

# Synchronized and Propagating States of Human Auditory Processing

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## Abstract:

Human brain dynamics combine external drivers (e.g. sensory information) and internal drivers (e.g. expectations and memories). How do the patterns of inter-regional coupling change when the balance of external and internal information is altered? To investigate this question, we analyzed intracranial (ECoG) recordings from human listeners exposed to an auditory narrative. We measured the latencies of coupling across consecutive stages of cortical auditory processing and we investigated if and how the latencies varied as a function of stimulus drive. We found that the latencies along the auditory pathway vary between no delay (“synchronized state”) and a small, nonzero delay (~20 ms, “propagating state”) depending on the external stimulation. The long-latency propagating state was most often observed in the absence of external information, during the silent boundaries between sentences. Moreover, propagating states were associated with transient increases in alpha-band (8-12 Hz) oscillatory processes. Both synchronized and propagating states were reproduced in a coupled oscillator model by altering the strength of the external drive. The data and model suggest that cortical networks transition between i) synchronized dynamics driven by an external stimulus, and ii) long-latency propagating dynamics in the absence of an external stimulus.

**Keywords:** ECoG; directionality; mode switching; auditory hierarchy; cortex.

## Motivation

Bottom-up information flow occurs when sensory information is sent to higher order regions of the cerebral cortex, and top-down information flow occurs

in the reverse direction (Honey, Newman & Schapiro, 2017). How does the balance of the bottom-up and top-down signaling vary over time? We addressed this question by measuring intracranial potentials in the human brain during a naturalistic auditory processing task and characterizing the time delays (latencies) between consecutive processing stages. We asked: (i) how variable are the delays between processing stages? (ii) how do the latencies between stages depend on the electrophysiological state of local circuits? (iii) how do the latencies between stages depend on the functional properties of the auditory stimulus?

## Method

Our analytic scheme is illustrated in Figure 1. We analyzed electrocorticographic (ECoG) signals from 4 human participants. Each participant listened to two repetitions of a 7-minute auditory stimulus with a narrative. First, we identified responsive channels by measuring the cross-run reliability (correlation between run 1 and run 2) for the time courses of alpha power responses (8-12 Hz) and also for broadband power responses (65-200 Hz). Second, in sliding 2 second windows, and for channel pairs along the superior temporal gyrus, we computed the cross-correlation of the voltage signal between adjacent sites. For each channel-pair in each time window, we identified the time lag of maximal inter-electrode correlation and defined it as the latency  $\tau$  between the channels. Third, we identified the time of sentence boundaries and tested how the latency  $\tau$  was altered at these moments. Finally, for each channel and 2 second



