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SUBHARMONICS AND AUDITORY NERVE TUNING CURVES IN GERBIL

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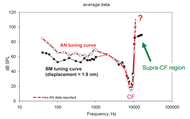
Introduction and Motivation

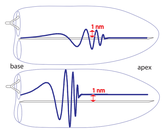
Question 1: Is there auditory nerve response in the plateau region?

Ruggero et al 2000 compared threshold tuning curves of chinchilla basilar membrane (BM) vibrations and auditory nerve (AN) fibers. They noted that the AN tuning curves lacked the higher-than-CF frequency plateaus that are present in BM responses and suggested that BM vibrations do not translate into AN responses at greater than BF regions. [1]



Ruggero et al's chinchilla BM tuning curves and neural tuning curve.[1] No neural response was recorded in the plateau region.

Implication of their study: a given amount of BM vibration within the BF region elicits a response in the AN, but the same amount of BM vibration in the plateau region did not produce any response in the AN.



Top: Stimulus frequency ≤ BF

(measuring BM in the short-wave region), a low SPL is required to drive the BM 1nm. Neural response observed.

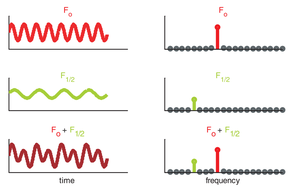
Bottom: Stimulus frequency >> BF

(measuring BM in the plateau region), a high SPL is required to drive the BM 1nm. No neural response observed.

To investigate this finding further, we recorded single unit AN responses in gerbils, to see if at high enough stimulus levels, we would observe a high frequency plateau in the AN responses. If so, what causes the diminished auditory nerve response in the plateau region?

In the literature, responses beyond the tip in the well supra-CF frequency region of a tuning curve had never been documented. In a study designed to explore that region specifically, we found plateau responses in the supra-CF region of several auditory nerve tuning curves at very high sound pressure levels (~120dB SPL). (Huang&Olson, ARO 2009, poster #623) However, a complicating issue at high sound pressure levels is the generation of subharmonics, which are likely generated in the eardrum (Dallos & Linnell 1966 JASA 40(3):561-564). Indeed, we found subharmonics in a subset of our gerbil ear canal pressure, and they might have contributed to the supra-CF responses.

Appearance of subharmonics:



STUDY 1 (Auditory Nerve) :
Here we present auditory nerve tuning curves in which supra-CF neural responses were present while subharmonics were beneath the noise floor in the ear canal pressure. Thus these detections of supra-CF neural responses did not seem to suffer from subharmonic "contamination."

In order to understand whether subharmonics that we can measure in the ear canal (EC) likely caused the measured plateau response in AN firing, we needed to know the relationship between the size of subharmonics in the EC and in the cochlea.

Outcome is not obvious – The eardrum motion is the source for the subharmonics in both the EC and the cochlea. Thus the normal relationship between EC pressure and cochlear pressure (typically ~ 20 – 25 dB of gain) cannot be expected.

Possibilities:
(1) Intracochlear subharmonics might be MUCH bigger than EC subharmonics (even more than 20 – 25 dB bigger). This would be a problem for our study, since if we can't measure EC subharmonics (and our noise level is ~ 20-30 dB SPL) they could still be of a size that is excitatory in the cochlea.

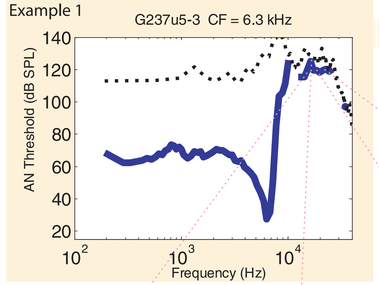
(2) Intracochlear subharmonics might be smaller than EC subharmonics. This would be advantageous to our study, since then unmeasurable EC subharmonics would in most cases be less than excitatory in the cochlea.

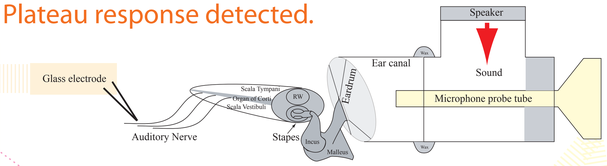
(3) Something in between 1 and 2.

