Effects of adaptation on orientation tuning in excitatory and inhibitory neurons in macaque V1 and V2

Daniel J. Thengone, Yunguo Yu, Jonathan D. Victor

Feil Family Brain and Mind Research Institute,
Weill Cornell Medical College, New York, NY 10065

contact: dat2011@med.cornell.edu

33.4100
VSS 2016

Introduction and Motivation

Sensory adaptation utilizes recent stimulus history to modify neuronal response properties to adjust to the ever-changing features of the visual world. To delineate the influence of adaptation on neural and network properties, we investigated its effect on orientation tuning in functionally distinct cell categories (excitatory vs. inhibitory) in V1 and V2 of the macaque.

Methods

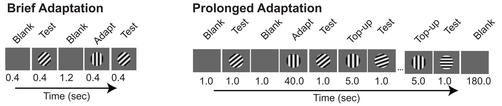
We performed multi-tetrode single-unit recordings to measure neural responses to drifting sinusoidal gratings before and after adaptation to preferred and non-preferred orientations.

Physiological Methods and Recordings

Macaque V1 and V2
Anesthesia: sufentanil and propofol
Neuromuscular blockade: rocuronium

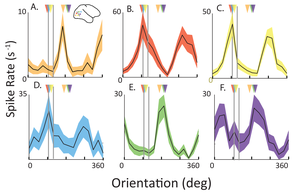
6-tetrode array, each independently movable
Spike sorting (KlustaKwik and Klusters)
Lesions and histology post experiment

Adaptation Paradigms



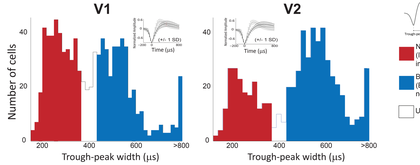
For each recording site, two adaptation experiments are performed, one at 0.4 sec and another at 40 sec duration. These times are chosen to demonstrate adaptation-induced effects in V1 (Patterson et al, 2013).

Selection of Adaptation Parameters



Based on online analysis of tuning measured at six tetrodes, the adapting orientations are chosen. In this example, neural activity at three of six tetrodes have peaks within 22.5 deg of a common direction. Orientations of 90 and 112.5 deg (indicated by vertical bars) are therefore selected for the adaptation experiments. Stimuli are presented at the spatial frequency that is optimal for at least one of the six tetrodes.

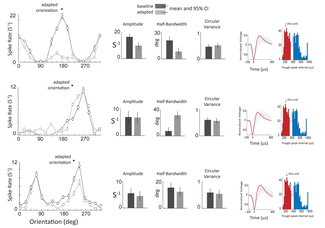
Extracellular wave shape analysis



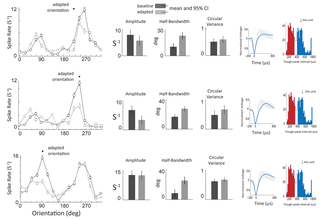
The bimodality in the distribution of trough to peak widths ($p < 0.01$ by the Hartigan dip test) was used to classify extracellular waveforms as narrow-spiking (< 405μs) putative inhibitory interneurons and broad-spiking (> 430μs) putative excitatory neurons (consistent with Mitchell et al., 2007). Neurons within 10% of the notch were labeled unclassified and not used in further analyses.

Single-unit Responses

V1 Supragranular Layer

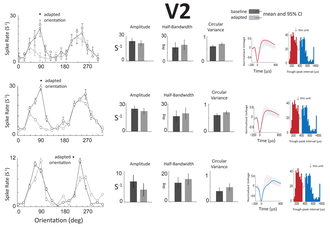


V1 Granular Layer



- Adaptation can induce changes in half-bandwidth, and the tuning curve peak shift can be either towards the adapter (attractive) or away from it (repulsive).
- Layer 4 shows a distinctive behavior: brief adaptation typically broadens the tuning bandwidth, while prolonged adaptation typically narrows it.
- In area V2 (shown below), adaptation both broadens and narrows half-bandwidth in the **inhibitory** units, while the **excitatory** units mostly narrow their half-bandwidths.
- Orientation tuning in the two cell types mostly shifts away from the adapter with brief or prolonged stimulation.

