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Research Report

Inferior colliculus stimulation causes similar efferent effects on ipsilateral and contralateral cochlear potentials in the guinea pig

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ARTICLE INFO

Article history:

Accepted 16 January 2006

Available online 28 February 2006

Keywords:

Hearing

Cochlea

Inferior colliculus

Efferent

Guinea pig

ABSTRACT

The inferior colliculus (IC) is a processing center in both the ascending and descending auditory pathways. It has been demonstrated anatomically to send descending projections to the region of the medial olivocochlear (MOC) neurons in the auditory brainstem. Activation of MOC system produces reductions in cochlear neural activity. Individual MOC fibers innervate relatively restricted regions of the cochlea. Recent studies have shown that selective electrical stimulation within the IC central nucleus (ICC) produces frequency-specific reductions of neural activity in the contralateral cochlea (Ota, Y., Oliver, D.L., Dolan, D.F., 2004. Frequency-specific effects on cochlear responses during activation of the inferior colliculus in the guinea pig. *J. Neurophysiol.* 91, 2185–2193). This efferent effect is likely mediated through selective activation of MOC cells. In this study, we investigated the effects of selective stimulation of one ICC on cochlear output in both ears in anesthetized and paralyzed guinea pigs to explore possible differences in the effective efferent innervation of the two ears. ICC stimulation had a similar tonotopically tuned effect on the distortion product otoacoustic emission (DPOAE) and the cochlear whole-nerve action potential (CAP) in each cochlea. The bandwidth of the efferent effect in each ear was measured and compared at different stimulation levels. For a given ICC stimulation site, the efferent effects were larger for the CAP response. The effect on each response measure was greater in the contralateral than the ipsilateral ear. The effective bandwidth of the efferent effect on the CAP was current-level-dependent but less so for the DPOAE. The results of transections at various locations within the brainstem suggest that the effects were mediated by the MOC system. From the results presented here, the descending efferent system, which originates in the auditory cortex, has frequency-specific, spatially restricted, bilateral effects. The effects are greater in the contralateral ear.

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1. Introduction

Portions of the ascending auditory system receive input from a descending, efferent system originating in various cortical

regions. The efferent pathway descends along a path that closely follows the ascending system. In general, the descending projections from the cortex go to the medial geniculate body (MGB) and inferior colliculus (IC), from the IC to the

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superior olivary complex (SOC) and cochlear nucleus (CN) (Huffman and Henson, 1990; Spangler and Warr, 1991). The IC is divided into a central nucleus (ICC) surrounded by a dorsal (ICD) and lateral cortex (LC) (Faye-Lund, 1985; Faye-Lund and Osen, 1985; Morest and Oliver, 1984). The IC sends projections to the dorsal nucleus of the lateral lemniscus and CN as well as the SOC and rostral periolivary region of the SOC where the cells of the olivocochlear system reside (Caicedo and Herbert, 1993; Schofield, 2001; Shore et al., 1991; Syka et al., 1988a,b; Thompson and Thompson, 1993; Vetter et al., 1993).

Each cochlea receives efferent innervation, which originates bilaterally from cells in the brainstem around the SOC (Brown, 1989; Guinan et al., 1983; Liberman and Brown, 1986; Rasmussen, 1946; Robertson, 1985; Warr, 1975, 1978, 1992; Warr and Guinan, 1979). The olivocochlear system is divided into two subsystems based on cell location within the SOC and destination within the cochlea (Guinan et al., 1983; Warr and Guinan, 1979). The cells giving rise to the lateral olivocochlear system (LOCS) are located in and around the lateral region of the SOC and terminate primarily on ipsilateral afferent dendrites under the inner hair cell (IHC) (Guinan et al., 1983; Liberman and Brown, 1986). The cells of the medial olivocochlear system (MOCS) are located in the medial region of the SOC and terminate on the outer hair cells (OHCs).

