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Corticofugal modulation of directional sensitivity in the midbrain of the big brown bat, *Eptesicus fuscus*

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Abstract

In our recent study of corticofugal modulation of collicular amplitude sensitivity of the big brown bat, *Eptesicus fuscus*, we suggested that the corticofugal modulation is based upon the best frequency (BF) differences and the relative amplitude sensitivity difference between collicular (IC) and cortical (AC) neurons but not the absolute amplitude sensitivity of IC and AC neurons. To show that corticofugal modulation is systematic and multiparametric, we studied corticofugal modulation of directional sensitivity in 89 corticofugally inhibited IC neurons in the same bat species under free field stimulation conditions. A neuron's directional sensitivity was expressed with the azimuthal range (AR) at 50% below the maximum of each directional sensitivity curve and the best azimuth (BAZ) at which the neuron discharged maximally. Cortical electrical stimulation did not affect the directional sensitivity of 40 (45%) neurons with $\mathrm{BF}_{\mathrm{IC-AC}}$ differences of 7.3 ± 4.4 kHz but sharpened the directional sensitivity of other 49 (55%) neurons with $\mathrm{BF}_{\mathrm{IC-AC}}$ differences of 2.3 ± 1.8 kHz. Corticofugal modulation sharpened directional sensitivity curves of IC neurons by decreasing the AR and shifting collicular BAZ toward cortical BAZ. The decrease in AR and the shift in BAZ increased significantly with $\mathrm{AR}_{\mathrm{IC-AC}}$ and $\mathrm{BAZ}_{\mathrm{IC-AC}}$ differences but not with absolute AR and BAZ of IC and AC neurons or $\mathrm{BF}_{\mathrm{IC-AC}}$ differences. Corticofual modulation also shifted collicular BF toward cortical BF. The shift in BF increased significantly with $\mathrm{BF}_{\mathrm{IC-AC}}$ differences but not with the BF of IC and AC neurons or BAZ shift. Consonant with our previous study, these data indicate that corticofugal modulation of collicular directional sensitivity is based on topographic projections between the IC and the AC and the difference in directional sensitivity but not the absolute directional sensitivity of IC or AC neurons.

Keywords: Auditory cortex; Bat; Corticofugal modulation; Directional sensitivity; Frequency; Inferior colliculus; Inhibition

1. Introduction

The fact that sound direction affects the responses of auditory neurons has been demonstrated in many studies. For example, using the bat as the mammalian model system, numerous studies have shown that most neurons in the central nucleus of the inferior colliculus (abbreviated as IC neurons) increase threshold and decrease the number of impulses when a sound azimuth changes from 40° contralateral (c40°) to 40° ipsilateral (i40°) within the frontal auditory space (Fuzessery and Pollak, 1985; Grinnell, 1963; Grinnell and Griennell, 1965; Grothe et al., 1996; Jen and Sun, 1984; Jen and Wu, 1993; Jen et al., 1987, 1989; Makous and O'Neill, 1986; Poon et al., 1990; Schlegel, 1977; Schlegel et al., 1988; Shimozawa et al., 1984; Sun and Jen, 1987; Wu and Jen, 1996; Zhou and Jen, 2000c, 2002, 2004). These studies also showed

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Abbreviations: AC, auditory cortex; AR, azimuthal range; BA, best amplitude; BAZ, best azimuth; BF, best frequency; IC, inferior colliculus; MT, minimum threshold; $\mathrm{AR}_{\mathrm{IC-AC}}$, $\mathrm{BAZ}_{\mathrm{IC-AC}}$, and $\mathrm{BF}_{\mathrm{IC-AC}}$, differences in AR, BAZ, and BF between IC and AC neurons; pps, pulses per second; PST, peri-stimulus time; SPL, sound pressure level

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that high best frequency (BF) neurons have sharper directional sensitivity than low BF neurons. In addition, the shape of directional sensitivity curves and the angle of maximal sensitivity of most neurons vary with sound amplitude (Grothe et al., 1996; Schlegel et al., 1988). Because sound pressure transformation at the pinna varies with sound direction (Chen et al., 1995; Jen and Chen, 1988) and pinna position affects the spatial sensitivity of auditory neurons (Jen and Sun, 1984; Sun and Jen, 1987), it has been suggested that the directional properties of the pinna and the binaural interaction contribute to the directional sensitivity of IC neurons (Fuzessery and Pollak, 1985; Schlegel et al., 1988; Wenstrup et al., 1988). Sound direction also affects the frequency tuning properties of auditory neurons. For example, the excitatory frequency tuning curves of most IC neurons are sharper when plotted at ipsilateral than at contralateral azimuths (Jen and Wu, 1993; Jen and Zhang, 2000; Zhang et al., 2000). A change of sound direction affects mostly on frequency tuning properties of IC neurons near the minimum threshold (MT) at the BF; similar to the studies in mice and frogs (Cain and Jen, 1999; Gooler et al., 1993, 1996; Xu et al., 1994; Zhang et al., 1999). Furthermore, it has been shown that the directional sensitivity and the direction-dependent frequency tuning properties of most IC neurons are primarily shaped by GABAergic inhibition (Jen and Zhang, 2000; Lu and Jen, 2001, 2003; Zhang et al., 1999; Zhou and Jen, 2002).

