Human auditory models of monaural processing: Physiological and functional aspects in the implementation of auditory-nerve firing models

Alejandro Osses

Human auditory models of monaural processing: Physiological and functional aspects in the implementation of auditory-nerve firing models

Alejandro Osses V.

E-mail: ale.a.osses@gmail.com

Laboratoire des Systèmes Perceptifs, École Normale Supérieure (ENS), PSL University, Paris, France

21 March 2022

Research seminar MOD 2022

My background

2003-2010 Engineering in Sound and Acoustics  (B.Sc. + “M.Sc.”)

2010-2012 Acoustic consultant 

2012-2014 KU Leuven  – “Predoc” in Cochlear Implant sound processing (prof. Jan Wouters)

2014-2018 TU Eindhoven  – Ph.D. in Auditory modelling (prof. Armin Kohlrausch)

2018-2020 UGent  – PostDoc in Auditory modelling (prof. Sarah Verhulst, prof. Dick Botteldooren)

2021 – ENS  : **fastACI** project with Léo Varnet

2020 – Developer within the Auditory Modelling Toolbox project amtoolbox.sourceforge.net (lead by dr. Piotr Majdak)

I hope I manage to bring you a “different perspective”

Motivation (1 / 2)

Based on:

Osses, Varnet, Carney, Dau, Bruce, Verhulst, Majdak (2022, Acta Acustica)
Preprint at https://arxiv.org/abs/2107.01753

Abstract:

A number of auditory models have been developed using diverging approaches, either physiological or perceptual, but they share comparable stages of signal processing, as they are inspired by the same constitutive parts of the auditory system. In this seminar, I will briefly describe the main stages of sound processing from the outer ear (or pinna) up to the inferior colliculus (midbrain) but I will focus on the physiological aspects that have been implemented in the model stages of inner hair cell (IHC) processing and auditory nerve (AN) synapse, at the beginning of the auditory neural pathway. I will also show auditory responses obtained from perceptual models that can capture specific neural processing properties.

Motivation (1 / 2)

Based on:

Osses, Varnet, Carney, Dau, Bruce, Verhulst, Majdak (2022, Acta Acustica)
Preprint at https://arxiv.org/abs/2107.01753

Abstract:

A number of **auditory models** have been developed using diverging approaches, either **physiological** or **perceptual**, but they share comparable stages of signal processing, as they are inspired by the same constitutive parts of the auditory system. In this seminar, I will briefly describe the main stages of sound processing from the outer ear (or pinna) up to the inferior colliculus (midbrain) but I will focus on the physiological aspects that have been implemented in the model stages of **inner hair cell** (IHC) processing and **auditory nerve** (AN) **synapse**, at the beginning of the auditory **neural pathway**. I will also show auditory responses obtained from perceptual models that can capture specific neural processing properties.

Motivation (2 / 2)

From Maxwell et al. (2020, JASA):

Model by Zilany et al. (2014)

> Note that this AN model is substantially different from peripheral models such as Dau *et al.* (1997), used in simulations of the notched-noise task in Derleth and Dau (2000) and similar masking tasks (with some changes to the model) in Jepsen *et al.* (2008). The Dau *et al.* (1997) model, and later modifications, did not include IHC saturation and did not aim to simulate physiological neural fluctuations and capture.

Another model

True

True, but this does not mean that a model may not account for neural fluctuations and capture

“Publish your code: it is good enough” (Barnes, 2010, Nature)

So, if a code is published, you can try it!

What is a model?

https://en.wikipedia.org/wiki/Model

“A model is an informative representation of an object, person or system”

Physical model [edit]

A physical model is a physical representation of an object, such as a miniature aeroplane representing a real aeroplane.

- ~~Model (art),~~ a person posing for an artist, e.g. a 15th-century criminal representing the biblical Judas in Leonardo da Vinci's painting *The Last Supper*
  - ~~Model (person)~~, a person who serves as a template for others to copy, often in the context of advertising commercial products
- Model (product), a particular design of a product offered by its manufacturer
  - Car model, a particular design of vehicle sold by a manufacturer
- Model organism (often shortened to *model*), a non-human species that is studied to understand biological phenomena present in other related organisms, e.g. a guinea pig starved of vitamin C to study scurvy, an experiment that would be immoral to conduct on a person
- ~~Model (mimicry)~~, a species that is mimicked by another species

Conceptual model [edit]

A conceptual model is a theoretical representation of a system, e.g. a set of equations attempting to describe the workings of the atmosphere for the purpose of weather forecasting.

- Conceptual model (computer science), a representation of entities and their relationships
- Mathematical model, a description of a system using mathematical concepts and language
- ~~Economic model~~, a theoretical construct representing economic processes
- Statistical model, a mathematical model that usually specifies the relationship between one or more random variables and other non-random variables
- ~~Model (CGI), a~~ mathematical representation of any surface of an object in three dimensions via specialized software
- Model (logic), a set along with a collection of finitary operations, and relations that are defined on it, satisfying a given collection of axioms
- ~~Model (MVC),~~ the central component of the model–view–controller software design pattern
- Standard model (disambiguation)
- ~~Medical model~~, a proposed "set of procedures in which all doctors are trained"
- ~~Model act, a la~~w drafted centrally to be disseminated and proposed for enactment in multiple independent legislatures

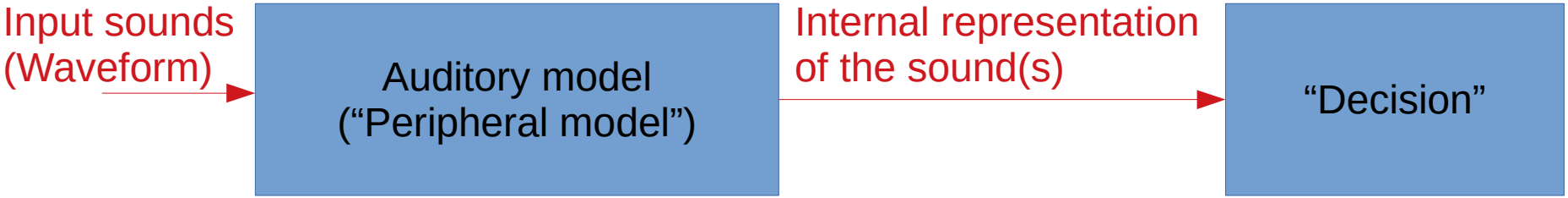
What is a computational model?

Computational modelling is the use of computers to simulate and study complex systems using mathematics, physics and computer science.

(https://www.nibib.nih.gov/science-education/science-topics/computational-modeling)

We will focus on computational models of the auditory system

(Video from https://en.wikipedia.org/wiki/Hair_cell)



Biophysical model
Phenomenological model
Functional effective model
Statistical model

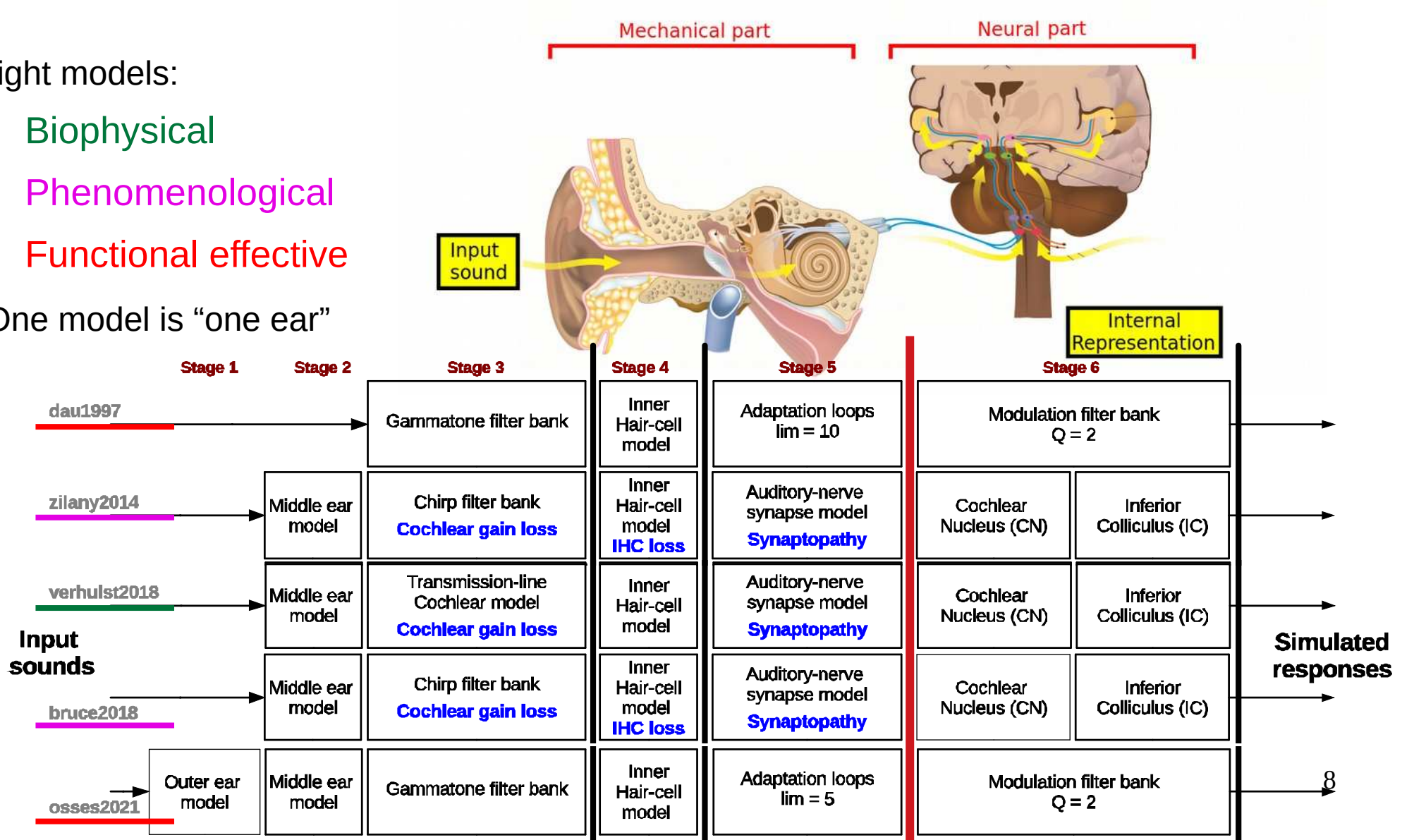
Simple task:
Yes, the target sound is present
No, the target sound is absent

I will show one auditory task:
- Not modulated by cognitive aspects
- Based on bottom-up evidence

Eight models:

- Biophysical
- Phenomenological
- Functional effective

One model is “one ear”

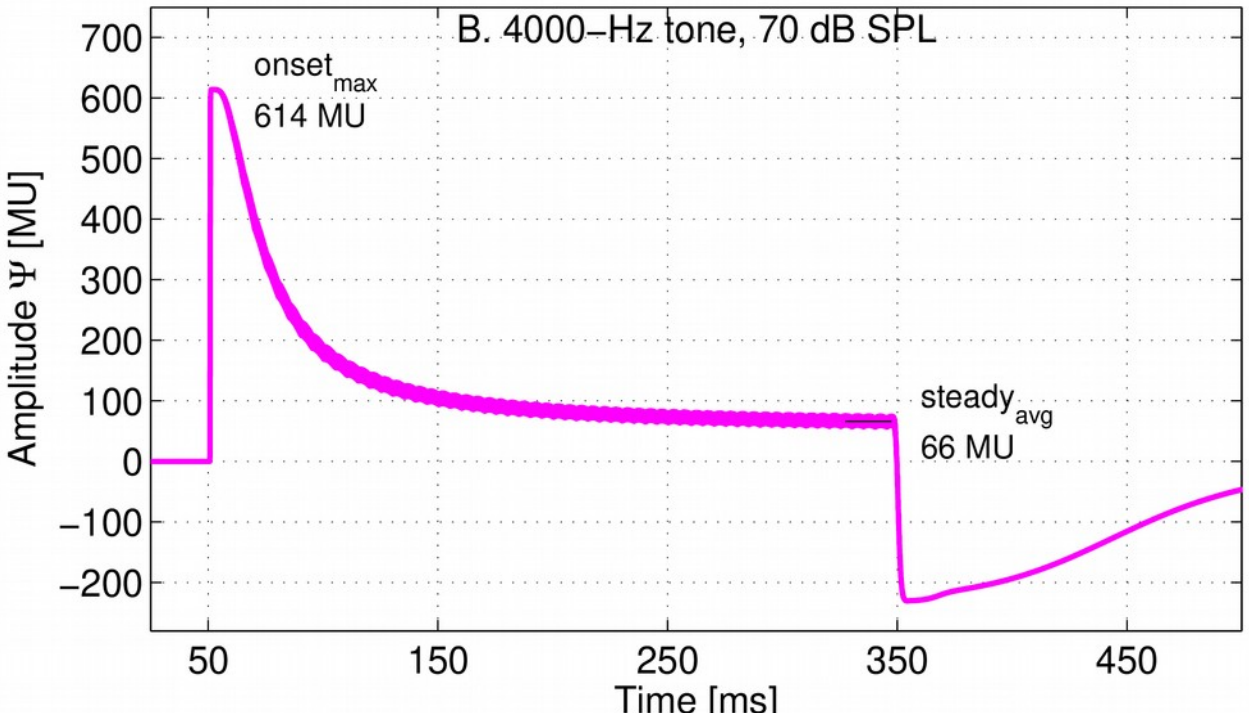


Differences between the models

- They were built using different rationales:
  - Physiologists don’t like functional effective (perceptual) models
  - Psychoacousticians do not always like the complexity of the biophysical and phenomenological models
  - Physiologists and psychoacousticians do not always use the same input stimuli in their model design
- **But in the end, all models are just an approximation...**

Stage 5: Auditory adaptation stage

- Learning from observations:



Approximation using “adaptation loops”
(used in dau1997, relanoiborra2019, osses2021)

Fig. C.11B
from Osses (2018, Ph.D. thesis)

Kohlrausch et al. (1992):

“The last class of investigated models tries to incorporate the adaptive properties of the auditory periphery. Adaptation means a change in the transformation characteristic according to the input level. Such an automatic gain control **can be** achieved with a feedback loop […].”