STUDY2 (Intracochlear Pressure) :
To probe this further, we delivered loud tones and compared ear canal pressure and intracochlear pressure at subharmonics frequencies, and the quantitative relationship between the two reinforced that subharmonics were probably not responsible for the supra-CF neural responses we measured.

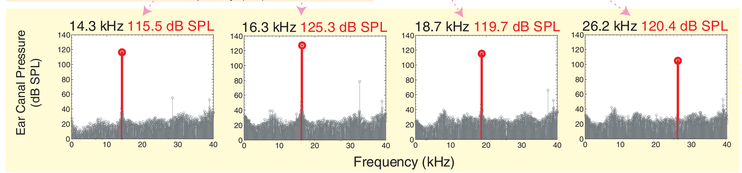
❖ Auditory Nerve Answer 1: Plateau response detected.

Example 1

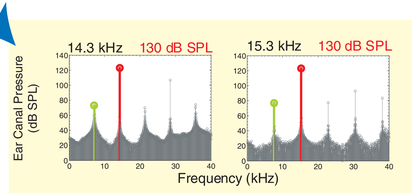




Method:
In vivo, single unit extracellular recording. Sokolich's surgical approach. [2,3] Tuning curve algorithm developed by Kiang,Moxon&Levine [4]. Threshold criterion = 10~20 spikes/sec. *No averaging performed in microphone data. Noise floor due to microphone and acoustic noise.



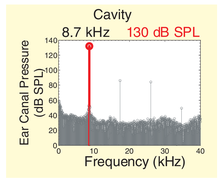
At the supra-CF plateau threshold levels, subharmonics in the ear canal were below the noise floor.



However, when the stimulus level is ~10dB higher, the eardrum-produced subharmonics emerged abruptly in the ear canal.

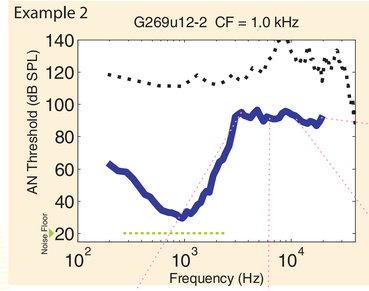
- Subharmonics emerge abruptly in the ear canal pressure at ~130dB SPL.

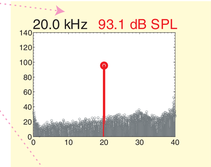
- No subharmonics can be observed at 130dB SPL in a cavity. Subharmonics observed in the ear canal were not produced in the speaker or microphone.

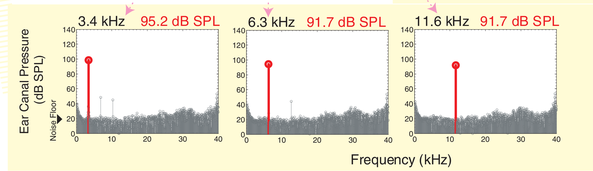


Noise Floor ≥ Subharmonic Level

Example 2







Results:
- For these 2 examples, the supra-CF plateau response is free from detectable subharmonic contamination in the ear canal pressure.

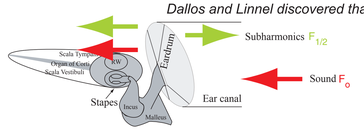
Example 2: No subharmonics can be seen above the noise floor ~20dB SPL. A minimum of 30dB SPL (tip threshold) is required to elicit a neural response
--> Subharmonics are too low in level to elicit a neural response.
--> Hence, the plateau resopnse is not caused by the subharmonics.

Answer 2: Subharmonics were not the basis for our auditory nerve plateau response.

(When subharmonics are in the noise, they are not big enough to be excitatory.)

Problem: Subharmonics discovered. They might have produced the plateau response.

Dallos and Linnel discovered that the subharmonics observed in the ear canal are generated in the eardrum [7,8,9].



- Fundamental frequency of the stimulus
- Subharmonics of the stimulus

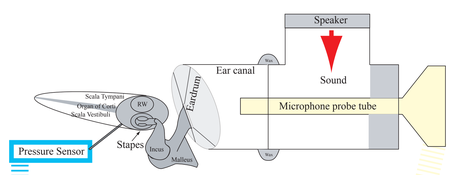
Intracochlear pressure shows that normal sound drive (fundamentals) and the subharmarmonics have a comparable relationship.

