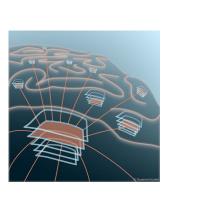
Long-range coordination patterns in cortex change with behavioral context

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Question

- Neural networks within a cortical area comprise a large number of neurons that mostly form short-range connections [1].
- Yet, neural activity is found to be confined to low-dimensional manifolds [2] which requires strong coordination also between distant neurons that are most likely unconnected.
- → Which dynamical mechanism causes such long-range neural coordination patterns?

Answer

Using tools from statistical physics of disordered systems [3,4,5,6,7], we show that networks can operate in a "dynamically balanced critical state", where pairs of neurons interact via a multitude of parallel paths through the network, giving rise to long-range covariances between individual neurons despite short-range connections [8]. This mechanism for long-range cooperation is not imprinted in specific connectivity structures but can change over time in a state-dependent manner, which we demonstrate in macaque motor cortex.

References

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Experimental Observations: macaque motor cortex activity during rest and a reach-to-grasp task

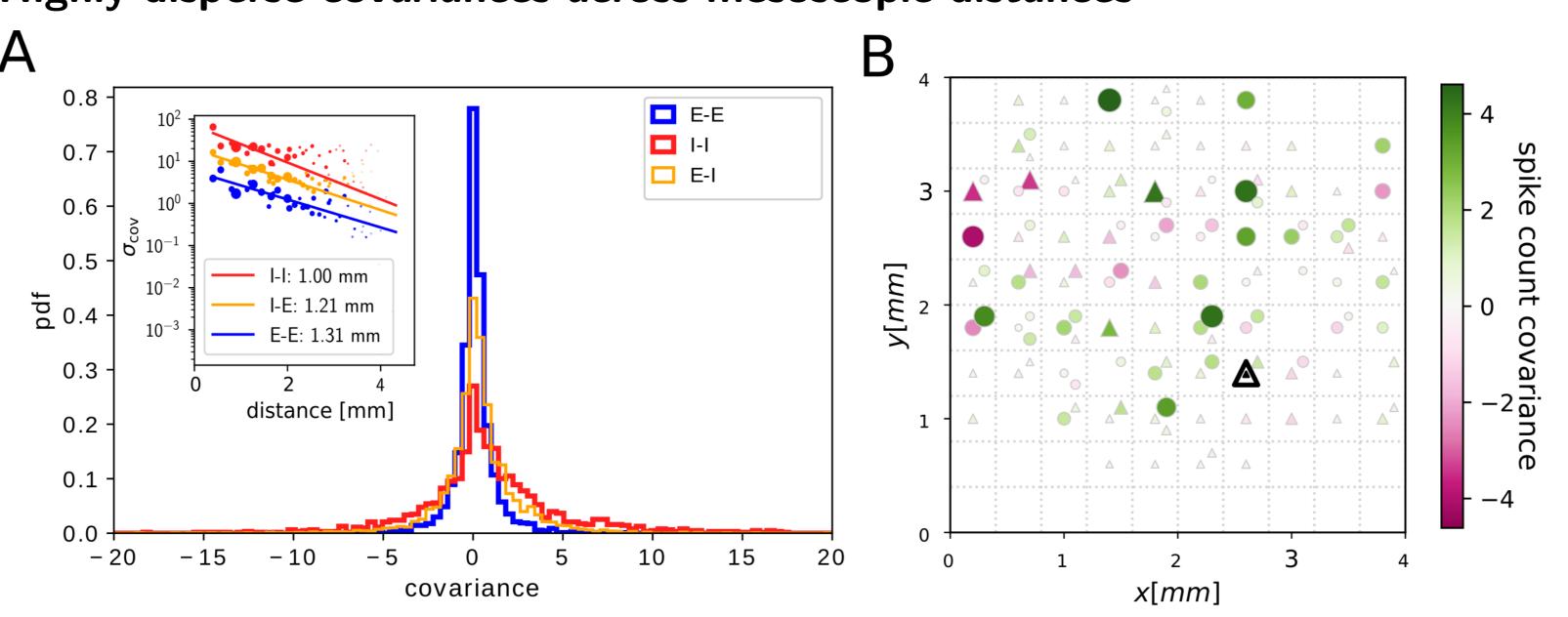
Setup

- 10×10 Utah electrode array in macaque motor cortex ($4 \times 4 \,\mathrm{mm}^2$)
- Resting state (RS) and reach-tograsp task (R2G) [9]
- Spike sorting into putative excitatory
 (E) and inhibitory (I) neurons
- Binning of spike trains (RS: 1s, R2G: 200 ms)
- → Spike-count covariances:

 $c_{ij} = \langle n_i n_j \rangle - \langle n_i \rangle \langle n_j \rangle$



Highly disperse covariances across mesoscopic distances



Which mechanisms give rise to the large dispersion of covariances? Does the long-range coordination rely on long-range connections?

