Key Note

# Chapter 14: Attention and awareness

## Key note 14B: Normalization- and attention-related neuronal co-variability

In addition to changing cell response strength, attention can also directly alter the variability of firing rates to repeated stimuli. Mitchell et al. (2007) recorded neurons in area V4 as monkeys performed an attention-demanding multiple object tracking task and observed attention-related increases in both the strength and reliability of neuronal responses over trials; attentional modulation of response variance (decrease in the ratio of neuron spike count variance to mean spike count) was larger among inhibitory (median 18.9%) than excitatory neurons (median 7.9%), suggesting the influence of attention on the former may be particularly important in diminishing noise in the neural signal. Attention also affects the response correlation between pairs of neurons. For example, a multi-electrode electro- physiology work showed that attending a single stimulus inside the receptive field decreases (spike-count) correlations for pairs of neurons with overlapping receptive fields (in the same hemisphere), relative to inattention (Cohen and Maunsell, 2009). Attention-driven reductions in spiking covariability or ‘noise correlations’ are assumed to reduce redundancy in signals from populations of neurons (at least for neurons with similar stimulus preferences), and may be more important in modulating the quality of neural representations than changes in response strength alone (Maunsell, 2015; Schmitz and Duncan, 2018).

Normalization models also have implications for attention-driven response correlation between pairs of neurons. For instance, Verhoef and Maunsell (2017) used implanted microelectrode arrays to record spike count correlations in (left hemisphere) V4 of monkeys that were cued to attend or not attend to single or multiple stimuli presented at locations near the neurons’ receptive field. When unattended, the addition of a non-preferred stimulus alongside a preferred stimulus (stimulus-induced suppression) markedly increased spike-count correlations between pairs of neurons with similar stimulus preferences, but decreased correlations between pairs of neurons with opposite stimulus preferences. However, attending to a preferred stimulus decreased spike-count correlations between pairs of neurons with strong preferences for the same stimulus compared with when attention was directed far from the receptive field, whereas attending to a non-preferred stimulus increased spike-count correlations of pairs of oppositely-tuned neurons. The authors suggested the effects of attentional modulation were a consequence of attention-related elevations in the responses in one population of neurons, which in turn, biased suppressive activity and yielded decreased (preferred) or increased (non-preferred) spike-count correlations according to neuron selectivity. Schmitz and Duncan (2018) argue that normalization mechanisms operate across many brain regions and are likely to account for the effects of visual attention on interarea communication, including, for example, an electrophysiology study with primates that has reported attention-modulated increases in spike count correlations between pairs of neurons in V1 and MT during a motion direction change detection task (Ruff and Cohen, 2016).

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Mitchell JF, Sundberg KA, Reynolds JH (2007) Differential attention-dependent response modulation across cell classes in macaque visual area V4. *Neuron* 55(1): 131–141.

Ruff DA, Cohen MR (2016) Attention increases spike count correlations between visual cortical areas. *Journal of Neuroscience* 36(28): 7523–7534.

Schmitz TW, Duncan J (2018) Normalization and the cholinergic microcircuit: a unified basis for attention. *Trends in Cognitive Sciences* 22(5): 422–437.

Verhoef BE, Maunsell JH (2017) Attention-related changes in correlated neuronal activity arise from normalization mechanisms. *Nature Neuroscience* 20(7): 969–977.