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Research paper

Development of functional organization of the pallid bat auditory cortex

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Abstract

The primary auditory cortex is characterized by a tonotopic map and a clustered organization of binaural properties. The factors involved in the development of overlain representation of these two properties are unclear. We addressed this issue in the auditory cortex of the pallid bat. The adult pallid bat cortex contains a systematic relationship between best frequency (BF) and binaural properties. Most neurons with BF <30 kHz are binaurally inhibited (EO/I), while most neurons with BF >30 kHz are monaural (EO). As in other species, binaural properties are clustered. The EO/I cluster contains a systematic map of interaural intensity difference (IID) sensitivity. We asked if these properties are present at the time the bat acquires its full audible range (postnatal day [P] 15). Tonotopy, relationship between BF and binaural properties, and the map of IID sensitivity are adult-like at P15. However, binaural facilitation is only observed in pups older than P25. Frequency selectivity shows a BF-dependent sharpening during development. Thus, overlain representation of binaural properties and tonotopy in the pallid bat cortex is remarkably adult-like at an age when the full audible range is first present, suggesting an experience-independent development of overlapping feature maps.

Keywords: Development; Auditory cortex; Feature maps; Binaural selectivity; Pallid bat; Tonotopy

1. Introduction

Both experience-dependent and -independent factors guide the development of topographic maps and response properties in the central nervous system. The relative contributions of these factors have been extensively studied in the visual and somatosensory systems (Fox, 1996; Katz and Shatz, 1996; Naegele et al., 1988). The general picture emerging from these studies is that experience-independent factors, such as gradients of chemicals and/or correlated spontaneous activity, guide the initial gross topography, while sensory-driven activity is involved in the subsequent refinement of maps. Similarly, response properties such as receptive field diameters (Carrasco et al., 2005), ocular dominance (Crowley and Katz, 2002) and orientation selectivity (Chapman et al., 1999) may also be initially shaped by experience-independent factors, and require visual experience for further refinement or maintenance.

Studies on the development of primary auditory cortex (A1) have focused on excitatory frequency selectivity and tonotopy. While the time course of maturation of tonotopy shows species-specific differences, the initial formation of tonotopy appears to be driven by experience-independent factors (Bonham et al., 2004; Eggermont, 1996; Pienkowski and Harrison, 2005; Zhang et al., 2001). Experience with sound is, however, important for either the refinement or maintenance of tonotopy, as evidenced by the effects of partial lesions of the cochlea or noise-rearing on tonotopy in A1 (Harrison et al., 1993; Zhang et al., 2001). Frequency

Abbreviations: A1, primary auditory cortex; BF, best frequency; CL, contralateral; EE, generic term for binaurally excited neuron; EI or EO/I, term for binaurally inhibited neuron; EO or EO/O, monaural neuron; EO/F, binaurally facilitated neuron; EO/FI, binaurally facilitated and inhibited neuron; FM, frequency modulated; IID, interaural intensity difference; IL, ipsilateral; IT, inhibitory threshold measured in IID values; P, postnatal day

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selectivity shows a protracted period of sharpening or broadening following hearing onset, and may depend on sensory-driven activity (Bonham et al., 2004; Zhang et al., 2001). Thus, A1 appears to be similar to other sensory cortices in the development of topographical representation of the receptor surface.

Besides tonotopy, A1 is characterized by non-random distributions of other response properties (reviewed in Brugge, 1985; Ehret, 1997; Read et al., 2002). The best studied of these is binaural selectivity. A consistent finding is that cortical neurons with similar binaural properties occur in clusters (Imig and Adrian, 1977; Middlebrooks et al., 1980; Reale and Kettner, 1986; Nakamoto et al., 2004; Kelly and Sally, 1988; Kelly and Judge, 1994; Liu and Suga, 1997; Shen et al., 1997; Recanzone et al., 1999; Rutkowski et al., 2000; Velenovsky et al., 2003). In cats and ferrets, clusters of neurons with different binaural properties such as binaural inhibition (EI) and excitation (EE) are represented orthogonal to the isofrequency contours (Imig and Adrian, 1977; Kelly and Judge, 1994). This form of organization has given rise to the idea that isofrequency contours form functional subunits in A1 (Read et al., 2002). Binaural cues change as the head and ear morphology change during development. It has been shown that binaural selectivity of individual A1 neurons is adult-like before ear and head morphology become adult-like (Brugge et al., 1988). That is, binaural properties are mature while frequency selectivity is still undergoing developmental changes. However, the maturation of the clustered representation of binaural selectivity and its relationship to tonotopy has not been studied. The main objective of this study was to address this issue in the auditory cortex of the pallid bat.