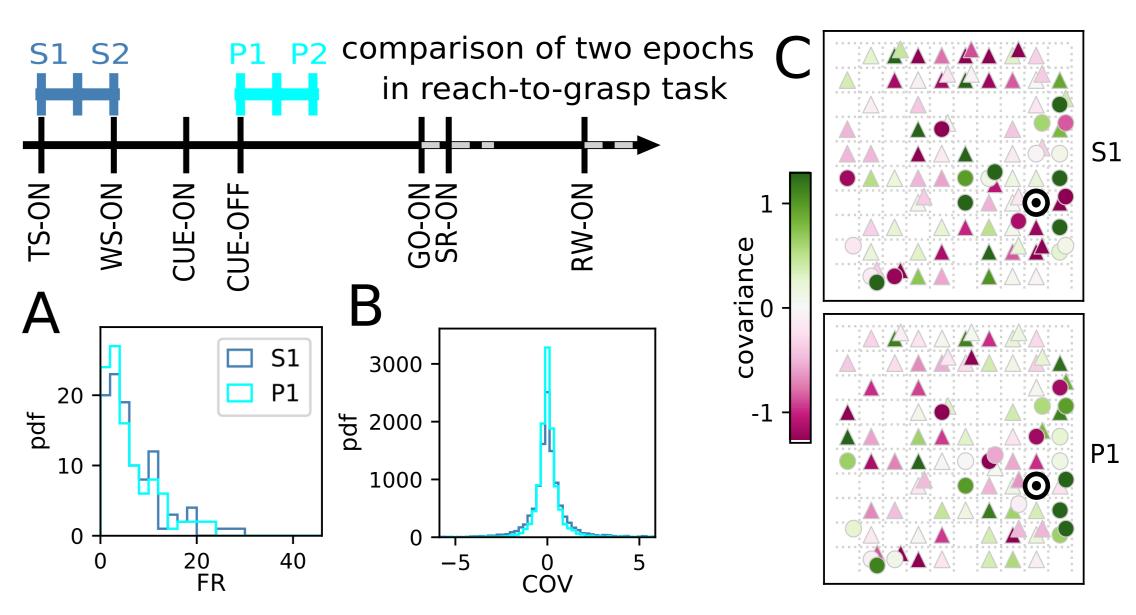
Covariances are:

- low on average
- large (negative and positive)
 for individual neuron pairs (across all distances)

Exponential decay of width of covariance distribution with decay constants:

- much larger (millimeter scale) than the range of direct connections (~ 300 microns [1])
- similar across neuron types

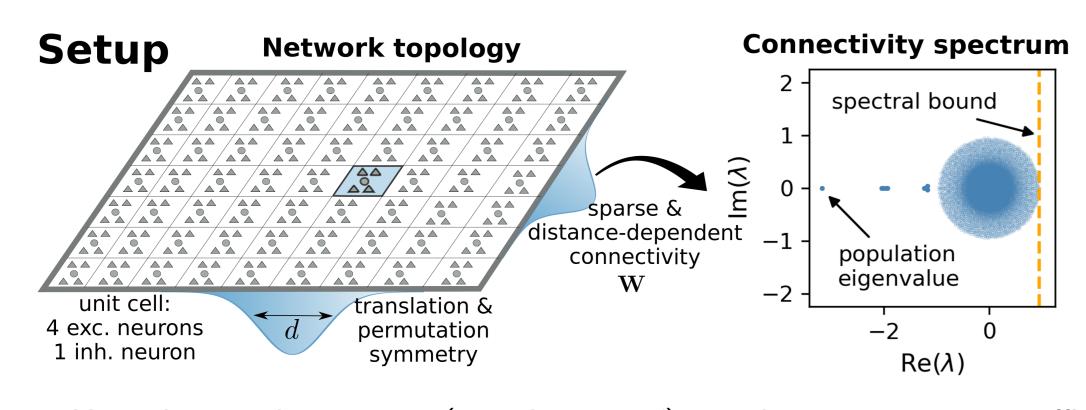
Coordination patterns change with behavioral context



 \bullet Firing rates and covariances have overall similar statistics but largely differ on the individual neuron level (corr. coeffs.: $\rho=0.69$ and $\rho=0.4)$

How are changes in firing rates and covariances related?