Stage 5: Auditory adaptation stage

- The “more accurate models”:
  - Auditory-nerve synapse models
- Next:
  - Brief overview of each processing stage: Key features
  - Some emphasis in the IHC and AN (adaptation) stage

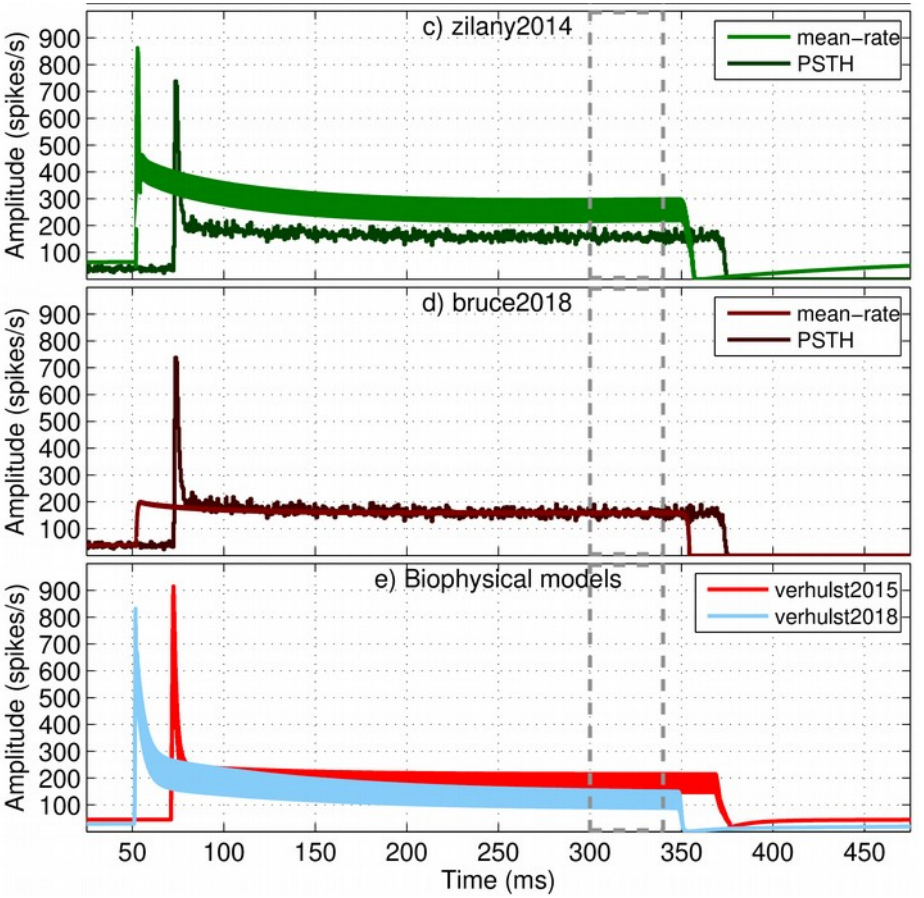
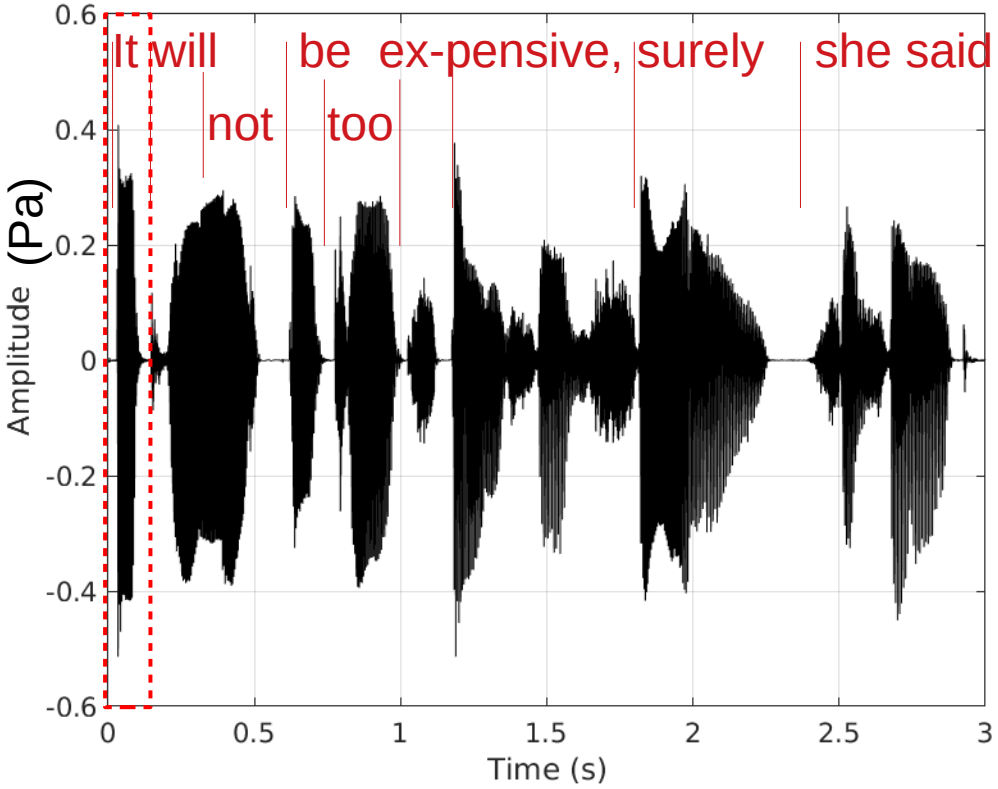
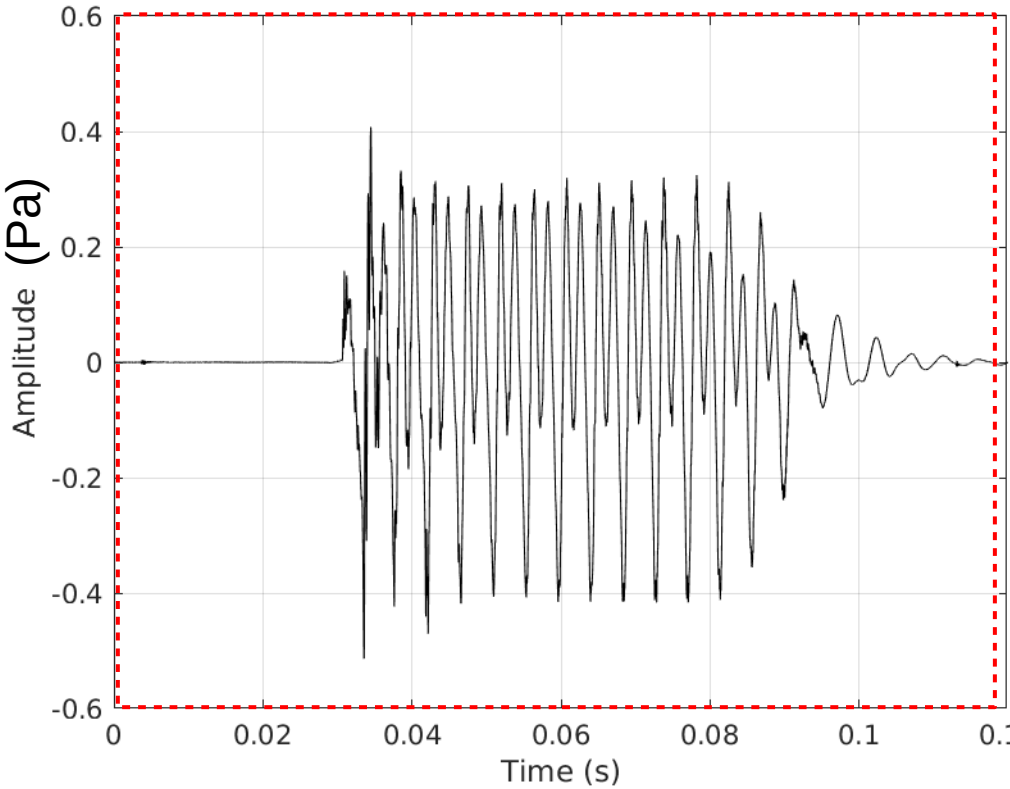


Fig. 9 from Osses et al. (2022)

An input signal: The waveform

- “It will not be too expensive, surely, she said”

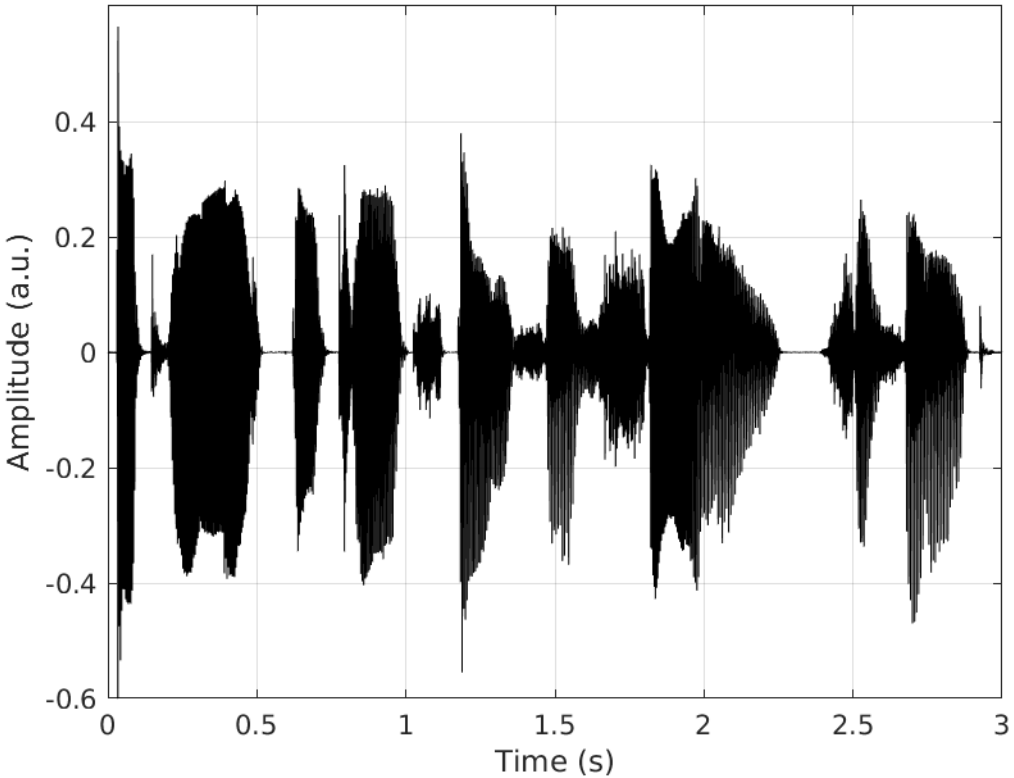


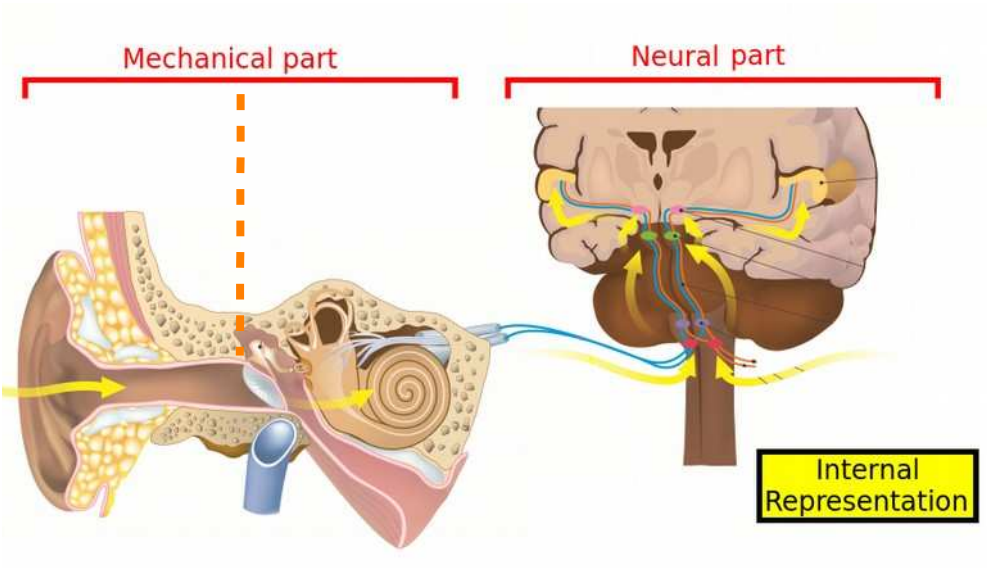


- This is fast-varying time information

Outer ear filtering

- The pinna acts as an equaliser
- The ear canal acts as a tube that resonates



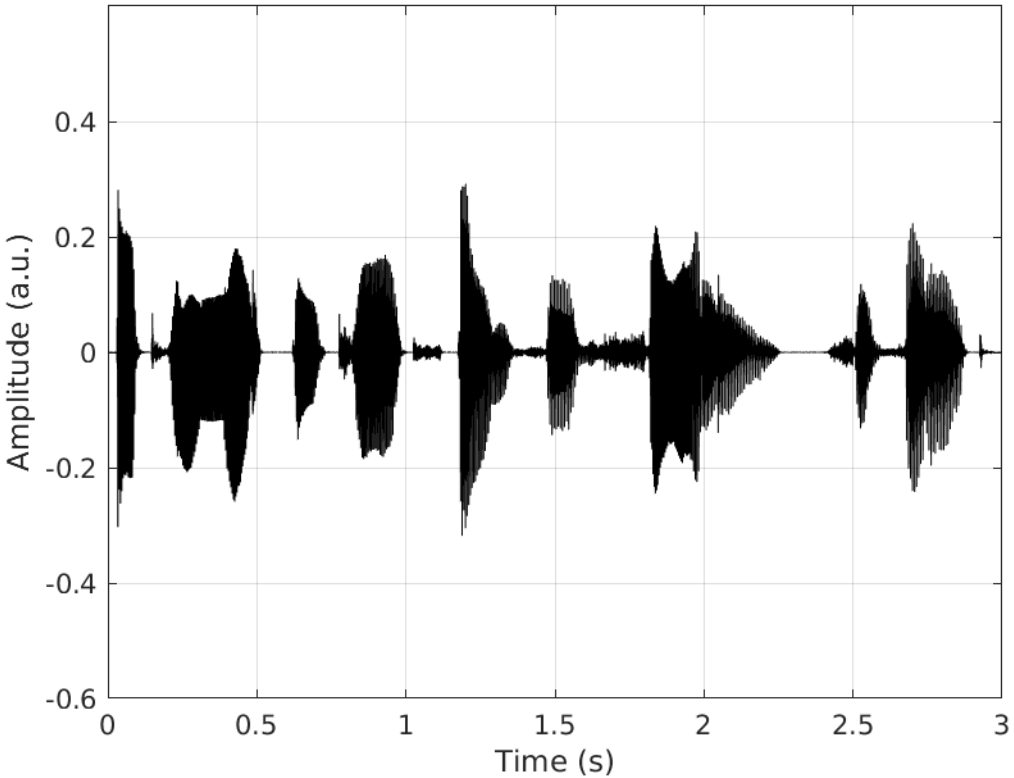


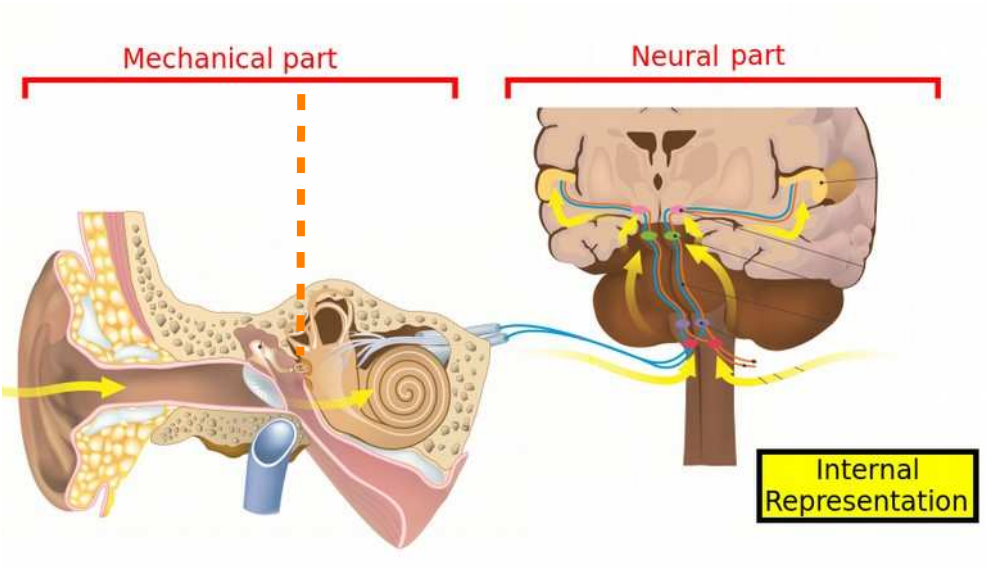
Physiological output:
Ear canal pressure (Pa)

- **This process is approximated as a linear filter**

Middle ear filtering

- It is an impedance matcher: Change of medium from air to fluids in the cochlea
- It acts as a filter with a non-null gain



