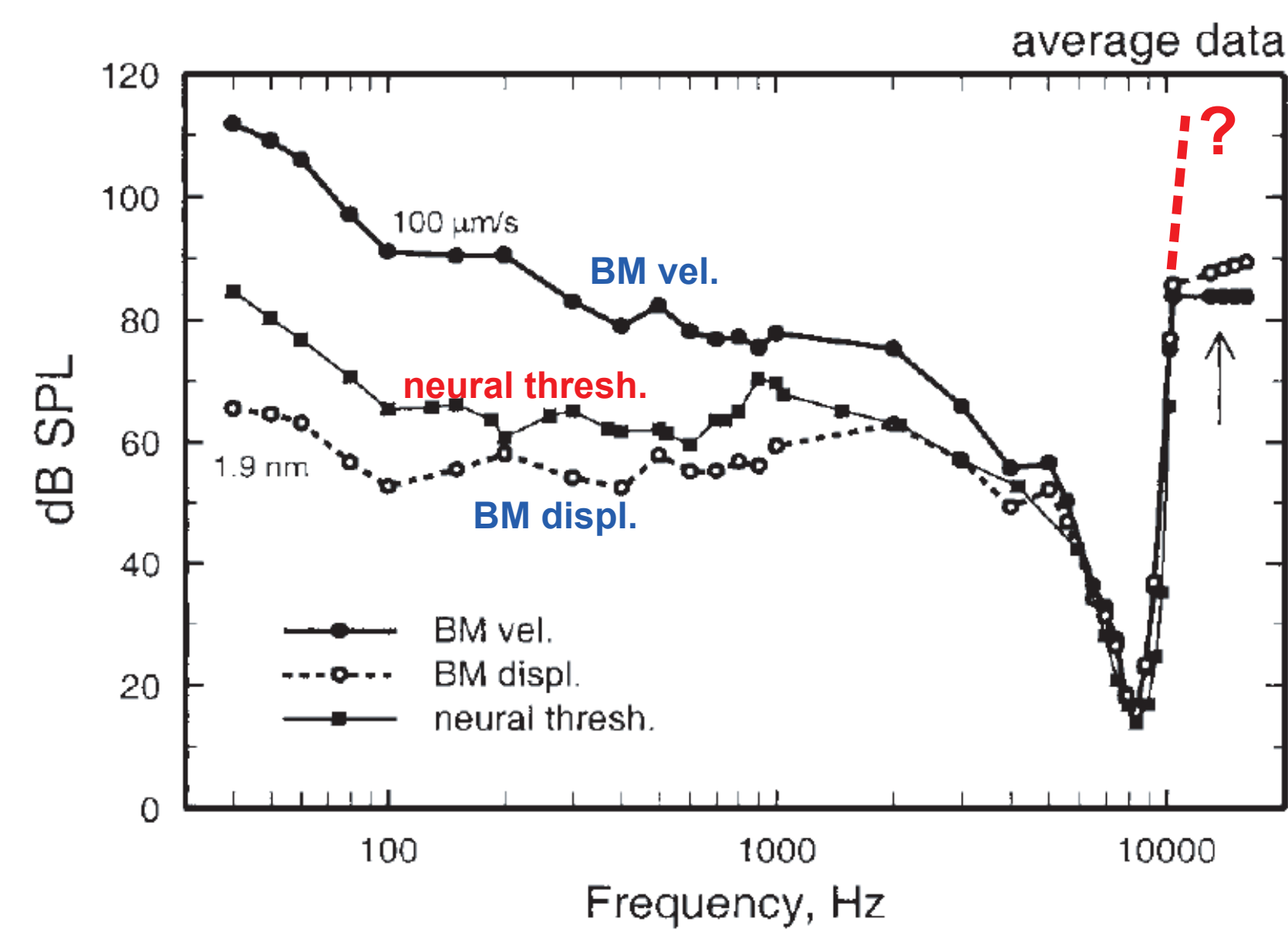


HIGH FREQUENCY PLATEAU IN GERBIL AUDITORY NERVE TUNING CURVES

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Introduction and Motivation

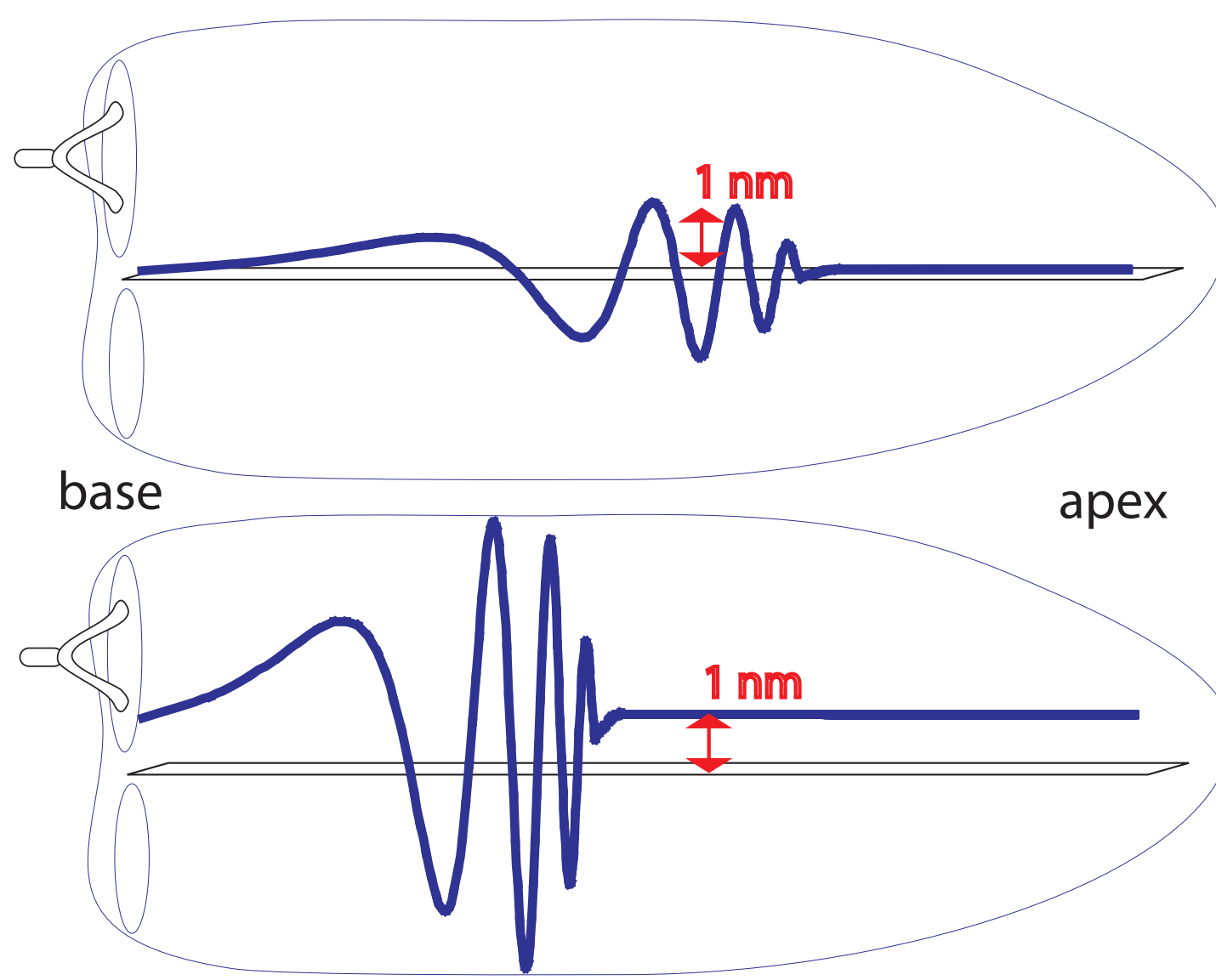
Ruggero et al 2000 compared threshold tuning curves of chinchilla basilar membrane (BM) vibrations and auditory nerve (AN) fibers. They noted that the AN tuning curves lacked the higher-than-CF frequency plateaus that are present in BM responses and suggested that BM vibrations do not translate into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

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



Bottom: Stimulus frequency \gg BF (measuring BM in the plateau region), a high SPL is required to drive the BM 1nm. No neural response observed.

However, exploring the plateau region was not a goal of Ruggero et al's study and they did not probe it in detail. To investigate this discrepancy 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?

