Simulating Physiological and Psychoacoustic Forward Masking in a Subcortical Model with Efferent Gain Control

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Introduction

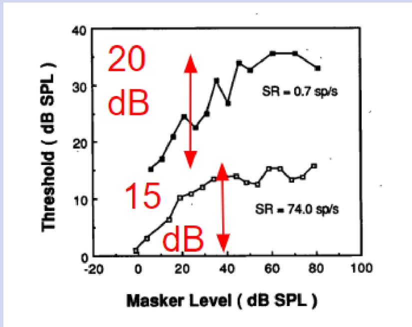
Forward Masking: Threshold for a short probe tone signal is elevated by a long preceding signal called the masker. In the cases examined here, the preceding masker is a tone.

Growth of Masking (GOM): As the sound level of the masker increases, the threshold for detecting the probe tone also increases.

Psychophysical GOM may extend over a wide range of masker levels. Thresholds for participants in behavioral experiments may increase by > 40 dB over a masker-level range of > 80 dB, for delays 10 ms or less (Plack and Oxenham, 1998; Oxenham and Plack, 1997).

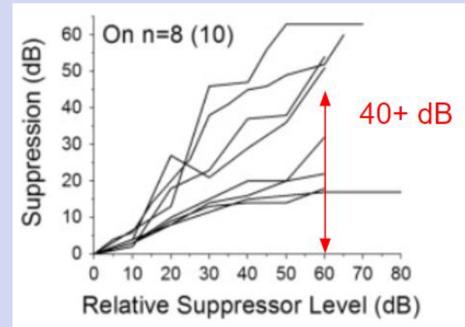
Physiological GOM in the auditory nerve has been unable to account for psychophysical GOM, as the maximum range of forward-masked thresholds has been limited to 15-20 dB (Relkin and Turner, 1988; Turner, Relkin, and Doucet, 1994).

Auditory Nerve (AN):



Relkin and Turner (1988): Barbiturate anesthesia Chinchilla

Inferior Colliculus (IC):



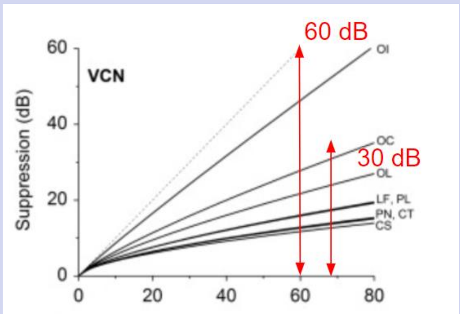
Ingham et al. (2016) – Urethane anesthesia Guinea Pig

Nelson et al. (2009) proposed that **physiological GOM in the inferior colliculus** could account for psychophysical GOM, with shifts in threshold similar to those measured psychophysically and growing over a similar range of masker levels. For most IC neurons, neural response to the masker was less than spontaneous rate at the 10-ms masker-probe delay where IC GOM was measured, suggesting that the mechanism underlying their forward-masking results was a reduction in the neural response to the probe rather than persistent neural excitation during the probe response. The GOM observed by Nelson et al. was greatest for onset-type neurons in the IC.

Guided by Nelson et al's results, modeling studies by Salimi et al. (2017) and Gai (2016) tried to account for forward masking in the IC through the inhibition of offset neurons in the superior paraolivary nucleus, or SPON.

More recently, GOM with a range of 30–60 dB was discovered in the cochlear nucleus (CN), challenging the hypothesis that substantial GOM first emerges in the IC (Ingham et al., 2016). Ingham et al. also corroborated the finding of substantial GOM in the IC. Additionally, Felix et al. (2015) found that inactivation of the SPON does not remove the suppression of probe responses for onset neurons in the IC.

Cochlear Nucleus (CN):



Ingham et al. (2016) – Urethane anesthesia Guinea Pig

This evidence suggests another source of suppression, emerging at or before the CN stage, that may explain physiologically-observed GOM for onset neurons at both CN and IC stages.

In the current study, a subcortical model designed to simulate MOC efferent-influenced activity in the IC (Farhadi et al., 2021) explained GOM in the IC and CN.

These model results suggest that substantial GOM occurs in the AN and is passed up to onset cells in the CN and IC. Less GOM observed in AN recordings may have been due to barbiturate anesthesia, as opposed to urethane or ketamine/xylazine anesthesia used in the GOM studies in the central nervous system (Guitton et al., 2004).

