ELSEVIER

Hearing Research 142 (2000) 102–112

HEARING RESEARCH

www.elsevier.com/locate/heares

Auditory perception in vestibular neurectomy subjects☆

Fan-Gang Zeng [a,*], Kristina M. Martino [b], Fred H. Linthicum [b], Sigfrid D. Soli [b]

[a] *Department of Hearing and Speech Sciences and Program in Neuroscience and Cognitive Science, 0100 Lefrak Hall, University of Maryland, College Park, MD 20742, USA*

[b] *House Ear Institute, 2100 West Third Street, Los Angeles, CA 90057, USA*

Received 14 August 1999; received in revised form 27 December 1999; accepted 27 December 1999

Abstract

The auditory efferent nerve is a feedback pathway that originates in the brainstem and projects to the inner ear. Although the anatomy and physiology of efferents have been rather thoroughly described, their functional roles in auditory perception are still not clear. Here, we report data in six human subjects who had undergone vestibular neurectomy, during which their efferent nerves were also presumably severed. The surgery had alleviated these subjects' vertigo but also resulted in mild to moderate hearing loss. We designed our experiments with a focus on the possible role of efferents in anti-masking. Consistent with previous studies, we found little effects of vestibular neurectomy on pure-tone detection and discrimination in quiet. However, we noted several new findings in all subjects tested. Efferent section increased loudness sensation (one subject), reduced overshoot effect (five subjects), accentuated 'the midlevel hump' in forward masking (two subjects), and worsened intensity discrimination in noise (four subjects). Poorer speech in noise recognition was also observed in the surgery ear than the non-surgery ear in three out of four subjects tested, but this finding was confounded by hearing loss. The present results suggest an active role of efferents in auditory perception in noise.

Key words: Olivocochlear bundle; Auditory efferent system; Anti-masking; Vestibular neurectomy; Signal detection in noise; Overshoot; Intensity discrimination; Forward masking

1. Introduction

The olivocochlear bundle, or the auditory efferent system, is a nervous feedback pathway that originates in the brain stem and projects to the inner ear. Auditory efferents have been identified for more than 50 years (Rasmussen, 1946) and their anatomy has been thoroughly described (e.g. Warr and Guinan, 1979; Liberman, 1980; Brown, 1987; Warr, 1992). While the efferent system was traditionally classified by crossed and uncrossed projections, the present view is that the efferent system consists of a medial subsystem and a lateral subsystem based on their origins in the brain stem. The medial efferents originate in the medial portion of the superior olivary complex and project to the outer hair cells; the lateral efferents originate in or near the lateral portion of the superior olivary complex and project to the dendrites of the auditory nerve fibers. Both medial and lateral efferents contain crossed and uncrossed projections.

Despite this rather thorough description of the efferent anatomy, the functional role of the efferents is still poorly understood and remains somewhat mysterious. One major cause for the mysterious efferent function is that many earlier studies reported negative findings on the role of efferents in absolute hearing thresholds, temporal threshold shifts, pure-tone intensity and frequency discrimination in quiet and in noise (e.g. Galambos, 1960; Trahiotis and Elliott, 1970; Igarashi et al., 1972, 1979a,b). Recently, there has been a rekindled interest in efferent functions (for a summary, see Rajan, 1990; Guinan, 1996; Walsh et al., 1998). Several hypotheses have been proposed for an efferent involve-

* Corresponding author. Tel.: +1 (301) 405-8688; Fax: +1 (301) 314-2023; E-mail: fzeng@hesp.umd.edu

☆ Portions of this work were presented at the 127th meeting of the Acoustical Society of America, Boston, MA, USA, 1994.

0378-5955/00/$ – see front matter
PII: S0378-5955(00)00011-3

ment in anti-masking (e.g. Liberman and Guinan, 1998), protection from damage due to loud noise (Cody and Johnstone, 1982; Handrock and Zeisberg, 1982; Rajan, 1990; Liberman and Gao, 1995), auditory and visual attention (Oatman, 1976; Igarashi et al., 1974; Scharf et al., 1994, 1997), and auditory development (Walsh et al., 1998). Among these hypotheses, the anti-masking effect has received the most extensive investigation, and perhaps the strongest empirical support.

Dewson (1968) first reported that efferent section in rhesus monkeys significantly impaired their ability to discriminate between two vowels ([i] and [u]) in noise but not in quiet. He interpreted his finding as increased 'perceptual' signal to noise ratio mediated by efferents. Nieder and Nieder (1970) were likely the first to coin the term 'anti-masking' when they observed that efferent stimulation significantly increased neural response to loud clicks in noise. This anti-masking function by efferents was subsequently confirmed by a large body of physiological studies which activated the efferents through either electrical stimulation or contralateral noise (Dolan and Nuttall, 1988; Guinan and Gifford, 1988; Winslow and Sachs, 1988; Kawase et al., 1993; Kawase and Liberman, 1993). It has been assumed that the efferents produce the anti-masking effect through an automatic gain control mechanism which reduces the outer hair cells' response to noise and increases the effective signal to noise ratio (e.g. Mountain, 1980; Liberman and Guinan, 1998; Winslow and Sachs, 1988). The anti-masking effect is most likely mediated by the medial efferents; it also takes time to develop and to decay and is most effective at moderate noise levels for mid- to high-frequency sounds (Warren and Liberman, 1989a,b; Guinan and Stankovic, 1996; Liberman and Guinan, 1998; Moulin and Carrier, 1998; Zheng et al., 1999).

Although behavioral studies of the efferent anti-masking function are rare compared with the large body of physiological literature in anti-masking, they are generally consistent with each other. For example, May and McQuone (1995) found that efferent section in cats significantly affects intensity discrimination in noise at 8 kHz but not at 1 kHz. In humans, Micheyl and Collet (1996) also found a possible relationship between detection of tones in noise and the strength of efferent activation, as measured by contralateral suppression of otoacoustic emissions (Littman et al., 1992; Williams et al., 1994; Maison et al., 1997). Similar to Dewson's (1968) finding, Hienz et al., (1998) showed that vowel formant discrimination in cats was adversely affected by bilateral efferent section only in high-level noise background but not at low noise levels. More recently, Giraud et al. (1997) measured speech in noise intelligibility in normally hearing listeners and in listeners who had undergone vestibular neurectomy, a surgical procedure that severs both the vestibular nerve and the efferent nerve to alleviate vertigo (House et al., 1984). They found a positive correlation between speech in noise intelligibility and the strength of emission suppression in normal listeners; in addition, the intelligibility was lower in the surgery ear than the non-surgery ear.

Scharf et al. (1994, 1997) also conducted extensive behavioral studies on vestibular neurectomy patients. In the case study, Scharf et al. (1994) systematically measured the effects of neurectomy on detection and discrimination of tones in noise. They found essentially no difference between the surgery ear and the non-surgery ear in detection of tones in broad-band noise (critical ratios), narrow-band noise (300–1800 Hz, overshoot), notched noise (frequency selectivity) and contralateral noise (central masking). They also measured suprathreshold intensity discrimination, frequency discrimination, gap detection, loudness growth and adaptation, pitch matching, and lateralization and found little difference between the surgery ear and the non-surgery ear. The only abnormal finding was that the efferent-sectioned patient could no longer focus his attention to a certain frequency region in an experiment requiring detection of expected and unexpected tones. Although the role of efferents in selective attention is still controversial (Michie et al., 1996), Scharf et al. (1997) were later able to replicate these basic findings in 16 case studies.