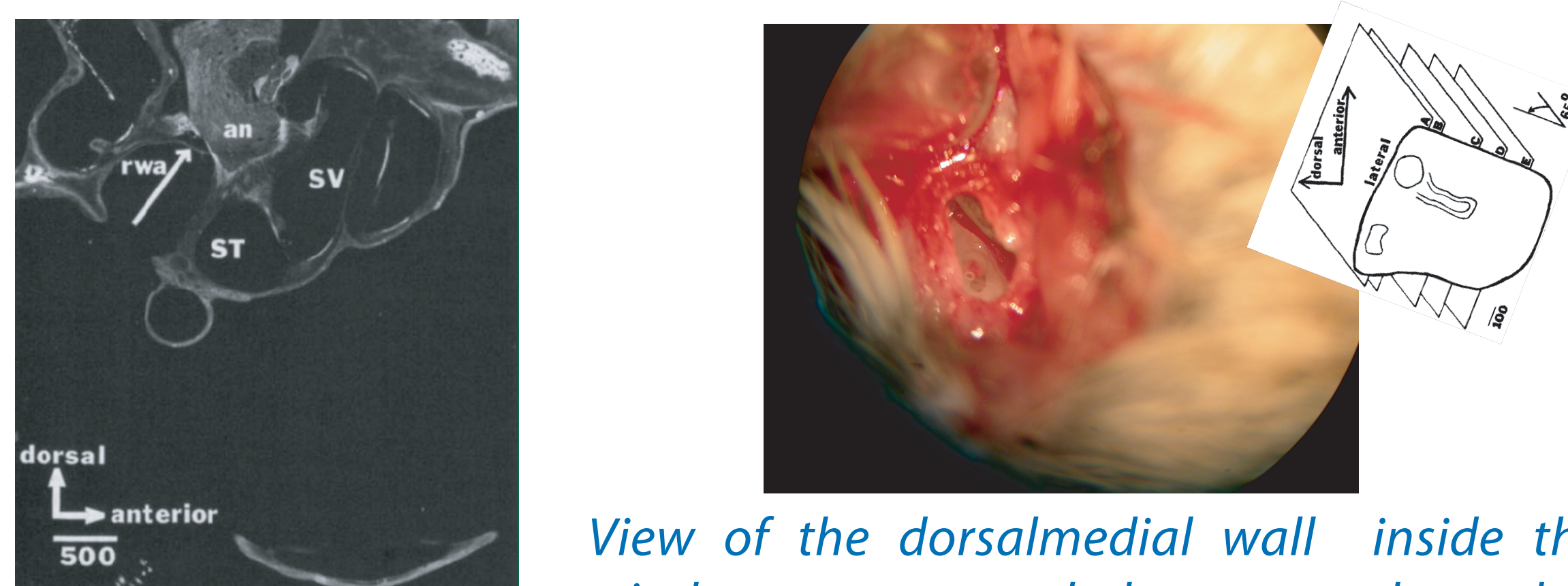
Hypotheses:

- 1) Curvature of the BM might play a role in determining whether hair cells get excited.
- 2) The feedforward model might include a mechanism where the hair cells in the plateau region are suppressed by the actions of the hair cells in the short-wave region.

This study might give us some clues to how the BM vibrations are translated into neural responses.

