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## Brainstem auditory time coding nuclei in the budgerigar: Anatomy

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In the avian auditory brainstem, auditory nerve afferents synapse upon the neurons of the magnocellular cochlear nucleus (MC), which in turn projects bilaterally to the nucleus laminaris (NL). This projection creates maps of interaural time difference (ITD) in the NL. The neurons of NL respond to interaural delays and project to the nuclei of the lateral lemniscus and the inferior colliculus. The organization of the ITD circuit differs among species of birds. We propose that this variation is correlated with time coding ability. The plesiomorphic pattern is found in the chicken where NL is composed of a monolayer of bipolar neurons, comprising a single map of ITD oriented in the medio-lateral direction (Young & Rubel, 1983). In comparison, the barn owl has a much larger multilayered NL. Since the budgerigar can localize sound, and since recording from the NL shows sharply tuned responses to ITD, we used immunohistochemical and Golgi techniques to examine the morphology of the NL in the budgerigar. The NL forms a multilayered structure like that of the barn owl. Like in other birds, NL neurons have dendritic arbors which change along the rostro-caudal axis, with caudal low best frequency cells having complex and long dendritic arborizations, while cells located in the rostral high best frequency region have many shorter dendrites. We also examined the relative distribution of glutaminergic excitatory and GABAergic inhibitory synapses throughout the tonotopic axis of both MC and NL by comparing the distributions of a synaptic vesicle marker (SV2) with that of glutamic acid decarboxylase (GAD). Most of the inputs to the NL cells are on their dendrites, and are therefore closer to their somas as dendrites become shorter. GAD immunohistochemistry revealed an increase in the number of GAD-positive boutons in low best frequency regions of NL. Such changes in the cell shape and distribution of inputs throughout the tonotopic axis may be associated with the ability to temporally code acoustic signals.

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