In the present report, we also conducted behavioral studies in six patients who had undergone a vestibular neurectomy procedure to alleviate their vertigo. Given the limited time that was typically available with these patients, we focused on psychophysical and speech measurements that are related to the anti-masking function proposed for the efferents. For example, we specifically examined the difference in detection of a brief tone presented at the onset and steady-state of a broad-band noise. In normal-hearing listeners, a brief tone is harder to detect at onset of a broad-band noise than at steady-state of the noise ('the overshoot' effect, see Zwicker, 1965a). We focused on overshoot because it had a time course similar to the efferent activation (Liberman and Brown, 1986) and a previous anecdotal report also found reduced overshoot in a vestibular neurectomy patient (Hafter, Viemeister and Schlauch, personal communication). Consistent with previous behavioral studies, we found little effects of vestibular neurectomy on detection and discrimination of tones in quiet. However, we did observe a significant reduction of the overshoot effect and degraded intensity discrimination in noise in the surgery ear. Speech recognition in noise was also impaired in the surgery ear for most patients but hearing loss might have confounded this result.

2. Materials and methods

2.1. Subjects

Six adult patients, four females and two males, who had undergone retrolabyrinthine vestibular nerve section (de la Cruz and McElveen, 1984; Nguyen et al., 1992) participated in this study. The surgical procedure significantly alleviated the pre-operative disabling vertigo in all patients. Table 1 shows basic personal and audiological information for these patients. While two subjects (RW and TG) showed significantly elevated thresholds (20 dB), they all had high levels of word recognition (80% or greater) in the surgery ear post-operatively. Four normal-hearing listeners, serving as experimental control, also participated in the speech experiment. Informed consent was approved by the local Institutional Review Board and obtained from each individual subject after the nature and possible consequences of the study were explained.

2.2. Stimuli

Stimuli in all psychophysical experiments were generated and controlled by a Tucker-Davis-Technologies system. Stimulus parameters will be described in each individual experiment as they varied from experiment to experiment. Hearing in noise test (HINT, Nilsson et al., 1994) was used to measure sentence speech reception threshold (SRT) in a control group of four normal-hearing subjects and in the surgery ear and the non-surgery ear of vestibular neurectomy subjects. HINT required a subject to recognize daily life sentences spoken by a male speaker in a broad-band noise whose long-term spectrum was matched to that of the male speaker. All stimuli, including tones, noises and speech sentences, were presented to the subject via TDH-49 headphones mounted in a MX-41/AR cushion. Regular calibration of the headphones in an NBS-9A coupler using a B and K sound level meter and/or a Hewlett–Packard dynamic signal analyzer (35660A) was conducted to ensure both fidelity and safety of the sound generation and delivery systems.

2.3. Procedures

A two alternative, forced choice, adaptive procedure was used in psychophysical experiments measuring pure-tone thresholds in noise and forward masking, and intensity discrimination in quiet, noise and forward masking. A three-up, one-down decision rule was used to produce 79.4% correct responses (Levitt, 1971). In the interaural loudness matching experiment conducted in one subject pre- and post-operatively, a pure-tone stimulus was presented to the non-surgery ear at a fixed level and served as a reference of loudness matching to the same pure-tone stimulus presented alternatively in the surgery ear. The subject was instructed to adjust the level of the stimulus in the surgery ear to make it just louder than, then just softer than and finally equally loud to the reference stimulus in the non-surgery ear. In the speech experiment, SRT (i.e. the speech to noise level achieving a 50% correct response) was obtained using the HINT material and procedure (Nilsson et al., 1994). To establish the baseline performance, we first measured SRTs as a function of the contralateral noise level in normal-hearing listeners. In subjects with vestibular neurectomy, the noise was presented dioti-

Table 1
Subject information

Subject	Sex	Age	Surgery ear	Cause of vertigo (and other symptoms)	Surgery date (month/day/year)	Test date(s)	Word recognition (post-operatively)
CM	M	68	R	Vestibular neuronitis (positional dizziness, totally disabling)	01/20/83	02/18/92–05/02/94	96%
JD	F	35	L	Vestibular neuronitis (panic attacks, sweating)	05/14/91	04/02/92–05/02/94	100%
PR	M	40	L	Meniere syndrome (tinnitus, hearing loss, fullness)	07/17/96	07/31/96	100%
RA	F	38	L	Meniere syndrome (tinnitus, hearing loss, fullness)	10/14/93	05/13/94	100%
RW	F	60	R	Trauma and fistula repair (constant numbness of hands and feet, totally disabled, positional dizziness, tinnitus, headache)	10/28/83	04/15/92–04/29/92	80%
TG	F	50	R	Meniere syndrome (drop attacks, tinnitus, fluctuating hearing loss, fullness)	12/07/93	N/A	88%

For subject RA, pre-surgical loudness balance data were collected on the same day when the surgery was performed. TG's test dates were not available as a result of a missing laboratory notebook.

cally at a 70-dB SPL overall level and the speech was presented either in the surgery ear or the non-surgery ear. Data are reported for all subjects tested.

3. Results

3.1. Pure-tone thresholds

Fig. 1 shows pure-tone thresholds collected clinically in the non-surgery ear and in the surgery ear pre-operatively (open symbols) and post-operatively (filled symbols). Except for subjects RW and TG, vestibular neurectomy had relatively minor effects on pure-tone thresholds with 10 dB or less shift after the surgery. For the two subjects who had greater hearing loss in the surgery ear post-operatively, both had Meniere syndrome and their loss might be due to continued hydrops that was not affected by the surgery. While little change in thresholds was reported in Scharf's (1997) study, the pure-tone average threshold could be elevated by an average of 4.1 dB in retrolabyrinthine approach and by 21.2 dB in middle fossa approach in other studies (de la Cruz and McElveen, 1984). We noted that three subjects, JD, PR and RA, had nearly normal pure-tone thresholds post-operatively in the surgery ear.

3.2. Loudness growth

In subject RA, we were able to obtain interaural loudness matching functions (Fig. 2) pre-operatively (open symbols) and post-operatively (filled symbols). At 1000 Hz (top panel), there was essentially no differ-

