# Temporal Weighting Functions Reveal a Precedence Effect in Neural Population, But Not Individual Unit, Responses in the Rat Inferior Colliculus

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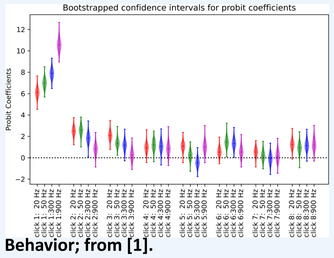
## Background

- To localize sounds in reverberant environments, the auditory system strongly favors spatial cues carried by the initial arriving wavefront over those of later reflections.
- Previously [1], rats showed strong **perceptual onset dominance** — the first click dominates lateralization judgements, and this onset weighting grows with click rate. Yet in **auditory cortex**, this dominance was **not** evident at individual recording sites and emerged only through population decoding.




**Behavior; from [1].**

- Whether **IC** shows onset dominance at the single-neuron level or similarly requires population-level readout remains unknown.

## Method

- **Subjects:**
  Nine normal hearing, young female Wistar rat
- **Stimulus Paradigm:**
  8-click trains at 4 click rates (20, 50, 300, 900 Hz)
  **ITD tuning trial**: 8 clicks in the train carried the same ITD ranging `from −0.123 ms to +0.123 ms in steps of 0.04 ms
  **TWF probe trial**: ITD of each click was drawn independently from a finer set of 13 ITD values, with 16 random-seed configurations spanning the same range

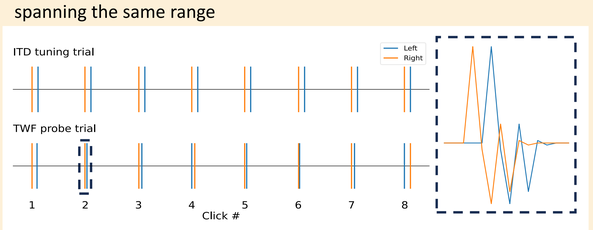



**Figure 1 Stimulus design.** Each trial was a train of 8 binaural clicks (blue, left ear; orange, right ear); the small time offset between the left and right click marks the interaural time difference (ITD) of that click. Inset, a single click on an expanded time scale, showing the left- and right-ear waveforms and their ITD.

- **Recording:**
  - Extracellular activity recorded from the IC of anesthetized rats
  - 32-channel linear silicon probe (50 µm spacing)
  - Responses quantified as analog multi-unit activity (AMUA), averaged from stimulus onset to 30 ms after the final click
- **Analysis**
  - **Univariate TWF**: variance explained ($\eta^2$) by each click's ITD, per multi-unit
  - **Multivariate TWF**: population decoding index (DI) from Mahalanobis distances between contralateral- and ipsilateral-leading population responses across all 32 channels

## Results: Example IC multi-units show clear ITD tuning

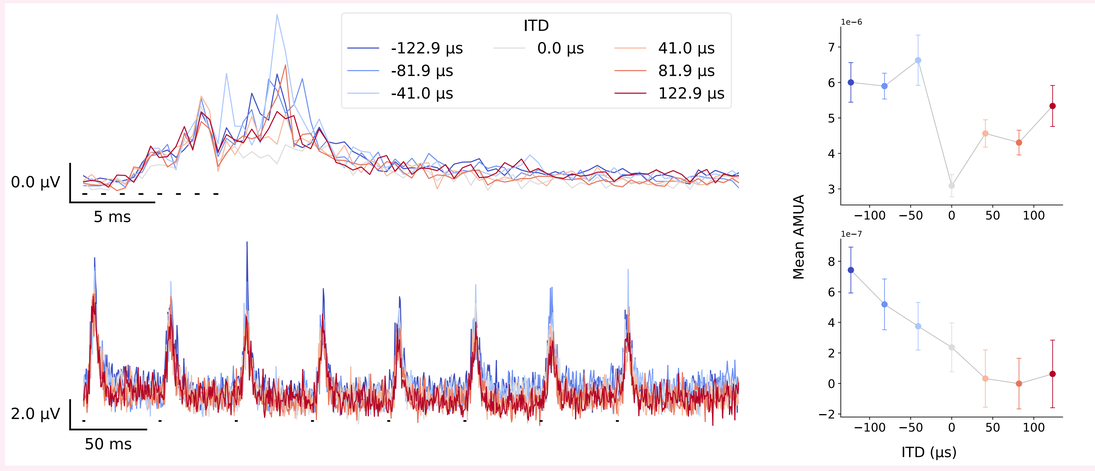



**Figure 2 AMUA responses and ITD tuning of two representative IC multi-units.** Each row shows one example unit responding to ITD tuning trials, in which all eight clicks carried the same ITD. **(A)** AMUA waveforms; colored traces denote the seven ITD values (blue, left-ear-leading negative ITDs; red, right-ear-leading positive ITDs; grey, 0 µs), and colored dashes beneath each trace mark click times. Top: unit recorded at a 900 Hz click rate, where the eight clicks fall within ~8 ms and merge into a single onset-dominated response; bottom: unit recorded at 20 Hz, where the clicks evoke eight discrete peaks. Horizontal scale bars, 5 ms (top) and 50 ms (bottom); vertical scale bars, as labelled. **(B)** Corresponding ITD tuning curves: mean AMUA amplitude over the analysis window (stimulus onset to 30 ms after the final click offset) versus ITD; error bars, SEM.

