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FREQUENCY SPECIFICITY OF THE MEDIAL EFFERENT SYSTEM

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INTRODUCTION

In the post "Bekesy era" evidence regarding the contribution of the medial olivo cochlear (MOC) system innervating the outer hair cells (OHCs), to the alterations in the basilar membrane biomechanics has accumulated (1). Many researches now seriously consider the possibility of the OHCs affecting the sensitivity of the basilar membrane mechanically through an active and non-linear biomechanical mechanism (2, 1, 3). Despite the large amount of research zeal injected into the illunderstood efferent system, reports regarding efferent effects of the crossed olivocochlear bundle (COCB) on cochlear frequency selectivity are scarce. In a study by Bonfils et al (4) the COCB was reported to have no role whatsoever to play in cochlear frequency selectivity. On the other hand Veuillet et al (5) found frequency specific suppression of evoked (tone pips) emissions using contralaterally presented narrow bands of noise. The functional relevance of the COCB thus, definitely merits a detailed exploration.

The present study was proposed to investigate this functional importance of COCB. The major landmark in such investigations relating to cochlear biomechanics has been the discovery of the otoacoustic emission (OAE) by kemp (6). These emissions provide a non invasive, effective method of observing the mechanical non-linearities of the basilar membrane which was until now, impossible. Previous attempts to study the medial efferent system's (MES) frequency specificity using TEQAEs (Transiently Evoked OtoAcoustic Emission) have been futile (7) and real frequency specific nature of the MES may have been obscured by the broad spectrum of the click stimulus used. Hence it would be imperative to use more frequency specific stimuli (Ex. Narrow Bands of Noise - NBN) to study the frequency specific nature of such a system. In this regard the utilization of DPOAE (Distortion Product - OAE) paradigms for their frequency specific site(s) of origin, would be indispensable. Thur our research protocol concerns the effect of contralateral acoustic stimulation using narrow bands of noise on various distortion product - OAE frequencies.

MATERIALS AND METHODS

1. Subjects - Seven adult volunteers were tested four subjects were women and three were men ranging in age from 18-22 years (mean=20.6 years). All subjects had no history of audiologic and otologic disorders and had normal pure tone hearing thresholds < 20dBHL (ISO 1979) across the frequency range from 250 - 8 KHz (tested at audiometric octave frequencies). Their tympanometric and acoustic reflex measures were normal on the day of the study.

2. DPOAE stimulus parameters - The emissions were recorded using the biologic scout plus otoacoustic emission analysing system (software version 3.2). The DPOAEs were measured at octave frequencies (.5,1,2, and 4KHz) and the frequency of the primaries (f1 & f2) are shown in table 1. The two primaries were presented at 70dBSPL (L1 = L2 = 70dBSPL).

TABLE-1

Depicts the primaries (f1 and f2), Geometric Mean (G.M.) and the difference - Intermodulation Distortion Products for each DP-octave point tested.

DP frequencies at	f1	f2	G.M	2*f1-f2
500Hz	415	488	450	342
1000Hz	855	1025	936	685
2000Hz	1660	2002	1823	1318
4000Hz	3296	3955	3610	2637

3. Contralateral acoustic stimulation - Contralateral 1/3 octave narrow bands of noise centred on four standard audiometric frequencies .5, 1. 2, 4 KHz were presented through a calibrated GSI-16 audiometer via an insert ear phone (AW 1000-wide). To avoid intracranial crosstalk and middle ear artifacts the investigators used contralateral noise levels not greater than 65 dB SPL.

4. Efferent Test procedure - The DPOAEs were measured in two conditions - a) DPOAEs recorded in the test ear at octave frequencies (.5,1,2 and 4KHz) without any NB noise in the contralateral ear, this was the "Baseline" condition.

b) DPOAEs were recorded in the test ear for the above octave frequencies with contralateral narrow band noise centred at .5,1.2 and 4 KHz (at 65 dB SPL).