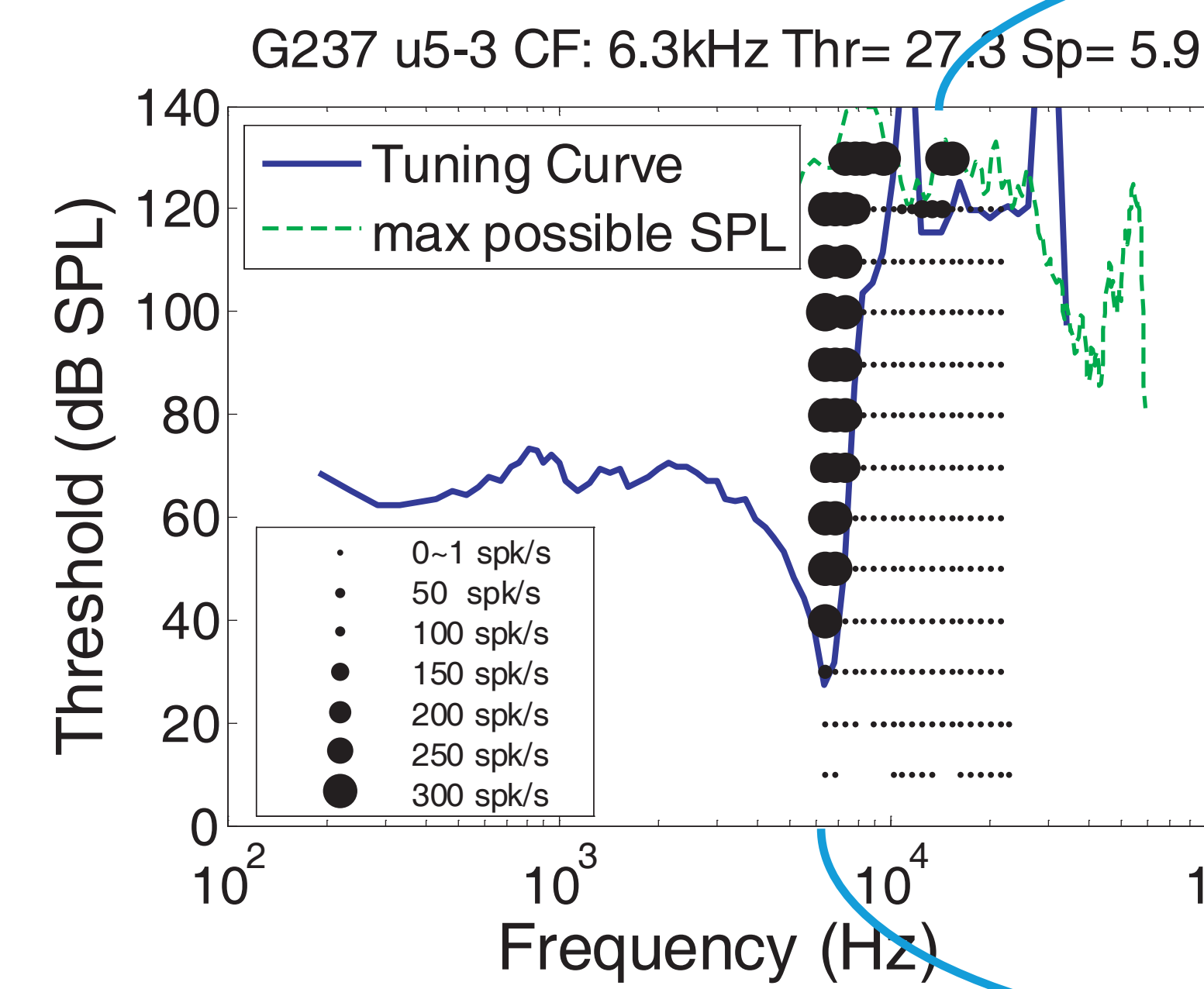
Methods

In vivo, in gerbil, with closed field pure tone stimulation. Single unit extracellular recording. Glass pipette microelectrode Z~50MΩ. AN is accessed surgically using Sokolich's approach. [2,3] Tuning curve algorithm developed by Kiang, Moxon & Levine [4]. Threshold criterion = 10~20 spikes/sec.