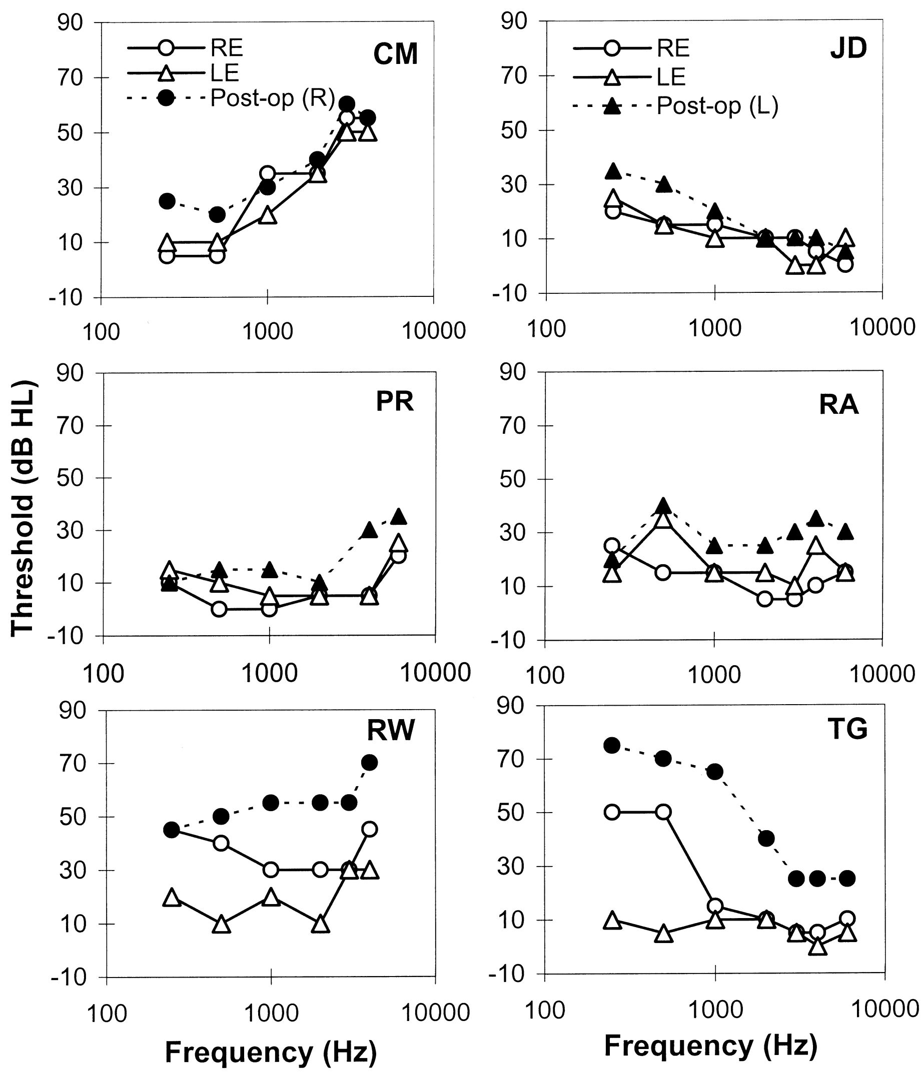

Fig. 1. Pure-tone thresholds. Open circles represent thresholds in the right ear and open triangles represent thresholds in the left ear. Filled symbols represent thresholds measured after vestibular nerve section.

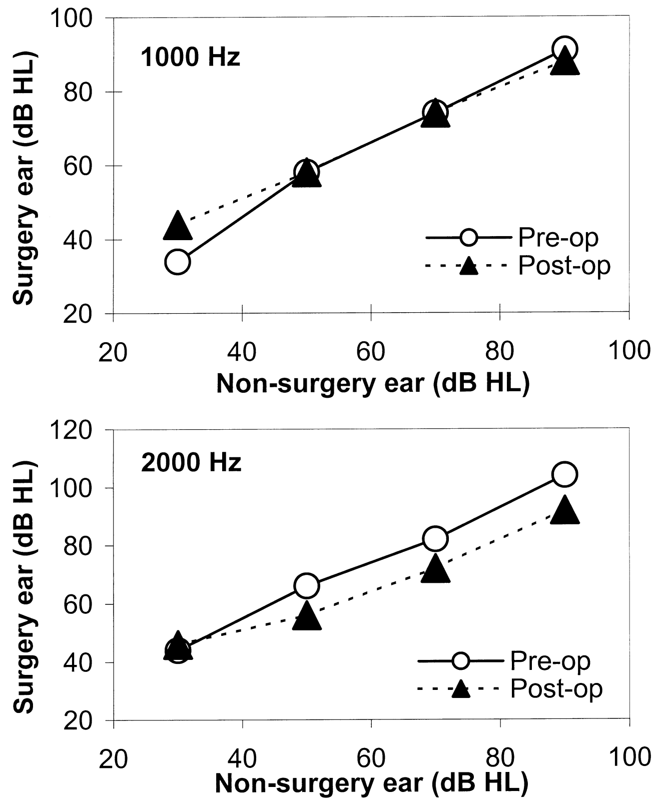

Fig. 2. Loudness matching functions at 1000 Hz (top panel) and 2000 Hz (bottom panel). The x-axis represents the level of a reference tone in the non-surgery ear; the y-axis represents the level of a comparison tone in the surgery ear to match the loudness of the reference. Open squares represent the function measured pre-operatively and filled triangles represent the function measured post-operatively.

ence in loudness growth between the pre- and the post-operatively conditions. However, at 2000 Hz, this subject consistently required lower levels (about 10 dB) in the surgery ear post-operatively than pre-operatively to match the loudness of the same reference stimulus in the non-surgery ear. In other words, a 2000-Hz tone of the same level would elicit louder sensation in the surgery ear than in the non-surgery ear.

3.3. Intensity discrimination in quiet

Fig. 3 shows a just noticeable difference (JND) in intensity, presented as level differences in dB and measured for a 25-ms, 1000-Hz pure-tone stimulus in three patients. Except for low stimulus levels (30 and 40 dB SPL) in subject JD, no apparent difference was found between the surgery ear (filled symbols) and the non-surgery ear (open symbols).

3.4. Forward masking

Forward masking measures the effect of prior stimulation on detection and discrimination of a following sound. No previous study has addressed forward masking in vestibular neurectomy patients. In the present study, the forward masker was always a 1000-Hz, 90-dB SPL, 100-ms tone. In the threshold recovery experiment, the probe tone was a 1000-Hz, 9-ms tone with 3-ms cosine-squired ramps. Signal delays, defined as the interval between the offset of the masker and the onset of the probe, ranged from 1 ms to 200 ms. In forward-masked intensity discrimination, the probe tone was 25 ms in duration and was presented always at 100-ms signal delay.

Fig. 4 presents threshold recovery from forward masking in one subject (top panel) and forward-masked intensity discrimination in two subjects (bottom two panels). The threshold recovery in the surgery ear was typical compared with normal-hearing listeners (e.g. Jesteadt et al., 1982). However, vestibular neurectomy accentuated the 'midlevel hump' in forward-masked intensity discrimination (Zeng et al., 1991) by producing both significantly worse discrimination at moderate levels and slightly better discrimination at low and high levels in the surgery ear than the non-surgery ear.

3.5. Overshoot in diotic noise

Overshoot is usually measured with both the signal and the noise presented to only one ear. Here, we presented the signal unilaterally but the noise binaurally in order to induce the strongest efferent effect (for 'binau-

