



Review article

Evolution of mammalian sound localization circuits: A developmental perspective

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ABSTRACT

Localization of sound sources is a central aspect of auditory processing. A unique feature of mammals is the smooth, tonotopically organized extension of the hearing range to high frequencies (HF) above 10 kHz, which likely induced positive selection for novel mechanisms of sound localization. How this change in the auditory periphery is accompanied by changes in the central auditory system is unresolved. I will argue that the major VGlut2⁺ excitatory projection neurons of sound localization circuits (dorsal cochlear nucleus (DCN), lateral and medial superior olive (LSO and MSO)) represent serial homologs with modifications, thus being paramorphs. This assumption is based on common embryonic origin from an Atoh1⁺/Wnt1⁺ cell lineage in the rhombic lip of r5, same cell birth, a fusiform cell morphology, shared genetic components such as Lhx2 and Lhx9 transcription factors, and similar projection patterns. Such a parsimonious evolutionary mechanism likely accelerated the emergence of neurons for sound localization in all three dimensions. Genetic analyses indicate that auditory nuclei in fish, birds, and mammals receive contributions from the same progenitor lineages. Anatomical and physiological differences and the independent evolution of tympanic ears in vertebrate groups, however, argue for convergent evolution of sound localization circuits in tetrapods (amphibians, reptiles, birds, and mammals). These disparate findings are discussed in the context of the genetic architecture of the developing hindbrain, which facilitates convergent evolution. Yet, it will be critical to decipher the gene regulatory networks underlying development of auditory neurons across vertebrates to explore the possibility of homologous neuronal populations.

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Abbreviations: aVCN, anterior ventral cochlear nucleus; DCN, dorsal cochlear nucleus; E, embryonic; GRN, gene regulatory network; LSO, lateral superior olive; MNTB, medial nucleus of the trapezoid body; MSO, medial superior olive; P, postnatal; pVCN, posterior ventral cochlear nucleus; SOC, superior olivary complex; VCN, ventral cochlear nucleus.

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An indefinite repetition of the same part or organ is the common characteristic (as Owen has observed) of all low or little-modified forms; . . . consequently it is quite probable that natural selection, during a long-continued course of modification, should have seized on a certain number of the primordially similar elements, many times repeated, and have adapted them to the most diverse purposes" (Darwin C.R., 1859).

1. Introduction

Sensory systems play a pivotal role in the exploration of the environment, in social communication, and survival. Consequently, increased sensitivity within existing senses provides broader windows to the external world. A striking example of such a process is the evolution of high frequency (HF) hearing in most mammals,¹ i.e., smooth extension of tonotopically organized hearing above 10 kHz (Fay, 1988; Grothe and Pecka, 2014; Heffner and Heffner, 2008; Manley, 2010a; Masterton et al., 1969). Most non-mammalian vertebrates do not hear significantly above this frequency range (Manley, 1971). HF hearing range in birds is limited to frequencies below 12 kHz (Dooling et al., 2000; Saunders et al., 2000) with auditory specialists, such as the barn owl, being situated at the upper limit (Gleich and Langemann, 2011; Köppl et al., 1993). Crocodiles, amphibians, and most fish do not hear above 5 kHz (Fay, 1988; Heffner and Heffner, 2008; Kenyon et al., 1998) with few conspicuous exceptions, such as some clupeiform (herring) fishes (up to 180 kHz) (Mann et al., 2001; Narins et al., 2014), some frogs (up to 34 kHz) (Feng et al., 2006; Narins et al., 2014), and pygopod (i.e. legless) geckos (up to 14 kHz) (Manley and Kraus, 2010). The extension of the mammalian hearing range into the HF region was likely positively selected for because of the benefit for sound localization (Frost and Masterton, 1994; Grothe and Pecka, 2014; Heffner and Heffner, 2008).

