in two auditory nuclei, nucleus magnocellularis (NM) and nucleus laminaris (NL) of the chick (Wadhwa et al., 1999; Alladi et al., 2002, 2005a). The enhanced acoustic stimulation is also responsible for the survival of neurons of the auditory nuclei (Alladi et al., 2005b). There is also an increase in the neuronal size as well as the proportion of CaBP neurons in the mediorostral nidopallium/hyperpallium ventrale (MNH), an auditory imprinting area (Panicker et al., 2002) and hippocampus of chick (Chaudhury et al., 2006). Both types of sound stimulation, when given prenatally, enhance the postnatal auditory response and preference of the chicks to only the species-specific maternal calls (Jain et al., 2004). Furthermore, music plays a role in the functioning of higher brain areas even at birth (Krumhansl and Jusczyk, 1990; Trehub, 1987). Leng and Shaw (1991) proposed that music could modulate the firing patterns and enhance the ability of the cortex to accomplish development, thus improving higher brain functions. Rauscher et al. (1997, 1998) reported improvement in spatio-temporal reasoning in preschool children and maze learning in rats following an early exposure to music. Music in the perinatal period is observed to enhance learning performance and alter BDNF/TrkB signaling in mice (Chikahisa et al., 2006). Studies by Kim et al. (2006b) show an increase in neurogenesis and spatial learning in rat pups following prenatal music exposure. Also, experience such as storing and retrieving food has an effect on growth and attrition of avian hippocampus (Clayton and Krebs, 1994). Thus, there is a possibility of the learning ability being influenced by context and experience of auditory information received during early phase of development.

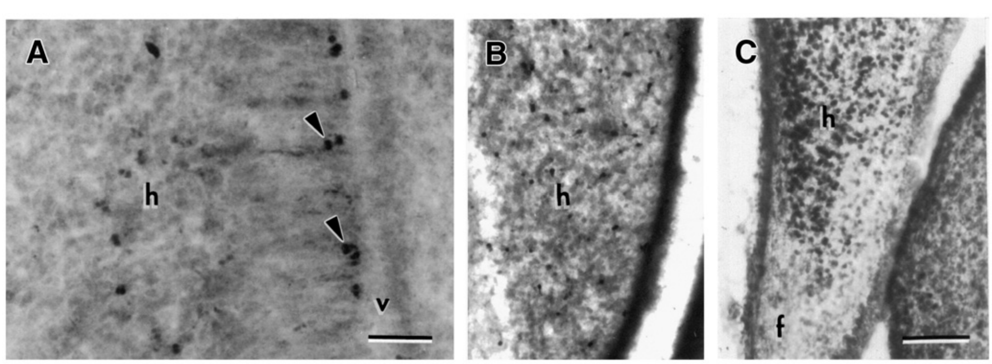

Fig. 2 – Photomicrographs of chick hippocampus at E12 show (A) the parvalbumin-positive neurons in the ventricular wall (arrowheads), and (B) distribution of parvalbumin immunoreactivity. At E16 (C), note the dense parvalbumin-positive neurons in the ventral region of the hippocampus (h). f—Fimbria, v—lateral ventricle. Scale bars—50 μm (A) and 100 μm (B, C).

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