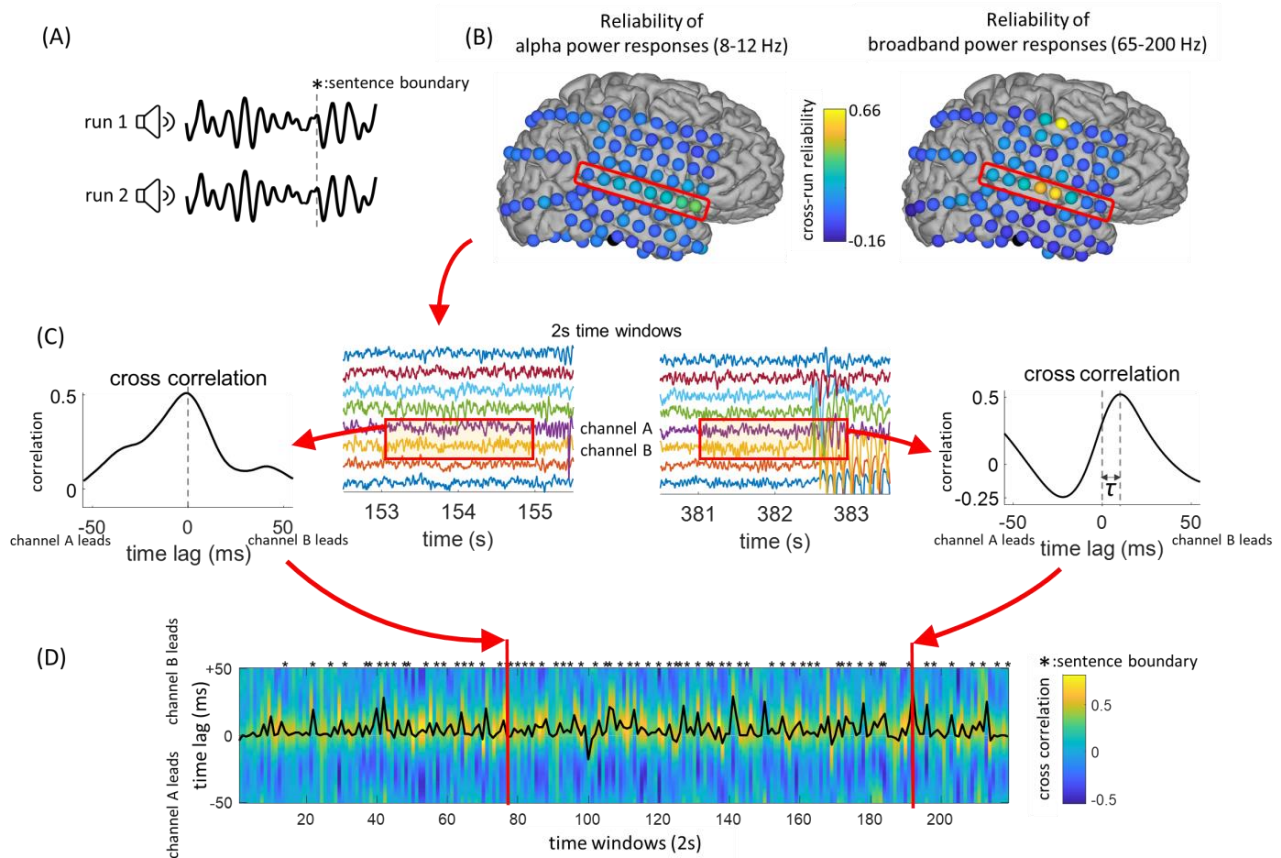


Figure 1. Schematic of analysis. (A) We presented a 7 minute auditory narrative twice to each participant. (B) We measured response reliability – how strongly each channel was locked to the stimulus. Channels with high reliability of alpha power (8-12Hz) & broadband power (65-200Hz) time courses were selected for further analysis. (C) Moving time windows were applied to each pair of chosen ECoG channels. For each time window, we measured the cross correlation between the chosen pair. The latency  $\tau$  was defined as the time lag yielding the maximum cross-correlation between the channels. (D) Cross correlation and latency  $\tau$  of this channel pair are illustrated for all time windows.

window we measured mean alpha (8-12 Hz) power and mean broadband (65-200 Hz) power.

## Results

### Inter-regional Latencies Vary Across Time

Consistent with prior reports (Zhang et al., 2018, Chapeton, Inati & Zaghoul, 2017), we found that the auditory pathway exhibited a gradient of delays, with posterior temporal regions leading anterior temporal regions on average. However, the latencies between stages of auditory processing were not stable, but fluctuated over time (mean of s.d. = 5.7 ms across 2 s time windows). Latencies become longer or shorter in the same pattern across repetitions of the same natural auditory stimulus (e.g. Spearman  $\rho = 0.25$

across repetitions), indicating that latency changes are not-random, but relate to a functional processing state.

Representative results from one subject are shown in Figure 2, which depicts the time delays between ECoG voltage signals from two electrodes in the middle superior temporal gyrus (STG). As shown in Panel (A), the inter-electrode delay  $\tau$  (location of the maximal cross-correlation) varied across time windows. Two distinct electrophysiological states were evident: one with longer inter-channel latencies (“*propagating state*”, blue brace, Figure 2A), and the other shorter latencies (“*synchronized state*”, red brace, Figure 2A).

### Latencies Correlates with Alpha Power Bursts

Latencies were longer during bursts of alpha power (propagating state) and were shorter during bursts of broadband power (synchronized state) (Figure 2B).