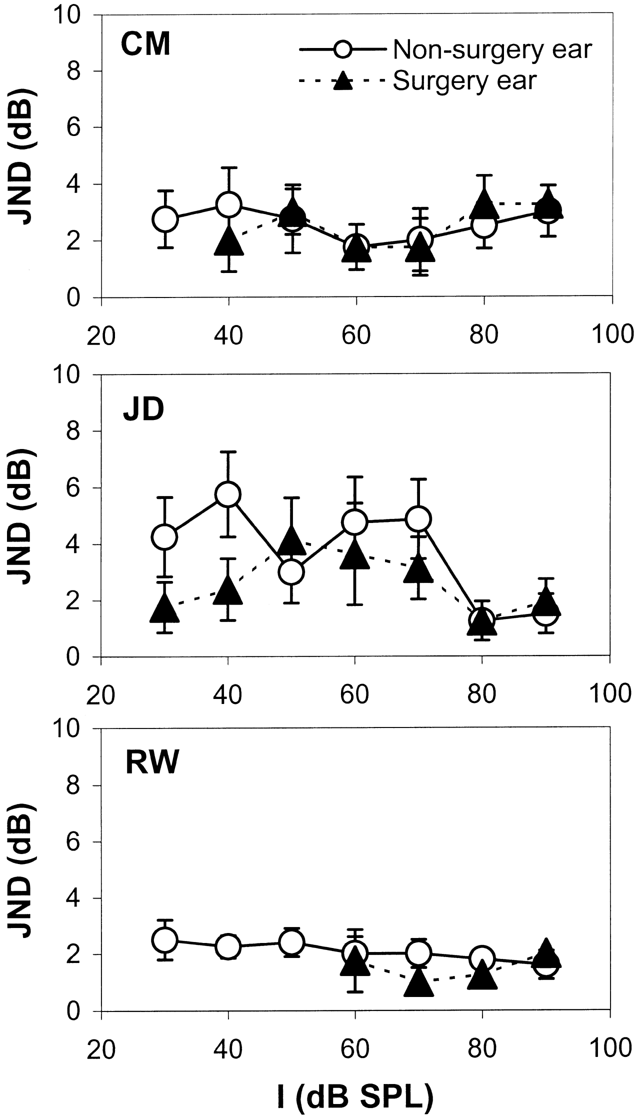

Fig. 3. Intensity discrimination in quiet. JND are plotted as a function of the pedestal level (x-axis). The open circles represent data obtained in the non-surgery ear and the filled triangles represent data in the surgery ear.

ral enhancement', see Liberman, 1988). In addition, a moderate to loud broad-band noise was chosen to maximize the overshoot effect (20–5000-Hz bandwidth with a spectrum level of 30 or 40 dB, see Bacon, 1990). The probe tone was 9 ms in duration and had 3-ms cosine-squared ramps. The probe tone was presented either at 3 ms or 300 ms after the onset of the noise, which had an overall duration of 425 ms and also 3-ms cosine-squired ramps. To minimize the effects of hearing loss on overshoot (Bacon and Takahashi, 1992), the probe frequency was chosen to be both 1000 Hz and 4000 Hz for subject JD, 4000 Hz for subject TG and 1000 Hz for the remaining subjects. At these frequencies, all subjects had 30-dB HL or better hearing thresholds. Except for subject PR whose overshoot effects were measured at 30- and 40-dB noise spectrum levels, other subjects performed the task at the 30-dB level.

Fig. 5 presents the difference in threshold between the 3-ms and the 300-ms conditions (i.e. overshoot effect) for both the non-surgery ear ('N' and open bars) and the surgery ear ('S' and filled bars) in five subjects. Compared with the non-surgery ear, overshoot was uniformly reduced in the surgery ear for all subjects and this reduction was statistically significant (paired t-test, $P < 0.01$). However, large individual variability was

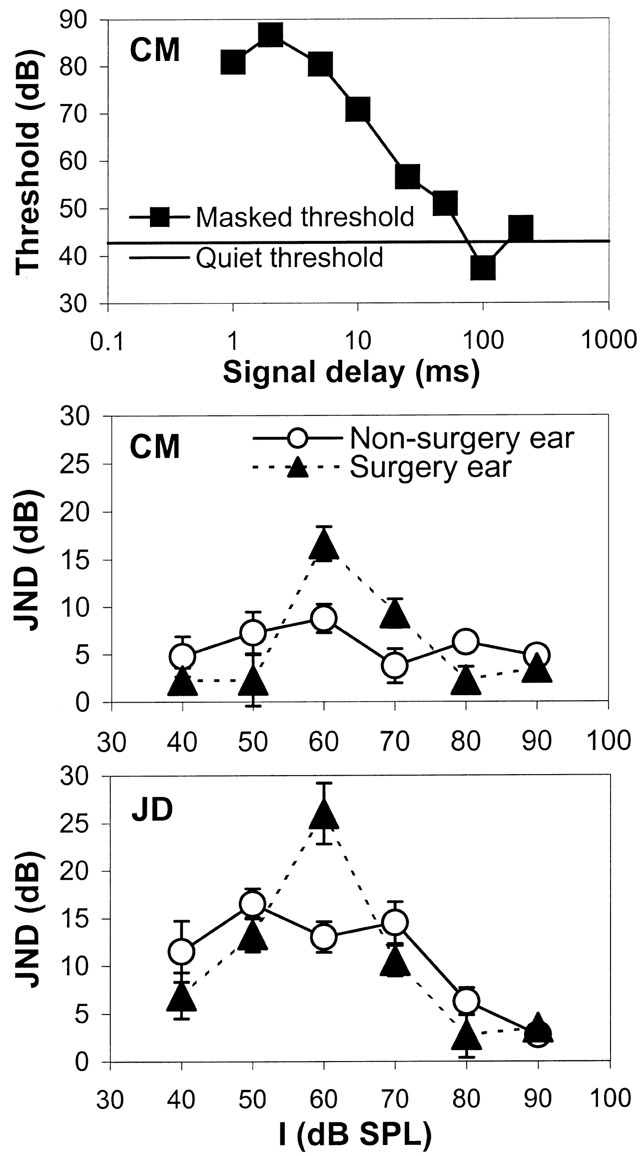

Fig. 4. Forward masking. Top panel: recovery from forward masking. Thresholds in dB SPL (y-axis) are plotted as a function of signal delay (x-axis). The threshold in the absence of masking (marked as 'Quiet threshold') is represented by the horizontal line. Middle and bottom panels: intensity discrimination in forward masking. Bottom panel: intensity discrimination. JND data are plotted as a function of the pedestal level for a forward-masked tone. Open circles represent data obtained in the non-surgery ear and filled triangles represent data in the surgery ear.

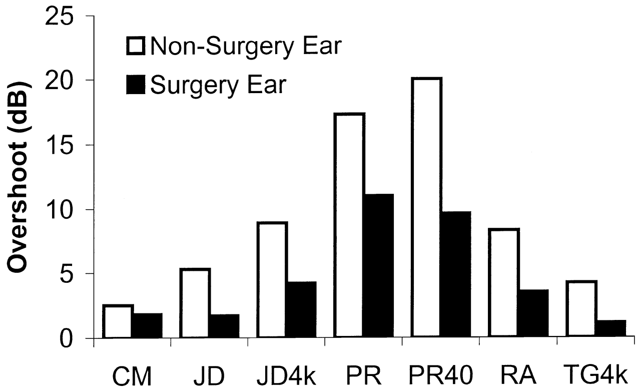

Fig. 5. Overshoot. Threshold differences in dB between the onset (3-ms delay) and the steady-state (300-ms delay) conditions. Open bars represent data obtained in the non-surgery ear and filled bars represent data in the surgery ear. All data were obtained for a 1000-Hz brief tone in the presence of a noise with 30-dB spectrum level except for (1) JD4k and TG4k which denoted a 4000-Hz tone in subjects, JD and TG, respectively, and (2) PR40 which denoted a noise spectrum level of 40 dB.