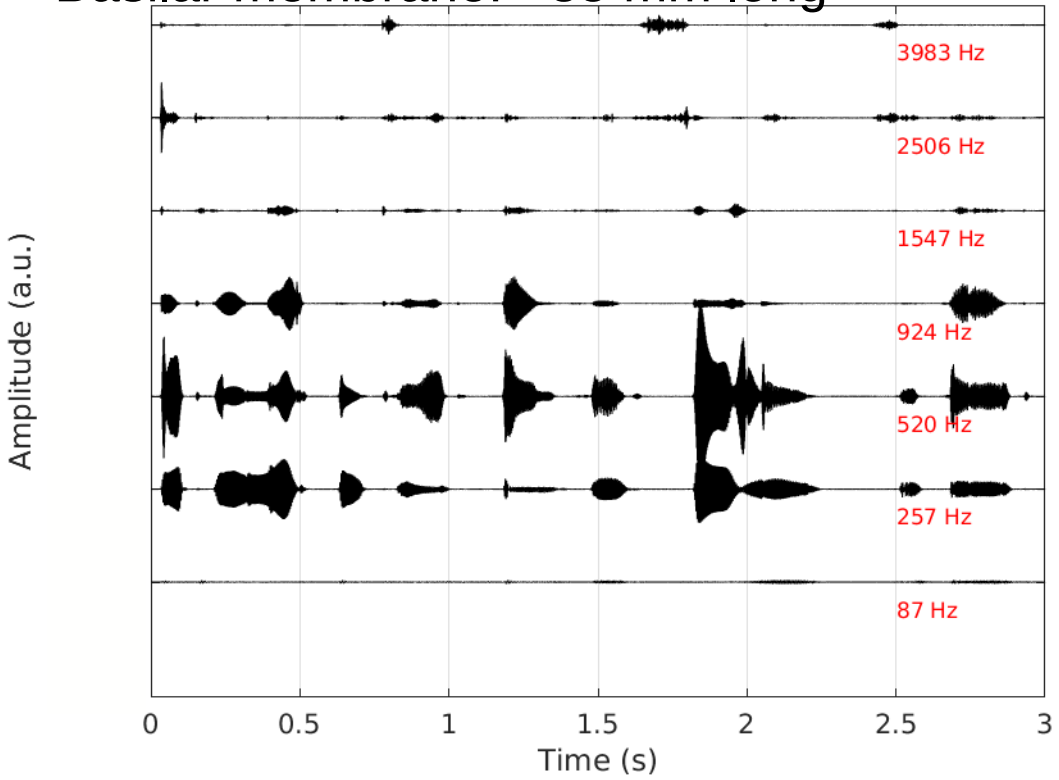


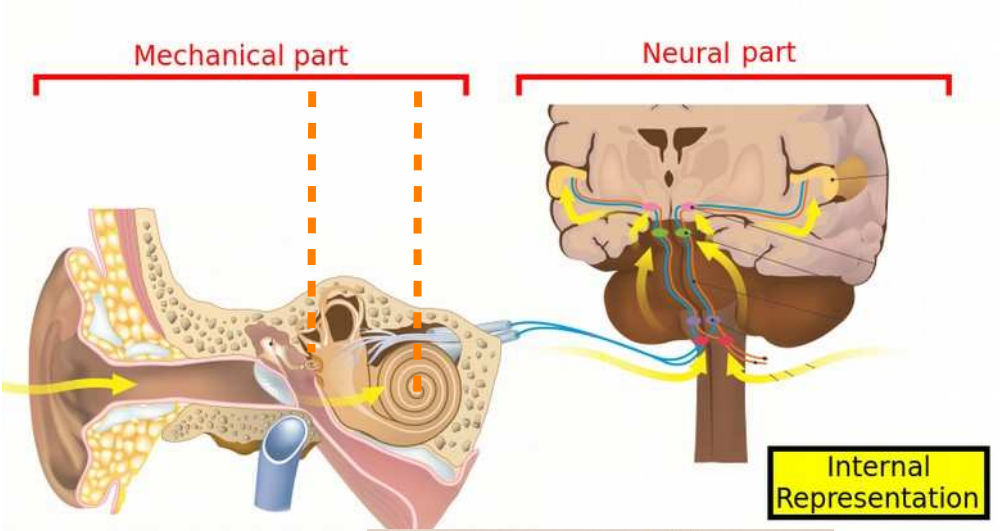
Physiological output: Stapes velocity (m/s)

- **This process is approximated as a linear filter too**

Cochlear filter bank

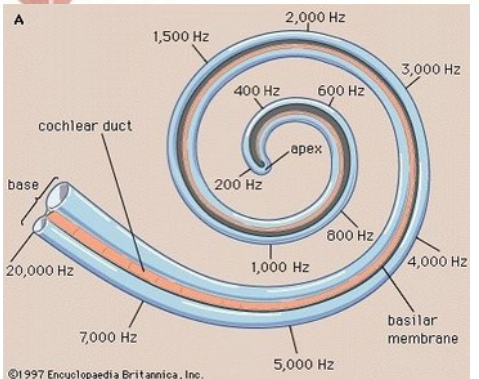
- It is a non-linear frequency analyser
- Basilar membrane: ~35 mm long





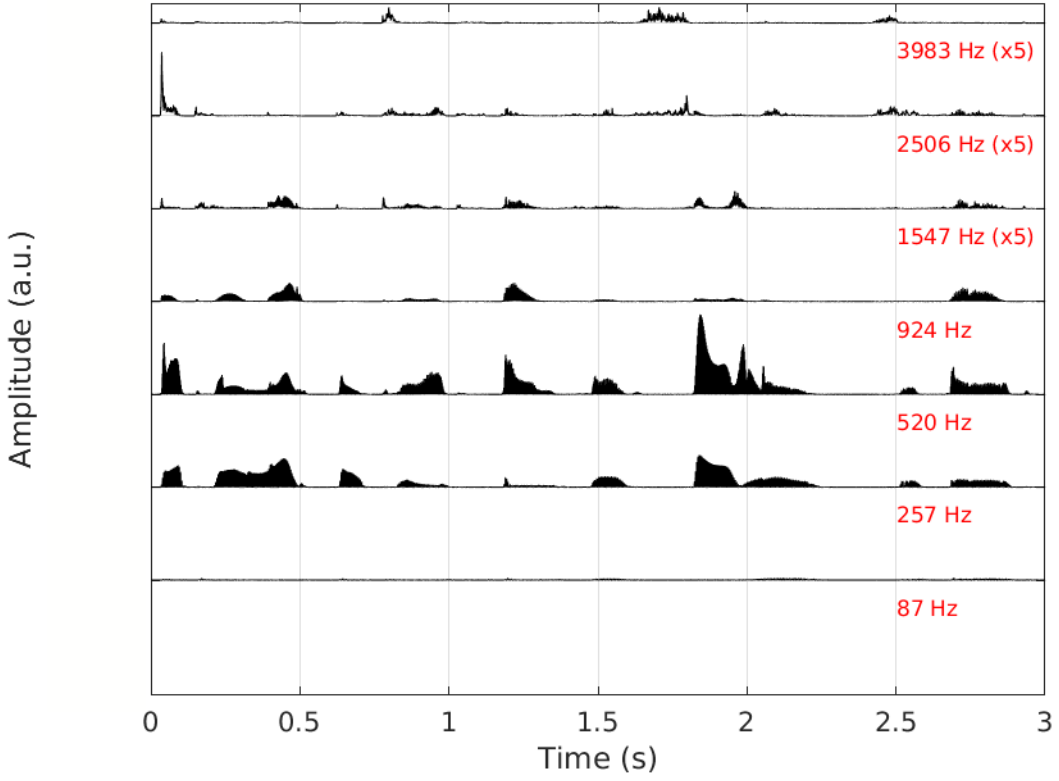
Physiological output:
Basilar membrane velocity (dB re. 1 m/s)

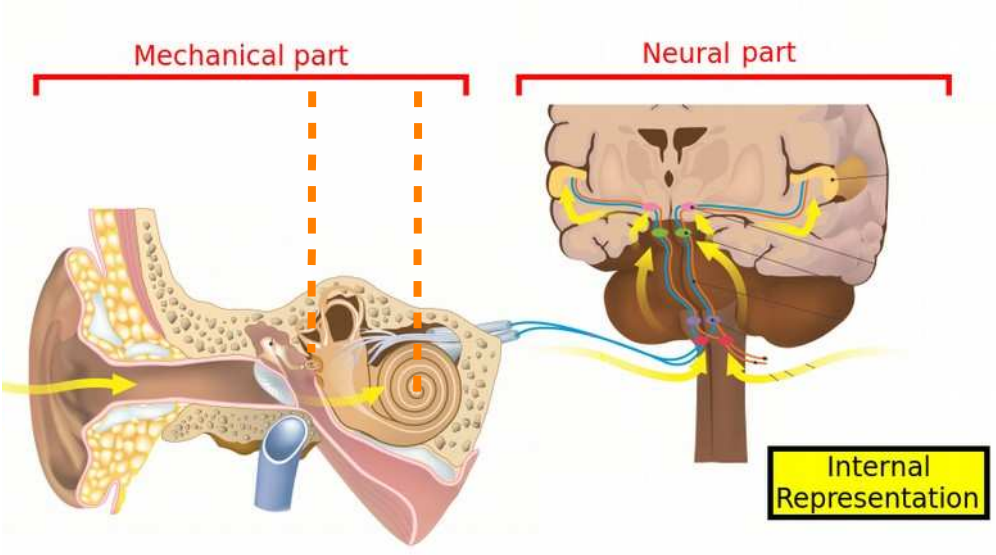
An schematic drawing:
(downloaded from here)



Inner-hair-cell processing

- Typically: Approximated as a half-wave rectification + low-pass filter





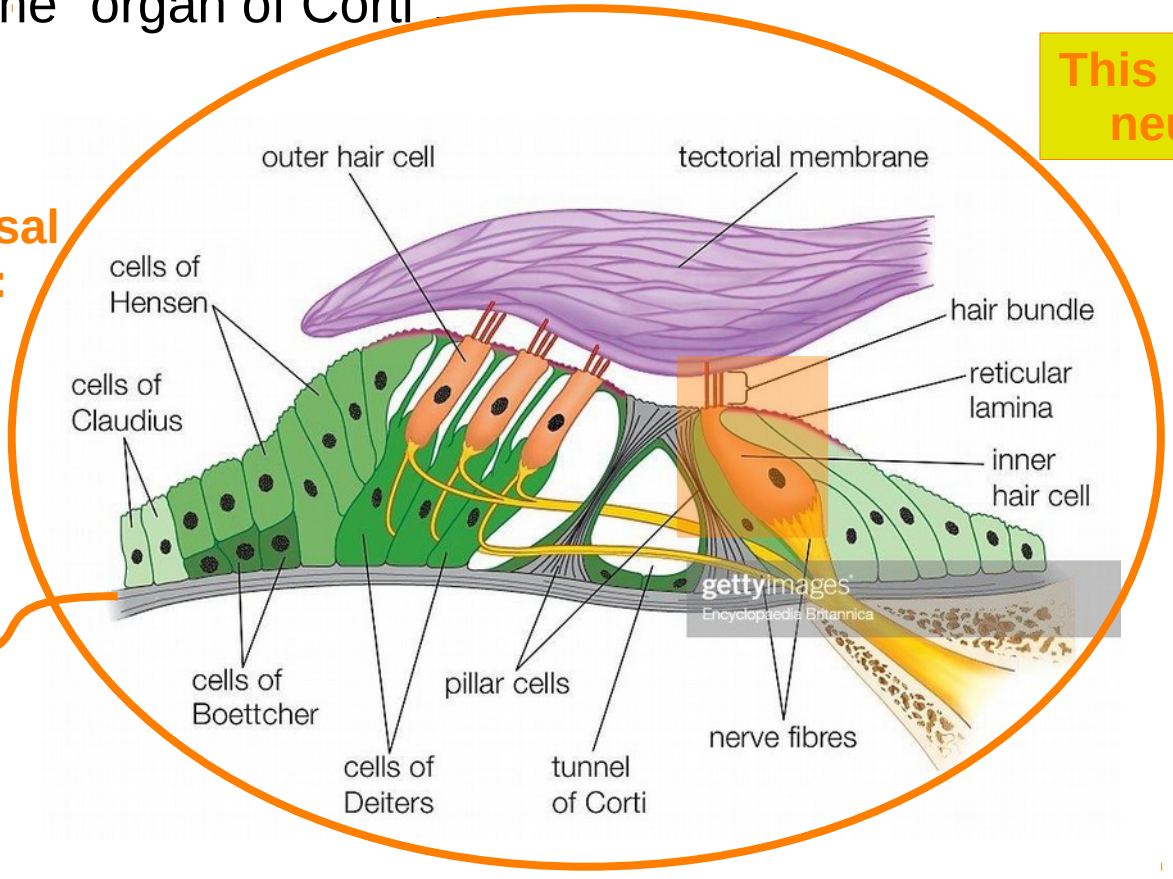
Physiological output:
Inner-hair-cell potential V_m (V)

Inner-hair-cell processing

- Mechanical basilar membrane oscillations into receptor potentials
- A zoom in into the “organ of Corti”:

This is the schematic of a neuron that can spike

A transversal section:



Actually, there are:
~3500 hair cells
~20 AN fibres / cell

Inner-hair-cell processing

- Model verhulst2018 simulates the IHC membrane potential Vm using a Hodgkin-Huxley circuit
  - Mechanoelectrical channel (MET)
  - Fast potassium channel (Kf)
  - Slow potassium channel (Ks)
  - No sodium channel
  - No leakage channel

Trigger the release of neurotransmitter

Generation of action potentials in the auditory nerve

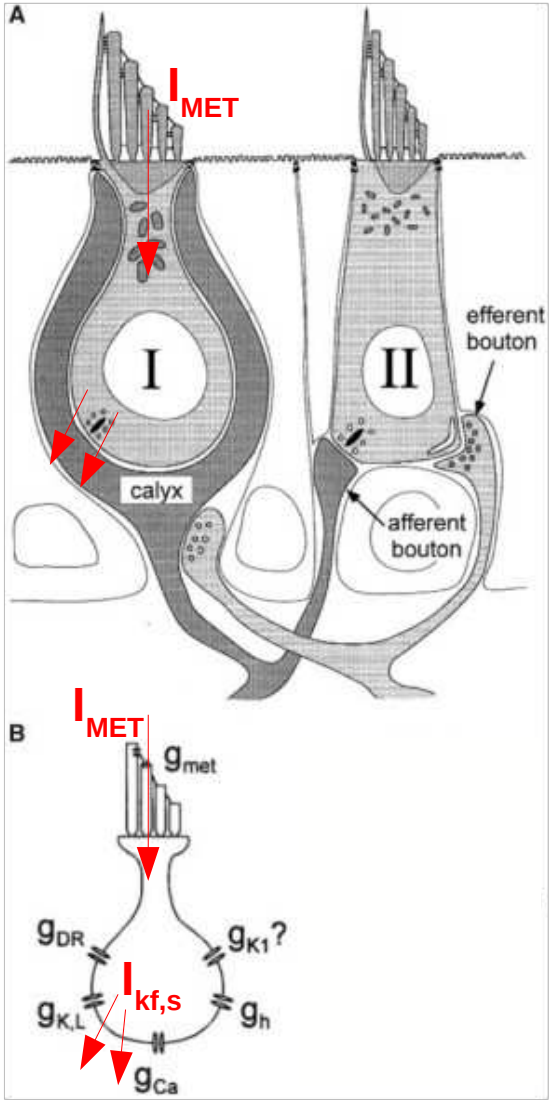
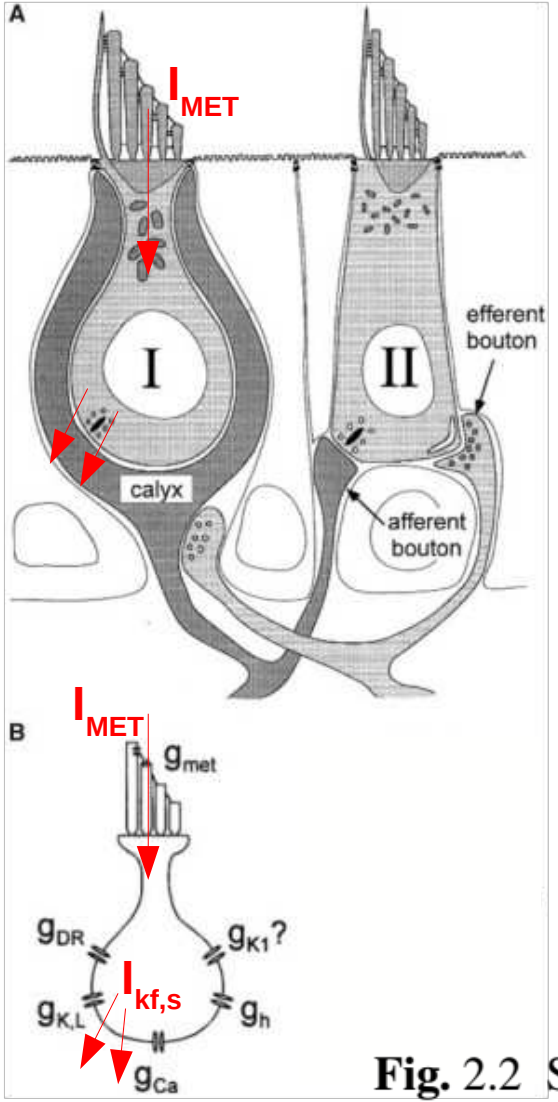