Comparative analyses have identified various features of mammalian ears that correlate with and enabled HF hearing (chapters 4, 5) (Manley, 2010a, 2012). In contrast, much less is known about the evolutionary trajectories of the mammalian neuronal circuits processing this information. As one important aspect of the auditory system is sound localization, the focus here is laid on neuronal circuits in the auditory brainstem that are involved in this task. Despite the fact that tetrapods (amphibians, reptiles, birds, and mammals) share a similar bauplan in the auditory brainstem, with an unusually high number of interconnected nuclei and an important role of inhibitory inputs (Fig. 1), the current view supports an independent evolution of these circuits in mammals and sauropsids (reptiles and birds) (Section 9.1) and that they represent homoplasious structures (Carr and Soares,

2002; Grothe et al., 2004; Grothe and Pecka, 2014). This likely reflects the fact that the tympanic ear evolved independently in all major tetrapod groups—the anurans, sauropsids, and mammals, as evidenced by the fossil record (Bolt and Lombard, 1985; Clack, 1997, 2002; Lombard and Bolt, 1979) and more recently by developmental genetics (Kitazawa et al., 2015) (Fig. 2).

Most models proposed so far with respect to the evolution of mammalian sound localization pathways are based on functional considerations (Carr and Soares, 2002; Christensen-Dalsgaard and Carr, 2008; Grothe et al., 2004; Grothe and Pecka, 2014). To understand the evolution of the auditory system, its development has to be analyzed as well, as changes in ontogeny underlie evolutionary changes in morphological structures (Carroll, 2008). Despite awareness of the importance of developmental information (Grothe et al., 2004), the lack of detailed data only 15 years ago precluded incorporation into previous evolutionary models. Fortunately, significant progress has been made recently in studies of the embryonic origins of auditory circuits and the gene regulatory networks (GRNs) underlying their formation (Nothwang et al., 2015; Willaredt et al., 2015b). Together with anatomical data, these studies provide novel insights into the evolutionary pathways leading to mammalian sound localization circuits.

As this review takes an evolutionary developmental perspective on the evolution of sound localization circuits, I will first outline current concepts relating to evolutionary processes in development. To understand how evolution has shaped auditory circuits, I will then provide an introduction to the acoustic cues for sound location. Then the hallmarks of the mammalian ear and the evolution of hearing in mammals will be briefly reviewed. Subsequently, anatomical and developmental data will be provided that indicate a close relationship between major thalian (marsupial and placental) projection neurons of sound localization circuits. This postulated model will represent an important framework for making predictions that can be approached experimentally. Finally, the phylogenetic relationships of vertebrate sound localization circuits will be discussed.

2. Concepts in evolutionary development

2.1. Evolutionary processes operating on development

Development produces the body plans of living organisms and novel structures are the outcome of mutational alteration of preexistent developmental programs (Carroll, 2008). Evolutionary changes are thus tightly linked to developmental processes. Three intimately interwoven evolutionary processes have been proposed to lead to new forms in organisms: (1) dissociation, (2) duplication and divergence, together with (3) co-option of developmental processes (Raff, 1996). Conducive to these processes are the modular organization of biological processes (Raff, 1996) and large genotype networks (Wagner, 2011; Wagner, 2014a).

- (1) Dissociation of developmental processes is required to allow the addition to, or subtraction of, features from an ontogeny to occur and this relies on the modular organization (see below)

¹ The definition of mammals is difficult in the fossil record, as the defining features evolved over different time periods and extinct mammals therefore represent mosaic forms (Manley, 2012; Vater et al., 2004). Concerning the middle ear, I will follow the criteria given for the definitive mammalian middle ear (DMME) *sensu* Allin and Hopson (1992); Luo (2011): an ectotympanic ring for the tympanic membrane, three middle ear ossicles, detachment of both the ectotympanic ring and the malleus from the mandible in the adult. Note that the DMME has likely evolved more than once (Allin and Hopson, 1992; Luo, 2011; Rich et al., 2005).

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