Model of MT spike count variability accounts for state-dependent tuning disparities

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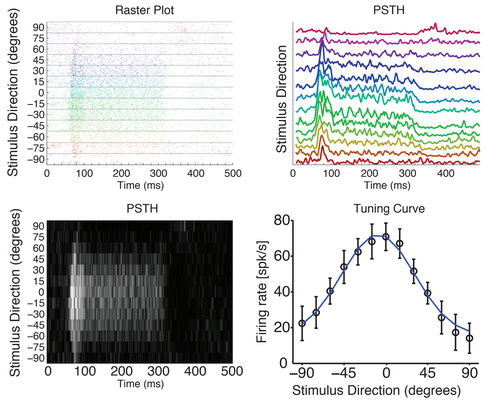
Summary

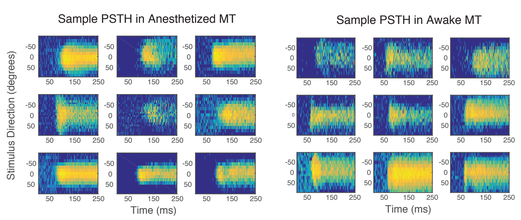
Sensory neurons have variable responses to repeated presentations of the same stimulus. The structure of this trial-to-trial variability within a population directly affects the ability to decode stimulus identity. We compared the spike-count variability of macaque MT neurons in both the awake and anesthetized state, finding a state-dependence of variability and variability tuning. In the anesthetized state, the data is well modeled by a Poisson process with variable multiplicative gain. This model predicts a variance to mean ratio, or Fano factor (FF), that is strictly increasing with spike count. However, in the awake state, inverted Fano factor tuning is observed, with decreasing FF at higher spike counts at preferred directions of motion. We developed a unified model of spike count variability that captures the U-shaped Fano factor tuning observed in the awake state, as well as the super-Poisson variability observed in the anesthetized state. In our model, the state-dependent FF tuning changes are mediated by a switch from a low gain fluctuation state in the awake state to a higher gain fluctuation state when anesthetized.



Experimental Methods

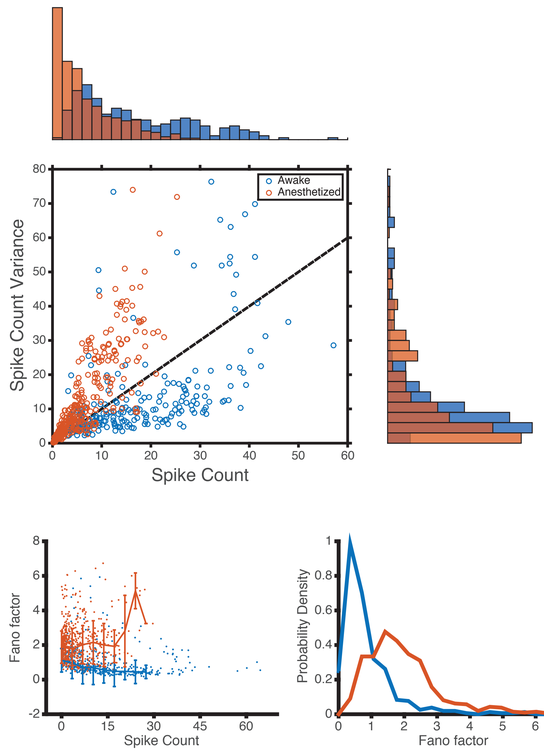
Neural data: Extracellular spikes were recorded in vivo from both anaesthetized paralyzed macaques and awake fixating macaques. A total of 80 single units were collected in cortical area MT/V5 during visual stimulation.

Stimuli: Smoothly translating random dot textures behind a stationary aperture presented in the receptive field of the recorded neurons. Stimulus was optimized in size and speed for each cell. Stimulus direction was randomly chosen from 13 or 24 directions in 15° increments around the preferred direction.



MT Response

- Responses exhibit gaussian tuning curves relative to stimulus direction
- Shape of responses is the same in awake and anesthetized states.
- Mean response of MT neurons decreases under anesthetsia



Spike Count Variance

- The variance of neural responses depends on such factors as attention, stimulus presentation, and conscious state.
- MT neurons in awake macaques exhibit a significantly lower Fano factor than in the anesthetized state.
- Firing in anesthetized state is super-poisson, increasing with spike count
- Firing in awake state is sub-poisson, decreasing with spike count
- Fano factor in anethetized state is consistent with Poisson mixture model, but awake state is not.

Fano Factor Tuning

- Many cells in awake MT exhibit a Fano factor that is tuned to stimulus direction.
- Fano factor has a distinct U- or M-shaped tuning: lower for preferredmotion direction and increasing for orthogonal directions
- This stimulus-dependence of variance is diminished or absent for anesthetized MT cells.
- The Fano factor tuning for individual neurons can be quantified with a tuning index.

