Local processing modifies spike timing in non-primary auditory cortex

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Possible origins of long and stimulus-modulated spike latencies in non-primary auditory cortex:

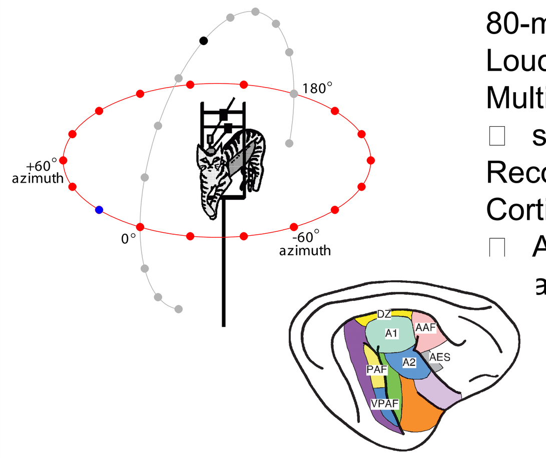
Delayed Input
- Long latencies reflect timing of input. (e.g. via slower excitatory pathway or feedforward processing delay)
- *Hypothesis: output latencies will covary with input latencies across recording sites and stimulus features.*

Local Processing
- Long latencies reflect local delay of early input. (e.g. responses slowed by tonic or early inhibition.
- *Hypothesis: input latencies will not vary between recording sites or with stimulus features. Output latencies will vary independently of input latencies.*

Approach: use local field potential (LFP) as marker of earliest detectable event in vicinity of recorded unit.

Compare LFP ("input") latency to spike ("output") latency

Recordings



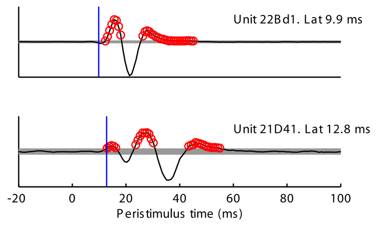
- Anesthetized cat, a-chloralose IV
- 80-ms Gaussian noise bursts, thr+20 dB
- Loudspeakers every 20° in azimuth
- Multi-channel probes with 16 sites spaced 100 or 150 mm
- Recordings in right hemisphere
- Cortical areas A1 (304 sites).
- AAF (140 sites), PAF (411 sites), and DZ (394 sites).

Analysis

Spike latency
- L_{spk}: Geometric mean of first spike latency across trials of given stimulus.
- Median L_{spk} (overall latency), ΔL_{spk} (range) computed across azimuth.

LFP signal processing
- Recordings low-pass filtered at 300 Hz, resampled at 1.25 kHz.
- Averaged LFP waveform is median across trials of each stimulus type.

LFP Latency calculation
- Threshold at 90th percentile of pre-stim voltages.
- L_{lfp}: Stimulus-specific latency
- Median L_{lfp}: overall across azimuth
- ΔL_{lfp}: range across azimuth
- L_{spk}-L_{lfp} or $\log(L_{spk}/L_{lfp})$: input/output delay

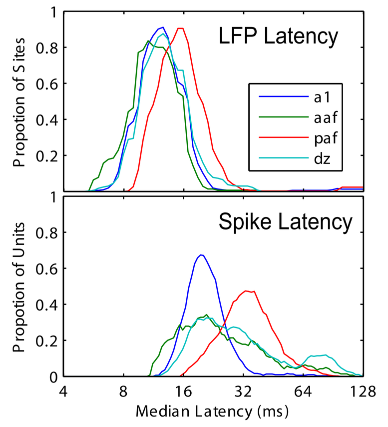


Multi-unit activity (MUA)
- Alternative to sorted spikes (spk). Recordings bandpass filtered at 1-4kHz, rectified and low-pass filtered to estimate envelope in spike band.
- Stats defined as for lfp.