Methods

Stimuli

Stimuli matched Ingham et al. (2016), Nelson et al. (2009), or Jesteadt et al. (2005) (see table below). For Jesteadt et al. (2005), in the 0-σ rove condition, the masker was always 70 dB SPL. In the 6-σ rove condition, the masker level was randomly selected from a Gaussian distribution with a mean of 70 dB SPL and a standard deviation of 6 dB.

Parameters for Conditions	Ingham et al. (2016)	Nelson et al. (2009)	Jesteadt et al. (2005)
Masker Tone Duration	100 ms	200 ms	200 ms
Masker Level	Varied	40 dB re Threshold	70 dB SPL; roved
Masker Ramps	2 ms	10 ms	2 ms
Probe Tone Duration	25 ms	20 ms	10 ms
Probe Ramps	2 ms	10 ms	5 ms
Masker-Probe Delay	2.83 ms	Varied 0-150 ms	0 and 30 ms
Masker and Probe Frequency	Varied, 4 kHz modeled	Varied, 4 kHz modeled	4 kHz

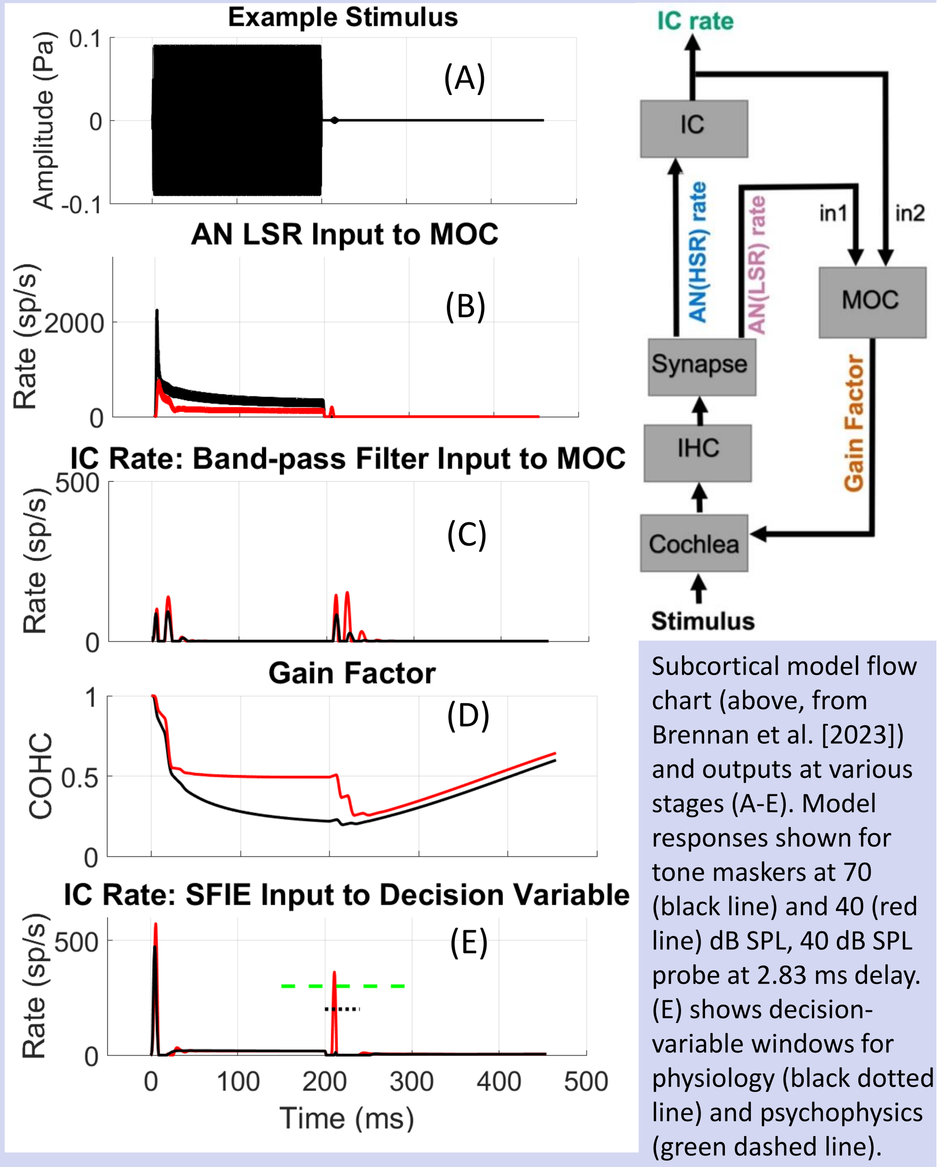
Models

Simulations *with MOC efferent control of cochlear gain:* Two signals are input to the MOC:

("in 1") Wide-dynamic range feedback controls cochlear (OHC) gain such that IHCs saturate in response to sound levels that are relatively high compared to the spectrum as a whole. As low-spontaneous-rate fiber (LSR) rate increases, gain decreases.

("in 2") Feedback from the IC decreases cochlear gain for fluctuating channels, but plays a relatively small role for tone maskers.

- Simulations *without efferents* used the AN model of Zilany et al. (2014).
- All AN models had human frequency selectivity (Ibrahim & Bruce, 2010).
- Time-varying AN responses were passed to SFIE IC model cells (Nelson and Carney, 2004) that had a band-enhanced modulation transfer function (MTF) with a best modulation frequency of 64 Hz.



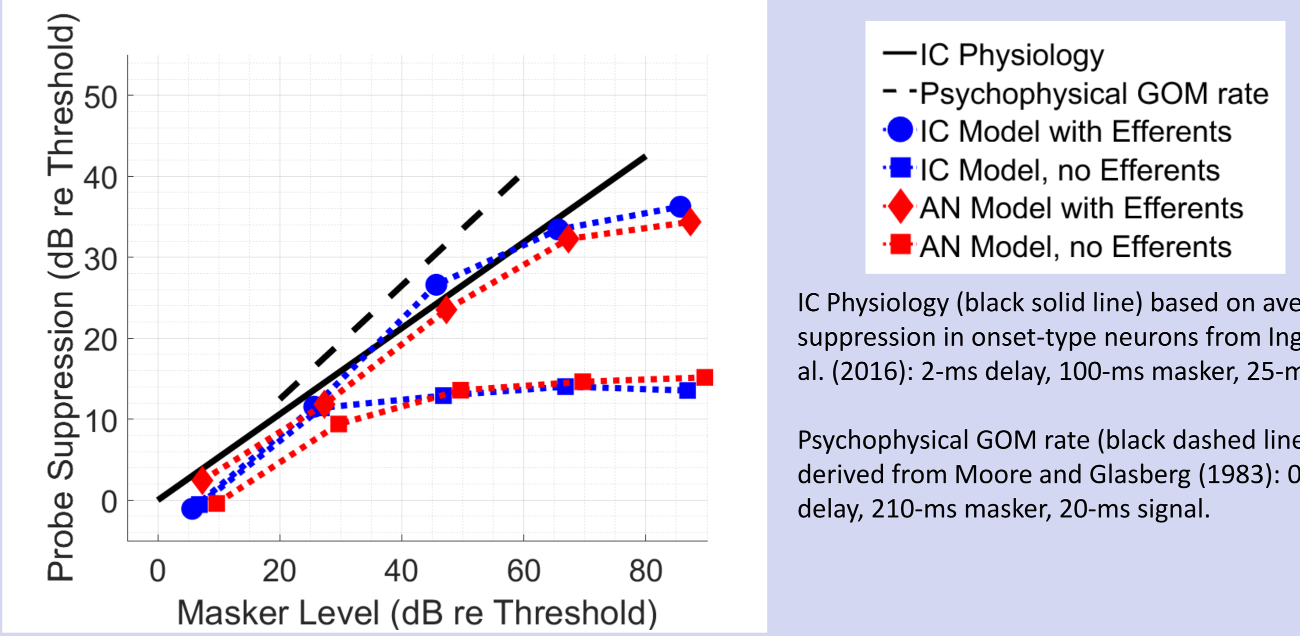
Subcortical model flow chart (above, from Brennan et al. [2023]) and outputs at various stages (A-E). Model responses shown for tone maskers at 70 (black line) and 40 (red line) dB SPL, 40 dB SPL probe at 2.83 ms delay. (E) shows decision-variable windows for physiology (black dotted line) and psychophysics (green dashed line).

