Spatiotemporal θ–γ waves organize hierarchical visual processing

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1 | Introduction: Spatiotemporal θ–γ code

Neural activity unfolds across diverse spatial and temporal scales. The **θ–γ code** describes how neural information can be encoded by interactions between slower θ activity (3–10 Hz) and a faster γ component (30–100 Hz) [1]. But the classical θ–γ code only treats the temporal dynamics of brain activity, whereas the brain itself is highly distributed and relies on communication between cortical layers and regions.

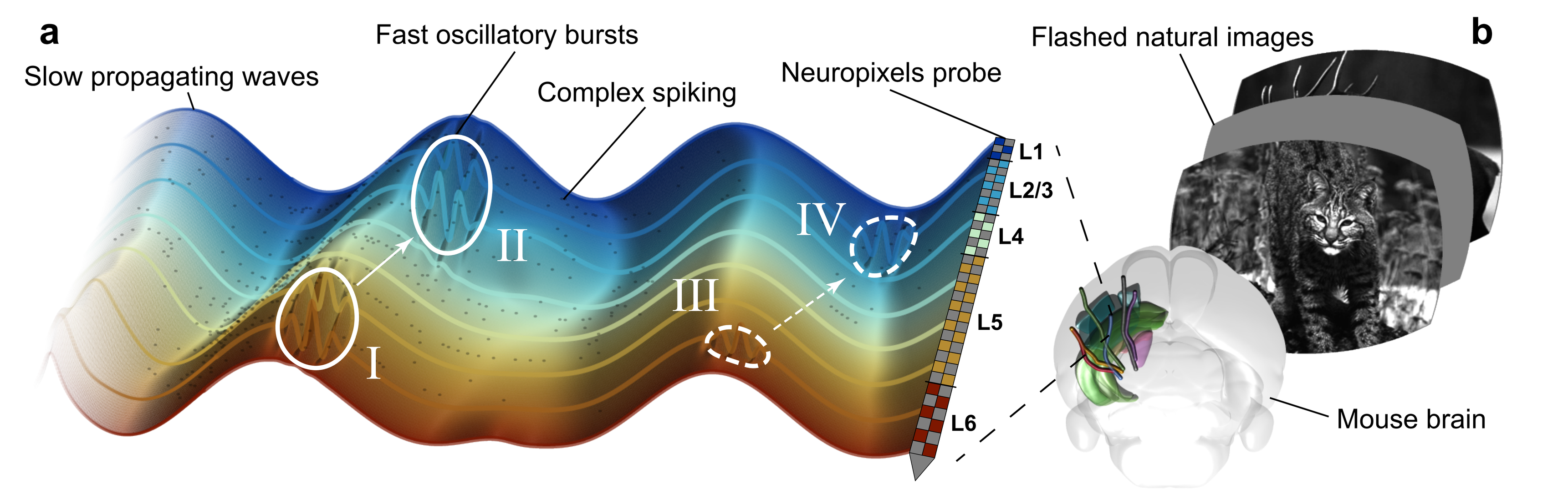
We put forward a **spatiotemporal** θ–γ code comprising:

1. A slower θ component that travels in **broad waves** over space [2]
2. A faster γ component that forms short-lived, spatially **localized 'packets'** [3, 4]

