Phase reorganization leads to diverse β-LFP spatial wave patterns in motor cortex during movement preparation

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1: *Transient* β-LFP wave events occur during movement preparation

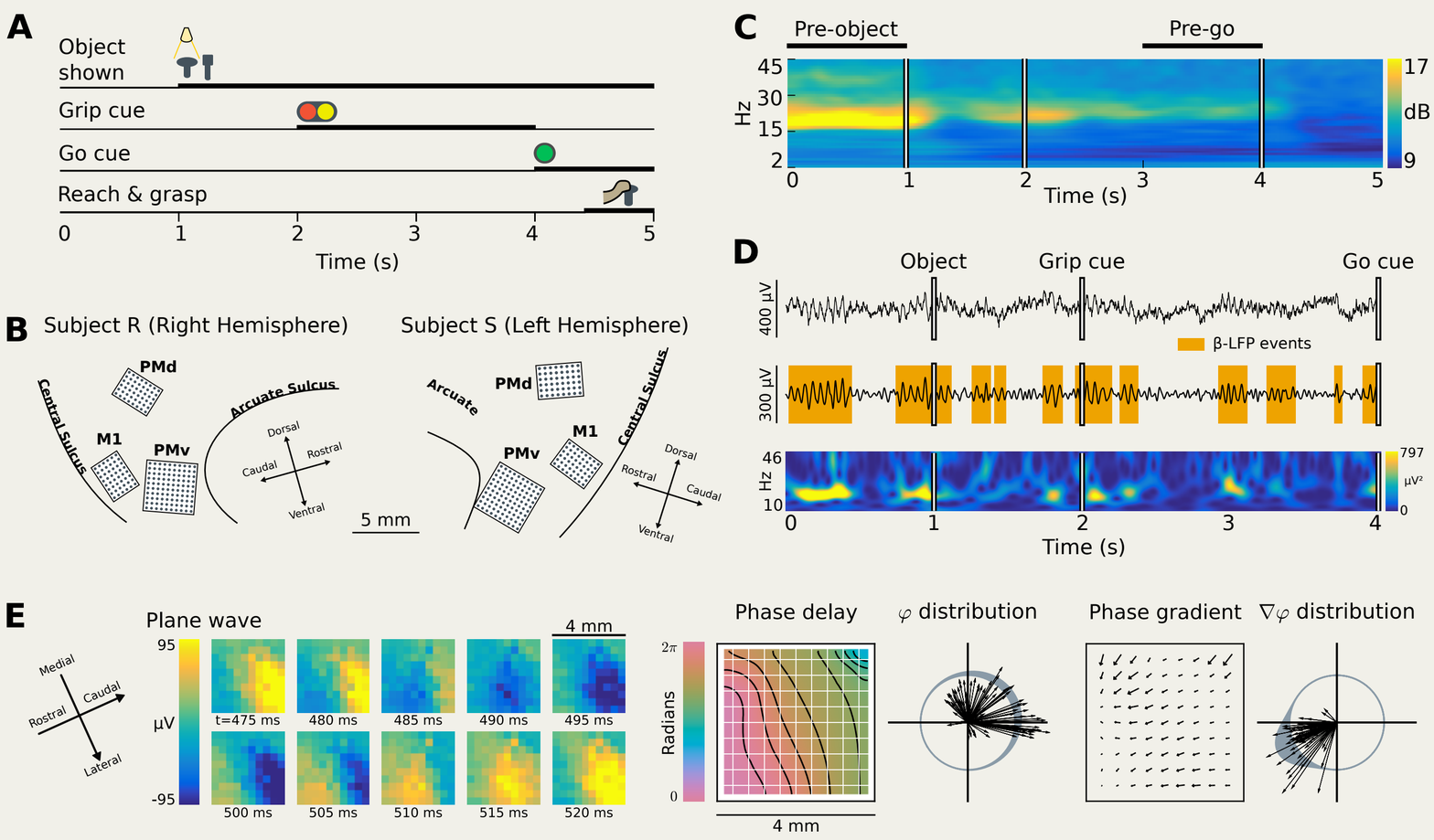

Figure 1. **A** We study the neural dynamics of movement preparation using a cued-reaching and grasping task with instructed delays. **B** Spatiotemporal β-LFP activity was recorded in motor areas M1, PMv, and PMd, in rhesus macaques (two subjects, R and S). **C** Trial-averaged β-LFP is elevated during preparatory steady-states (e.g. subject S). **D** Single-trial β-LFP activity is variable and transient. **E** β-LFP transients are known to organise as travelling waves along the rostro-caudal axis (**? ? ?**).