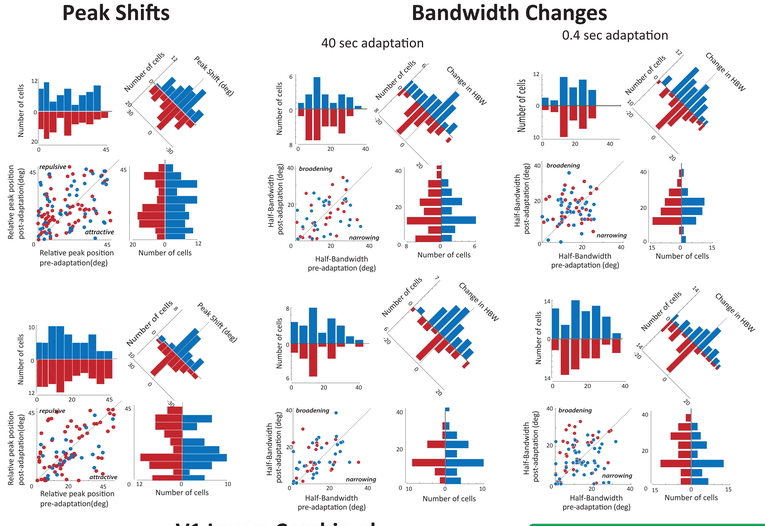
V2



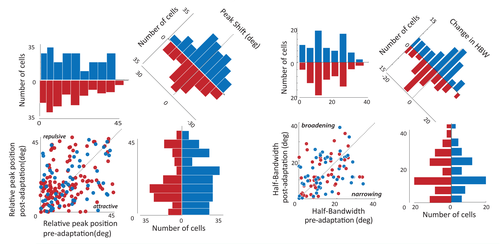
Population Responses

Peak Shifts

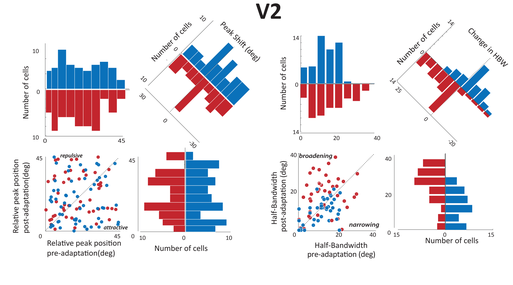
Bandwidth Changes



V1 Layers Combined



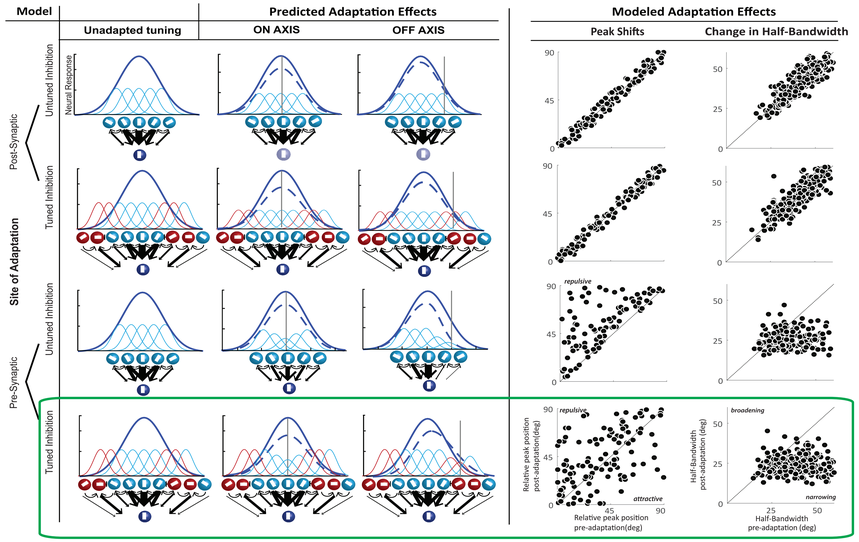
V2



Conclusions

- Excitatory and inhibitory neurons both show adaptive shifts of their orientation tuning curves, for brief and prolonged presentations of the adapting stimulus.
- In the granular layer of V1, brief adaptation of inhibitory celltypes mostly broadens tuning bandwidth while prolonged adaptation typically narrows it.
- In V2, adaptation mostly induces narrowing of orientation tuning in excitatory cells, but can increase or decrease the bandwidth of inhibitory cells. Both repulsive and attractive shifts in tuning are observed in V2.
- Both pre-synaptic adaptation and tuned inhibition are required to account for both repulsive and attractive shifts in tuning, as observed in the data.