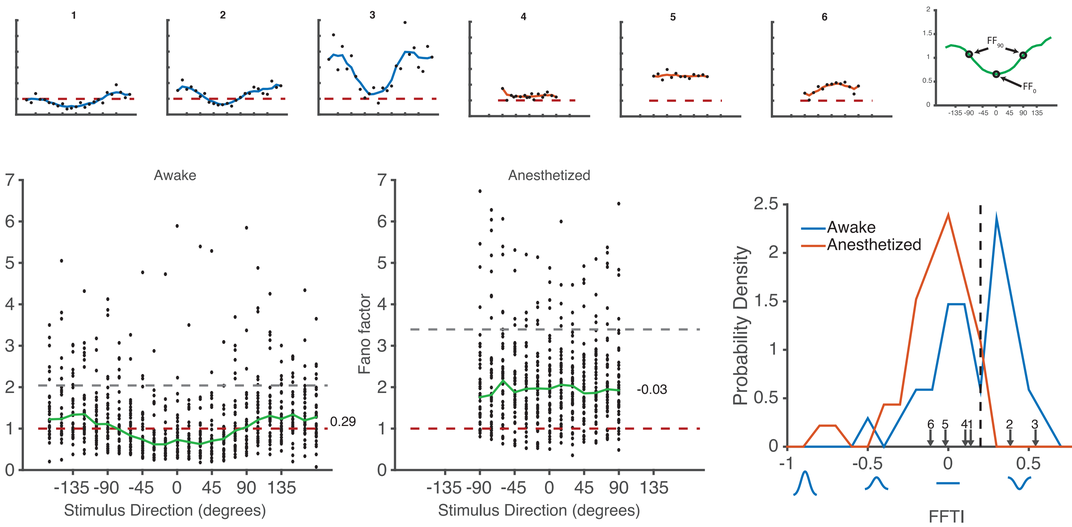
$$\mathrm{FF} = \frac{\mathrm{var}(x)}{\langle x \rangle}$$

$$\mathrm{FFTI} = \frac{\mathrm{FF}_{90} - \mathrm{FF}_{0}}{\mathrm{FF}_{90} + \mathrm{FF}_{0}}$$

Model

- Variability modeled as arising from two independent sources: an intrinsic variability and input gain fluctuations.
- Intrinsic variability of spike generation is modeled as a normal distribution with a mean μ and variance μ^{α}.
- Input μ is scaled by multiplicative gain.
- Variance of the gain fluctuations and the intrinsic variability parameter α determine spike count variability.

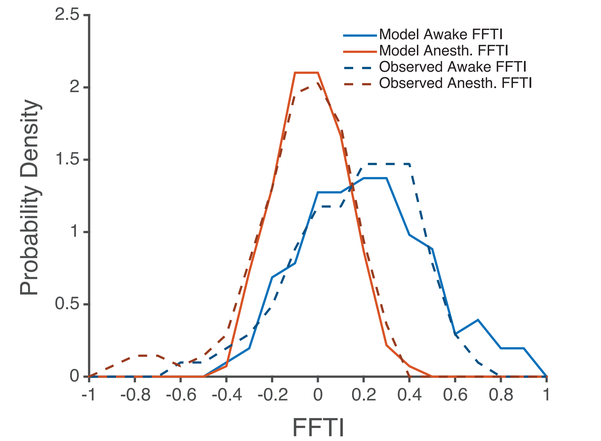
$$x \sim \mathcal{N}\left(\mu, \mu^{\alpha}\right) \qquad \mu = \lambda(\theta) \cdot g$$

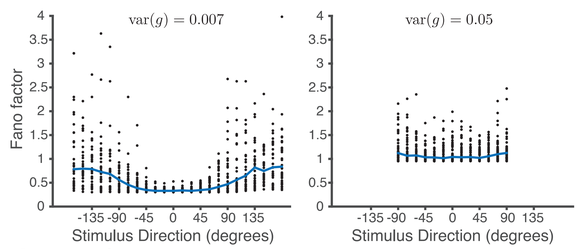


Model Results

- Variance can be decomposed into to two terms reflecting the contributions from intrinsic variability and gain fluctuations.
- These two contributions have opposing effects on the Fano factor tunings of neurons.
- This model can fit the distribution of observed Fano factor tunings
- An increase in the gain fluctuations in the anesthetized state can explain the difference in Fano factor tuning distributions observed.

$$\mathrm{var}(x) \approx \lambda(\theta)^{\alpha} + \lambda(\theta)^{2} \cdot \mathrm{var}(g)$$





Conclusions

- Spike count variability is stimulus-dependent and Fano factor is directionally tuned in MT neurons.
- Anesthesia not only increases variability, but diminishes stimulus-dependence of variability.
- The differences in Fano factor tuning are not attributable solely to differences in firing rate.
- State-dependent changes in Fano factor tuning can be explained by differences in gain fluctuations
- This model may extend to other factors that modulate variability structure and stimulus-dependence

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