1. How do input and output latencies relate across recording sites?

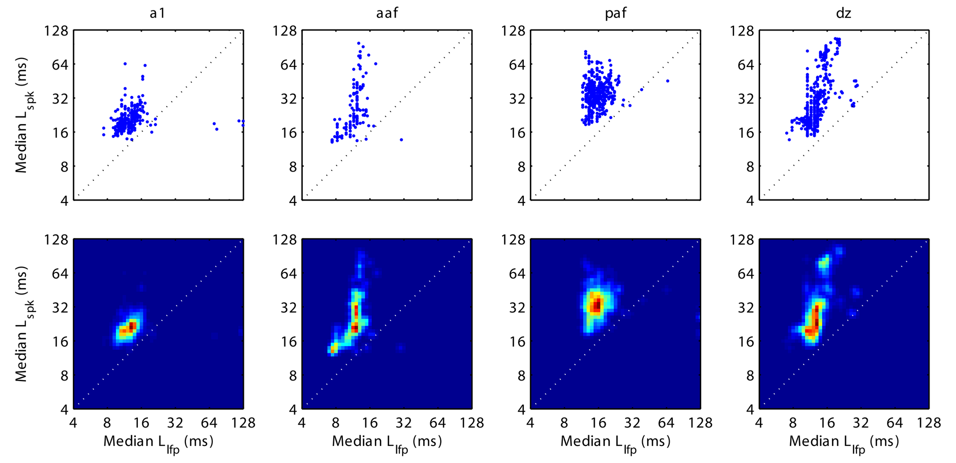
Different distributions of input, and output latencies in AC.

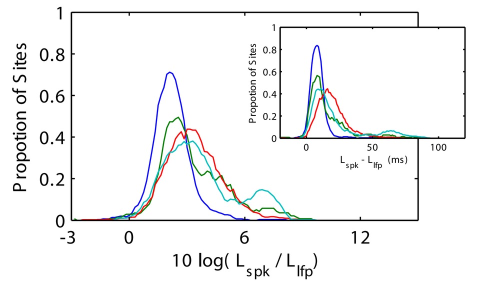
- LFP latencies are short, similar across fields.
- Non-primary spike latencies longer but not by common delay.



Median across sites

	L_{lfp}	L_{spk}
A1	10.7	19.8
AAF	10.7	20.8
PAF	13.6	33.8
DZ	12.3	30.1





Input-output delay varies between fields

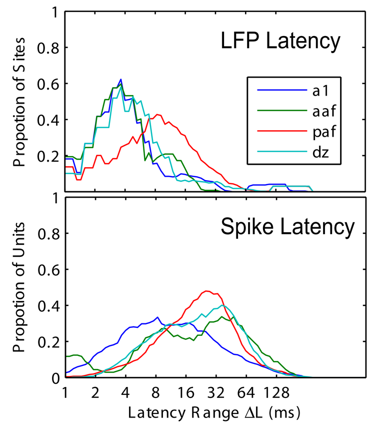
Median across sites

	L_{spk}-L_{lfp}
A1	8.9
AAF	10.4
PAF	12.7
DZ	17.3

2. Are input and ouput latencies equally sensitive to stimulus features?

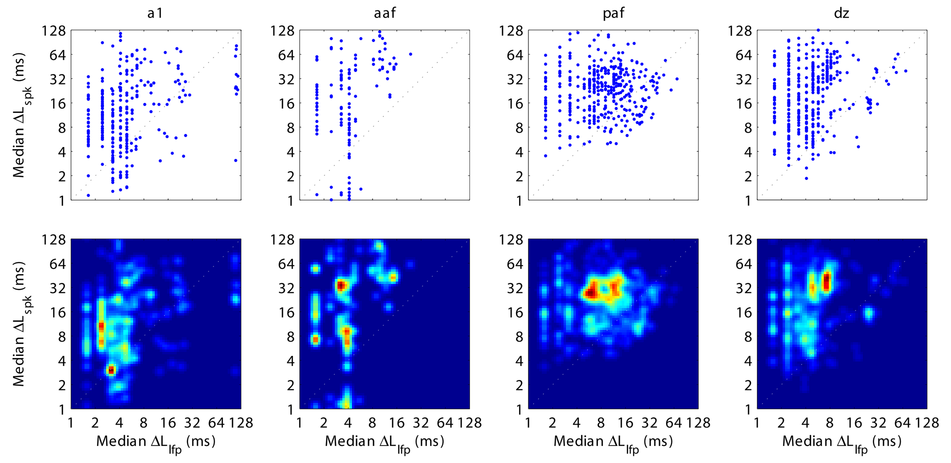
Greater azimuth sensitivity of spike than LFP latencies across cortical fields.