The pallid bat is well suited to address this developmental issue for three reasons. First, it is an altricial species in which hearing development has been well characterized (Brown, 1976). Second, the cortical representation of response properties has been studied in the adult. Binaural selectivity shows a frequency-dependent distribution in adult cortex (Razak and Fuzessery, 2002). Most neurons with best frequencies (BF) <30 kHz are binaurally inhibited (EO/I type), while most neurons with BF >30 kHz are not influenced by binaural stimulation (monaural or EO type). The pallid bat is a gleaning bat that uses passive hearing of prey-generated noise (5–35 kHz) for prey localization, while reserving echolocation (downward frequency-modulated sweeps, 60–30 kHz) for obstacle avoidance. In the adult cortex, most neurons with BF <35 kHz are selective for noise, while most neurons with BF >35 kHz are downward frequency-modulated (FM) sweep-selective. Because of the relationship between BF and noise- or FM sweep-selectivity, most noise-selective neurons are binaurally inhibited, while most FM sweep-selective neurons are monaural. Thus, binaural sensitivities are largely different in the two regions representing noise and downward FM sweeps, two sounds used in two different behaviors. In this study, we examined the development of frequency selectivity, binaural properties, and the systematic spatial relationship between these properties.

A second reason for studying the development of cortical binaural topography in the pallid bat is because it is the only species in which a systematic representation of interaural intensity difference (IID) sensitivity has been reported (Razak and Fuzessery, 2002). Within the noise-selective region, the cluster of EO/I neurons has a systematic representation of IID sensitivity (Razak and Fuzessery, 2000, 2002). This study examined the development of this IID map. We report that adult-like tonotopy, clustered organization of binaural properties, the relationship between BF and binaural type, and the systematic map of IID selectivity are present in the youngest pups examined. However, binaural facilitation is not present until P25 and frequency selectivity is not adult-like up to P40.

2. Materials and methods

Recordings were obtained from the auditory cortex of both cortical hemispheres in pallid bat pups that were born and raised in the University of Wyoming animal facility. Pregnant bats were netted in New Mexico and transported to the animal care facility at the University of Wyoming. The bats were maintained in cages and fed mealworms raised on ground Purina rat chow. Their room was heated, and maintained on a reversed 12:12 h light:dark cycle. When pups were born, the mom and her pups were moved to another cage to keep track of the pups' ages. Pups born within three days of each other were housed together. Therefore, the ages reported in this paper are accurate to within three days. The pups and moms remained in their cages until the day of recording from the pups.

2.1. Surgical procedures

The procedures used in pups were identical to those used in adults, and reported previously (Razak and Fuzessery, 2002). Recordings were obtained from bats that were anesthetized with Metofane (methoxyflurane) inhalation, followed by an intraperitoneal injection of pentobarbital sodium (30 μg/g body wt) and acepromazine (2 μg/g body wt). To expose the auditory cortex, the head was held in a bite bar, a midline incision was made in the scalp, and the muscles over the dorsal surface of the skull were reflected to the sides. The front of the skull was scraped clean and a layer of glass microbeads applied, followed by a layer of dental cement. The bat was then placed in a Plexiglas restraining device. A cylindrical aluminum head pin was inserted through a cross bar over the bat's head and cemented to the previously prepared region of the skull. This pin served to hold the bat's head secure during the recording session. The location of the auditory cortex was determined relative to the rostrocaudal extent of the midsagittal sinus, the distance laterally from the midsagittal sinus, and the location of a prominent lateral blood ves-