The processing of auditory information including sound direction has traditionally been explained by neural interactions of divergent and convergent projections within the ascending auditory system (Suga, 1997; Suga et al., 1998). However, recent studies showed that the massive corticofugal system adjusts and improves subcortical multi-parametric auditory signal processing in bats, cats, guinea pigs, mice, and rats (Jen and Zhang, 1999; Jen and Zhou, 2003; Jen et al., 1998, 2001, 2002, 2003; He, 1997, 2003; He et al., 2002; Ma and Suga, 2001a,b; Popelar et al., 2003; Suga et al., 1998, 2002; Sun et al., 1989, 1996; Syka and Popelar, 1984; Torterolo et al., 1998; Villa et al., 1991; Yan and Ehret, 2002; Yan and Suga, 1996; Zhang and Suga, 1997; Zhang et al., 1997, 2000; Zhou and Jen, 2000a,b). The corticofugal system also reorganizes (neuroplasticity) subcortical frequency map on the basis of sensory experience (including associative learning) (Gao and Suga, 1998, 2000; Suga et al., 1997; Yan and Ehret, 2001; Yan and Suga, 1998; Zhang and Suga, 2000). Anatomical studies have shown that the corticofugal system is topographically as well organized as the ascending auditory system (Andersen et al., 1980; Druga et al., 1997; Feliciano et al., 1995; Games and Winer, 1988; Herbert et al., 1991; Huffman and Henson, 1990; Kelly and Wong, 1981; Malmierca et al., 1996; Saldaña et al., 1996; Winer et al., 1998, 2001, 2002). For example, cortico-geniculate fibers originated from the deep layers of the auditory cortex (AC) topographically project to the ipsilateral ventral, ovoid, and dorsal nuclei of the medial geniculate body. The cortico-collicular fibers project bilaterally to the pericentral nucleus, the external nucleus, and the dorsomedial division of the IC, although the ipsilateral projection is much more extensive and topographically organized than the contralateral projection. In addition, cortical fibers also project bilaterally to the subcollicular nuclei such as the superior olivary complex and the cochlear nucleus.

In our studies of corticofugal modulation of collicular signal processing, we have shown that cortical electrical stimulation decreases the number of impulses, sharpens the frequency tuning curve, compresses the rate-amplitude function, and decreases the auditory spatial response area of IC neurons (Sun et al., 1989, 1996; Jen et al., 1998, 2001, 2002, 2003; Jen and Zhang, 1999; Zhou and Jen, 2000a,b). We have also shown that the effect of corticofugal modulation is direction-dependent. For example, cortical electrical stimulation increases the MT of IC neurons at a greater degree at i40° than at c40°. Conversely, cortical electrical stimulation sharpens the frequency tuning curves at a greater degree at c40° than at i40° (Zhang et al., 2000). However, these studies did not examine how corticofugal modulation of auditory signal processing of IC neurons was related to auditory sensitivity of AC neurons.

To determine the relationship of auditory sensitivity between IC and AC neurons during corticofugal modulation, we recently studied corticofugal modulation of amplitude sensitivity of IC neurons in the big brown bat, *Eptesicus fuscus* (Jen and Zhou, 2003). We showed that cortical electrical stimulation shifted collicular amplitude sensitivity toward cortical amplitude sensitivity when the $\mathrm{BF}_{\mathrm{IC-AC}}$ differences between IC and AC neurons were small ($1.6 \pm 1.4\,\mathrm{kHz}$) and IC neurons had lower MT than corresponding AC neurons. We have suggested that the corticofugal modulation is based upon $\mathrm{BF}_{\mathrm{IC-AC}}$ differences and amplitude sensitivity difference between IC and AC neurons but not the absolute amplitude sensitivity of IC and AC neurons.

To show that this systematic corticofugal modulation of collicular auditory sensitivity is multiparametric, we studied corticofugal modulation of directional sensitivity of IC neurons in the same bat species under free field stimulation conditions. Specifically, we examined how corticofugal modulation of directional sensitivity of IC neurons might be related to difference in the directional sensitivity between IC and AC neurons.

2. Materials and methods

As in our previous studies (Jen and Zhou, 2003; Jen et al., 1998, 2001; Sun et al., 1996; Zhou and Jen, 2000a,b), one or two days before the recording session, a 1.8 cm nail was glued onto the exposed skull of each of 30 Nembutal-