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Research paper

Effects of activation of the efferent system on psychophysical tuning curves as a function of signal frequency

Vinay [a,*], Brian C.J. Moore [b]

[a] *All India Institute of Speech and Hearing, Manasagangothri, Mysore 570006, India*
[b] *Department of Experimental Psychology, Cambridge University, Downing Street, Cambridge CB2 3EB, United Kingdom*

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A B S T R A C T

It has been shown that electrical stimulation of the efferent auditory system can influence neural tuning curves in animals. Here, we examined a psychophysical analog of this effect in humans. All of the 19 normally hearing subjects showed a reduction in the amplitude of otoacoustic emissions in one ear when contralateral broadband noise was presented, indicating a functioning efferent system. Psychophysical tuning curves (PTCs) were measured in simultaneous masking in the absence and presence of contralateral stimulation (CS). The CS was a continuous narrowband noise centered at the signal frequency and presented at a level of 50 or 60 dB SL. The CS had no consistent effect on the masker level at the tips of the PTCs. For the two highest signal frequencies (2000 and 4000 Hz), the CS reduced the masker level required for threshold on both the low- and high-frequency sides of the PTCs, and the sharpness of tuning, as measured by Q10, decreased significantly. For the two lowest signal frequencies (500 and 1000 Hz), the masker level required for threshold on the low-frequency sides of the PTCs increased with CS, and the Q10 values increased significantly. The general pattern of the results was consistent with that observed for electrical stimulation of the efferent system in animals.

1. Introduction

It is widely accepted that cochlear mechanics are influenced by an active mechanism which depends upon the operation of the outer hair cells (Robles and Ruggero, 2001). The operation of the outer hair cells can be influenced by the efferent system, in particular the medial olivocochlear (MOC) system (Guinan and Gifford, 1988; Guinan, 2006; Kawase et al., 1993; Liberman and Guinan, 1998; Russell and Murugasu, 1997; Winslow and Sachs, 1987, 1988). For tone bursts presented in continuous noise, activation of the efferent system by electrical stimulation or by stimulation with noise in the opposite ear can reduce adaptation to the noise and enhance the response to the tone bursts (Kawase et al., 1993; Winslow and Sachs, 1987). Guinan and Gifford (1988) studied the influence of electrical stimulation of the MOC on auditory-nerve frequency-threshold curves (tuning curves) in the cat. Efferent stimulation raised the thresholds for tones at the characteristic frequency (CF). The change was larger for neurons with low spontaneous rates than for neurons with high spontaneous rates. The sharpness of tuning of the neurons was quantified by the value of Q20, defined as the CF divided by the bandwidth measured at 20 dB above the threshold at CF. Efferent stimulation decreased the values of Q20 for most neurons, but it increased the values of Q20 for some neurons with CFs below 2000 Hz.

The role of the efferent system in humans has been studied by taking advantage of the finding that, in animals, a sound presented in the contralateral ear can activate the MOC system (Cody and Johnstone, 1982; Fex, 1962). In humans, contralateral stimulation has been found to have an influence on masking (Micheyl and Collet, 1996; Smith et al., 2000), intensity discrimination (Micheyl et al., 1997), the understanding of speech in noise (Giraud et al., 1997), and otoacoustic emissions (Chery-Croze et al., 1993; Collet et al., 1990; Moulin et al., 1993). Of particular interest here is a study of Kawase et al. (2000) which measured psychophysical tuning curves (PTCs) in the absence and presence of contralateral white noise. PTCs are thought to give a reasonable representation of the tuning of individual neurons in the auditory nerve (Chistovich, 1957; Small, 1959), provided that precautions are taken to prevent detection of beats and combination tones from having a strong influence on the results (Kluk and Moore, 2004; Moore, 2003). Kawase et al. (2000) used a single signal frequency of

Abbreviations: CF, characteristic frequency; CS, contralateral stimulation; MOC, medial olivocochlear; NBN, narrowband noise; PTC, psychophysical tuning curve; Q10, characteristic frequency or signal frequency divided by the bandwidth of a tuning curve measured 10 dB above the tip; Q20, characteristic frequency or signal frequency divided by the bandwidth of a tuning curve measured 20 dB above the tip; SL, sensation level

* Corresponding author. Address: 231, Shri Vinyasa, 9th Cross, 5th Main, Vijayanagar First Stage, Mysore 570 017, Karnataka, India. Tel.: +91 9448033966.
E-mail address: shrivinyasa@gmail.com (Vinay).

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2000 Hz. The masker (a 1/6th-octave wide band of noise) and contralateral white noise (level = 55 dB SPL) were presented synchronously for a duration of 495 ms, and the 20-ms signal was presented at a level of 35 dB SPL at various times during and just after the end of the masker. The addition of the contralateral noise tended to produce a small (<5 dB) decrease in masker level on the low-frequency "tail" of the PTC, with little effect around the tip. Hence, the sharpness of the PTC decreased slightly with addition of the contralateral noise. The effect of the contralateral noise tended to increase with increasing delay of the signal relative to the onset of the masker, and the effect was largest when the signal was presented just after the end of the masker (forward masking).