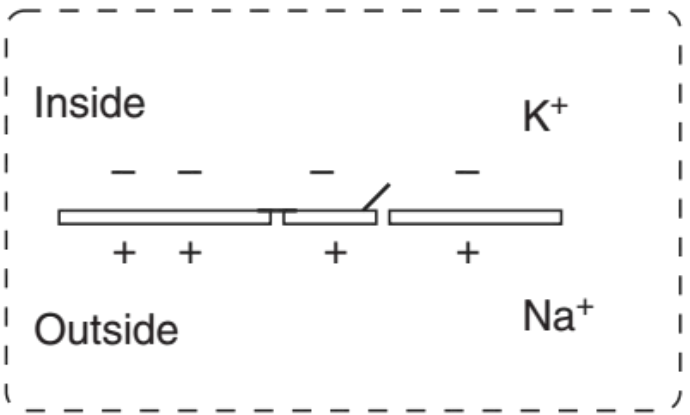
Fig. 4 Diagram of stereotypical type I and type II hair cells from a mammalian vestibular organ. (A) Note that a single primary

Fig. from McPherson (2018)

Inner-hair-cell processing

- The generic HH model:





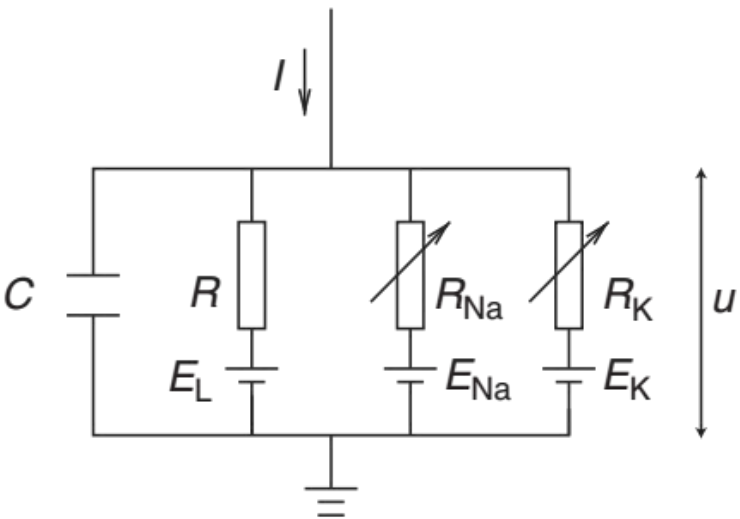


Fig. 2.2 Schematic diagram for the Hodgkin–Huxley model.

Fig. 4 Diagram of stereotypical type I and type II hair cells from a mammalian vestibular organ. (A) Note that a single primary

Fig. from Gerstner et al. (2014)

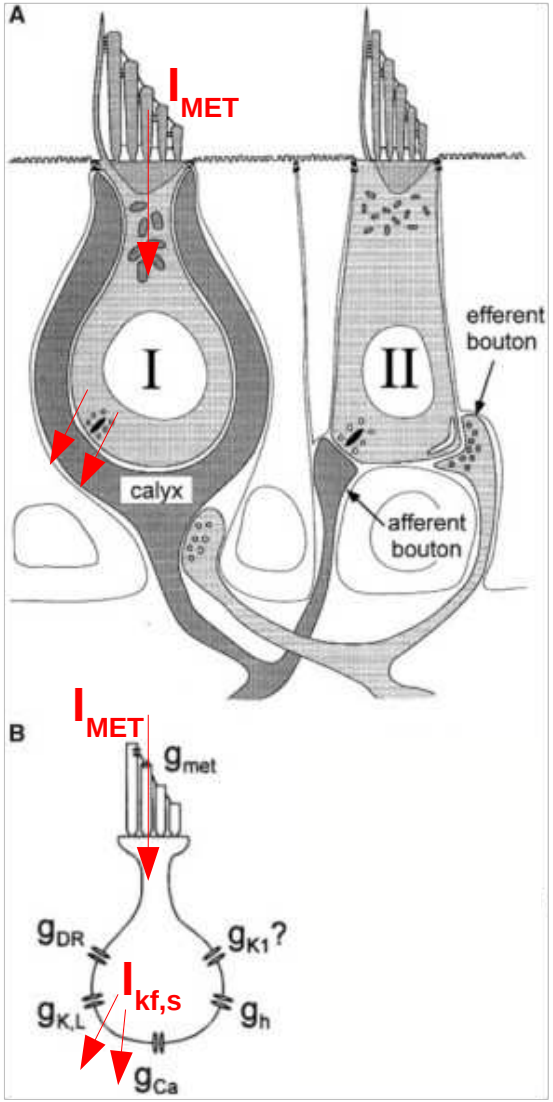


Fig. 4 Diagram of stereotypical type I and type II hair cells from a mammalian vestibular organ. (A) Note that a single primary

Inner-hair-cell processing

- Model verhulst2018 simulates the IHC membrane potential Vm using a Hodgkin-Huxley circuit
  - Mechanoelectrical channel (MET)
  - Fast potassium channel (Kf)
  - Slow potassium channel (Ks)
  - No leakage channel

"g" stands for conductance, with g = 1/R

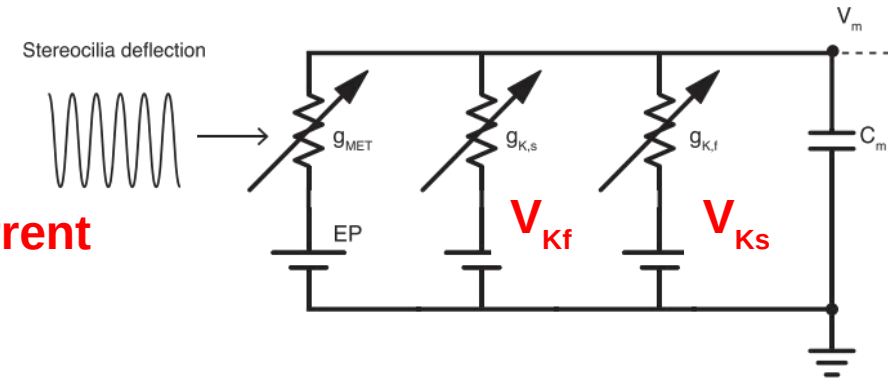


FIG. 1. Schematic of the model employed for this study.

Conservation of energy:

No external (injected) current

$$0 = I_{MET} + I_C + I_{Kf} + I_{ks}$$

$$-C\,dV/dt = I_{MET} + I_{Kf} + I_{ks}$$

$$I_{MET} = n_{MET} G_{MET,\,max} (V_m - EP)$$

$$I_{kf} = n_{kf} G_{kf,\,max} (V_m - V_{Kf})$$

$$I_{ks} = n_{ks} G_{ks,\,max} (V_m - V_{Ks})$$

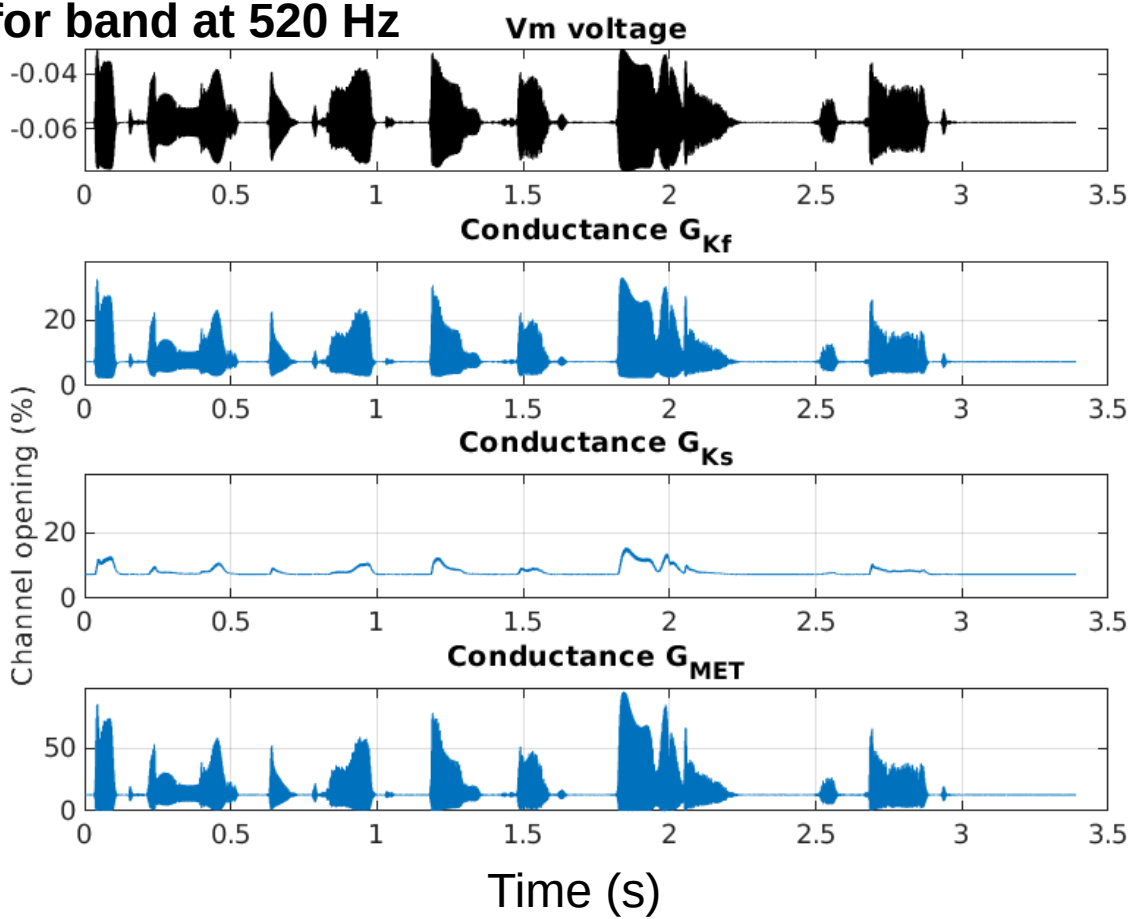
Ohm's law

Fig. from Altoè et al. (2017)

Inner-hair-cell processing

- The voltage-gated channels

Example for band at 520 Hz



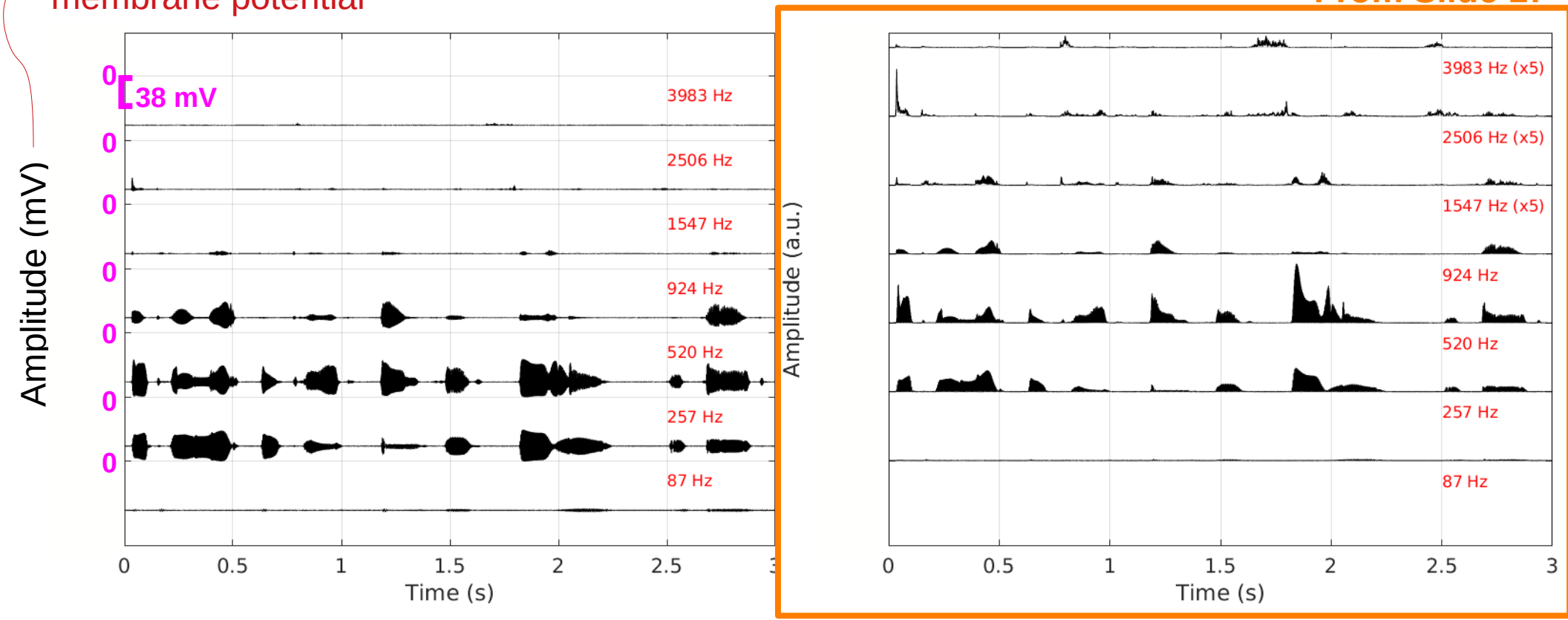
$$I_{MET} = n_{MET} G_{MET,\,max} (V_m - EP)$$
$$I_{kf} = n_{kf} G_{kf,\,max} (V_m - V_{Kf})$$
$$I_{ks} = n_{ks} G_{ks,\,max} (V_m - V_{Ks})$$

Described by a specific equation

Inner-hair-cell processing (3 / 3)

Simulated IHC membrane potential

From Slide 17



Negative potential (0 V for each channel indicated in magenta)

Asymmetric waveforms along V_{rest}

“Envelope extraction” too for high frequency channels

Auditory nerve firing

- One possibility was to use I_m to obtain spikes when reaching the neuron threshold