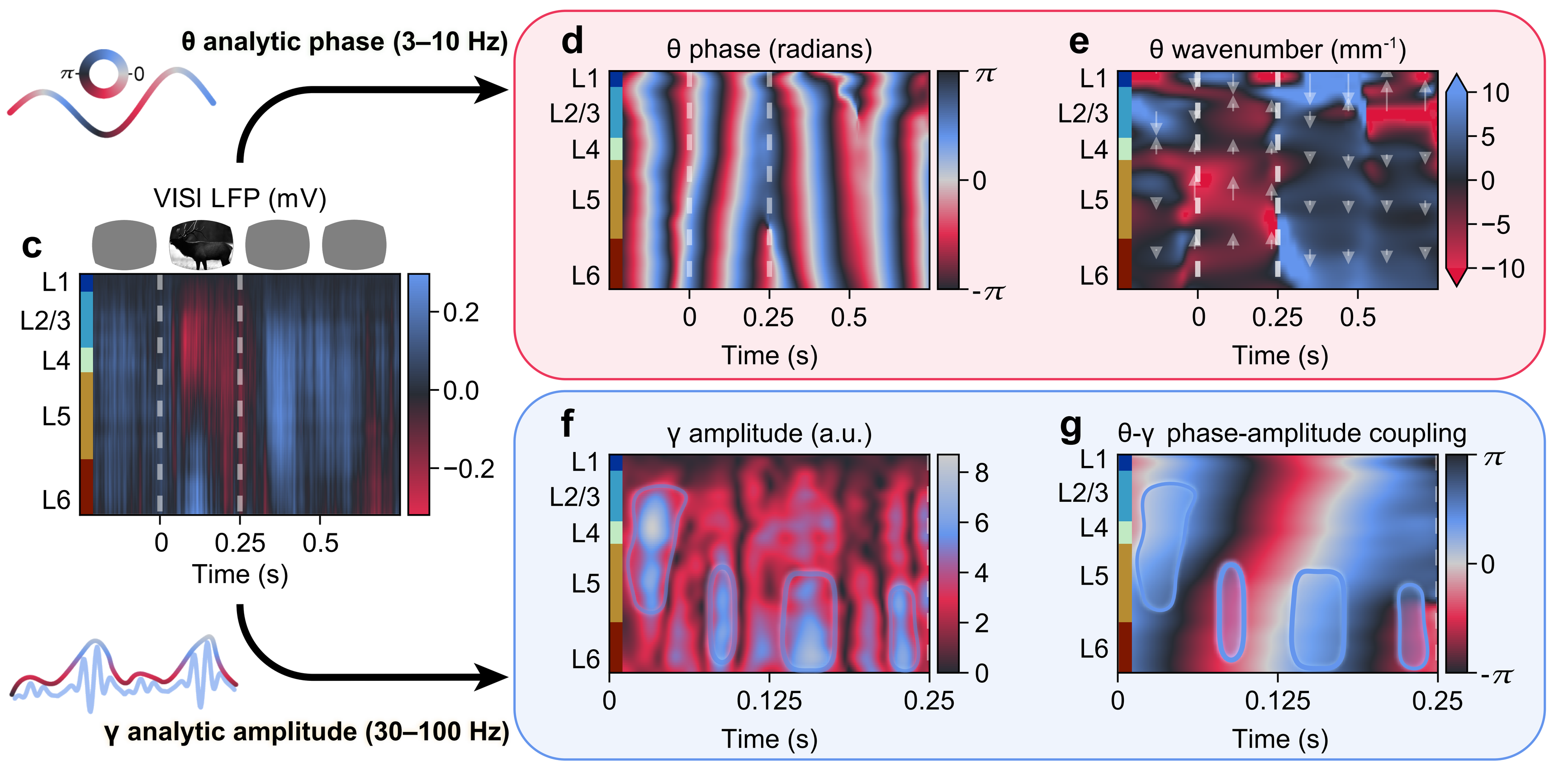
Thus detailed neural information may be **multiplexed** by local γ packets, which are broadly **modulated** by a traveling θ wave.

Below: A schematic of the spatiotemporal θ–γ code (**a**). γ packet I represents strong activation in deep layers, coinciding with a traveling θ wave that meets II at a peak, enhancing superficial γ. Conversely, packet III represents weak activity in deep layers coinciding with a stationary θ wave; thus packet IV occurs at a θ trough, and is suppressed.

We studied how this code may support hierarchical visual processing using the '**Allen Neuropixels—Visual Behavior**' dataset [5]: translaminar LFPs were recorded from six visual cortical regions in 53 mice tasked with identifying changes to flashed natural images (**b**).