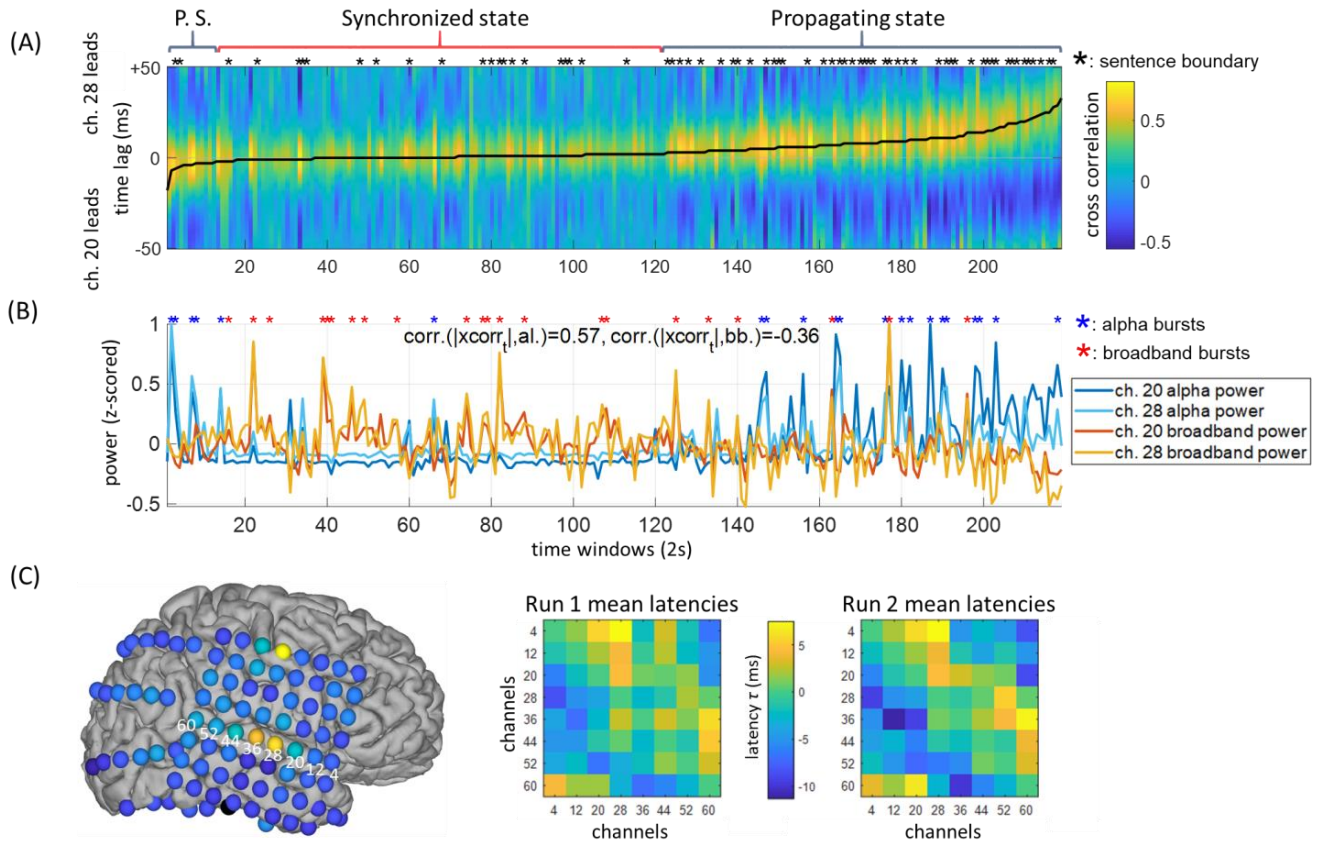


Figure 2. (A) Cross correlation between two chosen channels is shown for each time window, sorted by latency  $\tau$ , of the maximal cross correlation. Black line denotes the inter-electrode latency  $\tau$ . Asterisk (\*) denotes sentence onset. (B) Alpha and broadband power for each time window. Blue asterisk denotes alpha peaks; red asterisk denotes broadband power peaks. (C) Broadband reliability of the channels and the channel numbers for the auditory pathway are shown on the brain surface. Latency  $\tau$  matrices for run 1 and run 2 indicate that the mean latencies between channels are consistent across runs.

The alpha bursts and propagating states occurred preferentially in the silent boundaries between sentences as shown in Figure 2A (boundaries marked with \*; mean delay between nearest boundaries and alpha bursts: 0.77 s, mean delay for surrogate boundaries: 2.10 s).

The higher-order auditory cortex (channel 20) lagged behind the more sensory auditory cortex (channel 28), and this latency was larger when the alpha power increased across both sites (Figure 2B). Alpha-band power in a window is positively correlated with the latency for that window (Spearman  $\rho = 0.57$ ), while broadband power is negatively correlated with the latency (Spearman  $\rho = -0.36$ ).