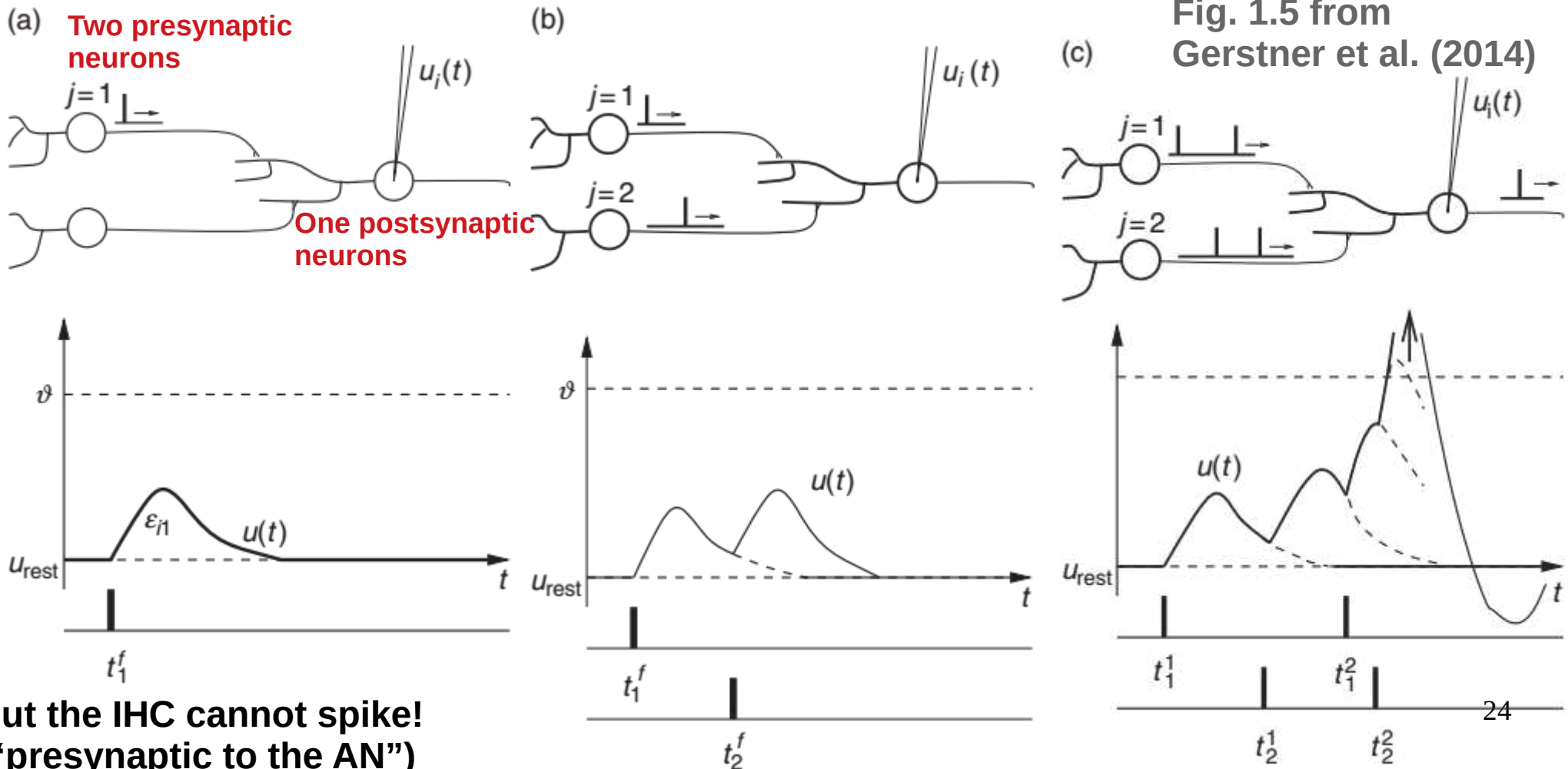
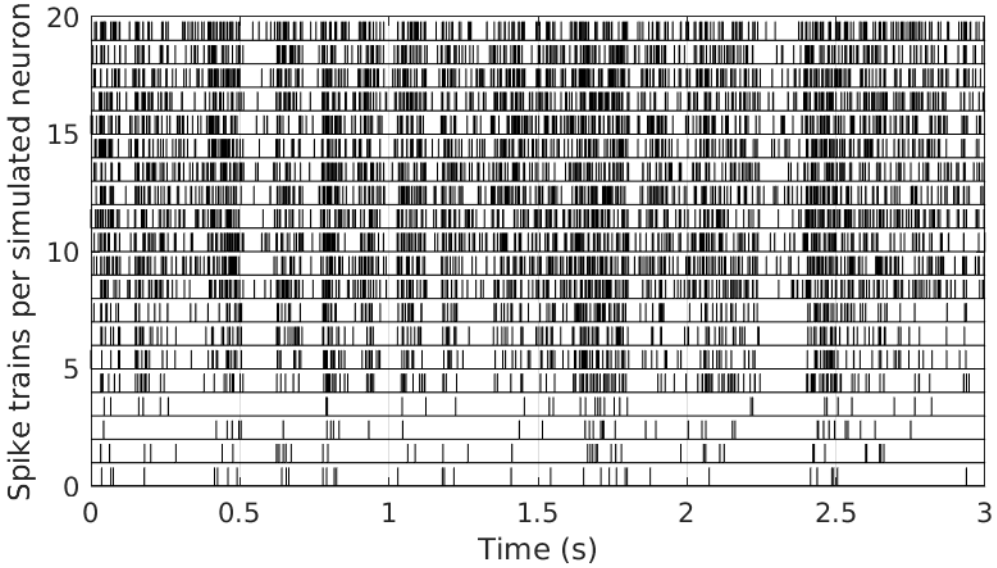


Fig. 1.5 from Gerstner et al. (2014)

But the IHC cannot spike!
(“presynaptic to the AN”)

Auditory nerve firing

Raster plots: **Speech**

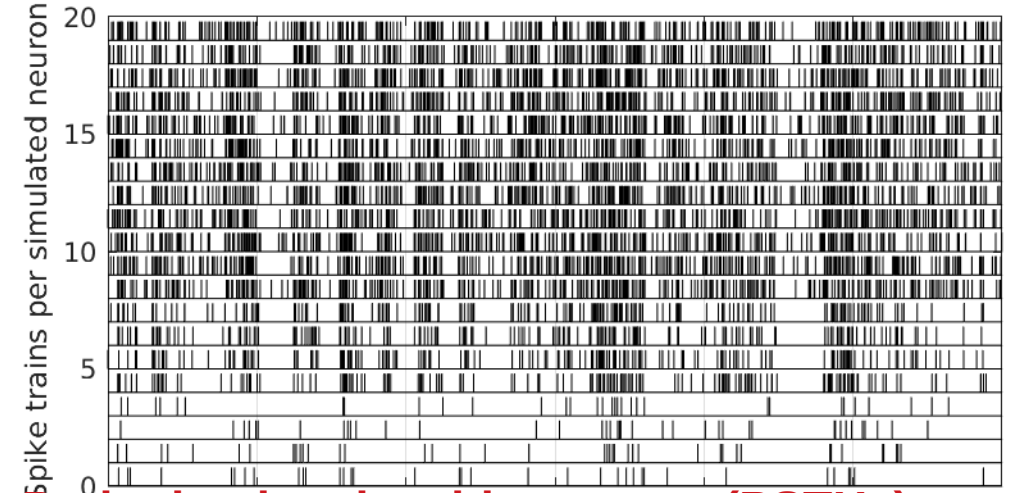


- Here I am showing the output of the spike model used in one of the models (“bruce2018” from Bruce et al., 2018)

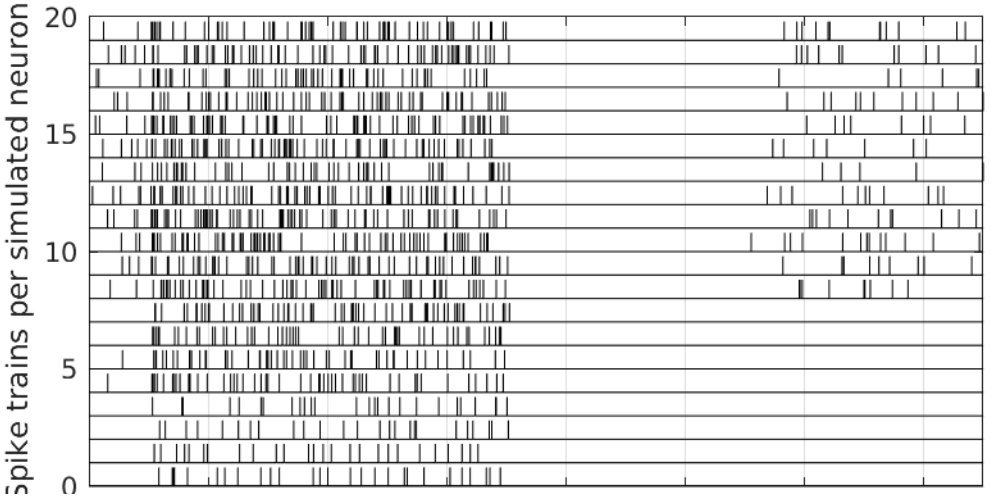
Auditory nerve firing

Raster plots:

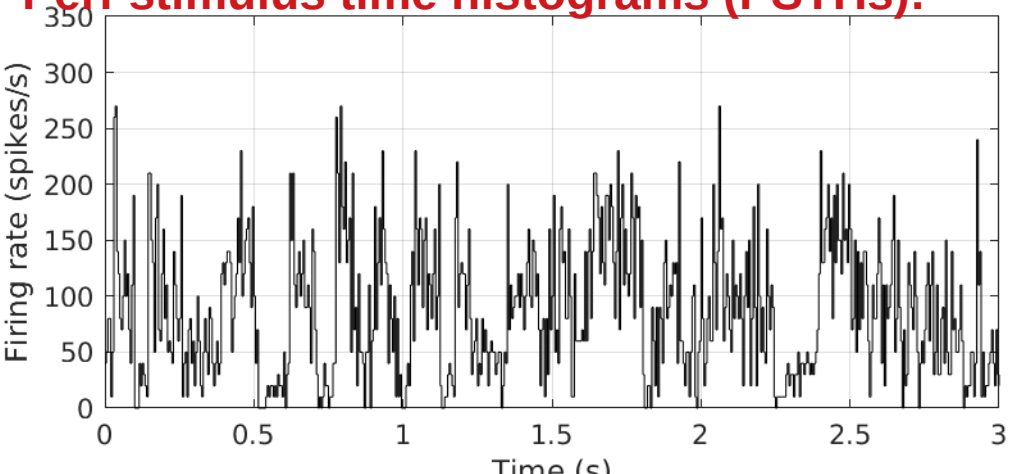
Speech

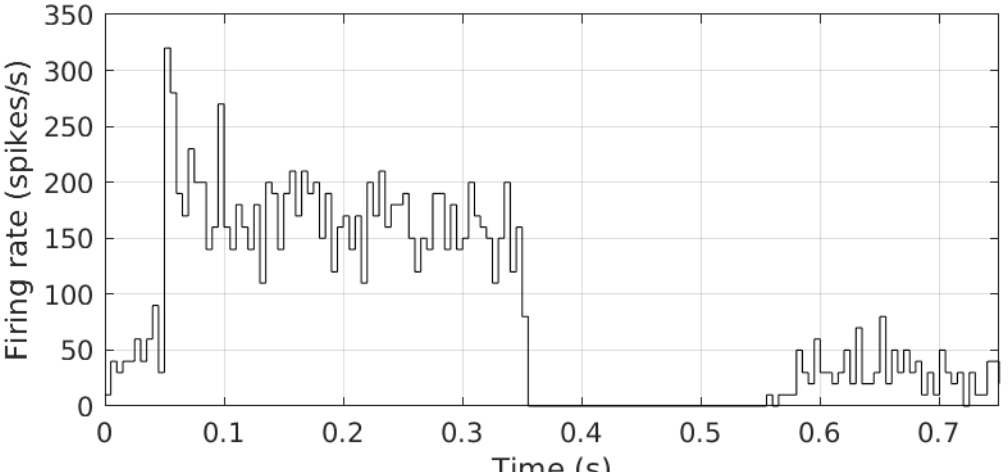


4-kHz pure tone



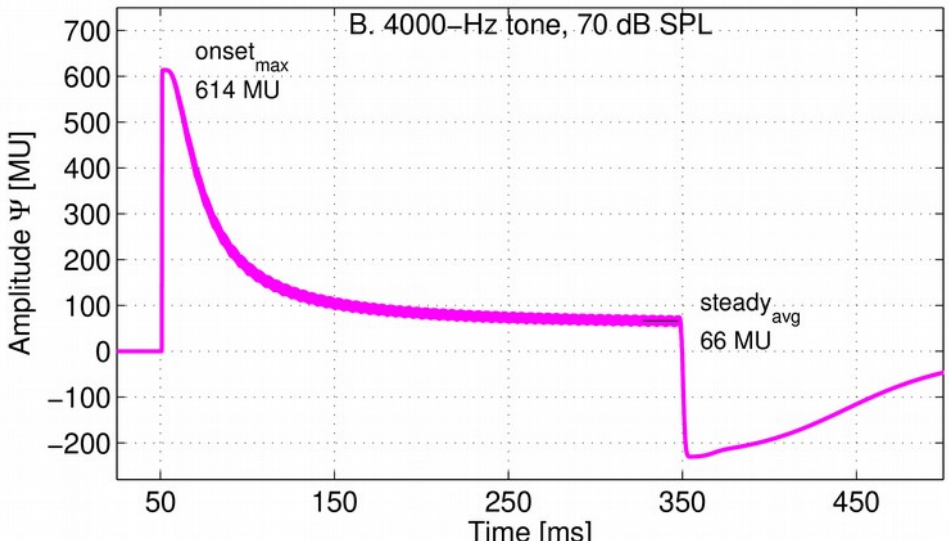
Peri-stimulus time histograms (PSTHs):



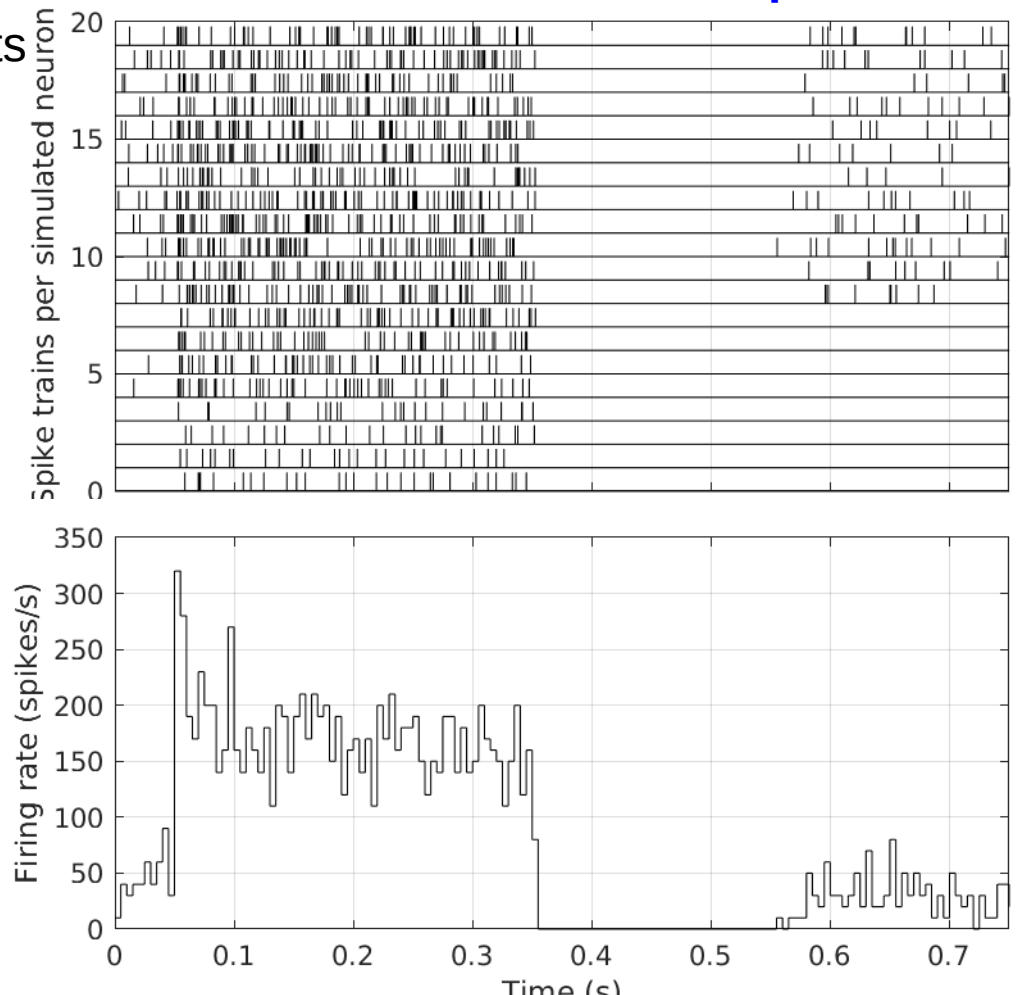


Auditory nerve firing

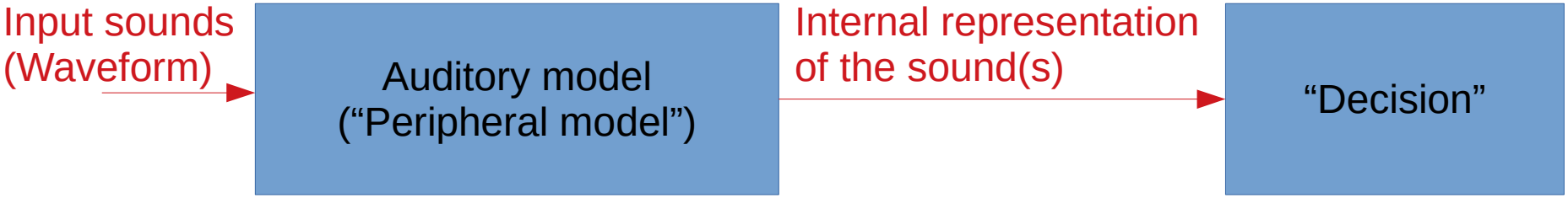
Maybe now we can compare across model outputs