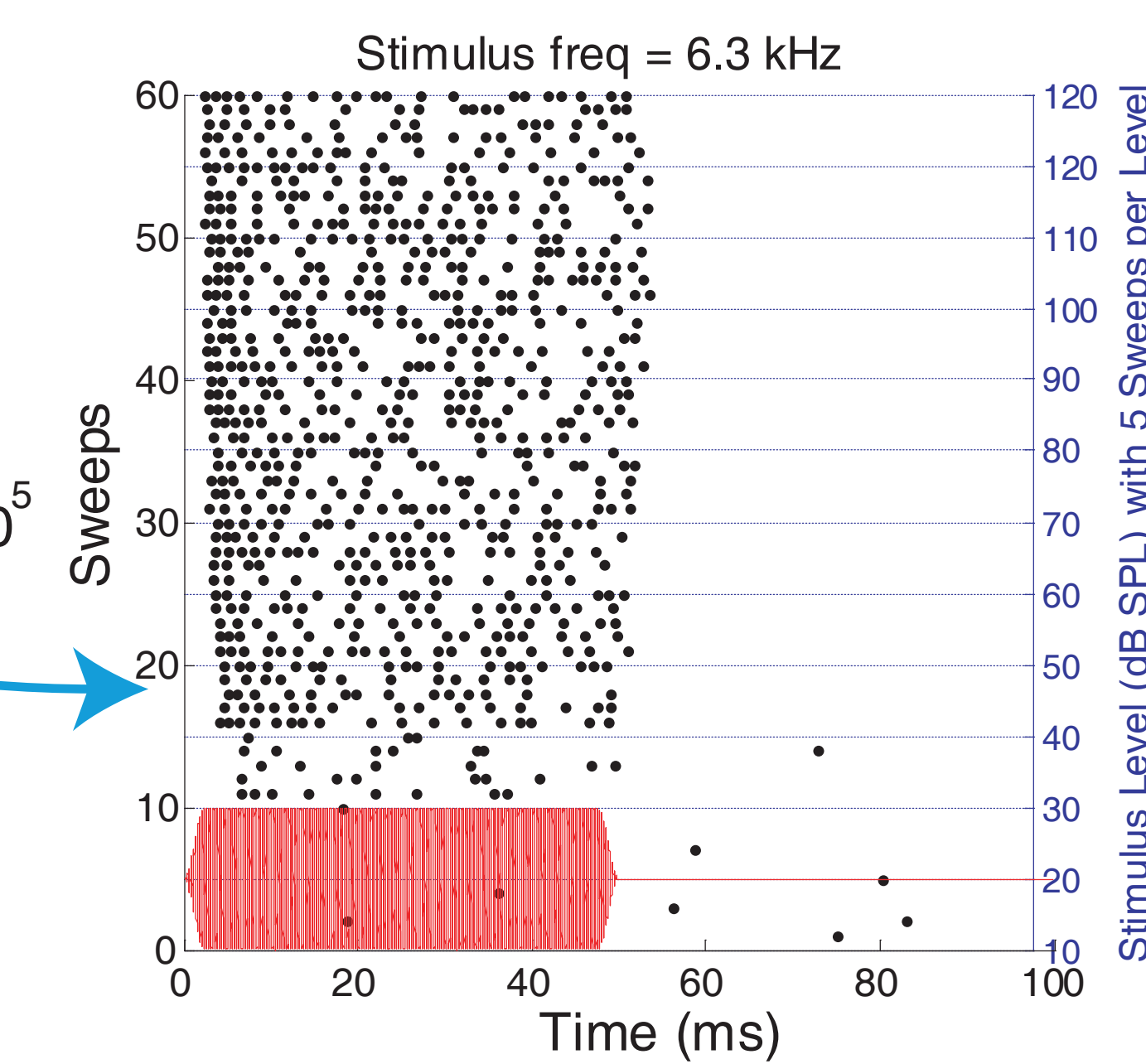


View of the dorsomedial wall inside the round window antrum and the approach angle to gain access to the AN. [3]

Recording tuning curves up to frequencies > CF



Monitor neural firing rates and patterns to verify tuning curves and their plateaus.