### Global Latencies Changes between States

The transitions between synchronized and propagating states generalizes beyond the auditory pathway to the

parietal, temporal and sensorimotor cortex. We observed that global latency patterns change between the synchronized state and the propagating state (Figure 3). When auditory drive was strong the latencies between many areas were reduced (smaller arrows), and when auditory drive was absent the latencies increased (larger arrows).

### Coupled Oscillator Model Exhibits Both States

The propagating and synchronous states could be reproduced using a canonical coupled oscillator model (Stuart-Landau model), containing a control parameter,  $D_0$ , for the external drive:

$$\dot{Z}_j(t) = \{\lambda_j + i\omega_j - |Z_j(t)|^2\} Z_j(t) + K \sum_{k=1}^N A_{jk} \{Z_k(t - \tau) + D_0 e^{i\alpha} Z_j\},$$

$$j = 1, 2, \dots, N.$$



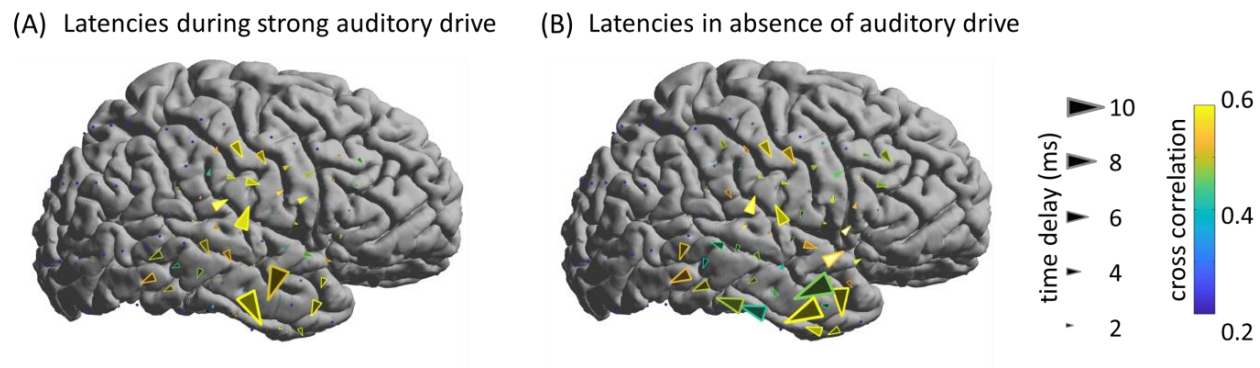


Figure 3. Latency pattern for strong vs. absent auditory drive. Arrow size and direction denote the mean latency and directionality of local voltage flow, for each channel relative to its local neighbors. Larger arrows indicate longer latencies. Warmer colors indicate stronger inter-regional couplings. (A) Voltage flow during the presence of strong auditory drive. (B) Voltage flow during quiet moments in auditory stimulus.

The synchronous state arises with large  $D_0$ , while the propagating state arises with small  $D_0$ .

propagating states (associated with weak external states and bursts of alpha-band power).

## Conclusions

How does human brain state change as we transition between internally-driven and externally-driven dynamics? We found that cortico-cortical coupling delays vary according to the strength of external stimulus drive in the human auditory pathway. Latencies across consecutive stages of auditory processing varied in a reproducible manner across repeats of the same minutes-long stimulus. The auditory pathway latencies exhibited two modes: time windows of zero latencies (*synchronous state*) and windows of nonzero latencies (*propagating state*). The long-latency propagating states often occurred in the silent boundaries between the sentences in the narrative. Moreover, the propagating state in the auditory pathway robustly co-occurred with bursts of alpha-band power, which are implicated in modulating corticocortical and thalamocortical interactions (van Kerkoerle et al., 2014). Thus, the changes in inter-regional latencies are not a random process, and reliably track features of the stimulus and endogenous dynamics.

The latency changes were not restricted to the auditory pathway, but could be observed at widespread temporal and somatomotor sites. We observed that widespread latencies were decreased (or increased) during strong (or absent) external drive. These widespread latency changes could be captured by a canonical coupled oscillator (Stuart-Landau) model in which we vary the strength of the external drive to the network. Altogether, the data and models suggest that human cortical dynamics reliably transition between synchronized states (associated with strong external drive and broadband power) and

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