Table 2
Overshoot

Subjects	S3ms	N3ms	(S−N)3ms	S300	N300	(S−N)300
CM	65.6	65.0	0.6	63.8	62.5	1.3
JD (1k)	63.9	60.0	3.9	62.2	54.7	7.5
JD (4k)	64.5	72.2	−7.7	60.3	63.3	−3.0
PR (30dB)	77.5	81.3	−3.8	66.5	64.0	2.5
PR (40dB)	92.4	93.0	−0.6	82.8	73.0	9.8
RA (1k)	66.4	78.0	−11.6	62.9	69.7	−6.8
TG (4k)	N/A	N/A	N/A	N/A	N/A	N/A

The unit for the threshold values is dB SPL. 'S' represents the surgery ear and 'N' represents the non-surgery ear. '3ms' represents the onset condition and '300' represents the steady-state condition. '1k' and '4k' represent the probe frequency of 1000 Hz and 4000 Hz, respectively. '30dB' and '40dB' represent noise spectrum level of 30 dB and 40 dB, respectively. '(S−N)3ms' represents the onset threshold difference between the surgery ear and the non-surgery ear and '(S−N)300' represents the steady-state threshold difference. TG's threshold data were not available as a result of a missing laboratory notebook.

also apparent with the difference in overshoot effect ranging from 0.7 dB in subject CM to 11.4 dB in subject PR. We note that this large individual variability in overshoot was directly related to hearing loss (see Bacon and Takahashi, 1992). The three subjects (JD, PR and RA) with the largest overshoot effect also had the least amount of hearing loss, whereas the two subjects (CM and TG) with the smallest overshoot also had the most significant hearing loss.

Table 2 presents the threshold values in dB SPL at 3-ms and 300-ms delays in both the surgery ear and non-surgery ear. These threshold values allowed us to examine whether the reduced overshoot effect was due to the lowered onset threshold, or the elevated steady-state threshold, or both. Column '(S−N)3ms' in Table 2 shows the onset threshold difference between the surgery ear and the non-surgery ear and column '(S−N)300' shows the steady-state threshold difference. Positive numbers mean higher thresholds in the surgery ear. Except for the subject PR at 40-dB noise level, which clearly showed that the reduced overshoot was due to the elevated steady-state threshold, all remaining cases had a mixed contribution of lowered onset threshold and elevated steady-state threshold to the reduced overshoot effect in the surgery ear.

3.6. *Intensity discrimination in diotic noise*

We are not aware of any previous reports that measured intensity discrimination of brief tones presented under overshoot conditions in either normal-hearing subjects or vestibular neurectomy subjects. Fig. 6 presents intensity discrimination data for a brief tone (1000 Hz or 4000 Hz) under the 3-ms delay condition (top panel) and the 300-ms delay condition (bottom panel). The pedestal level was at 80 dB SPL for all subjects except at 85 dB SPL for subject PR whose onset threshold was at 81.3 dB SPL (see Table 2). Intensity discrimination at the 3-ms delay produced mixed results, in which the JND values were greater in the

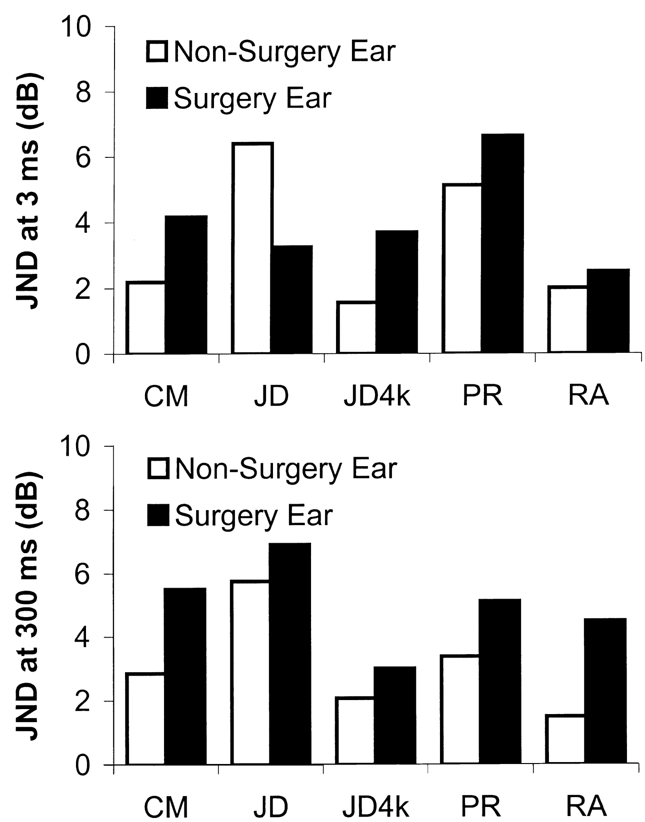

Fig. 6. Intensity discrimination in noise. Top panel: JND data in the onset (3-ms delay) condition. Bottom panel: JND data in the steady-state (300-ms delay) condition.

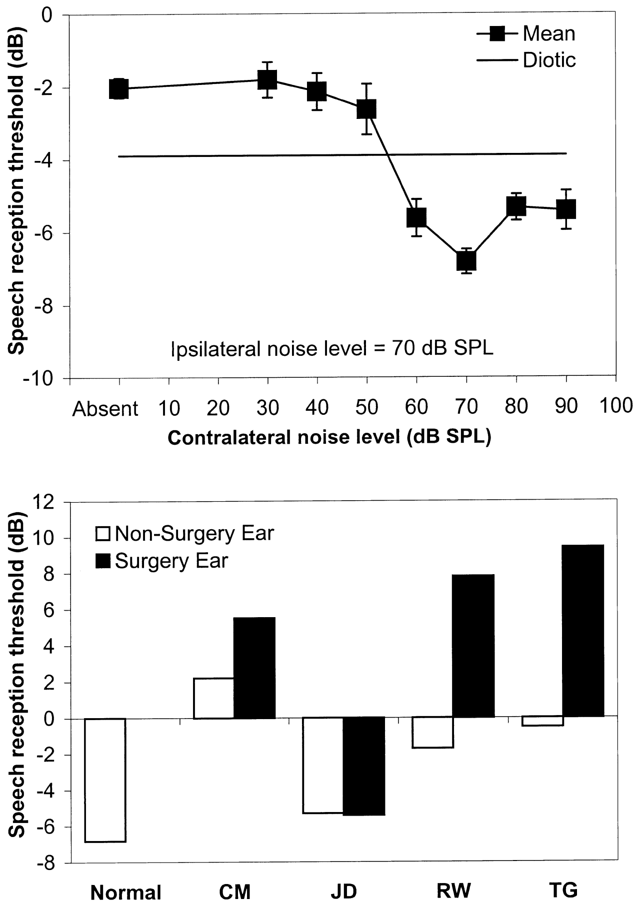

Fig. 7. Speech recognition in noise. Top panel: SRT in normal-hearing listeners as a function of the contralateral noise level. The ipsilateral noise level was fixed at 70 dB SPL. 'Absent' denotes the ipsilateral noise only condition. The horizontal line represents a diotic condition in which both speech and noise were presented identically to both ears. Bottom panel: SRT in vestibular nerve-sectioned listeners. The speech was presented ipsilaterally to either the non-surgery ear (open bars) or the surgery ear (filled bars). The noise was presented diotically to both ears.

surgery ear in one case and in the non-surgery ear in other cases. A paired *t*-test analysis revealed no statistical significance in JND values between the surgery ear and the non-surgery ear ($P = 0.29$). On the other hand, intensity discrimination at the 300-ms delay was uniformly poorer in the surgery ear than in the non-surgery ear. This difference was statistically significant (paired *t*-test, $P < 0.01$) and suggested a possible involvement of efferents in intensity discrimination in noise as previously proposed.