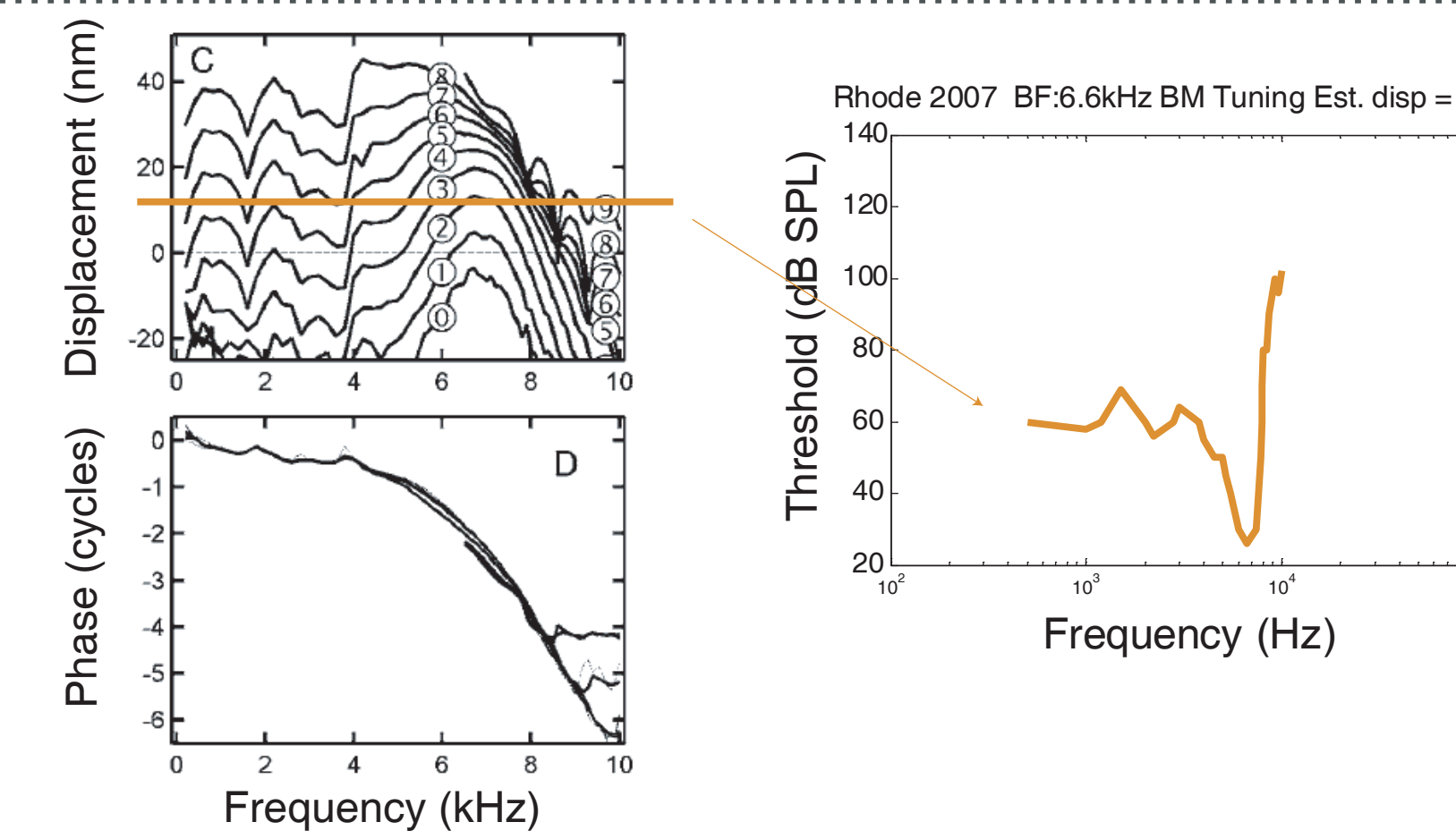
Firing pattern shows overall increase in neural firing rate, hence eliminating the possibility of false threshold detection due to transient responses.

Results 1: Comparison of mechanical and neural responses

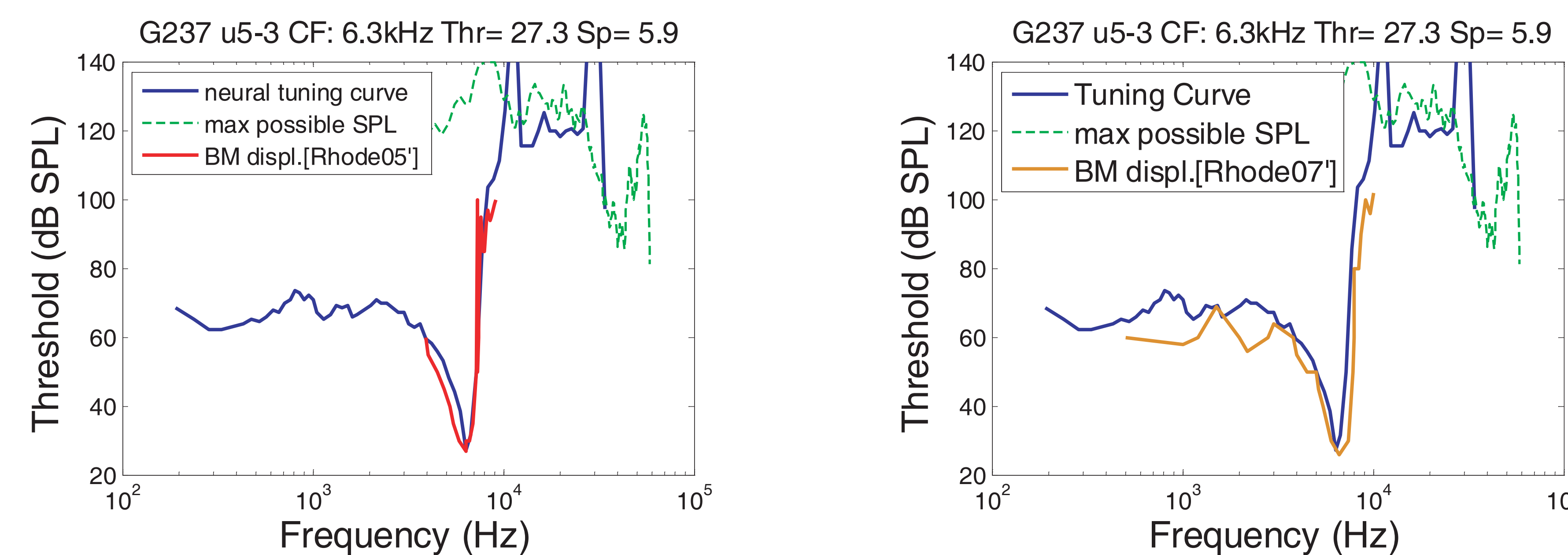
Method:

