

Stimulus onset quenches neural variability: a widespread cortical phenomenon

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A major goal of neuroscience is system identification: the brain is probed with repeated ‘trials’, and its dynamics are inferred from recorded responses (typically spikes). Most often, the mean across-trial response is all that is considered. By averaging, the experimenter hopes to combat the apparent noisiness of spiking, and estimate ‘the underlying firing rate’ of the neuron. However, one must presume that the underlying rate may differ across supposedly-identical trials, as indicated by optical-imaging studies (Arieli et al., 1996). Yet such variability usually remains a hidden dimension of the data, its presence inferred only when it correlates with behavior. Rarely is it considered that the rate variance might contain temporal structure comparable to that of the mean rate. However, such structure is expected for a variety of dynamics. Attractor networks may show declining variability as the network overcome initial variability. Integrator networks may show increasing variability as noisy signals are integrated. In fact, when distinguishing between candidate classes of dynamics, rate variability can be more informative than mean rate.

We investigated rate variance in seven cortical areas. We employed classical and newer mathematical methods for assessing variance, including an adaptation of the Fano factor and two variants of factor analysis. Critically, these methods can determine when an experimentally-observed change in variance is due to changes in underlying-rate variance, rather than changes in spiking regularity. This is essential, as spiking regularity can change with firing rate (e.g., due to refractoriness). Across all seven cortical areas, we found one remarkably consistent effect: stimulus onset drove a decline in underlying-rate variability.

The decline in variability occurred over a wide range of circumstances: during responses to simple sensory stimuli (sine-wave gratings for V1), during operantly-conditioned responses (reach targets for PRR and PMd), during reward-driven responses (OFC), under anesthesia (V1), during passive viewing (V4), and during active task performance (PRR, PMd, LIP, and MT). This decline may indicate that attractor dynamics are a prevalent feature of cortex. Alternately, it has recently been argued that a general feature of large recurrent networks is a tendency to produce chaotic spontaneous activity that is suppressed by an input (Rajan, Abbott & Sompolinsky, unpublished). Consistent with both interpretations, neural variability declined even when there was little change in mean rate. This observation underscores that a ‘non-responsive’ average rate can obscure robust responses on individual trials.

We further investigated trial-by-trial variability using an extension of factor analysis (GPFA, Yu et al., NIPS 2008) to reconstruct single-trial ‘neural trajectories’. Trajectories were initially variable, then converged to a common trajectory following stimulus onset. Taken together, our results indicate that a common property of cortical circuitry is that it is stabilized by an input. That said, we expect cortex to exhibit a variety of dynamics – yielding a variety of variability ‘signatures’ – under different circumstances (e.g., Churchland, Kiani & Shadlen, SFN 2006). Measurements of variability, and the reconstruction of single-trial responses, should be central to investigating those dynamics.