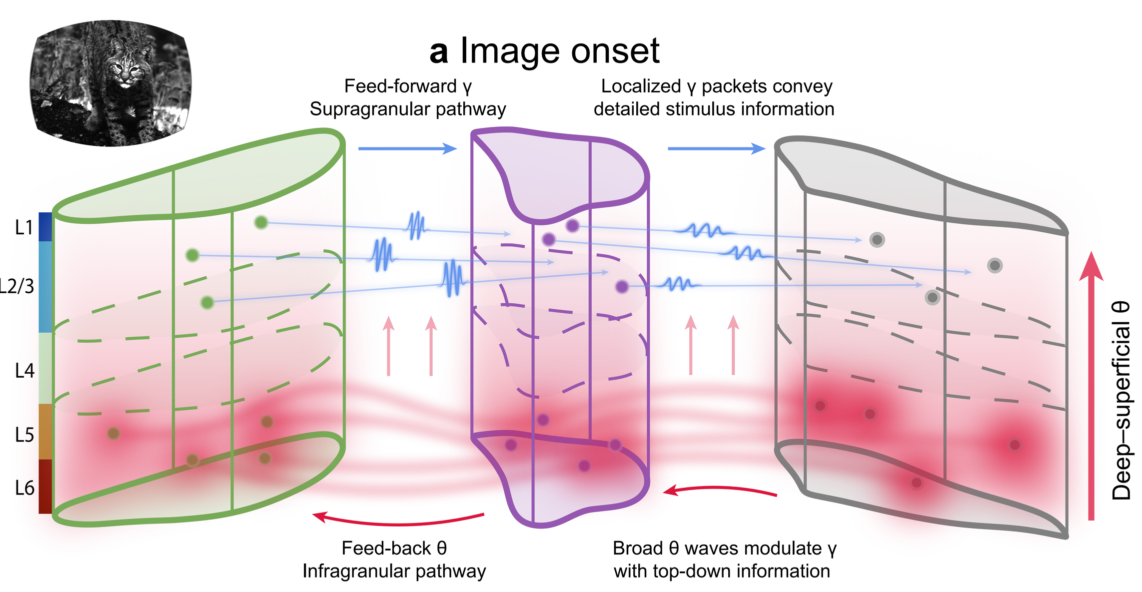


After band-pass filtering raw LFPs (**c**), we characterized θ as a traveling wave using the analytic phase (**d**) and quantified translaminar propagation with the negative spatial phase gradient (the **wavenumber**, **e**). We then used the analytic amplitude to detect non-stationary, spatially localized γ packets across layers (**f**). Finally, we extended classical **phase–amplitude coupling** measures to detect spatiotemporal θ–γ interactions that coordinate large-scale traveling θ waves with localized γ packets (**g**).



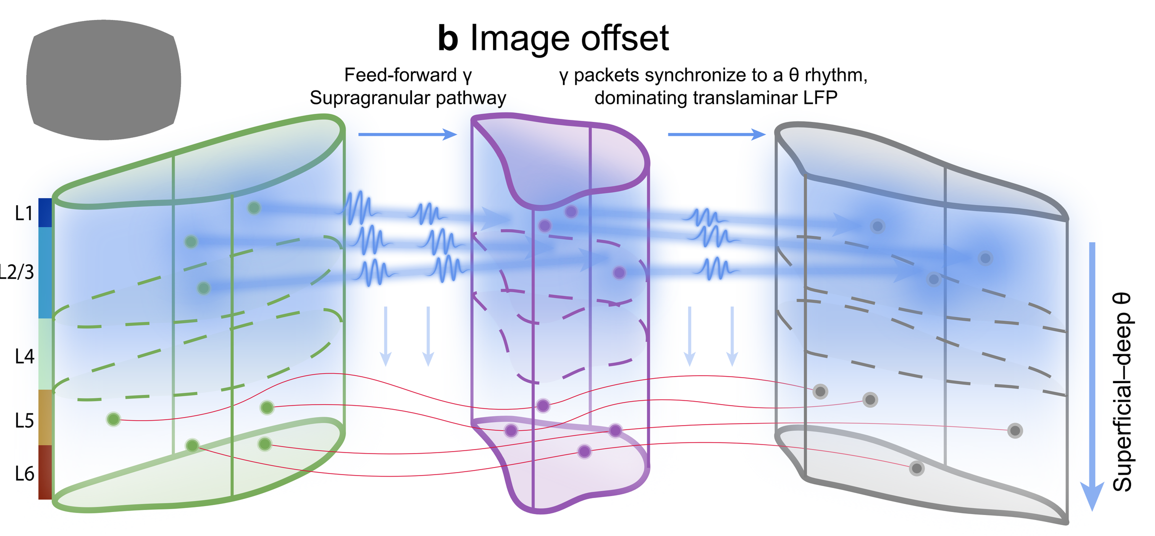
2 | Summary: Dual functional roles

We found that the onset and offset of changed stimuli evoked distinct **feed-back** and **feed-forward** modes of θ. Based on these modes, the spatiotemporal θ–γ code suggests θ has dual functional roles: top-down modulation and bottom-up synchronization



Left: Stimulus onset engages simultaneous feed-forward and feed-back streams. Superficial γ packets carry fine-grained bottom-up information, whereas traveling θ carries broad top-down information.