3.7. Speech perception in noise

We first establish the normative performance in ipsilateral, dichotic and diotic conditions. Fig. 7 (top panel) presents SRT as a function of contralateral noise level in four normal-hearing subjects. For the 70-dB SPL noise, the SRT was about −2 dB in the ipsilateral condition (labeled as 'Absent' on the *x*-axis depicting the contralateral noise level). This SRT value remained unchanged until the contralateral noise level reached 50 dB SPL and dropped abruptly to about −6 dB between 50- and 60-dB contralateral noise levels. The lowest SRT value of −7 dB was achieved at 70-dB contralateral noise level, i.e. the same level as the ipsilateral noise. Further increases in the contralateral noise levels (80- and 90-dB conditions) resulted in a slightly poorer performance (SRT = −6 dB). The diotic condition with speech and noise presented identically to both ears produced a SRT value of −4 dB (horizontal line). In other words, presenting a moderate to high level noise in the contralateral ear improved speech recognition in noise relative to the monaural condition (−6 dB vs. −2 dB) and the diotic condition (−6 dB vs. −4 dB).

Due to time availability, SRT was measured in four subjects. For subject JD, both the non-surgery ear and the surgery ear produced SRT values similar to normals, whereas for the three remaining subjects, the surgery ear produced significantly higher SRT values than the non-surgery ear. Unfortunately, there were two potential confounding factors in the present results. First, these three subjects had hearing loss in the surgery ear, which could lead to the higher SRT values in the surgery ear. Second, the same noise was presented to both ears, possibly resulting in binaural interactions other than the efferent activity. By using subjects with normal hearing in both ears and using an uncorrelated contralateral noise, Giraud et al. (1997) overcame both shortcomings in the present experiment and provided convincing evidence for the efferent anti-masking effect on speech recognition in noise.

4. Discussion

In this study, we compared pre-operative and post-operative pure-tone thresholds in six vestibular neurectomy patients and interaural loudness matching in one patient. In addition, we compared the surgery ear's performance with the non-surgery ear's performance in pure-tone intensity discrimination in quiet and in forward masking, detection (overshoot) and intensity discrimination of brief tones at onset and steady-state positions of a diotic broad-band noise, and sentence recognition in noise. Consistent with previous studies, no apparent effects of vestibular neurectomy were observed on pure-tone threshold, intensity discrimination in quiet, and recovery from forward masking.

However, several new findings were obtained in this study. In one case (2000 Hz in subject RA), the same intensity sound was louder (about a 10-dB effect) post-operatively than pre-operatively in the surgery ear.

Scharf et al. (1994) also noticed an abnormality in loudness matching function between the surgery ear and the non-surgery ear but could not determine whether such a difference was present pre-surgically. Our present finding appeared to be consistent with Borg's (1971) study which showed that rabbits' acoustic reflex threshold, particularly at high frequency, was lowered after the section of the efferents. More data are needed to test whether there is a relationship between efferent section and loudness growth.

We also noted a greater midlevel hump in forward-masked intensity discrimination in the surgery ear than in the non-surgery ear. While several central and peripheral factors have been identified to contribute to the midlevel hump (Plack et al., 1995; Schlauch et al., 1999; Zeng, 1998), efferents may also be involved in intensity discrimination under forward masking. In a contralateral forward masking paradigm, Zeng and Shannon (1995) observed a small but consistent midlevel hump for intensity discrimination of an ipsilaterally presented pure tone. Zeng and Shannon ruled out the possibility of a cross-talk masking effect and suggested that there might be an efferent component in the midlevel hump. While the present finding is consistent with this suggestion, it remains unclear how exactly the efferent nerve affects forward masking.

The most interesting finding in this study is the reduced overshoot effect and the deteriorated steady-state (300-ms delay) intensity discrimination in the presence of diotic noise. Because hearing loss generally reduced the overshoot effect through the lowered onset thresholds and because even mild to moderate hearing loss could significantly reduce the overshoot (Carlyon and Sloan, 1987; Bacon and Takahashi, 1992), the reduced overshoot in the present study might be due to hearing loss. However, some of the greatest reductions in overshoot were observed in subjects with normal hearing, suggesting an efferent involvement in overshoot reduction. The degraded intensity in the steady-state condition provided additional support for an efferent involvement. Physiological studies showed that the efferent action usually takes tens to hundreds of ms to develop and to decay (Liberman and Brown, 1986; Warren and Liberman, 1989a,b), indicating that an anti-masking effect would not be observed at the onset of a noise but only in a steady-state condition.

Three previous studies also measured overshoot in three vestibular neurectomy subjects and showed a reduction in overshoot effect in the surgery ear. Hafter, Viemeister and Schlauch (personal communication) reported reduced overshoot in a vestibular neurectomy subject, but their observation seemed to be confounded by hearing loss ($\sim$40 dB HL) at the test frequency. Scharf et al. (1994, 1997) also measured overshoot in the presence of monaural noise in two patients and found that overshoot was reduced by 2 dB (13.5 vs. 15.3 dB) in the operated ear in one patient and by 1 dB (10.6 vs. 11.7 dB) in the other. Because of this relatively small reduction in overshoot in the operated ear, Scharf et al. (1997) did not measure overshoot for the remaining 14 subjects in their 16 case study.

The present positive results suggest that one should not dismiss a possible relationship between overshoot and efferent function. There were significant differences in stimulus paradigm between the present study and the Scharf et al. (1994, 1997) studies. One difference was the noise used in each experiment. The present study used a broad-band noise (20–5000 Hz) with a spectrum level of 30 or 40 dB. Scharf et al. used a much lower noise spectrum level, which was 10 dB (42-dB SPL overall level and 1500-Hz bandwidth) and 3 dB (39 dB SPL and 8000 Hz) in their 1994 and 1997 studies, respectively. While existing literature shows little overshoot effect at these low noise spectrum levels (e.g. Bacon, 1990), Scharf et al. (1994, 1997) found an unusually large overshoot effect (10–15 dB) in their two subjects. These unusually large overshoot effects could be due to individual variability but also other factors such as training and practice.

The other difference was that the noise was presented to both ears in the present study, but only to the ipsilateral ear (relative to the signal) in the Scharf et al. (1994, 1997) studies. There is evidence for an involvement of contralateral noise in overshoot. For example, Chatterjee and Zeng (1996) found that overshoot was slightly greater (about 2 dB) in the diotic noise condition than the ipsilateral noise condition. In addition, Turner and Doherty (1997) found that a contralateral forward masker was also effective in reducing the overshoot effect. Bacon (personal communication) was able to replicate Turner and Doherty's findings in some of his subjects. Had Scharf et al. used a contralateral noise, they might have been able to observe greater than 1–2-dB overshoot reduction in the surgery ear of their patients.

Finally, Scharf et al. (1997) did not pursue overshoot also because they found no significant differences in tone in noise thresholds between the operated and unoperated ears. However, detection of long tone in noise and overshoot are two phenomena having totally different underlying mechanisms. The detection of a long-duration tone in noise is mostly mediated by noise components close to the tone frequency (i.e. critical band). On the other hand, overshoot (threshold differences in detection of a brief tone in noise at various signal delays) is mostly mediated by noise components remote from the tone frequency (Zwicker, 1965b; McFadden, 1989; Carlyon and White, 1992; Wright, 1997). In other words, a more reasonable comparison would be between overshoot and detection of a tone in notched noise. Scharf et al. (1997) indeed provided such data in seven subjects (their Fig. 3), in which subjects had to detect a 500-ms, 1000-Hz tone in the presence of two 400-Hz wide band noises whose frequency separation was varied from 0 to 800 Hz. While there were no differences in tone threshold between the operated and unoperated ears for the no notch condition, all subjects, except one (HO), showed that, as the notch width was increased, the tone threshold became increasingly higher in the operated ear than the unoperated ear. While the higher threshold in the operated ears could be partially attributed to the difference in absolute thresholds (Scharf et al., 1997), we noted that there was still at least a 10-dB masking effect even in the widest notch (800 Hz) condition. This masking effect could not be attributed to any on-frequency masking but had to be caused by the off-frequency masking (possibly the same mechanism underlying the overshoot). The major contribution of off-frequency components to overshoot found psychophysically is consistent with the wide (as much as an octave) and more basal projection by the efferent nerve to outer hair cells in the cochlea (Liberman and Brown, 1986; Warr, 1992).