4-kHz pure tone



Example of an application: Simultaneous masking

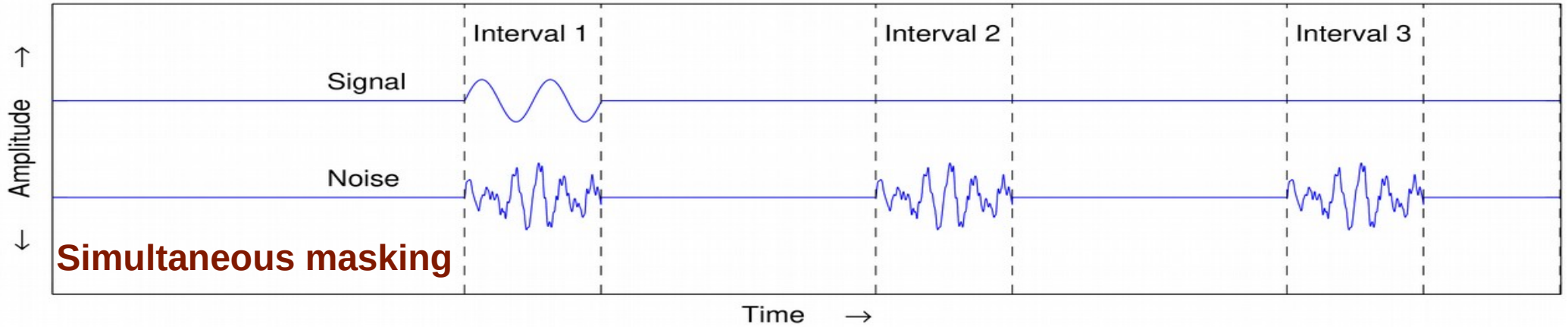


Simple task:
Yes, the target sound is present
No, the target sound is absent

I will show one auditory task:
- Not modulated by cognitive aspects
- Based on bottom-up evidence

m-Alternative Forced Choice (m-AFC) paradigm

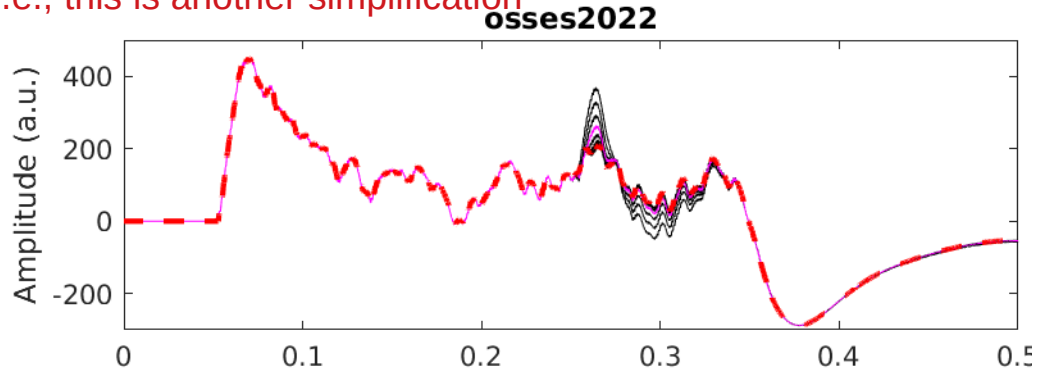
- There are *m* intervals (sounds), the listener is asked to pick up one:

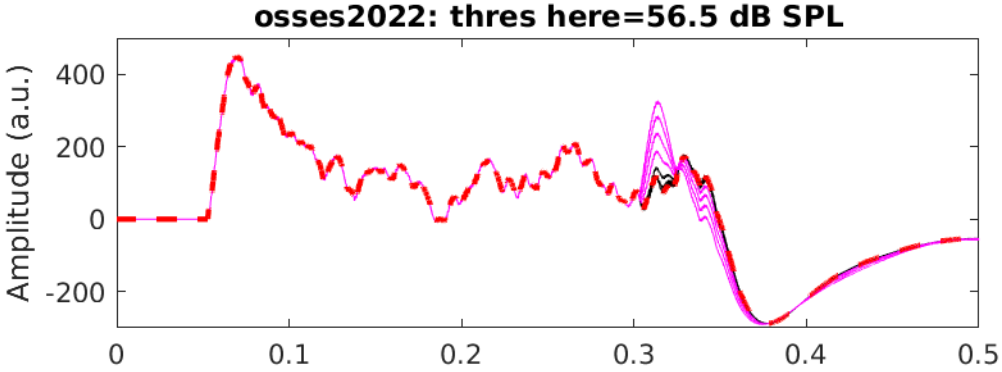


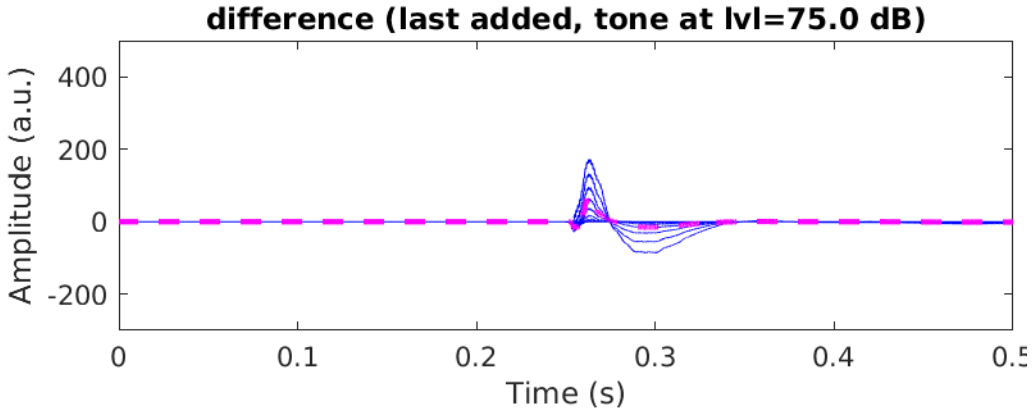
- If *m* = 3: “Which sound is different from the other two?”
- I will show a task where:
  - The noise is 300 ms long
  - The tone is 10 ms long in three conditions: simultaneously or after the noise
  - We look for the tone level at which the signal+noise interval is correctly detected

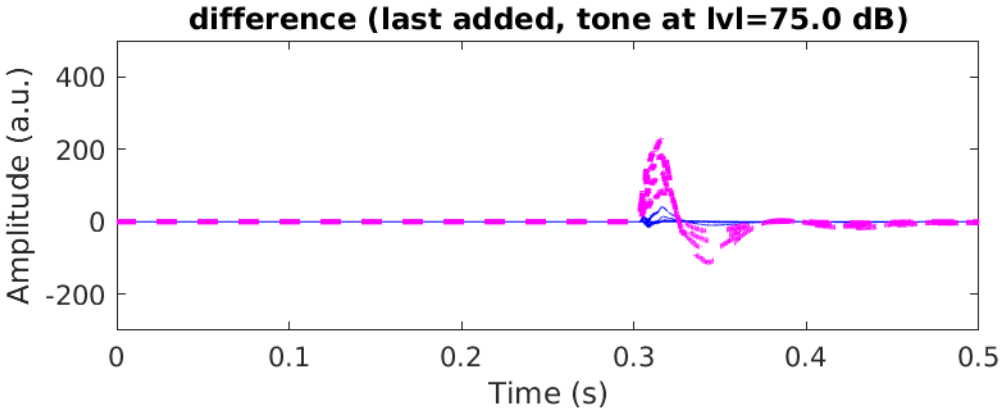
m-Alternative Forced Choice (m-AFC) paradigm

Remark: For this schematic figures I am using the target sounds (tone+noise) and only one of the two noise-alone sounds i.e., this is another simplification