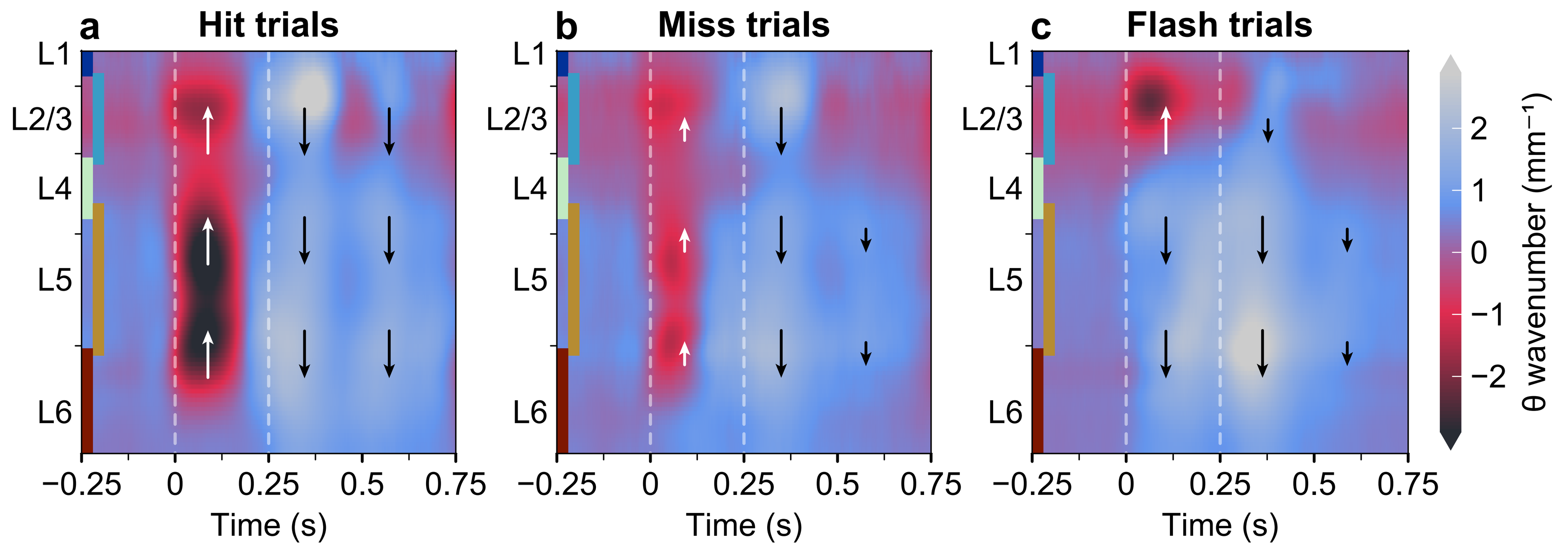
Right: Stimulus offset is dominated by coherent γ packets synchronized to θ. This feed-forward θ may provide windows of bottom-up quiescence to prevent the featureless stimulus from interfering with ongoing higher-order processes.



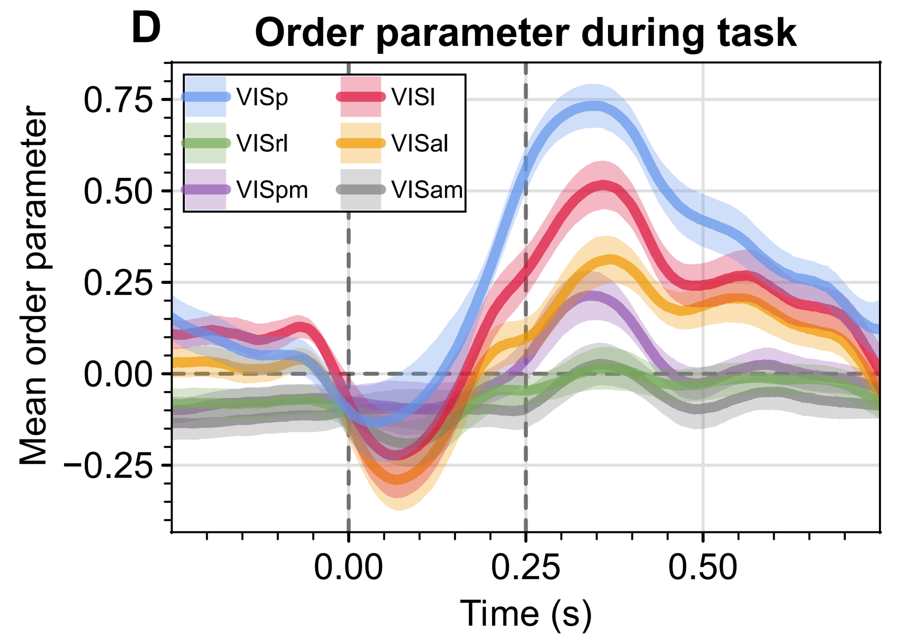
3 | θ travels between layers in bidirectional waves