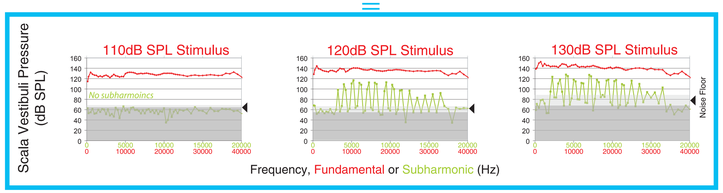
Thus, equipped with this relationship, we can treat subharmonics like fundementals to determine if subharmonic levels in the ear canal are high enough to elicit an auditory nerve response.

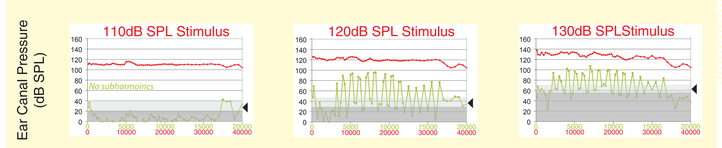
Question 2: Could these eardrum-produced subharmonics result in a stimulating pressure in the cochlea?

❖ Intracochlear Pressure

Method:
Miniature fiber-optic based pressure sensor is placed behind the stapes in the scala vestibuli to measure intracochlear pressure.







Results:

1. Subharmonics were recorded in the ear canal pressure and in the intracochlear pressure for 120 and 130 dB SPL stimulus drives in this gerbil

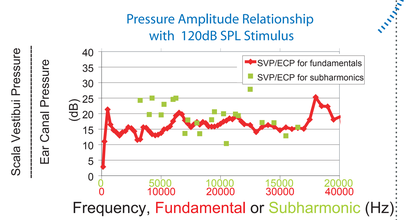
2. Subharmonics are not present for every stimulus frequency.

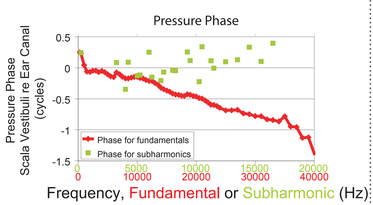
3. Subharmonics emerge abruptly at high SPL in the intracochlear pressure. This is also consistent with Dallos and Linnel's observed properties of subharmonics in the cochlear microphonics [7,8,9].

4. When the stapes is disarticulated, the subharmonics persist in the ear canal pressure. This result confirms Dallos and Linnel's finding that the even-order subharmonics come from the eardrum [7,8,9]. (not shown)

5. Information obtained:
Scala vestibuli to ear canal pressure ratio is similar for the stimulus drive (fundamentals) and the subharmonics.

$$\left[\frac{SVP}{ECP}\right]_{subharmonics} \approx \left[\frac{SVP}{ECP}\right]_{fundamentals}$$





6. Subharmonic phase shows ~ zero delay, reinforcing that subharmonics originated in the middle ear (not speaker) .

Clinical Implications of our Measurements:

1. Human subjects do perceive subharmonics when exposed to 130+ dB SPL sound [10]. Potential problems with hearing aids at high SPLs: Patients with band limited or high frequency hearing loss require such high SPLs within the hearing loss frequencies that subharmonics are produced within their normal hearing frequencies. As a result, patients might perceive subharmonics to be louder than the intended fundamentals.

2. Many high power hearing aids capable of 130+ dB SPL, at which level the patients' eardrums can be driven to produce subharmonics.

Make	Model	Possible Power (dB SPL)
Phonak	SuperFront PP-C-L-4	142
	SuperFront PP-SC	140
Siemens	Centra HP	136
	Centra P	131
	Motion P	130
Oticon	Sumo DM	144
Widex	BV-8	131
	AK-m	130
	m4-m	132

Conclusion:

We recorded a plateau response in the supra-CF region of AN tuning curves in the gerbil. Eardrum-produced subharmoincs emerge when the stimulus level exceeds ~120dB SPL. They do not likely contribute to the supra-CF plateau response, when subharmonics are beneath the noise floor, as in the examples here.

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