For each frequency of conralaterally presented narrow band noise the DPOAEs were measured across the frequency range (.5-4KHz). Statistical analyses were carried out using SPSS (Statistical Software Package on a Apple II Computer). A repeated measure MANOVA (Multivariate analysis of variance) was used to measure the effects of contralateral NBN on DPOAE amplitudes across frequencies.

RESULTS

A repeated measure MANOVA that was used to measure the effects of contralateral NBN on DPOAE amplitudes across frequencies with a measure of suppression equalised for shifts in base line viz. relative suppression (ΔDBSPL/Baseline amplitude) failed to yield any significant interaction or main effects for the narrow bands of noise. Hence the groups were collapsed over the four conditions of contralateral noise and then were analysed for differences between suppression at various frequencies (Table-2).

TABLE-2

Comparison between frequencies of narrow bands of noise for statistical significance of suppression effects using MONOVA.

Groups Compared	F values	P values
Suppression at 500Hz Vs 1KHz	3.1484	.1264
Suppression at 1KHz Vs 2KHz	.4873	.5113
Suppression at 2KHz Vs 4KHz	4.3786	.0813*
Suppression at 500Hz Vs 2KHz	8.1119	.0293**
Suppression at 500Hz Vs 4KHz	20.0552	.0042***
Suppression at 1KHz Vs 4KHz	.0004	.9855

* Significant at .1 level, ** Significant at .05 level, *** Significant at .01 level.

The comparison revealed that only for 2KHz Vs 4 KHz ($P<.1$), 0.5KHz Vs 2KHz ($P<0.05$) and 0.5KHz Vs 4KHz ($P<0.05$) there was a significant suppression in the difference measure. Further to determine if specific frequency noise bands in contralateral ear influenced their corresponding DPOAE sites in the test ear, planned comparisons were conducted and result are summarised in Table-3.

TABLE-3

Shows amplitude suppression effect of NBN (contralaterally presented) on its corresponding DPOAE frequency.

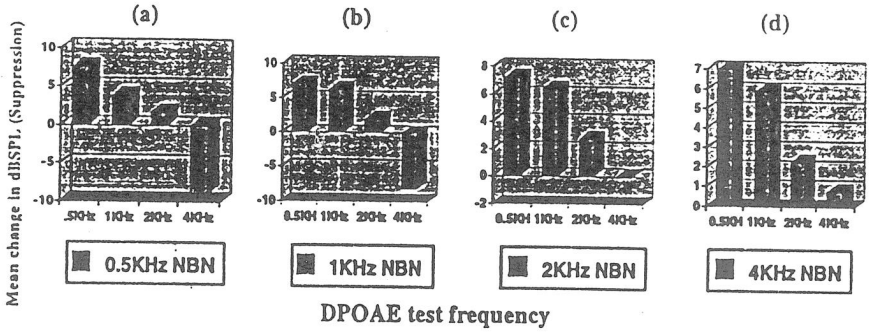
Effect Tested	F values	P values
500Hz NBN on 500Hz DPOAE amplitude	28.0436	.0018*
1KHz NBN on 1KHz DPOAE amplitude	.1103	.7511
2KHz NBN on 2KHz DPOAE amplitude	.1792	.6868
4KHz NBN on 4KHz DPOAE amplitude	.2541	.6321
* Significant at .01 level.		

Table-3 does suggest a significant frequency specific suppression effect, but only for 500Hz, however it would be fallacious to assume that other frequency bands of contralateral noise have no effect on DPOAEs in the test ear. The reasons for the same shall be discussed in the next heading. Despite rigorous statistical procedures little could be gained from further analysis of these data.

Figure-1, represents the mean change in dBSPL (Suppression) when plotted as a function of DPOAE frequencies for each contralateral noise band and lucidly demonstrates the "suppression" effect.

FIGURE-1

Displays suppression (mean change in dBSPL) as a function of DP frequencies tested for each contralaterally presented narrow band noise.