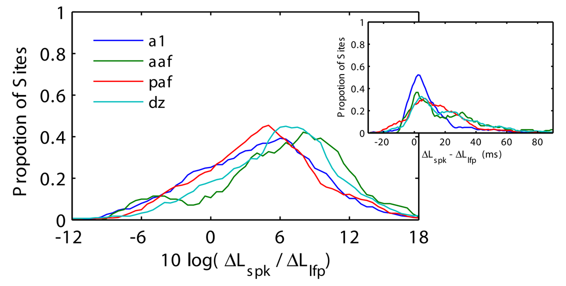
- LFP mainly insensitive to azimuth.
- Greatest spike-latency modulation in non-primary fields.



Median across sites

	ΔL_{lfp}	ΔL_{spk}
A1	4.1	7.6
AAF	4.1	14.1
PAF	4.9	25.3
DZ	4.1	26.9





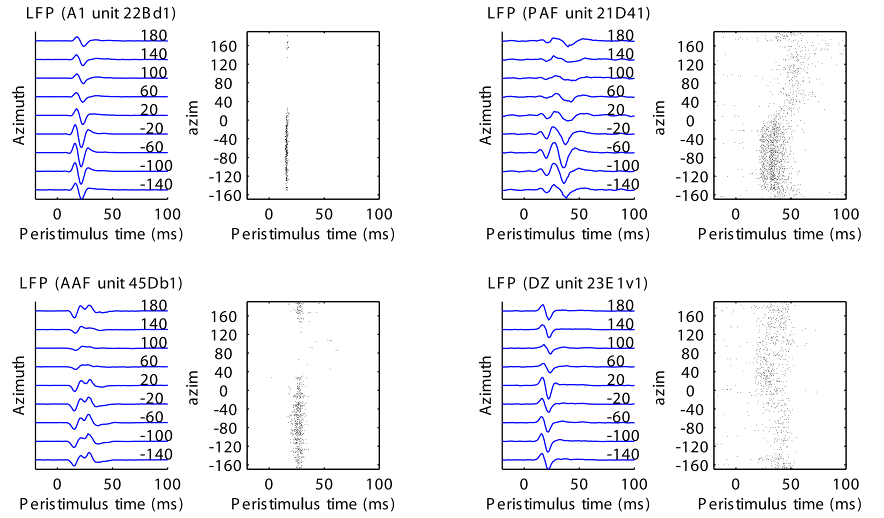
Increase in azimuth sensitivity of output latency is similar across fields.

Median across sites

	ΔL_{spk}-ΔL_{lfp}
A1	3.0
AAF	9.6
PAF	16.0
DZ	19.6

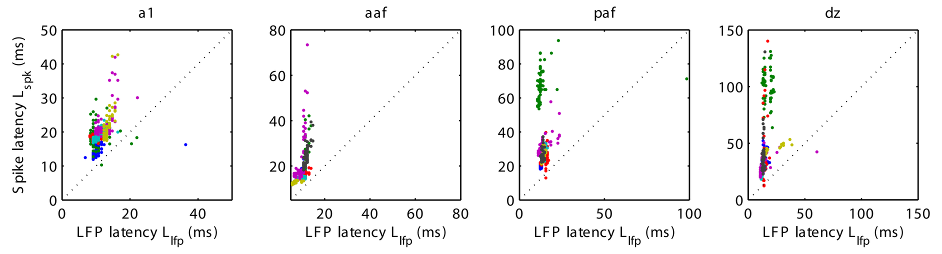
3. Do input and output latencies covary across azimuth?