2: Multiple underlying mechanisms can explain travelling waves

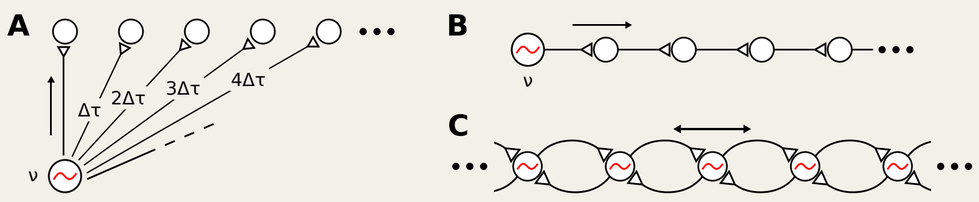

Figure 2. Redrawn from (**?**).

A Anatomical conduction: β-LFP oscillations may propagate from a common source with varied delays. **B Excitatory waves:** Waves may propagate as travelling waves in an excitable medium. **C Coupled oscillators:** Phase gradients in local β-LFP oscillations can create apparent waves.

3: Wave patterns are *diverse*, not fixed

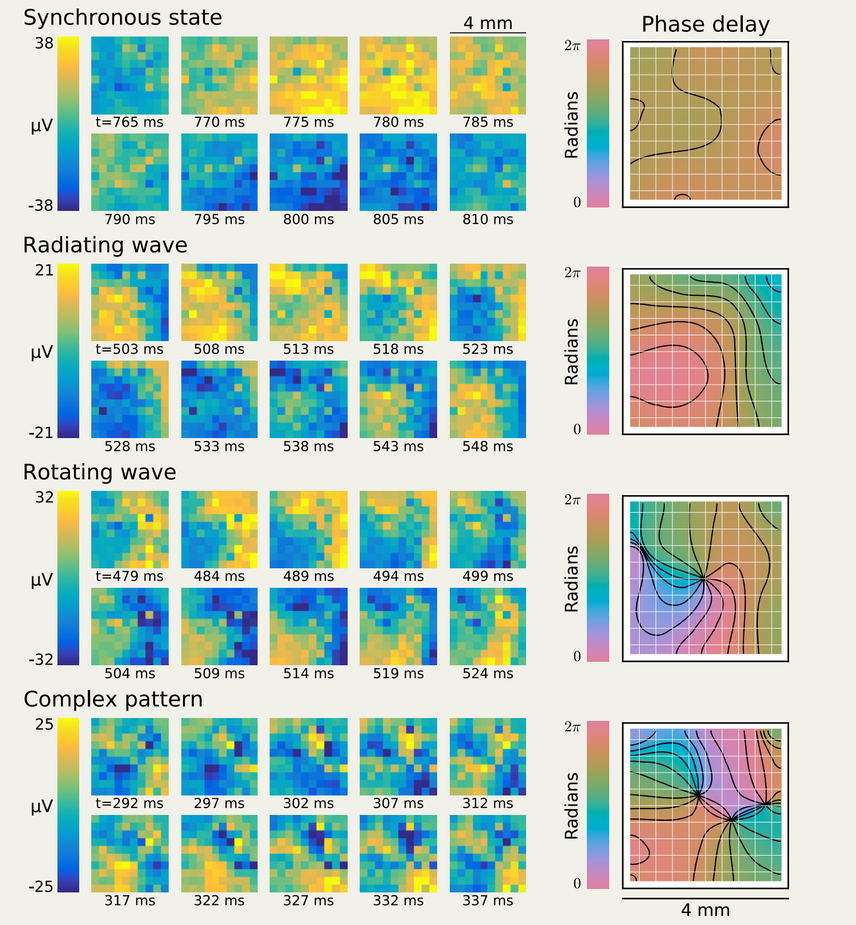

Figure 3. Example β-LFP wave events from area PMv of subject S.

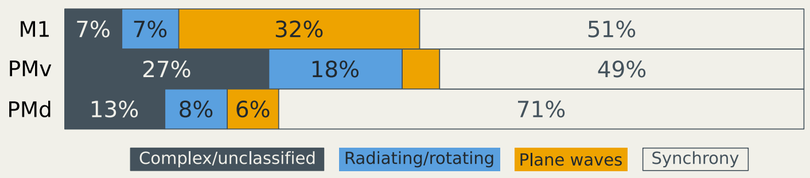

Figure 4. Synchrony, radiating, rotating, and complex patterns are prevalent in preparatory steady-states (subjects R, S combined).