Further it is evident from Figure-1 that all contralaterally presented narrow bands of noise produced suppression at .5KHz, however lower frequency of NBN (viz. .5 and 1KHz) evoked and increase in DPOAE amplitudes at the basal end (4KHz). This is depicted by the negative shift of the amplitude function for .5KHz and 1KHz at 4KHz DPOAE test frequency (Figure-1. a,b) . On the other hand higher frequency of NBN (viz. 2 and 4KHz) produced a lesser negative shift and in Fig. 1-d a slight positive shift relative to their low frequency counterparts, at 4KHz (Figure-1.c,d)

Thus in concise, though the raw data (not shown here) and the above analysis are suggestive of a greater suppression effect in the lower frequencies esp. 500Hz, irrespective of the frequency of contralateral NBN, a certain degree of caution is warranted when interpreting these results.

DISCUSSION

To state succinctly, irrespective of the frequency of NBN used in the contralateral ear, it was the lower frequency (.5KHz and to a lesser extent 1KHz and 2 KHz - in order of decreasing effect) DPOAEs that were

suppressed. Further the difference measure (Table-2), though not entirely representative of the frequency specificity of the MES, does depict the differential amplitude "suppression effect" across DPOAE frequencies. Deducing from the above, irrespective of the frequency of noise in the contralateral ear, the maximum amplitude disparity occurred between .5KHz Vs 2 & 4KHz and 2KHz Vs 4KHz (DPOAE test frequencies), potraying the general tendency of greater suppression to occur at lower DPOAE frequency (viz. .5KHz).

Reverting back to our original discussion on the frequency specificity of the MES, our findings are in concordance with findings in literature, demonstrated using a variety of evoked emission methods. Veuillet et al (8) demonstrated similar frequency specific effects by using narrow bands of noise with centre frequencies (C.F.) between 0.9 and 2.9KHz, that produced maximum suppression for the emission (emissions were evoked by tone pips) frequency band centred on the C.F. of the noise, however he found less frequency specificity for higher frequencies of noise.

In a similar vein, Norman and Thornton (7) found more evidence of frequency specificity for the 1KHz noise band than for the higher frequency bands. They reported a gradual decrease in frequency specificity with increase in contralaterally presented noise frequency. Also Moryl (9) studied the suppression of (click-evoked) emissions using contralaterally presented pure tones and found suppression in some frequency bands of the emission from 250-500Hz tones but no significant suppression from higher frequency tones. At this juncture an intriguing question about the frequency specific effect of MES is that of its "causation". The tonotopic organization of the MES is the central tenet of our discussion. Researches (10) have identified a more basal shift in the crossed olivo cochlear bundle's (COCB) projections from the medial olivocochlear neurons to the OHCs of the contralateral cochlea. Further there COCB fibres are peaked around 1KHz to 2KHz region of the contralateral cochlea. These anatomical observations suggest that the maximum suppression could be obtained at these frequeacies than else where. Though the tonotopic organization of the MES seems convincing enough, it still does not adequately explain our peculiar findings.

It is now well established that the usage of high (sound pressure) levels of the primaries (f1 & f2) may drive the "cochlear transformer" in to the linear region (11). At such high sound levels, as Guinan (12) states "the active mechanisms in the OHCs may be unimportant" and the passive elements may contribute more to the mechanical effects of the efferent activity. Moreover at levels 70dB SPL different DPOAE generation mechanisms may be involved (13) that utilize lesser active processes. Further, findings in animals (14) and other theoretical considerations suggest that primary level are most effective when L1 is 5 to 10dB>L2 (L1>L2 ; 15). Therefore the optimum level for the primaries that would have made the experiment more sensitive would be 65 and 50 or 55 and 40dB SPL (for L1 & L2 respectively), the same is supported by recent work of Sumitrajit Dhar (pers.comm).

