



Review

Conserved mechanisms of vocalization coding in mammalian and songbird auditory midbrain



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ARTICLE INFO

Article history:

Received 17 December 2012

Received in revised form

23 March 2013

Accepted 11 May 2013

Available online 31 May 2013

ABSTRACT

The ubiquity of social vocalizations among animals provides the opportunity to identify conserved mechanisms of auditory processing that subserve communication. Identifying auditory coding properties that are shared across vocal communicators will provide insight into how human auditory processing leads to speech perception. Here, we compare auditory response properties and neural coding of social vocalizations in auditory midbrain neurons of mammalian and avian vocal communicators. The auditory midbrain is a nexus of auditory processing because it receives and integrates information from multiple parallel pathways and provides the ascending auditory input to the thalamus. The auditory midbrain is also the first region in the ascending auditory system where neurons show complex tuning properties that are correlated with the acoustics of social vocalizations. Single unit studies in mice, bats and zebra finches reveal shared principles of auditory coding including tonotopy, excitatory and inhibitory interactions that shape responses to vocal signals, nonlinear response properties that are important for auditory coding of social vocalizations and modulation tuning. Additionally, single neuron responses in the mouse and songbird midbrain are reliable, selective for specific syllables, and rely on spike timing for neural discrimination of distinct vocalizations. We propose that future research on auditory coding of vocalizations in mouse and songbird midbrain neurons adopt similar experimental and analytical approaches so that conserved principles of vocalization coding may be distinguished from those that are specialized for each species.

This article is part of a Special Issue entitled "Communication Sounds and the Brain: New Directions and Perspectives".

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1. Introduction

Vocal communication is common among animals. The ubiquity of this behavior provides the opportunity to identify conserved mechanisms of auditory processing that underlie perception of

communication sounds. By identifying mechanisms of auditory-vocal processing that are shared across vocal communicators, we can gain insight into how human auditory processing leads to speech perception. In employing this comparative approach we can also distinguish shared mechanisms from those that are specialized for the demands of particular species, thereby providing a better understanding of the evolution of auditory processing mechanisms.

In this review, we compare auditory response properties and neural coding of social vocalizations in the auditory midbrain of laboratory mice (*Mus mus*), Mexican free-tailed bats (*Tadarida brasiliensis*) and zebra finches (*Taeniopygia guttata*). These animal groups are phylogenetically distant and have divergent behavioral repertoires, yet they all use acoustically complex vocal signals for social communication. Because these animal groups differ considerably in evolutionary history, mechanisms of vocalization processing that are common among groups are likely to represent conserved principles of auditory-vocal processing that support complex vocal communication.

Abbreviations: A1, primary auditory cortex; CF, characteristic frequency; dB, decibels; DCN, dorsal cochlear nucleus; DNLL, dorsal nucleus of the lateral lemniscus; IC, inferior colliculus; ICC, central nucleus of the inferior colliculus; INLL, intermediate nucleus of the lateral lemniscus; kHz, kilohertz; LLD, dorsal nucleus of the lateral lemniscus; LLI, intermediate nucleus of the lateral lemniscus; LLV, ventral nucleus of the lateral lemniscus; LSO, lateral superior olive; MGB, medial geniculate body; MLd, lateral dorsal mesencephalon; MSO, medial superior olive; ms, millisecond; NA, nucleus angularis; NL, nucleus laminaris; NM, nucleus magnocellularis; OC, olivocochlear nucleus; Ov, nucleus ovoidalis; RA, robust nucleus of the arcopallium; SON, superior olivary nucleus; SPN, superior paraolivary nucleus; VCN, ventral cochlear nucleus; VNLL, ventral nucleus of the lateral lemniscus.

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Our focus is on the auditory midbrain because it is the first region in the ascending auditory system where individual neurons show complex tuning properties that are correlated with the acoustics of social vocalizations. This is true in mammals (Andoni et al., 2007; Holmstrom et al., 2007; Andoni and Pollak, 2011; Mayko et al., 2012) birds (Woolley et al., 2005, 2006, 2009; Schneider and Woolley, 2010, 2011) and frogs (Edwards et al., 2002, 2007; Elliott et al., 2011), and is therefore a general principle of auditory processing. The coding properties of auditory midbrain neurons are also important to understand because they provide the major input to the thalamus and cortex. Distinguishing between response properties that emerge in the cortex and those that are inherited from subcortical circuits requires an understanding of midbrain response properties. Indeed, it is well known that several response properties important for coding complex sounds emerge at the level of the auditory midbrain rather than the auditory cortex (Casseday et al., 1994; Portfors and Wenstrup, 2001; Nataraj and Wenstrup, 2005; Woolley et al., 2005, 2006; Xie et al., 2005; Schneider and Woolley, 2011).