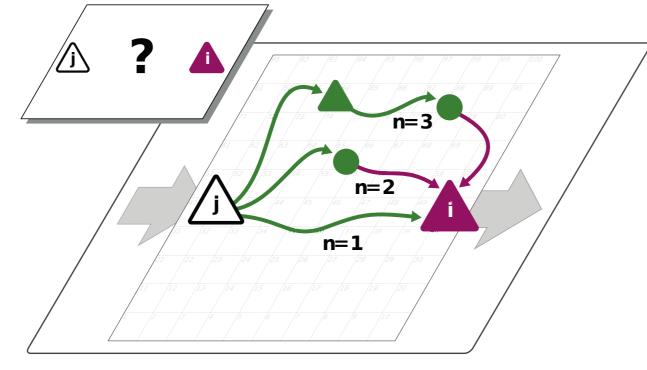
Theory and Simulation: balanced random network model with short-range connectivity



- ullet Hypothesis: short-range (length scale d), random connectivity sufficient to explain experimental observations
- Linear response theory [10,11,12] relates spike-count covariances to the effective connectivity ${m W}$: ${m c} = [{m 1} {m W}]^{-1} {m D} [{m 1} {m W}]^{-T}$

There is a critical regime [7], where the maximum eigenvalue (spectral bound) $R = \max(\text{Re}(\lambda)) \lesssim 1$

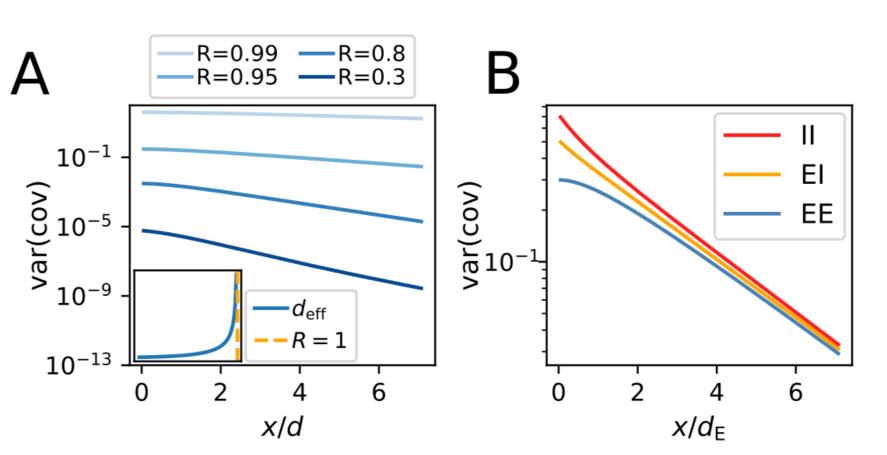
Interactions via indirect connections



- ullet Neuronal interactions are not only mediated via direct connections, but also via indirect paths: $[{f 1}-{m W}]^{-1}=\sum_{n=0}^\infty {m W}^n$
- \rightarrow larger reach and superposition of contributions from excitatory and inhibitory neurons

In the critical regime, covariances are dominated by multi-synaptic interactions

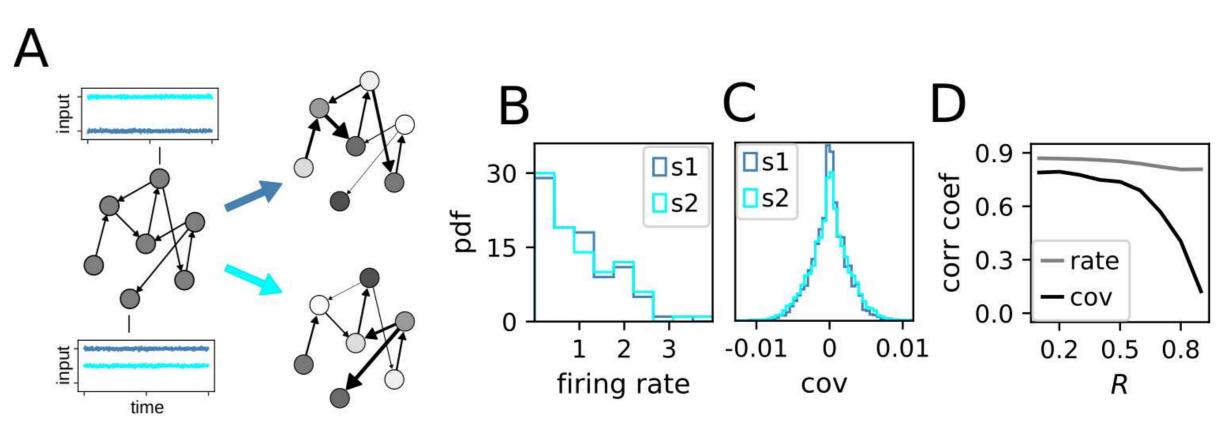
Decay of covariances depends on spectral bound



ullet Beyond mean-field theory for spatially organized random E-I networks: ullet exponential decay of variance of covariances on length scale $d_{\rm eff}$, determined by spectral bound $d_{\rm eff}/d \sim \sqrt{R^2/(1-R^2)+{
m const.}}$

Length scale of covariances diverges at critical point $R \to 1$

Covariance patterns depend on effective connectivity of network states



- ullet Anatomical connections + firing rates o effective connections
- ightarrow Effective connectivity is dynamic \Rightarrow covariance patterns are dynamic

In the critical regime, small changes in firing rates induce large changes in covariances

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