Another current issue in active cochlear biomechanics and the generation of DPOAE is the "fine structure", which the present study has neglected. It is important to understand that DPOAE level recorded at the earcanal is a combination of the waves generated at the primary sites, DPOAE site (2*f1 - f2) and their phase relationships. In this regard due to our limitation in fine resolution recording of DPOAEs and by not knowing the phase relationship between these two sites (Eg. f2 site Vs 2*f1-f2) in our data points, it would be extremely difficult to fully explain our findings. However, it can be argued that in some cases the recording may have been at the "minimum of the amplitude function" (when the two sites are out of phase) and therefore evidenced an enhancement of DPOAE level in such conditions. Further reports in literature also support our findings of DP enhancement (16). Thus one could attribute the same to our findings of DPOAE enhancement in some subjects especially at high frequency DPOAE data points. However at this stage it remains unknown as to why only for lower frequency contralateral NBNs (.5 and 1KHz) a greater " enhancement" effect was evidenced.

On the other hand, at a more basic level, the band width of NBN used in the current study may have also contributed to the mixed results obtained. The present study utilized 1/3 octave noise bands which failed to coincide with or adequately suppress high frequency DPOAE sites especially at 2 and 4KHz, leading to poor suppression effect at these frequencies. In addition, the contralaterally presented NBN in the current study mainly concentrated on the regions around the geometric mean and the primaries. It is well established that there is more than one source of DPOAEs (13,17,18) and our experimental protocol failed to influence the combination tone or 2*f1-f2 site, this may well be considered as the most serious limitation of the present study. If so, then the explanation for the lower frequency (.5Khz) DPOAE suppression would be more complicated by the fact that even for low frequency DPOAEs the narrow bands of noise (contralaterally presented) failed to overlap with the 2*f1-f2 site.

These results should be considered in the light of Norman and Thornton's (7) study, where in suppression appeared to increase with noise band width, although their results showed a significant increase in suppression with band width only for the 1 and 2KHz bands, they obtained a much greater suppression with the wide band contralateral noise (WBN). Thus there is evidence for a general trend of wider noise bands obtaining better suppression and therefore by employing broader band widths for NBN, we may have been able to demonstrate a more specific suppression effect.

In speculation, the lack of suppression at high frequencies may also be attributed to a greater "cochlear amplifier" effect at the basal (high frequency) end. Thus in such cases the active negative damping is greater than the passive positive damping and hence the contralateral efferent effects altering biomechanical properties of OHCs and therefore the level of DPOAEs may not be equal across the length of the cochlear partition. These factors in cohesion could explain our results in the planned comparison (Table-3) wherein significant suppression were obtained only for the 500Hz (NBN) on 500Hz DPOAE amplitude condition.

Unlike the above convoluted reasoning, it is much easier to explain as to "why irrespective of NBN used (in contralateral ear) that there always was a suppression for low frequency DPOAEs" (Figure-1). It may be reasonably argued that the higher frequency NBN find it much easier to suppress low frequency DPOAE's because the generation force is not as great for these emissions as it it for the emissions from the basal end (Sumitrajit Dhar - pers.comm).

Finally, however it would be pretentious to consider any of these factors in isolation, owing to the fact that the amplitude and spectral characteristics of DPOAEs measured in the ear canal may be reflective of not only the intermodulation/distortion products of the various sites of vibration, but also the reverse transmission characteristics of the middle ear, the acoustical properties of the earcanal and the frequency response of the recording equipment. Thus the confounding influences of the above mentioned factors on each other are inextricably meshed and seem to underscore the perplexing results obtained.

CONCLUSION

In the light of the now-known studies on anatomical and physiological peculiarities of the medial efferent (COCB) system, it is unequivocally suggestive of a system having a high degree of frequency specificity. Although our findings demonstrate some degree of frequency specificity of the COCB, to a major part is quite deficient in resolving unambiguously the issue of frequency specificity of the COCB. The equivocal findings in the present study can be attributed to technical limitations, choice of noise band width, high intersubject-suppression variability, and most important of all the inherent nature of the mechanism(s) generating the DPOAEs. However, carefully planned future experiments by researchers utilizing both physiologic and psychoacoustic measures may prove more fruitful in discovering the frequency specific nature of the medial efferent system.

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