The 2000-Hz signal frequency used by Kawase et al. (2000) was on the boundary between the two frequency regions found by Guinan and Gifford (1988); recall that electrical stimulation of the efferent system decreased the value of Q20 for most neurons, but increased the value of Q20 from some neurons with CFs below 2000 Hz. In a more recent study, Quaranta et al. (2005) measured PTCs in simultaneous masking using signal frequencies of 1000 and 4000 Hz. The signal was pulsed on and off and the masker was presented continuously. The contralateral sound (when present) was a narrowband noise centered at the signal frequency and presented at a sensation level (SL) of 40 dB. It is not entirely clear from the description of Quaranta et al. whether or not the contralateral sound was continuous; however, it was produced by a clinical audiometer, and so presumably was continuous. They quantified the sharpness of tuning of the PTCs using measures analogous to the Q20 measure described earlier: Q10 and Q20 were defined as the signal frequency divided by the width of the PTC at a level 10 (for Q10) or 20 (for Q20) dB above the level at the tip of the PTC. They found that the presence of the contralateral sound led to a significant increase in Q10 at 1000 Hz and a significant decrease in Q10 at 4000 Hz (although no correction to the p values was made to allow for multiple comparisons). Changes in Q20 were not statistically significant. Generally, the effects were very small. For the 1000-Hz signal, in the presence of the contralateral sound the masker level required for threshold was increased by 1–4 dB for masker frequencies of 800 Hz and below and was decreased by 1–3 dB for masker frequencies of 1400 Hz and above. For the 4000-Hz signal, in the presence of the contralateral sound the masker level required for threshold was decreased by 1–2 dB for masker frequencies of 3200 Hz and below and was decreased by 1–5 dB for masker frequencies of 4200 Hz and above. Changes in masker level resulting from the contralateral sound were not significant at any frequency.

The effects of contralateral stimulation on sharpness of tuning found by Quaranta et al. (2005) were broadly similar to the effects of electrical stimulation of the efferent system in the cat found by Guinan and Gifford (1988). However, there are some problems in interpreting the results of Quaranta et al. (2005). Firstly, their masker was a sinusoid. It has been shown that PTCs determined using sinusoidal maskers can be strongly influenced by the detection of beats (Kluk and Moore, 2004), which means that they do not give a valid indication of the sharpness of tuning of the auditory system. Secondly, the PTCs of Quaranta et al. for the 4000-Hz signal seem unusually broad. For example, for the PTC without contralateral stimulation, the masker level required for threshold was only about 30 dB higher for a masker frequency of 8000 Hz than for a masker frequency of 4000 Hz. PTCs in the literature for a 4000-Hz signal frequency are usually sharper than that, especially when the masker is a sinusoid (Kluk and Moore, 2004; Moore, 1978; Moore et al., 1984). Finally, as noted above, the effects found by Quaranta et al. were very small, perhaps because of the low level of the contralateral stimulation that they used.

In the present study, the effects of contralateral stimulation on PTCs were measured for four signal frequencies, 500, 1000, 2000 and 4000 Hz, to give a more representative measure of the effect of the efferent system on frequency selectivity as a function of signal frequency. To avoid problems with beat detection, a narrowband noise was used as a masker, as recommended by Kluk and Moore (2004). In an attempt to get larger effects than those found by Quaranta et al. (2005), we used two relatively high levels of contralateral stimulation, 50 and 60 dB SL.

It has been shown that otoacoustic emissions can be used to record the activity of the efferent system, by measuring the change in the emissions in one ear produced by contralateral stimulation (Chery-Croze et al., 1993; Collet et al., 1990; Moulin et al., 1993). We used such a method to check that the efferent system was effective for each subject used in the present experiment.

2. Method

2.1. Subjects

Nineteen subjects were tested, eight female and 11 male. Their ages ranged from 18 to 26 years. None had any history of ear disease, significant noise exposure, ototoxicity, familial hearing loss or cardiovascular disease. None of the subjects had non-auditory neural conditions. All subjects had audiometric thresholds at or better than 15 dB HL for audiometric frequencies from 0.25 to 8 kHz for air conduction and 0.5 to 4 kHz for bone conduction. All subjects had normal middle ear function as assessed using a GSI Tympstar Immittance meter. The purpose of the study was explained to the subjects, and their consent was obtained for participation in the study.

2.2. Measurement of otoacoustic emissions

Transient evoked otoacoustic emissions (TEOAEs) were measured using an ILO 292 Otodynamics analyzer. Stimuli were trains of 80 μs clicks, three with positive polarity and one with negative polarity, the latter having a level 9.5 dB higher than the former, and stimulus processing was based on the non-linear mode. Each TEOAE response was based on the average response to 260 of the four-click trains, which were presented at a rate of approximately 50 trains per second. The stimulus level was 84 dB peak equivalent SPL and the artifact rejection level was set to 47.3 dB SPL. TEOAEs were present for all of the subjects. The effect of applying white noise to the contralateral ear at 50 dB SL was then assessed. This noise was generated using a Maico 53 dual-channel clinical audiometer, and it was presented via an ER3A insert earphone. Table 1 shows the overall level of the TEOAE for each subject, without and with contralateral stimulation (CS). The TEOAE magnitude was reduced by at least 1 dB by the CS for all subjects, indicating that the CS did produce effects of the efferent system in the ear opposite to the CS.

2.3. Measurement of PTCs

PTCs were measured for the right ear only, in the presence and absence of CS. PTCs were measured using a Maico 53 dual-channel clinical audiometer. The audiometer was set to dual-frequency mode. The signal tone was generated in one channel. It was presented at 10 dB SL and was pulsed on and off in a regular sequence (0.25 s on, 0.25 s off). A narrow band noise (NBN) masker was selected in the other channel. The NBN conformed to the specifications given in ANSI-S3.6 (2004), and had a bandwidth between 1/3 and 1/2 oct. The relatively large bandwidth is required to reduce the influence of beats on the PTCs (Kluk and Moore, 2005). The two channels were mixed in order to present the tone and NBN to the same ear, using one earpiece of a set of TDH39 headphones