Interpolate BM tuning curves from published BM data. Match threshold SPL of the tip. Overlay BM tuning curves on gerbil neural tuning curves. Compare plateau sound pressure level.

Note: BM data in the plateau region is not abundant.



Comparing Rhode's chinchilla BM tuning data [5,6] to gerbil neural data:



Result: A plateau in the AN response was observed.

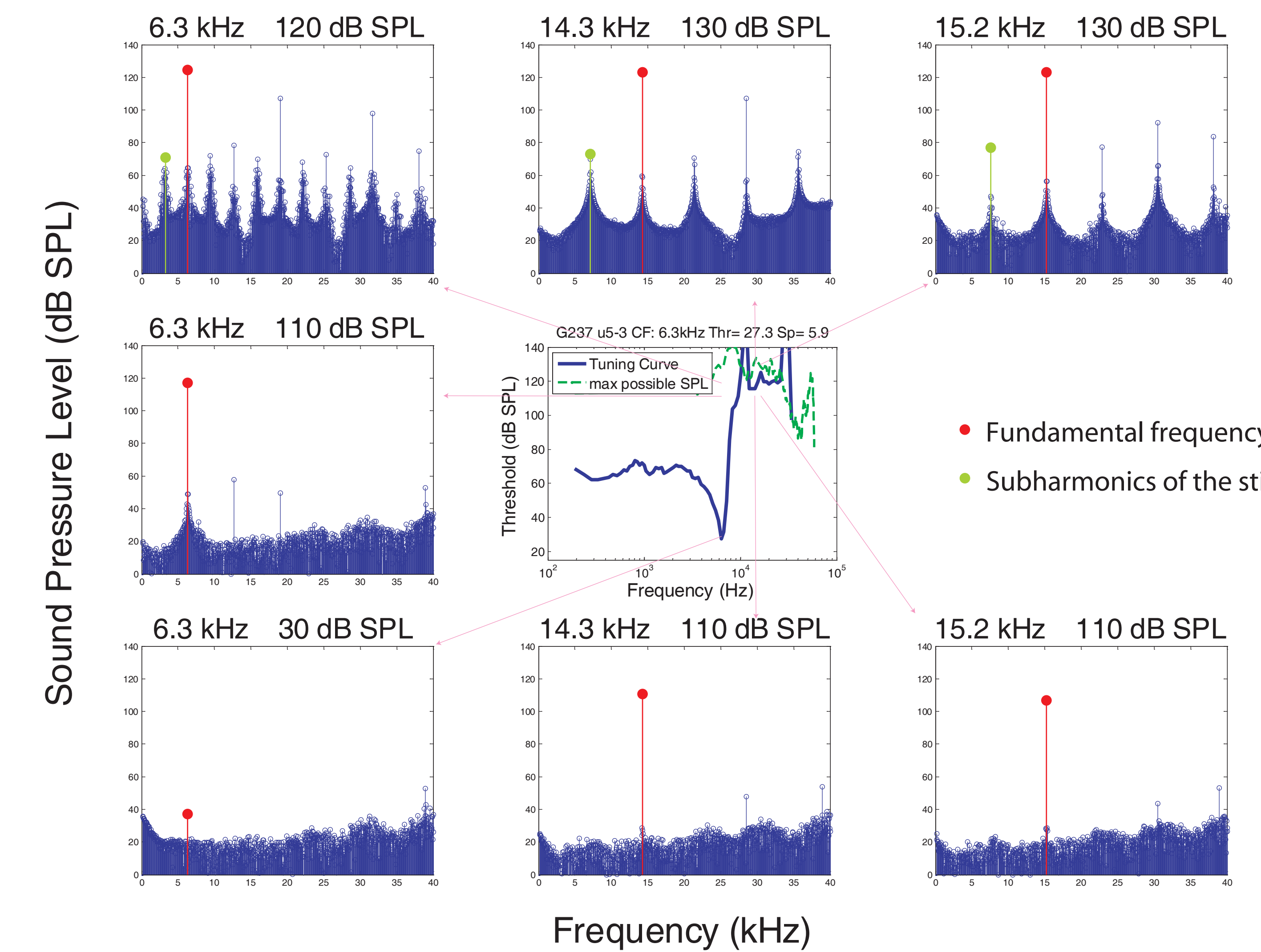
- When matching chinchilla data to gerbil data: The neural plateau in the gerbil is at least 10~15 dB higher than the BM plateau in the chinchilla. (The available BM magnitude data is limited in frequency range so does not show a very clear plateau. However, the presence of the plateau could be clearly identified in the BM phase data.)