Threshold Calculation

- Model responses were used to decide, for each trial, whether the tone was in interval 1 or 2.
- Physiological simulations: on each trial, the interval with the higher **maximum** response during a 40-ms decision-variable window (matching windows in Nelson et al. and Ingham et al.) was selected as the target interval.
- Psychophysical simulations: Same as above except that the decision-variable window extended from 150 to 300 ms to reflect less *a priori* knowledge about the time of the probe response.
- Percent correct was tabulated over 100 trials. A logistic curve was fit to the data across tone levels to estimate threshold (61% to match Ingham et al., 70.7% in all other cases).

Results and Discussion

Subcortical Model Including Efferents Explains Growth of Masking (GOM)

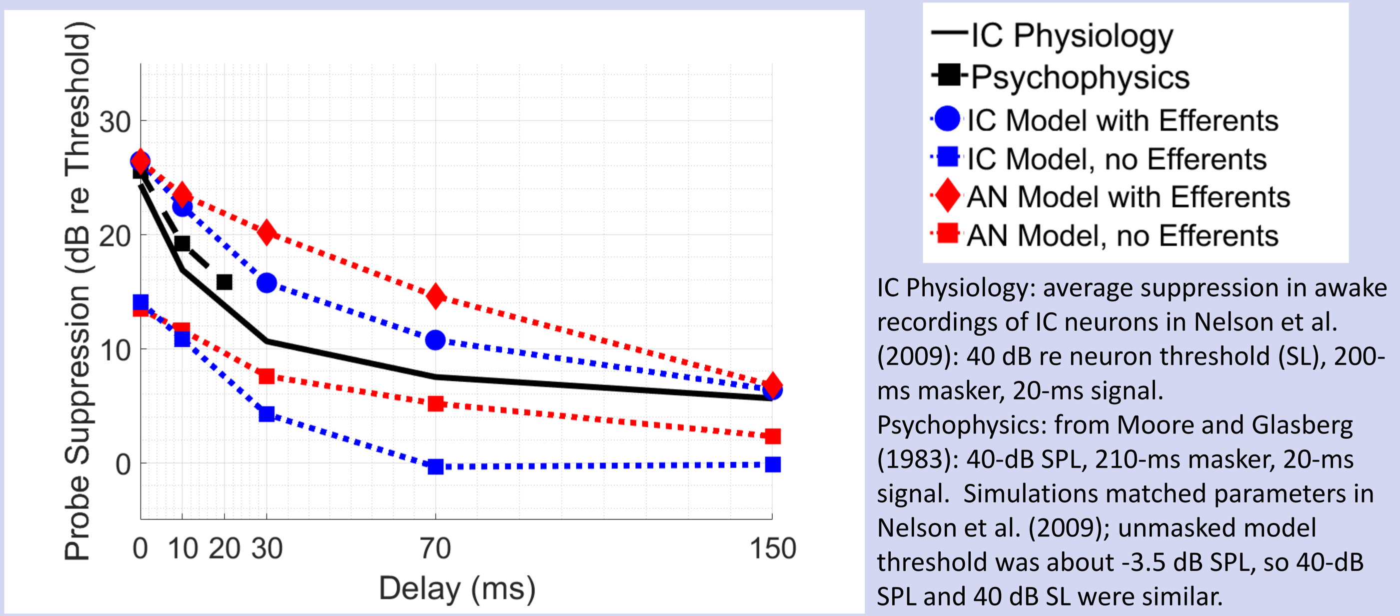


IC Physiology (black solid line) based on average suppression in onset-type neurons from Ingham et al. (2016): 2-ms delay, 100-ms masker, 25-ms signal.

Psychophysical GOM rate (black dashed line) derived from Moore and Glasberg (1983): 0-ms delay, 210-ms masker, 20-ms signal.

- Suppression in AN and IC Models with efferents (red diamonds, blue circles) was similar to IC onset-type neurons (black solid line). The IC Model with efferents inherited suppression properties from the AN model with efferents. GOM was substantially greater for the AN model with efferents (red diamonds) than AN model without efferents (red squares).
- GOM rate is similar for psychophysics and IC physiology; degree of difference depends on comparison in SL or SPL (see below).
- IC Physiology (Ingham et al, 2016) used urethane anesthesia, with potentially less impact on efferents than barbiturates (Guitton et al., 2004).
- All values are expressed re unmasked threshold (SL) for each neuron, model neuron, or listener, except for the SPL-matched psychophysical data (x-position shifted to match SPL, rather than SL, of model conditions, using unmasked threshold average from Oxenham & Plack, 1998). The physiological results were available as SL only; however, efferent function is likely to be similar for matched SPL.