In summary, the present study showed that vestibular neurectomy (1) did not affect absolute thresholds and intensity discrimination in quiet condition, (2) increased post-surgical loudness sensation, (3) accentuated the midlevel hump in forward-masked intensity discrimination but had no effects on threshold recovery from forward masking, (4) reduced the overshoot effect, (5) worsened intensity discrimination in noise in the steady-state condition but not the onset condition, and (6) degraded speech recognition in noise in some but not all subjects. These results, taken together with previous studies, suggest that the efferent system is involved in auditory perception in noise.

Acknowledgements

We thank Tino Trahoitis for his guidance in the planning stage of this project. We thank Ann Masuda for her help in scheduling patients and Shawn Gao, Michael Nillson and Jean Sullivan for their help in speech experiments. We also thank Sid Bacon, Holly Burrows, Ginger Grant, Leslie Prather, Walt Jesteadt, Bertram Scharf and an anonymous reviewer for their helpful comments on the manuscript. This work was supported by NIH (DC02267).

References

Bacon, S.P., 1990. Effect of masker level on overshoot. J. Acoust. Soc. Am. 88, 698–702.

Bacon, S.P., Takahashi, G.A., 1992. Overshoot in normal-hearing and hearing-impaired subjects. J. Acoust. Soc. Am. 91, 2865–2871.

Borg, E., 1971. Efferent inhibition of afferent acoustic activity in the unanesthetized rabbit. Exp. Neurol. 31, 301–312.

Brown, M.C., 1987. Morphology of labeled efferent fibers in the guinea pig cochlea. J. Comp. Neurol. 260, 591–604.

Carlyon, R.P., Sloan, E.P., 1987. The 'overshoot' effect and sensory hearing impairment. J. Acoust. Soc. Am. 82, 1078–1081.

Carlyon, R.P., White, L.J., 1992. Effect of signal frequency and masker level on the frequency regions responsible for the overshoot effect. J. Acoust. Soc. Am. 91 (2), 1034–1041.

Chatterjee, M. and Zeng, F.-G., 1996. Overshoot in monaural, diotic, and contralateral masking paradigms. In: Popelka, G.R. (Ed.), Abstracts of the 19th ARO Midwinter Research Meeting. p. 140.

Cody, A.R., Johnstone, B.M., 1982. Temporary threshold shift modified by binaural acoustic stimulation. Hear. Res. 6, 199–206.

de la Cruz, A., McElveen, J.T., Jr., 1984. Hearing preservation in vestibular neurectomy. Laryngoscope 94 (7), 874–877.

Dewson, J.H., 1968. Efferent olivocochlear bundle: some relationships to stimulus discrimination in noise. J. Neurophysiol. 31, 122–130.

Dolan, D.F., Nuttall, A.L., 1988. Masked cochlear whole-nerve response intensity functions altered by electrical stimulation of the crossed olivocochlear bundle. J. Acoust. Soc. Am. 83, 1081–1086.

Galambos, R., 1960. Studies of the auditory system with implanted electrodes. In: Rasmussen, G.L. and Windle, W.F. (Eds.), Neural Mechanisms of the Auditory and Vestibular Systems. C.C. Thomas, IL, pp. 137–151.

Guinan, J.J., 1996. Physiology of olivocochlear efferents. In: Dallos, P., Popper, A.N. and Fay, R.R. (Eds.), The Cochlea. Springer-Verlag, New York, pp. 435–502.

Guinan, J.J., Gifford, M.L., 1988. Effects of electrical stimulation of efferent olivocochlear neurons on cat auditory-nerve fibers. I. Rate-level functions. Hear. Res. 33, 97–113.

Guinan, J.J., Stankovic, K.M., 1996. Medial efferent inhibition produces the largest equivalent attenuations at moderate to high sound levels in cat auditory-nerve fibers. J. Acoust. Soc. Am. 100, 1680–1690.

Giraud, A.L., Garnier, S., Micheyl, C., Lina, G., Chays, A., Chery-Croze, S., 1997. Auditory efferents involved in speech-in-noise intelligibility. NeuroReport 8 (7), 1779–1783.

Handrock, M., Zeisberg, J., 1982. The influence of the efferent system on adaptation, temporary and permanent threshold shift. Arch. Otorhinolaryngol. 234, 191–195.

Hienz, R.D., Stiles, P., May, B.J., 1998. Effects of bilateral olivocochlear lesions on vowel formant discrimination in cats. Hear. Res. 116, 10–20.

House, J.W., Hitselberger, W.E., McElveen, J., Brackmann, D.E., 1984. Retrolabyrinthine section of the vestibular nerve. Otolaryngol. Head Neck Surg. 92, 212–215.

Igarashi, M., Alford, B.R., Nakai, Y., Gordon, W.P., 1972. Behavioral auditory function after transection of crossed olivocochlear bundle in the cat. I. Pre-tone threshold and perceptual signal-to-noise ratio. Acta Otolaryngol. 73, 455–466.

Igarashi, M., Alford, B.R., Gordon, W.P., Nakai, Y., 1974. Behavioral auditory function after transection of crossed olivocochlear bundle in the cat. II. Conditional visual performance with intense white noise. Acta Otolaryngol. 77, 311–317.

Igarashi, M., Cranford, J.L., Nakai, Y., Alford, B.R., 1979a. Behavioral auditory function after transection of crossed olivocochlear bundle in the cat. IV. Study on pure-tone frequency discrimination. Acta Otolaryngol. 87, 79–83.

Igarashi, M., Cranford, J.L., Allen, E.A., Alford, B.R., 1979b. Behavioral auditory function after transection of crossed olivocochlear bundle in the cat. V. Pure-tone intensity discrimination. Acta Otolaryngol. 87, 429–433.

Jesteadt, W., Bacon, S.P., Lehman, J.R., 1982. Forward masking as a function of frequency, masker level, and signal delay. J. Acoust. Soc. Am. 71, 950–962.

Kawase, T., Delgutte, B., Liberman, M.C., 1993. Antimasking effects of the olivocochlear reflex. II. Enhancement of auditory-nerve response to masked tones. J. Neurophysiol. 70 (6), 2533–2549.

Kawase, T., Liberman, M.C., 1993. Antimasking effects of the olivocochlear reflex. I. Enhancement of compound action potentials to masked tones. J. Neurophysiol. 70 (6), 2519–2532.

Levitt, H., 1971. Transformed up-down methods in psychoacoustics. J. Acoust. Soc. Am. 49, 467–477.

Liberman, M.C., 1980. Efferent synapses in the inner hair cell area of the cat cochlea: an electron-microscopic study of serial sections. Hear. Res. 3, 189–204.