Correlating latency across azimuth at each recording site:

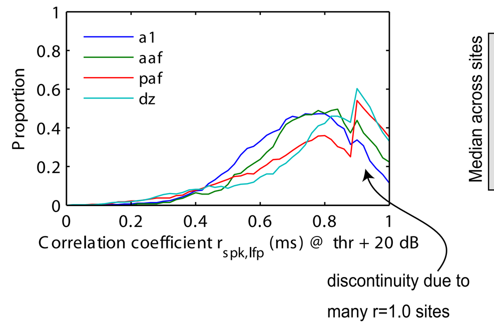


Input and output latencies are correlated across azimuth.

- Examples of stimulus-specific spike latency vs LFP latency:
- Seven random example units (colors) from each field.



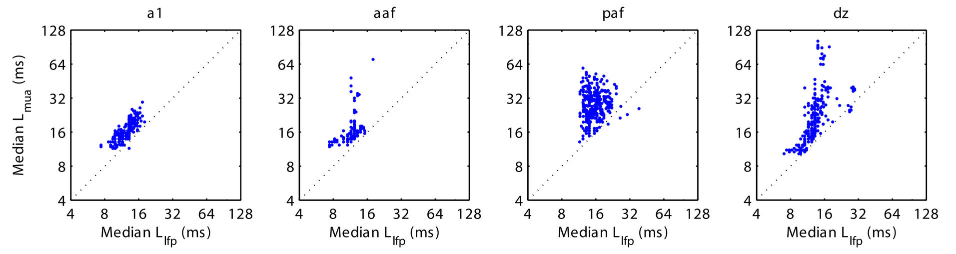
Degree of correlation is similar across cortical fields.

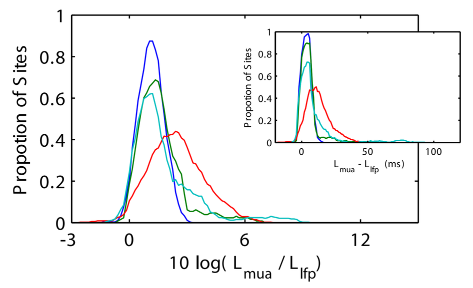


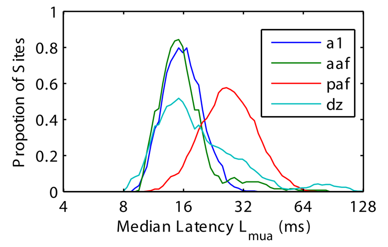
Median across sites

	$r_{spk\text{-}lfp}$
A1	.74
AAF	.81
PAF	.77
DZ	.70

1b. What about MUA latencies?