θ travels from deep layers to superficial layers after the onset of the stimulus, and from superficial to deep layers after stimulus offset. θ propagation coherence is strongest when the mouse correctly identifies changes in the stimulus (balanced accuracy 0.65±0.11, median ± IQR across sessions, 5 folds, 20 repeats, $p < 10^{-13}$).

Below: θ wavenumbers across time and cortical layers for hit (**a**), miss (**b**), and flash (**c**) trials.

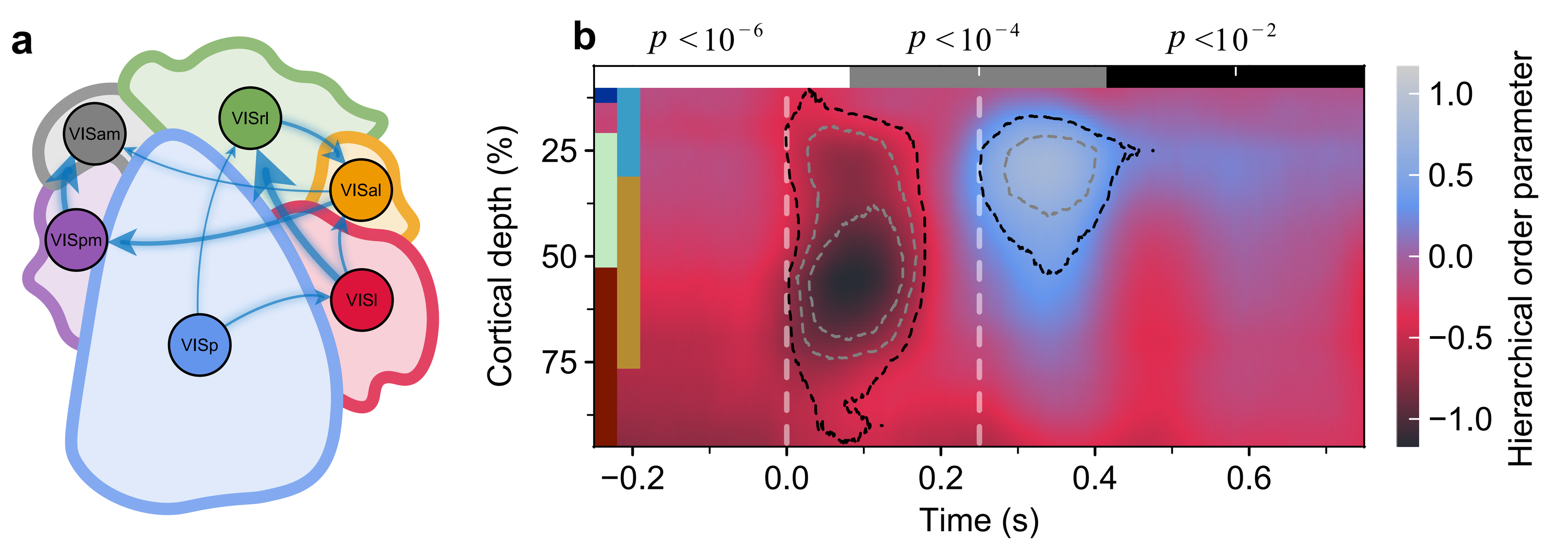


Right: θ order parameters, which measure the average direction of θ propagation, across trial time periods and visual areas (**d**). The order parameter shows the bidirectional pattern of θ is strongest in lower-order visual areas. In particular, the order parameter following stimulus offset has a group-level correlation −0.54 with hierarchical scores (Kendall's τ, $p < 10^{-6}$, 95% CI=[−0.57,−0.50]).