Liberman, M.C., 1988. Response properties of cochlear efferent neurons: Monaural vs. binaural stimulation and effects of noise. J. Neurophysiol. 60, 1779–1798.

Liberman, M.C., Brown, M.C., 1986. Physiology and anatomy of single olivocochlear neurons in the cat. Hear. Res. 24, 17–36.

Liberman, M.C., Gao, W.Y., 1995. Chronic cochlear de-efferentation and susceptibility to permanent acoustic injury. Hear. Res. 90, 158–168.

Liberman, M.C., Guinan, J.J., 1998. Feedback control of the auditory periphery: anti-masking effects of middle ear muscles vs. olivocochlear efferents. J. Commun. Disord. 6, 471–482.

Littman, T.A., Cullen, J.K., Bobbin, R.P., 1992. The effect of olivocochlear bundle transection on tuning curves and acoustic distortion products. J. Acoust. Soc. Am. 92, 1945–1952.

Maison, S., Micheyl, C., Chays, A., Collet, L., 1997. Medial olivocochlear system stabilizes active cochlear micromechanical properties in humans. Hear. Res. 113, 89–98.

May, B.J., McQuone, S.J., 1995. Effects of bilateral olivocochlear lesions on pure-tone intensity discrimination in cats. Audit. Neurosci. 1, 385–400.

McFadden, D., 1989. Spectral differences in the ability of temporal gaps to reset the mechanisms underlying overshoot. J. Acoust. Soc. Am. 85 (1), 254–261.

Micheyl, C., Collet, L., 1996. Involvement of the olivocochlear bundle in the detection of tones in noise. J. Acoust. Soc. Am. 99, 1604–1610.

Michie, P.T., LePage, E.L., Solowij, N., Haller, M., Terry, L., 1996. Evoked otoacoustic emissions and auditory selective attention. Hear. Res. 98, 54–67.

Moulin, A., Carrier, S., 1998. Time course of the medial olivocochlear efferent effect on otoacoustic emissions in humans. NeuroReport 9 (16), 3741–3744.

Mountain, D.C., 1980. Changes in endolymphatic potential and crossed olivocochlear bundle stimulation alter cochlear mechanics. Science 210, 71–72.

Nieder, P., Nieder, I., 1970. Antimasking effect of crossed olivocochlear bundle stimulation with loud clicks in guinea pig. Exp. Neurol. 28, 179–188.

Nilsson, M., Soli, S.D., Sullivan, J.A., 1994. Development of the Hearing In Noise Test for the measurement of speech reception thresholds in quiet and in noise. J. Acoust. Soc. Am. 95, 1085–1099.

Nguyen, C.D., Brackmann, D.E., Crane, R.T., Linthicum, F.H., Jr., Hitselberger, W.E., 1992. Retrolabyrinthine vestibular nerve section: evaluation of technical modification in 143 cases. Am. J. Otol. 13 (4), 328–332.

Oatman, I.C., 1976. Effects of visual attention on the intensity of auditory evoked potentials. Exp. Neurol. 51, 41–53.

Plack, C.J., Carlyon, R.P., Viemeister, N.F., 1995. Intensity discrimination under forward and backward masking: role of referential coding. J. Acoust. Soc. Am. 97 (2), 1141–1149.

Rajan, J., 1990. Functions of the efferent pathways to the mammalian cochlea. In: Rowe, M. and Aitkin, L. (Eds.), Information Processing in Mammalian Auditory and Tactile Systems. Alan R. Liss, New York, pp. 81–96.

Rasmussen, G.L., 1946. The olivary peduncle and other fiber projections of the superior olivary complex. J. Comp. Neurol. 84, 141–219.

Scharf, B., Magnan, J., Collet, L., Ulmer, E., Chays, A., 1994. On the role of the olivocochlear bundle in hearing: A case study. Hear. Res. 75, 11–26.

Scharf, B., Magnan, J., Chays, A., 1997. On the role of the olivocochlear bundle in hearing: 16 case studies. Hear. Res. 103, 101–122.

Schlauch, R.S., Clement, B.R., Ries, D.T., DiGiovanni, J.J., 1999. Masker laterality and cueing in forward-masked intensity discrimination. J. Acoust. Soc. Am. 105 (2), 822–828.

Trahiotis, C., Elliott, D.N., 1970. Behavioral investigation of some possible effects of sectioning the crossed olivocochlear bundle. J. Acoust. Soc. Am. 47, 592–596.

Turner, C.W. and Doherty, K.A., 1997. Temporal masking and the 'active process' in normal and hearing-impaired listeners. In: Jesteadt, W. (Ed.), Modeling Sensorineural Hearing Loss. Lawrence Erlbaum Associates, New Jersey, pp. 387–396.

Walsh, E.J., McGee, J., McFadden, S.L., Liberman, M.C., 1998. Long-term effects of sectioning the olivocochlear bundle in neonatal cats. J. Neurosci. 18, 3859–3869.

Warren, E.H., III, Liberman, M.C., 1989a. Effects of contralateral sound on auditory-nerve responses. I. Contributions of cochlear efferents. Hear. Res. 37, 89–104.

Warren, E.H., III, Liberman, M.C., 1989b. Effects of contralateral sound on auditory-nerve responses. II. Dependence on stimulus variables. Hear. Res. 37, 105–121.

Warr, W.B., 1992. Organization of olivocochlear efferent systems in Mammals. In: Webster, D.B., Popper, A.N. and Fay, R.R. (Eds.), The Mammalian Auditory Pathway: Neuroanatomy. Springer-Verlag, New York, pp. 410–448.

Warr, W.B., Guinan, J.J., 1979. Efferent innervation of the organ of Corti: Two separate systems. Brain Res. 173, 152–155.

Williams, E.A., Brookes, G.B., Prasher, D.K., 1994. Effects of olivocochlear bundle section on otoacoustic emissions in humans: efferent effects in comparison with control subjects. Acta Otolaryngol. 114 (2), 121–129.

Winslow, R.L., Sachs, M.B., 1988. Single-unit intensity discrimination based on auditory-nerve rate responses in backgrounds of quiet, noise, and with stimulation of the crossed olivocochlear bundle. Hear. Res. 35, 165–190.

Wright, B.A., 1997. Detectability of simultaneously masked signals as a function of masker bandwidth and configuration for different signal delays. J. Acoust. Soc. Am. 101 (1), 420–429.

Zeng, F.-G., 1998. Interactions of forward and simultaneous masking in intensity discrimination. J. Acoust. Soc. Am. 103 (4), 2021–2030.

Zeng, F.-G., Turner, C.W., Relkin, E.M., 1991. Recovery from prior stimulation. II: Effects upon intensity discrimination. Hear. Res. 55, 223–230.

Zeng, F.-G., Shannon, R.V., 1995. Possible origins of the non-monotonic intensity discrimination function in forward masking. Hear. Res. 82, 216–224.

Zheng, X.Y., Henderson, D., McFadden, S.L., Ding, D.L., Salvi, R.J., 1999. Auditory nerve fiber responses following chronic cochlear de-efferentation. J. Comp. Neurol. 406 (1), 72–86.

Zwicker, E., 1965a. Temporal effects in simultaneous masking by white-noise bursts. J. Acoust. Soc. Am. 37, 653–663.

Zwicker, E., 1965b. Temporal effects in simultaneous masking and loudness. J. Acoust. Soc. Am. 38, 132–141.