2. Ascending inputs to the auditory midbrain in mammals and birds

The ascending auditory pathways in mammals and birds are highly conserved (Butler and Hodos, 2005; Butler et al., 2011). The auditory midbrain is a nexus of auditory processing; it receives and integrates information from multiple parallel pathways and provides the ascending auditory input to the thalamus (Fig. 1). The avian auditory midbrain is traditionally called the lateral dorsal mesencephalon (MLd) because of its anatomical location, but this nucleus is homologous to the mammalian central nucleus of the inferior colliculus (IC; Grothe et al., 2004; Covey and Carr, 2005). The IC and MLd receive inputs directly from contralateral and ipsilateral cochlear nuclei, from lateral lemniscal nuclei and from the contralateral auditory midbrain (Conlee and Parks, 1986; Krutzfeldt et al., 2010; see Fig. 1 for details). The IC and MLd also receive ascending input from other brainstem nuclei, including the

superior olivary complex and superior paraolivary nucleus in mammals (Winer and Schreiner, 2005 for review), and the superior olivary nucleus in songbirds (Wild et al., 2010).

One major difference in the auditory systems of mammals and songbirds is the organization of descending projections to the midbrain. The IC receives descending input from the auditory thalamus and cortex (Saldana et al., 1996; Winer et al., 1998). The songbird MLd receives descending input from the pathway that parallels and surrounds the song motor pathway, specifically the “cup” surrounding the robust nucleus of the arcopallium (RA), a motor cortex-like forebrain region that is necessary for song production (Fig. 1B; Mello et al., 1998). Thus, top-down influences on midbrain auditory processing may differ considerably between mammals and songbirds. Descending inputs to IC contribute to plasticity and learning (Gao and Suga, 2000; Zhang and Suga, 2005; Bajo et al., 2010), whereas the functional roles of descending inputs to MLd are unknown. The projections from RA cup to MLd and its surrounding region may convey information about vocal motor commands to the ascending auditory system. However, the sensory–motor interactions between descending vocal control circuits and subcortical auditory circuits remain to be studied.

3. Mice, bats and songbirds are good models for auditory processing

Our focus in this review is on mice, bats and songbirds because the neural mechanisms underlying vocalization coding in the auditory midbrain have been most well studied in these groups and, as described below, each group offers unique advantages for understanding mechanisms of auditory processing. A few studies in mammals with low frequency hearing (cat, guinea pig) have examined neural responses to vocalizations in the IC (Aitkin et al., 1994; Suta et al., 2003). In all of these studies, the stimuli were limited to a few representative vocalizations and analyses included only basic measures of response properties such as average firing rate. In general, vocalizations tend to evoke higher firing rates in the IC of cat and guinea pig compared to pure tones, noise or

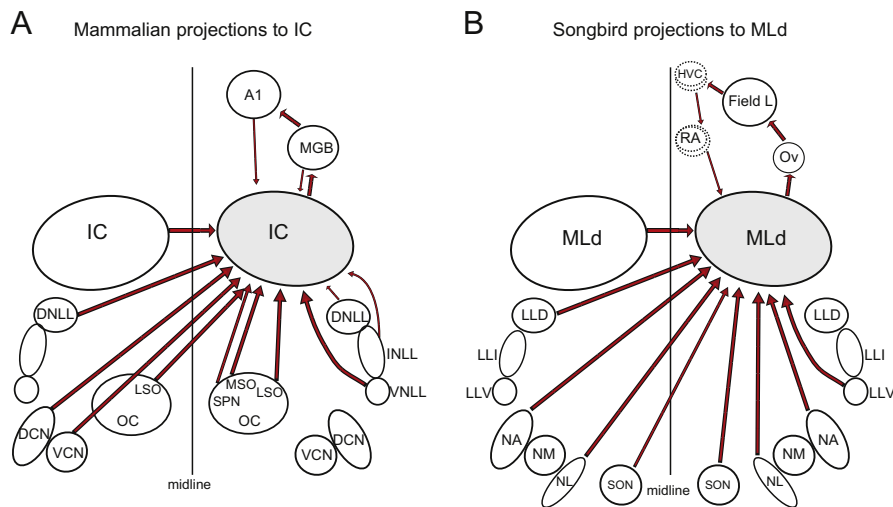


Fig. 1. Schematic diagram of the major pathways to and from the right side auditory midbrain. To facilitate focusing solely on auditory midbrain projections, we have omitted projections in the brainstem that do not go to the midbrain. A. Inferior colliculus (IC) of the mouse. Abbreviations are A1, primary auditory cortex; DCN, dorsal cochlear nucleus; DNLL, dorsal nucleus of the lateral lemniscus; INLL, intermediate nucleus of the lateral lemniscus; LSO, lateral superior olive; MGB, medial geniculate body; MSO, medial superior olive; OC, olivocochlear nucleus; SPN, superior paraolivary nucleus; VCN, ventral cochlear nucleus; VNLL, ventral nucleus of the lateral lemniscus. B. Dorsal lateral mesencephalon (MLd) of the songbird. Abbreviations are LLD, dorsal nucleus of the lateral lemniscus; LLI, intermediate nucleus of the lateral lemniscus; LLV, ventral nucleus of the lateral lemniscus; NA, nucleus angularis; NL, nucleus laminaris; NM, nucleus magnocellularis; Ov, nucleus ovoidalis; RA, robust nucleus of the arcopallium; SON, superior olivary nucleus. Note: HVC is the proper name of the primary vocal control nucleus. The dashed lines around HVC and RA refer to the “shelf” and “cup” regions, respectively. These regions and their projections form a descending pathway to MLd and the region surrounding MLd.

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