The observed pattern diversity is incompatible with fixed anatomical conduction delays: zero-lag spatial phase synchrony, rotating, and complex wave patterns cannot be explained in terms of β oscillations propagating from a common source with varying delay.

4: β waves differ from travelling waves

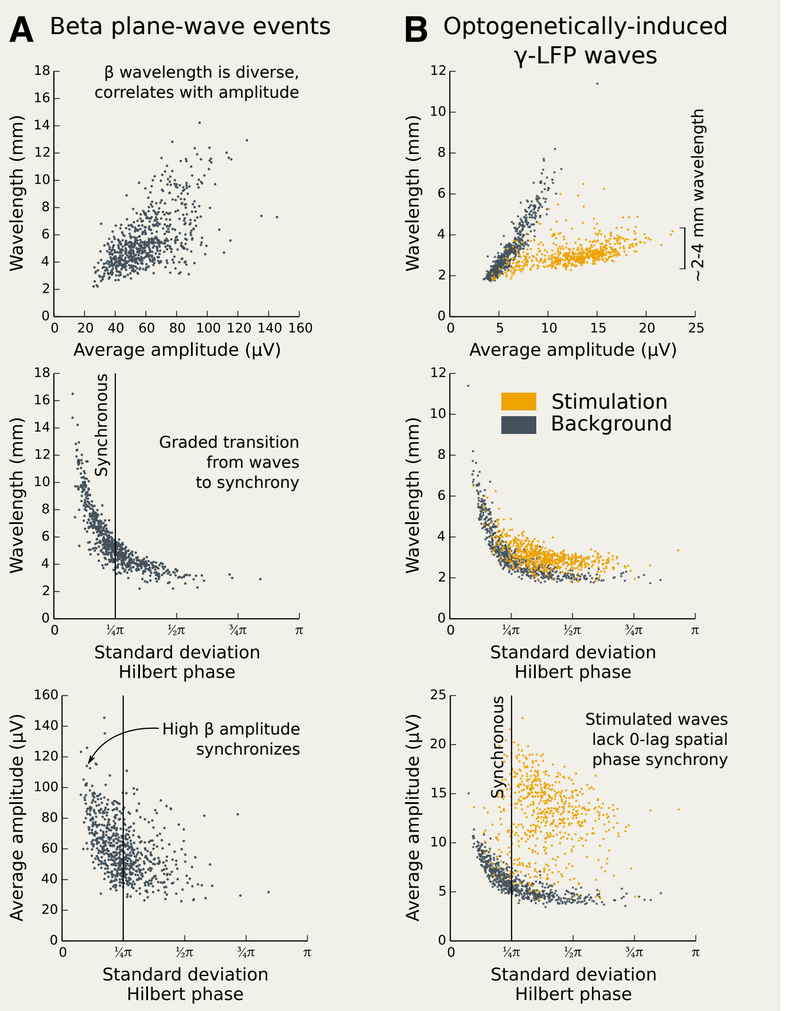

Figure 5. **A** β wavelength increases with amplitude, & high-amplitude events are more synchronous. **B** Optogenetic stimulation induces true travelling γ-LFP waves (**?**) with characteristic ∼2-4 mm wavelength that desynchronise γ-LFP.

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5: Single neurons show *sustained* β-rhythmic spiking at diverse frequencies (?)

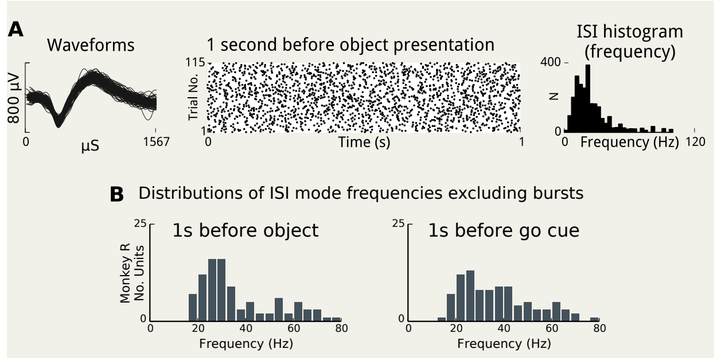

Figure 6. 90% (264/292) of neurons that fired during delays exhibited β-rhythmic spiking (e.g. **A** subj. S, PMd), suggesting that coupled-oscillator dynamics may explain the diverse & transient nature of β-LFP waves. **B:** Mode firing-frequencies do not exhibit a single frequency, but are broadly distributed between approximately 15 and 45 Hz (e.g. Subj. R).