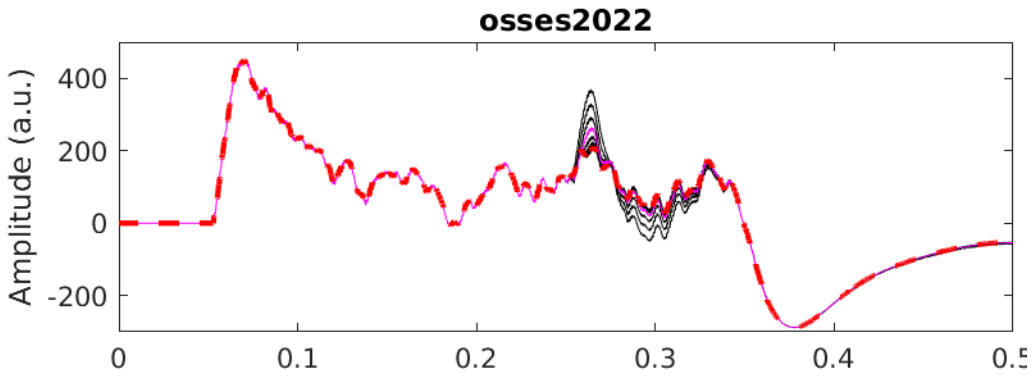


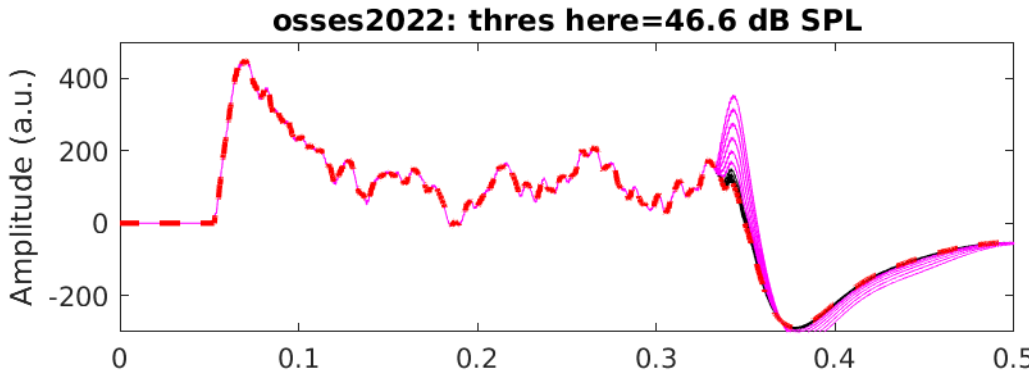


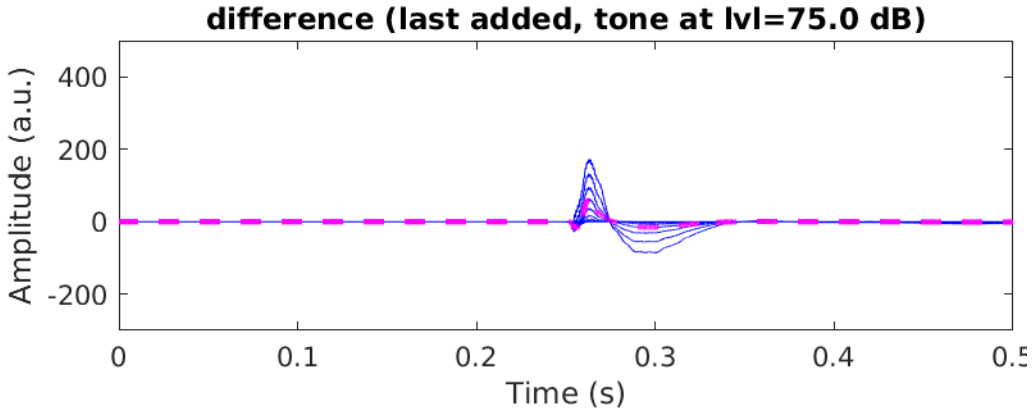
Tone onset at time 250 ms

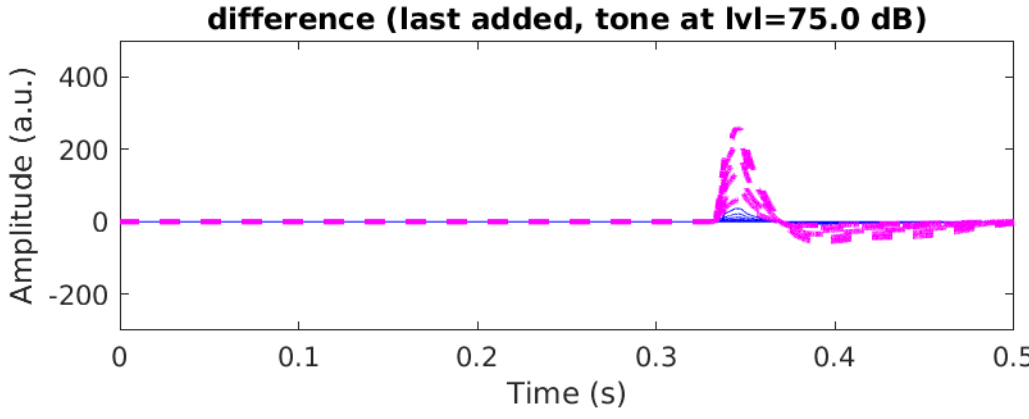
Tone onset at time 300 ms

m-Alternative Forced Choice (m-AFC) paradigm





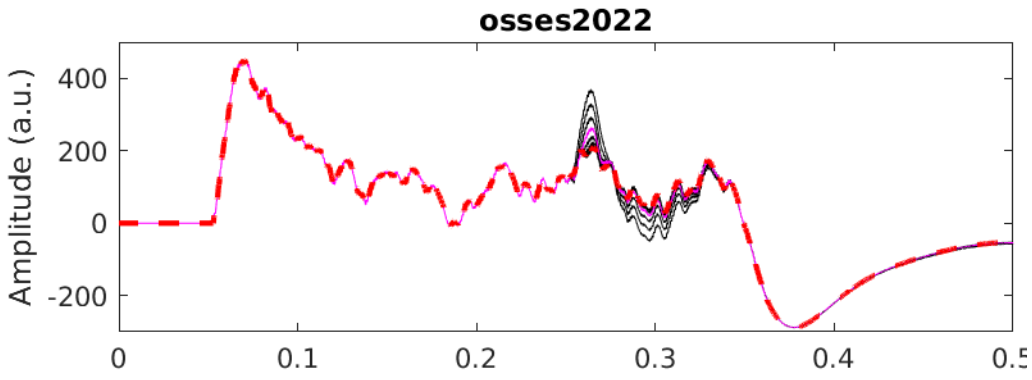


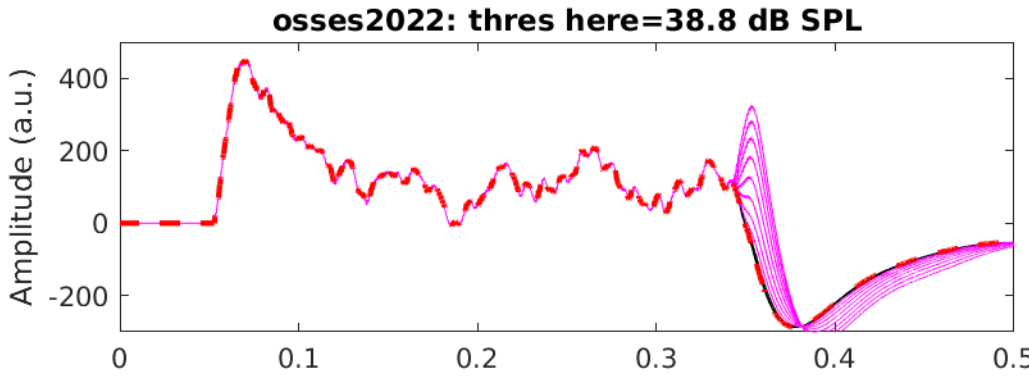


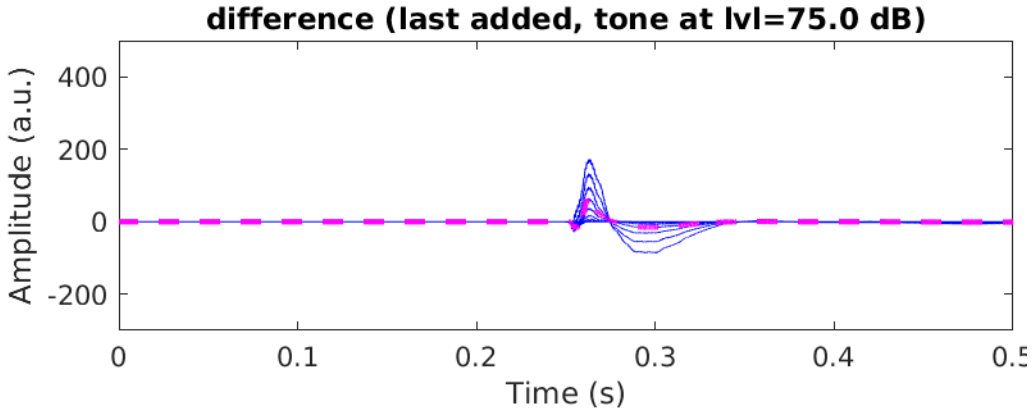
Tone onset at time 250 ms

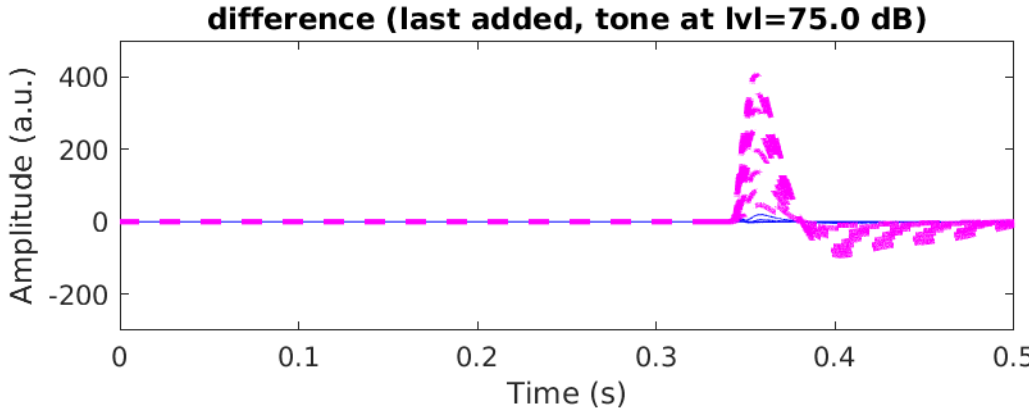
Tone onset at time 330 ms

m-Alternative Forced Choice (m-AFC) paradigm





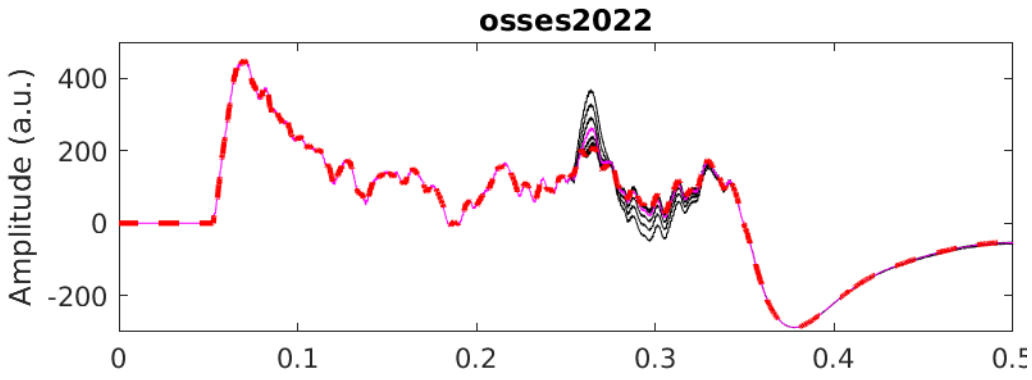


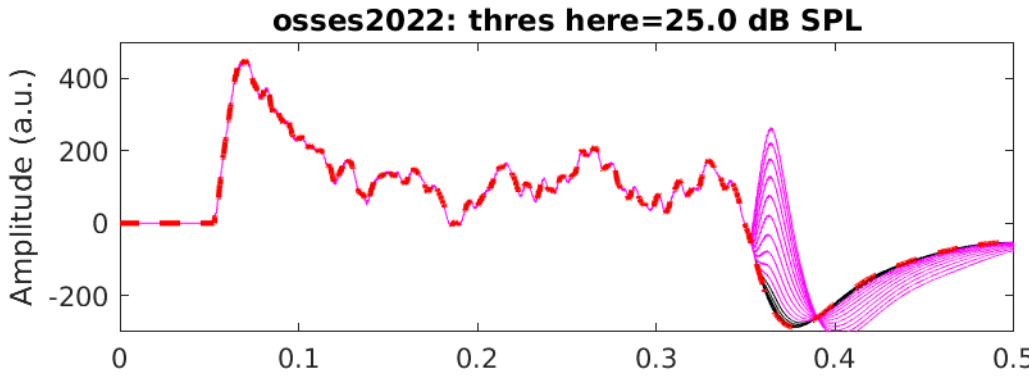


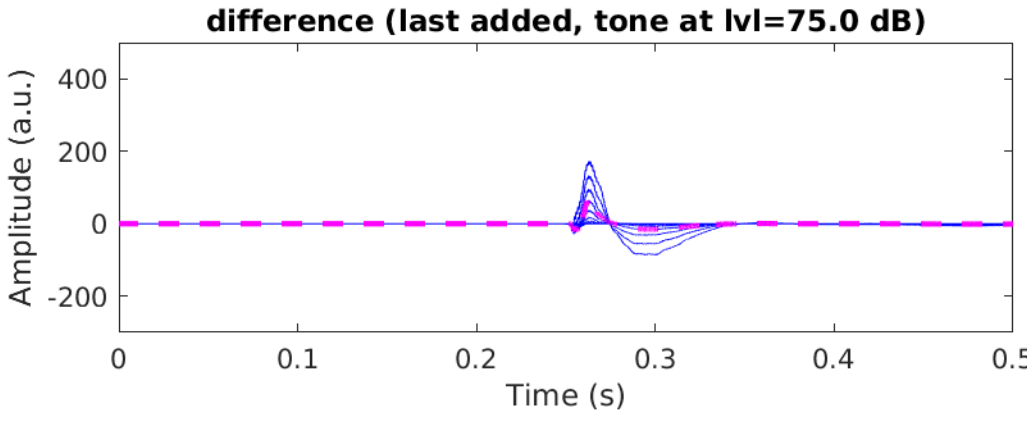
Tone onset at time 250 ms

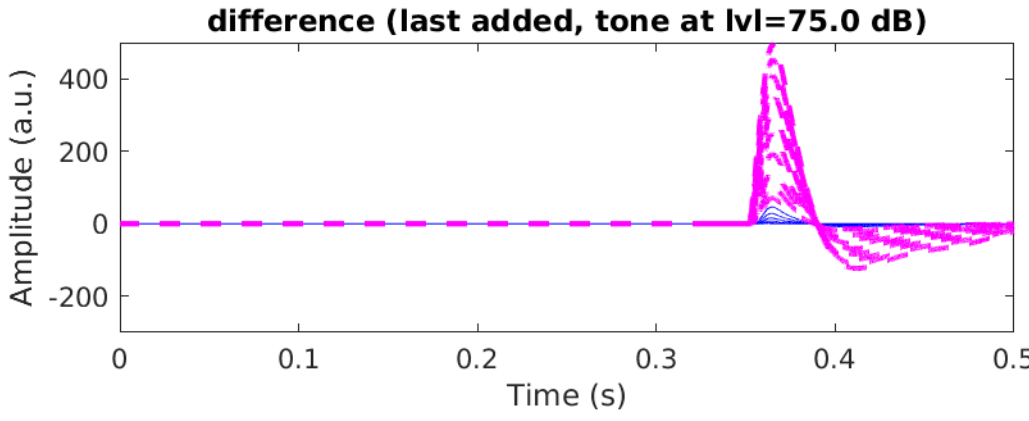
Tone onset at time 340 ms

m-Alternative Forced Choice (m-AFC) paradigm





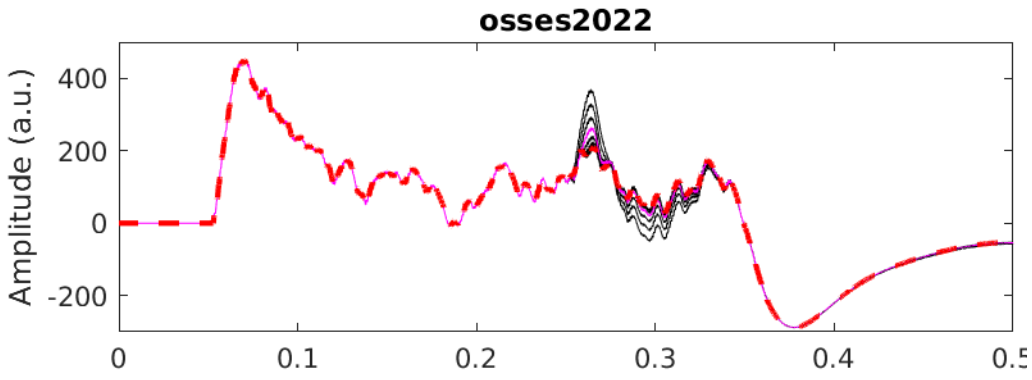


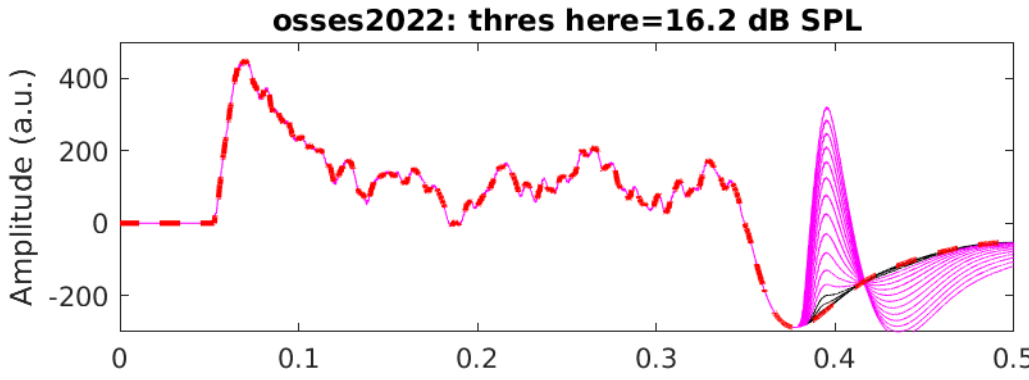


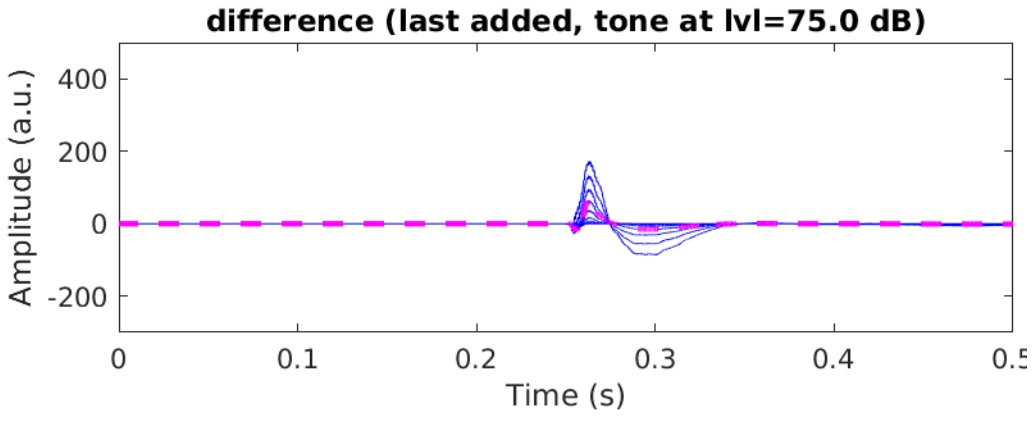
Tone onset at time 250 ms

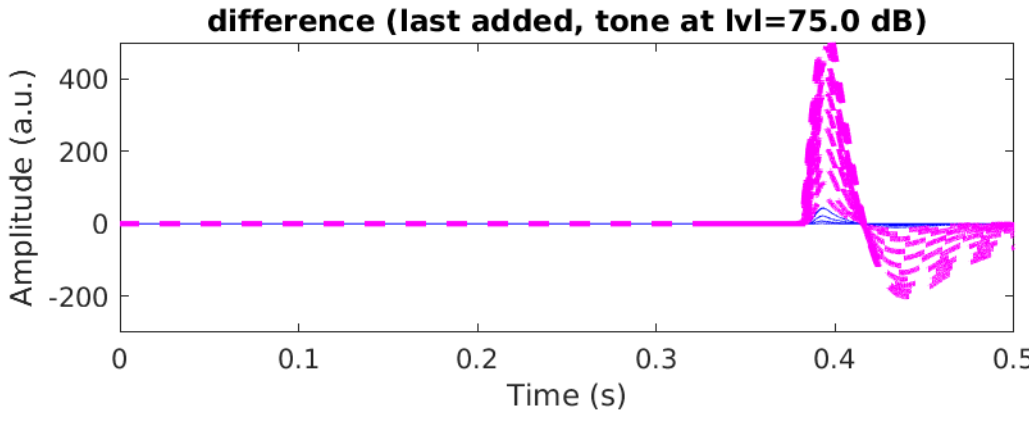
Tone onset at time 350 ms
(Post-masking)

m-Alternative Forced Choice (m-AFC) paradigm





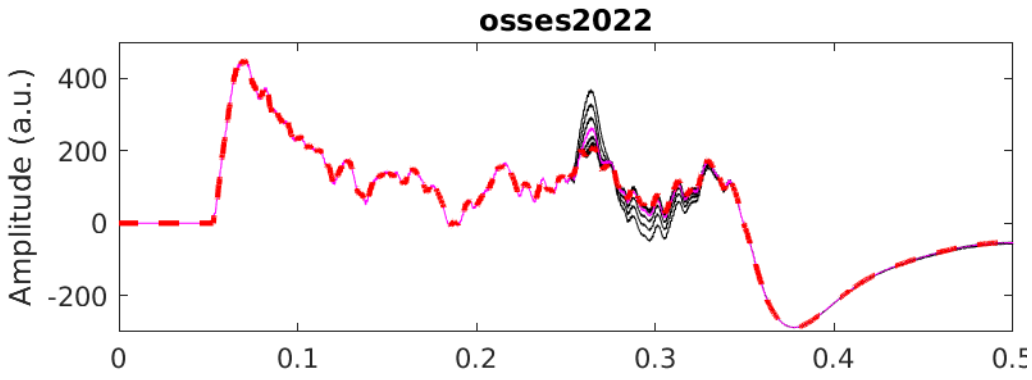


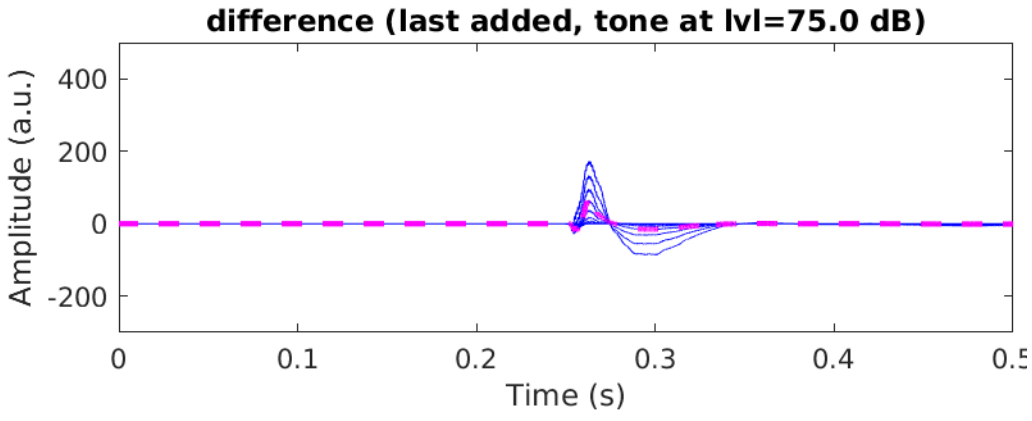


Tone onset at time 250 ms

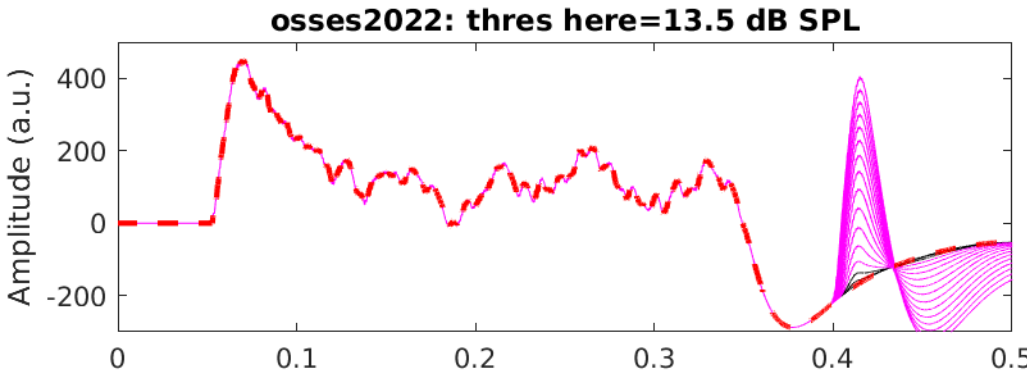
Tone onset at time 380 ms
(Post-masking)