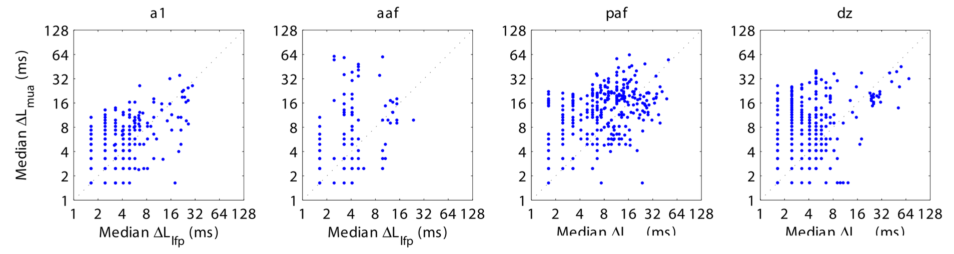


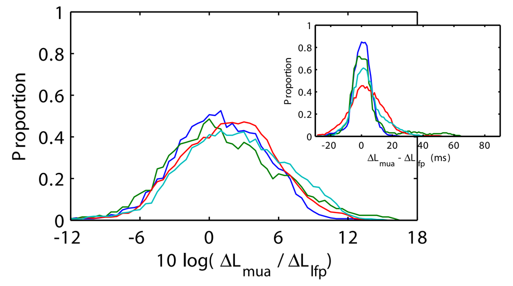


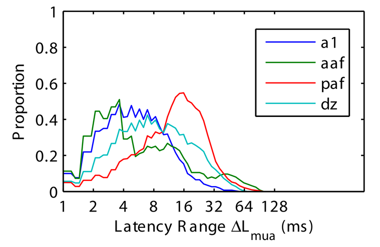
Median across sites

	L_{mua}	L_{mua}-L_{lfp}
A1	14.4	4.1
AAF	14.0	4.1
PAF	24.6	11.2
DZ	17.2	4.9

2b. What about MUA latencies?



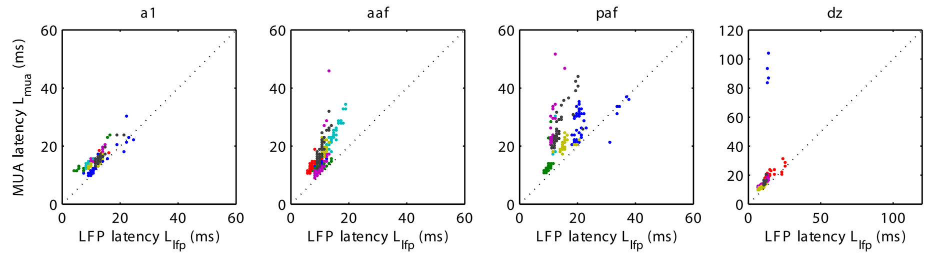


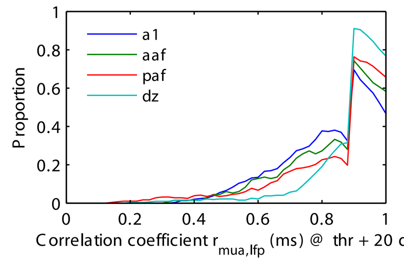


Median across sites

	ΔL_{mua}	ΔL_{mua}-ΔL_{lfp}
A1	3.3	0.0
AAF	4.1	0.0
PAF	13.4	6.1
DZ	7.4	2.5

3b. What about MUA latencies?





Median across sites

	$r_{mua\text{-}lfp}$
A1	.85
AAF	.89
PAF	1.0
DZ	1.0

Conclusions and Questions

Local processing? YES
- Spike latency ≠ LFP latency + fixed delay.
- LFP latencies are similar across cortical fields. Spike latencies are not.
- LFP latencies are weakly modulated by azimuth.
- Spike latencies are strongly modulated by azimuth.
- Stimulus-specific delay (L_{spk}-L_{lfp}) varies between fields.

Delayed input? YES
- Some evidence for longer LFP latencies in non-primary cortex.
- In all fields, high correlation between spike and LFP latency across azimuth.
- Latencies reflect both delayed input and local processing
- Input-output delay is multiplicative, not additive (local process not independent of input timing).
- "Large-print" theory (latency coding for the temporally impaired?)

Primary vs non-primary fields
- Non-primary fields (PAF, DZ) noted for long spike latencies.
- Non-primary LFP latencies are longer than in primary AC, but input/output delay is even greater still.
- Spike latency codes stimulus features in both primary and non-primary fields.
- Non-primary fields similar to primary but temporally exaggerated?

Inhibited or Inhibiting?
- Does early activity visible in LFP reflect (1) subthreshold excitation or (2) early non-specific inhibition?
- Why are MUA latencies intermediate between LFP and spike latencies, and why is their stimulus sensitivity similar to LFP, not spikes?
  - -Contamination by slow wave?
  - -Exaggerated latency range with sorted spikes?
  - -Contribution of local interneurons?

LFP waveform structure in primary and non-primary fields.
- Do later deflections relate to late spike timing?

Acknowledgments

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