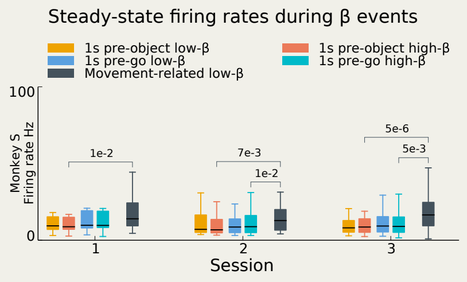

Figure 7. Unlike β suppression related to movement (grey bars), β-LFP amplitude transients during preparatory steady-states are not associated with changes in the underlying single-neuron firing frequencies. (e.g. subj. S).

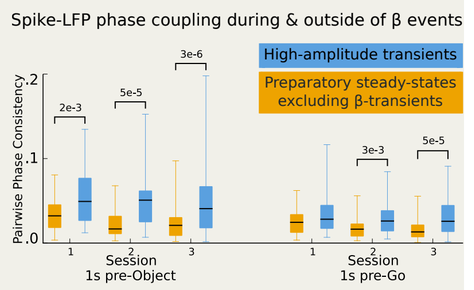

Figure 8. Single neurons are weakly coupled to β-LFP during delay periods. No significant phase coupling exists outside of transient events, but there is a small statistically significant increase in spike-field phase coupling during β-LFP transients (e.g. subj. S).

6: Heterogeneous frequencies → phase reorganisation → diverse β transients

- Unlike previous studies, which found travelling waves & posited directed information transfer, we find:
  1. ***Diverse*** waves that cannot be explained by anatomical conduction delays
  2. **Transient** variations *in both spatial patterns and wavelengths* that differ from travelling waves
  3. Coexistence with ***sustained*** β-rhythmic single neuron firing, despite weak spike-LFP phase coupling

Conclusion: Spatiotemporal dynamics in β-LFP do not reflect only signal conduction: they also reflect ongoing reorganisation of coupled oscillatory populations.

Conjecture: Frequency diversity encodes planned and upcoming actions (**?**). This diversity limits phase coupling of neurons to a single common β-LFP frequency, which necessarily gives rise to diverse β-LFP transients via a mechanism akin to 'beating'.

Future:

- Diverse wavelengths are incompatible with existing models of motor-cortex β-LFP (**?**): modified models are needed.
- The 'beating' theory of β-LFP transients contrasts with the thalamic-input theory of somatosensory β-LFP transients (**?**).
- Reconcile the oscillator hypothesis with the theory that β-LFP waves reflect directed spiking communication.
- Understand the neural mechanisms of preparatory steady-states in motor cortex

References

[1] Takahashi K, et al. Propagating waves in human motor cortex. *Front Hum Neurosci*, 2011.

[2] Takahashi K, et al. Large-scale spatiotemporal spike patterning consistent with wave propagation in motor cortex. *Nat Commun*, 2015.

[3] Rubino D, et al. Propagating waves mediate information transfer in the motor cortex. *Nat Neurosci*, 2006.

[4] Ermentrout GB et al. Traveling electrical waves in cortex: insights from phase dynamics and speculation on a computational role. *Neuron*, 2001.

[5] Lu Y, et al. Optogenetically-induced spatiotemporal gamma oscillations and neuronal spiking activity in primate motor cortex. *J Neurophysiol*, 2015.

[6] Rule ME, et al. Dissociation between sustained single-neuron spiking β-rhythmicity and transient β-lfp oscillations in primate motor cortex. *J Neurophysiol*, 2017.

[7] Vargas-Irwin CE, et al. Linking objects to actions: Encoding of target object and grasping strategy in primate ventral premotor cortex. *J Neurosci*, 2015.

[8] Heitmann S, et al. A computational role for bistability and traveling waves in motor cortex. *Front Comput Neurosci*, 2012.

[9] Sherman MA, et al. Neural mechanisms of transient neocortical beta rhythms: Converging evidence from humans, computational modeling, monkeys, and mice. *PNAS*, 2016.