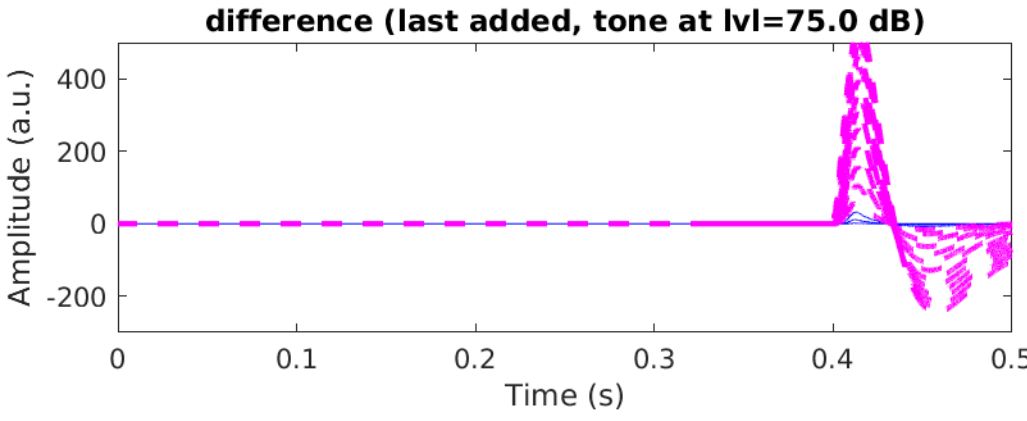
m-Alternative Forced Choice (m-AFC) paradigm





Tone onset at time 250 ms

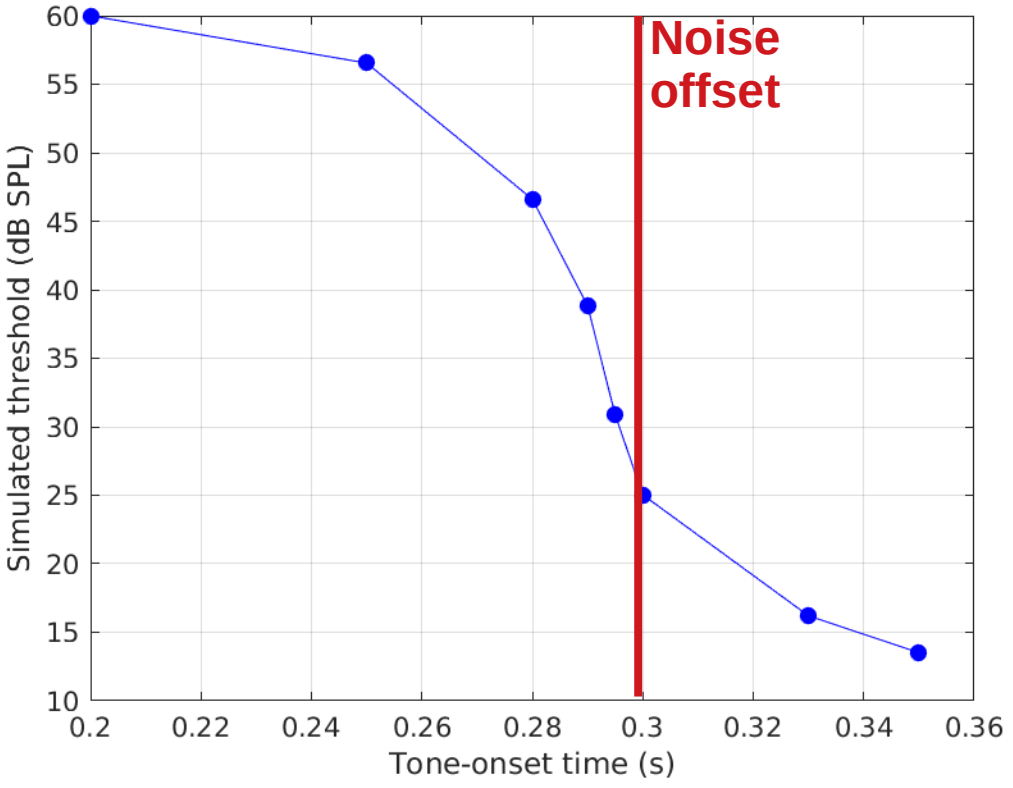




Tone onset at time 400 ms
(Post-masking)

m-Alternative Forced Choice (m-AFC) paradigm

- Putting all the simulation thresholds together:
- This is a non-linear problem



Summary

- This study (the paper) compares different models and use them on the same set of sounds, independent of the rationale of each model
- Different models will give different (but hopefully comparable) results:
  - Make sure you are aware of the capabilities of the specific models
  - **Warning**: Not all model descriptions are always available (codes somewhere?)
- In this lecture, I showed some physiological aspects that have inspired “functional implementations”
- I showed an example of application (not shown in the paper)
- Different models have been validated with different sounds and more complex models are not necessarily best to other models (you need to check that, if not shown in the literature)
- Make sure your simulations are replicable, and that you can use your model with different sets of parameters without having to re-program:
  - For instance, use 

References

Altoè, A., Pulkki, V., & Verhulst, S. (2017). Model-based estimation of the frequency tuning of the inner-hair-cell stereocilia from neural tuning curves. *J. Acoust. Soc. Am.*, *141*, 4438–4451. doi:10.1121/1.4985193

Barnes, N. (2010). Publish your computer code: It is good enough. *Nature*, *467*(7317), 753. doi:10.1038/467753a

Bruce, I. C., Erfani, Y., & Zilany, M. S. A. (2018). A phenomenological model of the synapse between the inner hair cell and auditory nerve: Implications of limited neurotransmitter release sites. *Hear. Res.*, *360*, 40–54. doi:10.1016/j.heares.2017.12.016

Gerstner, W., Kistler, W., Naud, R., & Paninski, L. (2014). *Neuronal Dynamics: From Single Neurons to Networks and Models of Cognition*. Cambridge University Press.

Majdak, P., Hollomey, C., & Baumgartner, R. (2021). *AMT 1.0: the toolbox for reproducible research in auditory modeling*.

Maxwell, B., Richards, V., & Carney, L. (2020). Neural fluctuation cues for simultaneous notched-noise masking and profile-analysis tasks: Insights from model midbrain responses. *J. Acoust. Soc. Am.*, *147*, 3523–3537. doi:10.1121/10.0001226

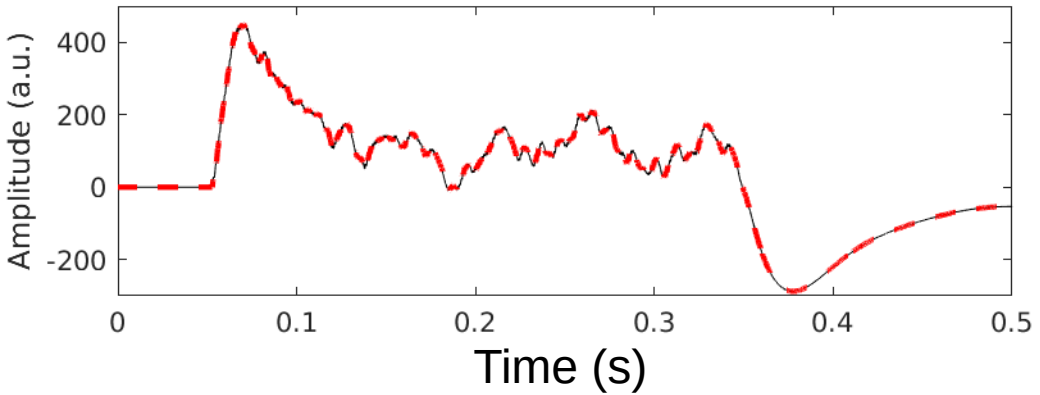
Osses, A., Varnet, L., Carney, L., Dau, T., Bruce, I., Verhulst, S., & Majdak, P. (2022). A comparative study of eight human auditory models of monaural processing. *ArXiv*, 1–24. doi:10.1051/aacus/2022008

Osses, A. (2018). *Prediction of perceptual similarity based on time-domain models of auditory perception*. Technische Universiteit Eindhoven.

Verhulst, S., Altoè, A., & Vasilkov, V. (2018). Computational modeling of the human auditory periphery: Auditory-nerve responses, evoked potentials and hearing loss. *Hear. Res.*, *360*, 55–75. doi:10.1016/j.heares.2017.12.018

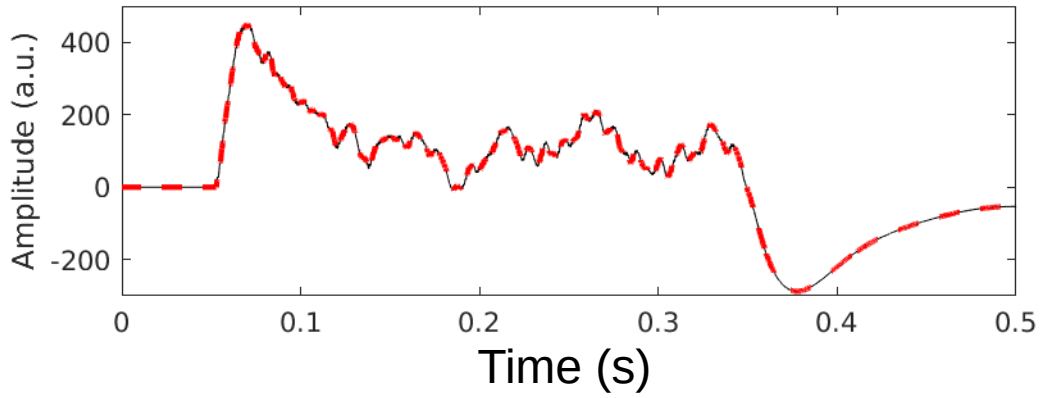
Extra slide (not shown during the lecture)

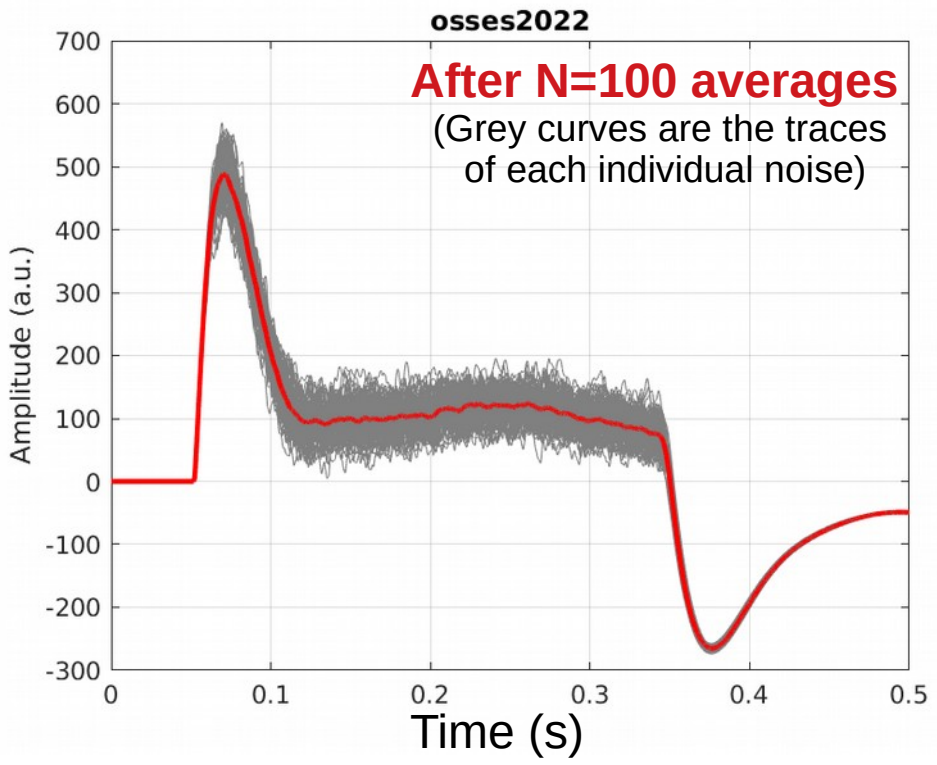
Out colleague/classmate Hugo didn't like the stochastic shape of the internal representation of the noise-alone interval (obtained from one noise) of slide 30:



Extra slide (not shown during the lecture)

Out colleague/classmate Hugo didn't like the stochastic shape of the internal representation of the noise-alone interval (obtained from one noise) of slide 30:





As discussed during the lecture, my opinion is that stochasticity is a desired and natural property in neuronal signals.

In this talk I used only one noise (a "frozen noise") to better illustrate the auditory tasks.

References with hyperlinks

Altoè, A., Pulkki, V., & Verhulst, S. (2017). Model-based estimation of the frequency tuning of the inner-hair-cell stereocilia from neural tuning curves. *J. Acoust. Soc. Am.*, *141*, 4438–4451. doi:10.1121/1.4985193

Barnes, N. (2010). Publish your computer code: It is good enough. *Nature*, *467*(7317), 753. doi:10.1038/467753a

Bruce, I., Erfani, Y., & Zilany, M. (2018). A phenomenological model of the synapse between the inner hair cell and auditory nerve: Implications of limited neurotransmitter release sites. *Hear. Res.*, *360*, 40–54. doi:10.1016/j.heares.2017.12.016

Gerstner, W., Kistler, W., Naud, R., & Paninski, L. (2014). *Neuronal Dynamics: From Single Neurons to Networks and Models of Cognition*. Cambridge University Press.

Majdak, P., Hollomey, C., & Baumgartner, R. (2022). AMT 1.x: A toolbox for reproducible research in auditory modeling. *Acta Acustica*, *6*, 19. doi:10.1051/aacus/2022011

Maxwell, B., Richards, V., & Carney, L. (2020). Neural fluctuation cues for simultaneous notched-noise masking and profile-analysis tasks: Insights from model midbrain responses. *J. Acoust. Soc. Am.*, *147*, 3523–3537. doi:10.1121/10.0001226

Osses, A. (2018). *Prediction of perceptual similarity based on time-domain models of auditory perception*. Ph.D. thesis. Technische Universiteit Eindhoven. (tel-03871102)

Osses, A., Varnet, L., Carney, L., Dau, T., Bruce, I., Verhulst, S., & Majdak, P. (2022). A comparative study of eight human auditory models of monaural processing. *Acta Acust.*, *6*, 17. doi:10.1051/aacus/2022008 (hal-03666259)

Verhulst, S., Altoè, A., & Vasilkov, V. (2018). Computational modeling of the human auditory periphery: Auditory-nerve responses, evoked potentials and hearing loss. *Hear. Res.*, *360*, 55–75. doi:10.1016/j.heares.2017.12.018