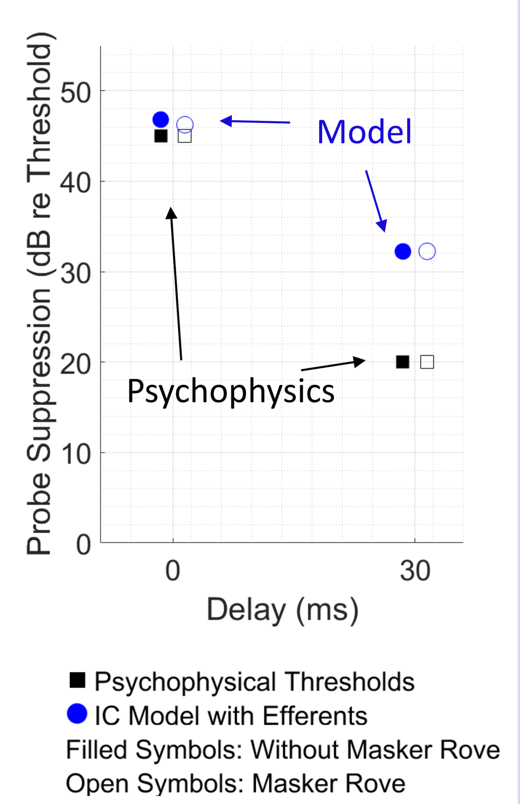
Subcortical Model with Efferents Explains Change in Threshold with Probe Delay



IC Physiology: average suppression in awake recordings of IC neurons in Nelson et al. (2009): 40 dB re neuron threshold (SL), 200-ms masker, 20-ms signal.
Psychophysics: from Moore and Glasberg (1983): 40-dB SPL, 210-ms masker, 20-ms signal. Simulations matched parameters in Nelson et al. (2009); unmasked model threshold was about -3.5 dB SPL, so 40-dB SPL and 40 dB SL were similar.

- Suppression is expressed re unmasked threshold (SL) for each neuron, model neuron, or listener.
- Suppression in IC Model with efferents (blue circles) is close to that of IC physiological recordings (black line) at short and long delays.
- IC Model with efferents inherited some suppression from AN model with efferents (red diamonds), although the IC-model sensitivity to onsets improved thresholds at moderate delays.
- Suppression was substantially greater for AN model with efferents (red diamonds) than for AN model without efferents (red squares).
- Similarities are present between forward masking in psychophysical and physiological data (solid black line and dashed black line with squares) at short delays.

Subcortical Model with Efferents Explains Thresholds Robust to Masker Rove



- In good agreement with human thresholds (Jesteadt et al., 2005), model thresholds changed very little in the presence of masker rove.
- Note that the detection process required only general a priori knowledge of when the tone would occur (~100ms before/after the end of the masker). Detection required peak rate during the probe response to exceed peak rate during the masker response (as in Brennan et al., 2023).
- Thresholds were robust to rove due to multiple factors, including the peak-based decision variable and saturation of the average rates of HSR fibers during the masker.
- The present model accounts for a result that is difficult to explain using a standard persistence model. The persistence model would integrate masker energy, without saturation.
- Model suppression was similar to human participants in the 0-ms delay condition. ~10 dB of extra suppression in the model for the 30-ms delay condition was attributable to the gap between the IC Model and physiological suppression at the 30-ms delay (see Results, Suppression vs. Delay).

Conclusions

- A model of the subcortical auditory system that incorporates the MOC efferents (Farhadi et al., 2022) can account for:
  - physiological growth of forward masking in the IC
  - changes in IC thresholds with increasing delay between masker and probe tones, and
  - results from analogous psychophysical paradigms, including difficult-to-explain roving-level masker conditions.
- Simulation results suggest that the MOC efferents may play an essential role in forward masking:
  - Physiological forward masking may be caused by decreased OHC gain, driven by MOC efferents, rather than adaptation or central inhibition.
- Psychophysical forward masking may be more closely related to peripheral physiology than previous studies (Relkin and Turner, 1988; Nelson et al., 2009) suggested.
- Previous consensus that sufficient GOM did not exist in the AN may have been a result of barbiturate anesthesia (Relkin and Turner, 1988) that suppresses MOC efferent activity (Guitton et al., 2004).

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