BM plateau data from literature. This table summarizes the levels of plateau that have been observed in BM motion:

First Author	Year	Journal	Animal	data type	BF (kHz)	BM displ.(nm)	BM vel.(μm/s)	Plateau (dB SPL)	matched to	CF (kHz)	CF thresh(dB SPL)	Notes
Rhode	2005	Aud.Mech.	chinchilla	BM	6.3	6		~100	my AN data	6.3	27	
Rhode	2007	J.Acoust.Soc.Am	chinchilla	BM	6.6	16		~100	my AN data	6.3	27	
Ruggero	2000	PNAS	chinchilla	BM	9.5	1.9	100	85-90	Ruggero	9.5	12	Mossbauer, prior BM data
Ruggero	2000	PNAS	chinchilla	BM	9.5	2.7	164	90-100	Ruggero	9.5	12	Laser vibrometer, same cochlea
Rocheffoucauld	2007	biophysj	gerbil	BM	20-25		30	100				passive, assume linear to SPL
Ren	2001	Hear.Res.	gerbil	BM	13	1	60	100-110	my AN data	11.6	54	

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Results 2: Subharmonics at high sound pressure levels



The spectrum of the sound pressure measured in the ear canal. Red markers indicate the stimulus frequency and SPL introduced in the ear canal

Result: Subharmonics were recorded in the ear canal at high SPLs

Mostly even-order subharmonics; some odd-order subharmonics too

No subharmonics can be observed in the speaker even at a very high sound pressure level in a controlled fake ear cavity. Subharmonics observed here were not produced in the speaker or the recording devices.

Dallos and Linnell did a series of studies on subharmonics in the ear. Even-order subharmonics come from the ear drum, odd-order subharmonics from the cochlea. [7,8,9]

Discussion and Relevance of the Findings to Cochlear Activity

We observed neural response in the supra-CF plateau region. Neural plateau (gerbil) is at least 10~15 dB higher than BM plateau (chinchilla).

1. Gerbil BM data is usually in the high-BF region. We lack high-CF AN units to compare at this point.
2. Windowing problem: it is possible that the synaptic/neural delay is not correctly accounted for. ie. spikes during a tone-on period are mistaken for a tone-off period. This problem would lead to false positive threshold attainment. However, this problem is eliminated by monitoring overall firing rate increase with the use of rate level functions.
3. Spectral splatter problem: on ramp/off ramp in the stimulus envelope introduce frequencies other than the stimulus itself. It is conceivable that this frequency splatter could cause spurious transient response. This can be mostly avoided by a) inspecting raster plots to identify the transient response, 2) using only the steady-state response, 3) monitoring firing rates. (see Methods)
4. It is possible for the high SPL stimuli to cause AN threshold shift and/or hearing damage.
5. Subharmonics could be the source of the AN plateau response. AN units have a lower threshold (near CF) at subharmonics frequencies of the stimulus. (see Future Studies)
6. The BM motion data acquired by Laser measurement could be contaminated by the round window motion artifact at plateau frequencies.

Future Studies

Identify the source of the plateau in the neural response

Look at firing patterns and calculate vector strength at phase locking frequencies to probe possible subharmonic response

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