## Results: Individual multi-units do not upweight the first click

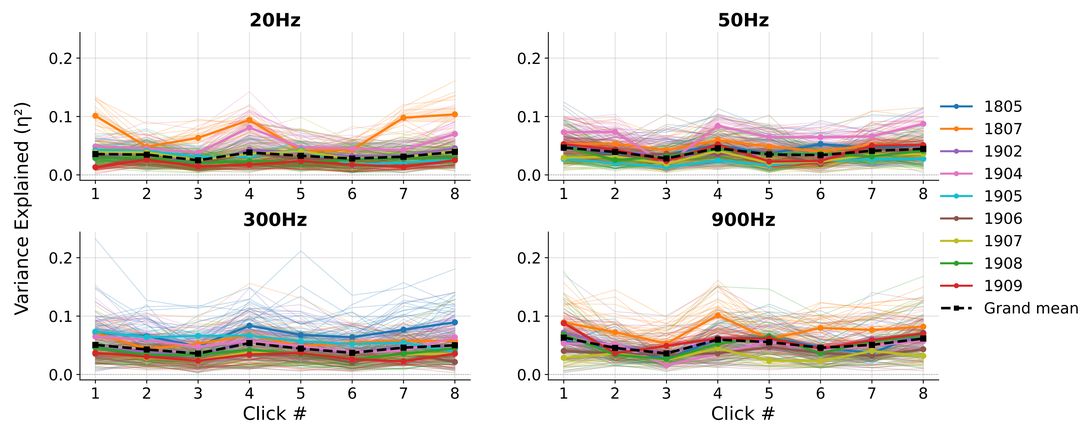



**Figure 3 Univariate temporal weighting functions show no onset dominance at the single-unit level.** Univariate level TWFs for each click rate (20, 50, 300, 900 Hz). For each ITD-sensitive multi-unit, variance explained ($\eta^2$) by the ITD at each click position (1–8) was computed from random-ITD trials, in which every click carried an independently assigned ITD. Thin translucent lines, individual ITD-sensitive multi-units; thick colored lines, per-animal means (animal IDs in legend); black dashed line, grand mean across all multi-units. The grand mean remains approximately flat across click positions and shows no elevation at click 1, indicating that the first click does not dominate at the individual multi-unit level.

## Results: The population upweights the first click

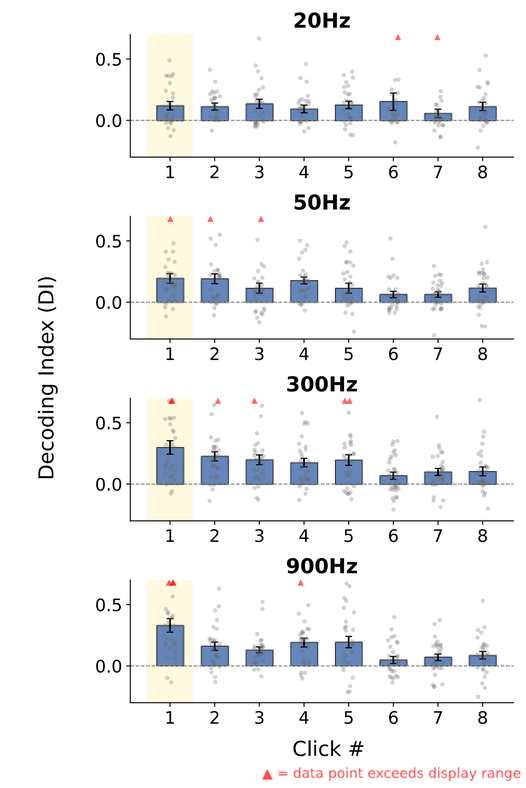



**Figure 4 Multivariate temporal weighting functions reveal onset dominance at the population level.** For each penetration, a multivariate decoding index (DI) was computed at each click position from leave-one-out Mahalanobis distances between contralateral- and ipsilateral-leading population response vectors across the 32 channels; higher DI indicates that the ITD at that click position is more strongly represented in the population response. Bars, mean DI across penetrations; error bars, SEM; grey dots, individual penetrations.

## Summary

- Individual multi-units are ITD-sensitive but show no onset dominance
- Population responses upweight the first click at high click rates (300, 900 Hz)
- Onset dominance in the IC appears at the population, not the individual multi-unit level

**Reference**:
(1) Li, K., Auksztulewicz, R., Chan, C. H., Mishra, A. P., & Schnupp, J. W. (2022). The precedence effect in spatial hearing manifests in cortical neural population responses. BMC biology, 20(1), 48.