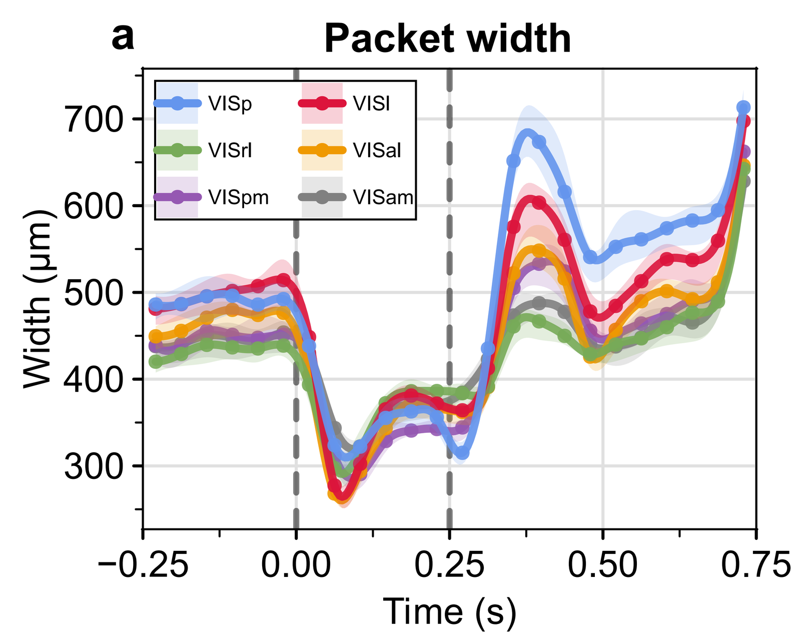


4 | Bidirectional θ travels across the visual hierarchy

Below: Comparing anatomical hierarchical scores (**a**) to θ phases shows that θ tends to travel toward lower visual areas (feed-back, red) in deep layers after stimulus onset, and toward higher areas (feed-forward, blue) in superficial layers following offset (**b**).

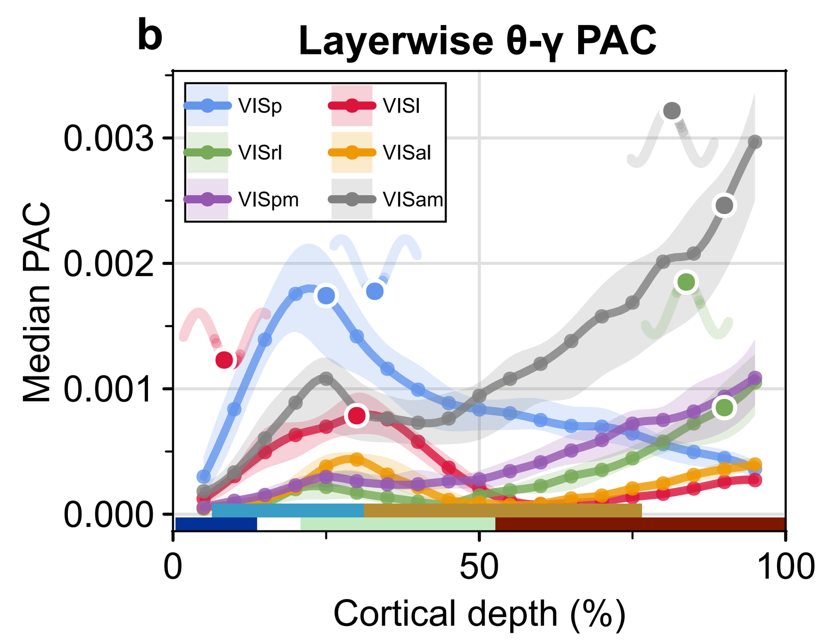


5 | θ modulates localized γ packets



Left: γ packets are highly localized after stimulus onset (**a**), but broaden after stimulus offset. Packet width after offset decreases along the hierarchy (group-level median Kendall's τ = −0.28, 95% IQR [-0.33, -0.21], $p < 10^{-6}$).

Right: γ packets are locked to θ waves, particularly in supragranular layers of lower-order areas and infragranular layers of higher areas (**b**). γ packets in superficial layers prefer θ troughs, whereas deep layers prefer peaks.



References

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2. Xu et al., *Interacting spiral wave patterns underlie complex brain dynamics and are related to cognitive processing*, Nat. Hum. Bev. (2023).
3. Meyerolbersleben et al., *Anatomically resolved oscillatory bursts reveal dynamic motifs of thalamocortical activity during naturalistic stimulus viewing*, Neuron (2025)
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