Adaptation-induced tuning shifts in models of orientation selectivity



Model Characteristics

Common to all Models

- Feedforward architecture
- 80% excitatory neurons
  20% inhibitory neurons
- Input neuron orientation tuning modeled with von Mises functions
- Tuning function parameters drawn from our neural data
- Output neuron activity modeled as Poisson spike trains

Distinguishing between Models

- Tuned vs. untuned inhibition
- Post-synaptic vs. pre-synaptic adaptation

Adaptation Rules

- Post-synaptic adaptation influences connection strengths of all inputs by a common factor, determined by post-synaptic neuron
- Pre-synaptic adaptation influences connection strengths proportionally to the pre-synaptic unadapted response

	Symbol	Mean	25th percentile	50th percentile	75th percentile
Excitatory Input Neurons					
Half-Bandwidth (deg)	n/a	26.3	20.5	24.5	50.2
Concentration	β_j	1.9	2.6	2.4	0.5
Amplitude (s^{-1})	M_j	11.5	6.2	8.2	29.2
Baseline Firing Rate (s^{-1})	B_j	9.5	3.2	9.5	12.2
Inhibitory Input Neurons					
Half-Bandwidth (deg)	n/a	32.3	18.6	35.5	60.2
Concentration	β_j	1.1	2.8	0.8	0.2
Amplitude (s^{-1})	M_j	12.2	8.4	14.2	35.8
Baseline Firing Rate (s^{-1})	B_j	12.4	7.6	8.5	12.5

Network parameters	Typical	Min	Max
Average number of inputs	1000	100	1000
Fraction of inhibitory inputs	0.2	0.05	0.5
Connectivity Rule width (deg)(σ)	20	5	60
Adaptation strength(α)	0.5	0.1	0.75

Input Neuron (von Mises function)

$$R_{input}(\varphi_{stim}, j) = B_j + M_j e^{\beta_j \cdot \cos(2(\varphi_{stim} - \varphi_j))}$$

Connectivity

$$P_e(j,k) = \frac{1}{K} e^{-(\varphi_j - \varphi_k)^2/2\sigma^2} \quad \textit{excitatory}$$

$$P_{i_{tuned}}(j,k) = \frac{1}{K}\left(e^{-(\varphi_j - \varphi_k)^2/2\sigma^2} + e^{-(\varphi_j - \varphi_k + \pi)^2/2\sigma^2}\right) \quad \textit{tuned inhibitory}$$

$$P_{i_{untuned}}(j,k) = constant \quad \textit{untuned inhibitory}$$

Adaptation Factor

$$f(\varphi_{adapt}, j) = 1 - \alpha\left(\frac{R(\varphi_{adapt}, j) - R_{min}(j)}{R_{max}(j) - R_{min}(j)}\right)$$

$$R_{min}(j) = \min_x(R(\varphi_{stim}, j))$$

$$R_{max}(j) = \max_x(R(\varphi_{stim}, j))$$

Output Neuron

$$R_{output}(\varphi_{stim}, k) = \sum_{allpairs} C(j,k) A(j,k) R_{input}(\varphi_{stim}, j)$$

$C(j,k) = 1$ *with probability* $P(j,k)$ *and 0 otherwise*
$A(j,k) = 1$ *before adaptation*
$A(j,k) = f(\varphi_{adapt}, j)$ *for pre-synaptic adaptation*
$A(j,k) = f(\varphi_{adapt}, k)$ *for pre-synaptic adaptation*

References

1. Abbott, L.F., Varela, J.A., Sen, K., & Nelson, S.B. (1997). Synaptic depression and cortical gain control. Science, 275(5297), 221-224.
2. Dragoi, V., & Sur, M. (2004). Plasticity of orientation processing in adult visual cortex. Visual Neurosciences, 1654-1664.
3. Kohn, A. (2007). Visual adaptation: physiology, mechanisms, and functional benefits. Journal of Neurophysiology, 97(5), 3155-3164.
4. Mitchell, J.F., Sundberg, K.A., & Reynolds, J.H. (2007). Differential attention-dependent response modulation across cell classes in macaque visual area V4. Neuron, 55(1), 131-141.
5. Patterson, C.A., Wissig, S.C., & Kohn, A. (2013). Distinct effects of brief and prolonged adaptation on orientation tuning in primary visual cortex. The Journal of Neuroscience, 33(2), 532-543.
6. Shapley, R., Hawken, M., & Ringach, D. (2003). Dynamics of orientation selectivity in the primary visual cortex and the importance of cortical inhibition. Neuron, 38(5), 689-699.

Support: EY9314
The Fred Plum Fellowship

We thank Mary M. Conte for assistance with poster design and creation.