Dynamic causal communication channels between neocortical areas

Summary: Dynamic pathways of information flow between distributed brain regions underlie the diversity of behaviour. However, it remains unclear how neuronal activity in one area causally influences ongoing population activity in another, and how such interactions change over time. Here we introduce a causal approach to quantify cortical interactions by pairing simultaneous electrophysiological recordings with neural perturbations. We found that the influence primary visual cortex (V1) and higher visual area LM had on each other was surprisingly variable over time. Both feedforward and feedback pathways reliably affected different subpopulations of target neurons at different moments during processing of a visual stimulus, resulting in dynamically rotating communication dimensions between the two cortical areas. The influence of feedback on V1 became even more dynamic when visual stimuli were behaviourally relevant and associated with a reward, impacting different subsets of V1 neurons within tens of milliseconds. Importantly, these fast timescales of change in communication were in stark contrast to, and could not be explained by, the much slower dynamics of activity in either cortical area. To understand the function of dynamically rotating communication dimensions, we used a linear dynamical system to model the population activity in V1 in terms of its local recurrent dynamics and external inputs. We found that the fast rotation of the feedback communication dimension momentary aligned these long-range influences with local dynamical modes and with the visual input. This created a selective, transient time window for integrating visual information with the feedback input. Interestingly, we found that only during this brief (<100 ms) time window, the feedback input to V1 was relevant for decision making in a visual discrimination task. In summary, using a causal method for measuring long-range cortical interactions, we found that communication subspaces between visual areas are dynamically rotating. This rotation leads to momentary alignments of external inputs and local dynamics, and results in the formation of transient windows for integration and decision making.

Background and questions: Despite decades of research on communication in the brain, we know surprisingly little about how neuronal activity in one area influences activity in another. The main reason is that inter-areal interactions in the neocortex have so far been inferred from statistical relations of simultaneously recorded neural activity in different areas. However, inferring cause-effect relationships from activity statistics is inherently ambiguous, and therefore the existing analytic methods can not capture how brain areas causally influence each other (Das and Fiete, Nat. Neurosci. 2020; Reid et al., Nat. Neurosci. 2019). Therefore, it is still unclear to what degree causal inter-areal communication can be flexibly regulated and how it might change over time or in different behavioural contexts.

Methods: We developed a causal approach to measure long-range cortical communication, using simultaneous electrophysiological recordings and locally targeted and transient optogenetic silencing of anatomically interconnected regions (Fig1A). Using linear discriminant analysis, we identified the dimensions along which the local population activity of each area changed when silencing the activity in the other area. These dimensions, capturing the causal influence of distributed neural populations on each other, were termed communication dimensions (Fig1B). Furthermore, by varying the onset time of optogenetic perturbation, we were able to track the dynamics of interareal communication over time (on timescales of tens of milliseconds). We quantified both feedforward communication (the influence of V1 on activity inLM) and feedback communication (the influence of LM on V1 activity) in mice engaged in a visual discrimination task (Fig1A).

Results: We measured communication dimensions between V1 and LM at different time points and quantified their similarity over time using pairwise dot products. We found that these similarities decay over time with time constants of around 100 ms. We showed that this fast decay cannot be accounted for by the temporal dynamics of population activity in either area or trial-to-trial noise. This indicated a rotation in communication dimensions over time. Moreover, we found that the feedback communication dimension, specifically, rotated at much faster rates when the visual stimulus was coupled to a reward and therefore behaviourally relevant (Fig1C).. What function do such fast rotations of communication subspace serve? Cortical feedback is thought to be involved in the modulation of cortical responses according to the context *(Briggs, F. Annu. Rev. Vis. Sci. 2020),* and we find that the behavioral context selectively controls the rotation speed of feedback communication dimensions. This suggests a potential role of subspace rotations in sensory processing. To assess this role, we used a Poisson linear dynamical system to distinguish the contributions of local dynamics, visual input, and feedback influences to shaping visual responses in V1. To understand how external inputs - such as feedback from LM - interact with local dynamics, we examined the alignment of their influence with the dynamical modes of the V1 network. These analyses revealed transient alignment of LM feedback influence with visual inputs and specific dynamical modes of V1, only during the time window in which LM feedback on V1 was relevant for decision making.

Conclusion: We characterized the causal influence of two visual cortical areas on each other, and found a novel principle of cortical communication: communication subspaces between visual cortical areas dynamically rotate. These rotations serve to momentarily align long-range influences with other inputs and local dynamics and form brief time windows of computation that are critical for behavior.

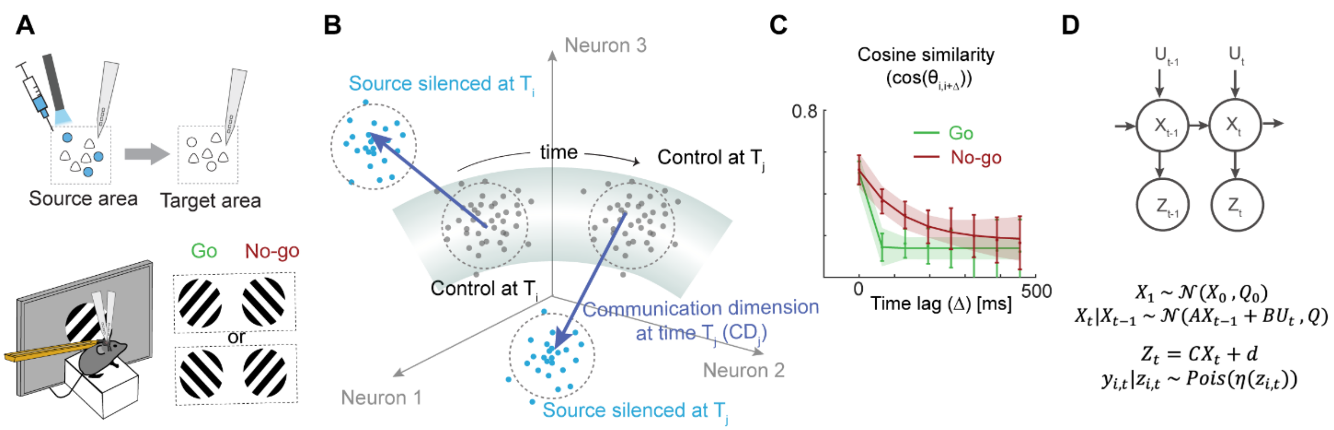

Figure 1 - A, *Experimental design.* ***B,*** *Population analysis framework, describing the causal influence of a source on a target area using communication dimensions.* ***C,*** *The similarity of feedback communication dimensions decays over time (indicative of the dimensions rotating over time) at a rate that depends on the contingency of the visual stimulus. The green and red curves correspond to Go and No-go trials respectively.* ***D,*** *The Poisson linear dynamical system used to model V1 population activity.* X_t *denotes the state at time* t*, and* $y_{i,t}$ *the activity of neuron* i *at time* t*.*