While the most extensively studied of these two efferent systems is the MOCS, a recent study (Groff and Liberman, 2003) suggests a significant role for the LOCS. The MOCS forms a feedback loop in which acoustic activation causes efferent fiber discharge activity in the cochlea (Brown, 1989; Liberman, 1988a,b; Liberman and Brown, 1986; Robertson, 1984; Robertson and Gummer, 1985). MOCS fibers are divided in terms of their response to acoustic stimulation. The suppressive effects of these efferents are mediated by releasing acetylcholine (ACh), which binds to the $\alpha 9/\alpha 10$ ACh receptors causing Ca^{2+} to enter, resulting in the activation of K^+ channels (Housley and Ashmore, 1991). MOC fibers innervating a given ear respond preferentially to one ear or the other (Brown, 1989; Liberman, 1988a,b). Most MOC neurons responding to sound in the ipsilateral ear have their cell bodies on the side of the brainstem opposite the ear they innervate. The neurons responsive to the contralateral ear have cell bodies on the same side of the brainstem as the ear they innervate (Liberman and Brown, 1986). The majority of efferent fibers respond only to stimulation of one ear. The percent of ipsilateral vs. contralateral responsive efferent fibers closely matches the percent of labeled cells in the ipsilateral vs. contralateral brainstem (Brown, 1989; Liberman and Brown, 1986; Robertson, 1985; Robertson and Gummer, 1985; Warr, 1978). Acoustic stimulation of both ears simultaneously revealed complex binaural interactions not predicted by the simple monaural stimulation studies (Liberman, 1988a,b). The sound-activated feedback loop of the olivocochlear system may involve the descending projections from the IC to the SOC (Caicedo and Herbert, 1993; Mulders et al., 2003; Mulders and Robertson, 2002; Schofield and Cant, 1999; Thompson and Thompson, 1993; Vetter et al., 1993). These binaural interactions may take place as a result of interactions within the SOC or from higher central nervous system inputs to the SOC region.

In contrast to acoustic activation, the MOCS can be activated by electrically stimulating the crossed olivocochlear

bundle (COCB), at the floor of the 4th ventricle, where the crossing MOC fibers converge (Desmedt, 1962; Dolan and Nuttall, 1988; Galambos, 1956; Wiederhold and Kiang, 1970). Gross electrical stimulation of the COCB activates most, if not all, of the crossing MOC fibers and causes broad suppressive effects throughout the cochlea. The olivary brainstem regions giving rise to the peripheral MOCS receive descending projections from higher brainstem locations. Recent studies have shown that electrical stimulation of the IC results in functional efferent effects on the cochlea (Groff and Liberman, 2003; Mulders and Robertson, 2000, 2002, 2005; Ota et al., 2004; Popelar et al., 2002; Rajan, 1988, 1990; Scates et al., 1999). Ota et al. (2004) showed that ICC stimulation caused localized, frequency-specific reductions of the CAP in the contralateral ear. This is consistent with a tonotopic feedback projection from the ICC to the lower brainstem (Malmierca et al., 1996).

This study compares the effect of localized electrical stimulation of one ICC on the CAP and the DPOAE in both the ipsilateral (to the stimulated ICC) and contralateral ears. The bandwidth of the efferent effect in each ear was measured and compared at different stimulation levels. The DPOAE and CAP represent different aspects of cochlear function. The CAP is the neural output and the end product of the cochlear transduction processes. The DPOAE reflects activity of the OHC. This study addresses the functional issue whether localized activation within the ICC causes a similar efferent effect in each ear. The results showed that, in general, the frequency region of the efferent effect on the two responses was similar in both ears. The efferent effects were always greater in magnitude in the contralateral ear. Transection of the commissure of the IC had no effect on the efferent reduction in either ear. Transection of the floor of the 4th ventricle eliminated the efferent effect in the contralateral ear but not the ipsilateral ear. An off-midline transection eliminated the efferent effect in the ear on the side of the cut. The bandwidth of the efferent effect on the CAP in the contralateral ear was dependent on current level. There was no significant difference in the bandwidth of the effect on the CAP between the two ears. With the exception of one current level, there were no significant differences in the bandwidth of the effect on the DPOAE between the two ears. With one exception, within-ear comparisons of the bandwidth of the efferent effect on the two response measures were similar.

2. Results

2.1. Contralateral and ipsilateral ears

A comparison of the effects of ICC stimulation on the CAP recorded from the contralateral and ipsilateral ears from three animals are shown in Figs. 1A–C. The current level applied to the ICC in each case (and for each subsequent figure) is shown in the figure. In each case, the tone burst was set at 10 dB above threshold. For each ear, the reduction in CAP amplitude was expressed as percent of the control response. In each case, the affected frequency region was similar in the two ears. In general, the efferent effect was greater in the contralateral ear. Data shown in Fig. 1A show an efferent effect at a higher frequency compared to Figs. 1B and C. This is consistent with

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