Adaptation-induced tuning shifts in excitatory and inhibitory neurons of the primary visual cortex

Daniel J. Thengone , Yunguo Yu , Eyal I. Nitzany, Jonathan D. Victor

Brain and Mind Research Institute, Weill Cornell Graduate School of Medical Sciences, New York, NY, 10065

contact: dat2011@med.cornell.edu

Introduction and Motivation

The brain employs a variety of strategies to adjust to changes in the external world. Adaptation is one such strategy, as it modifies responses based on recent inputs. As with other modulatory influences (such as attention) that affect network dynamics, adaptation is likely to involve a broad range of processes at the neuronal level. Here we study how adaptation influences neuronal responses in functionally distinct cortical cell-categories (excitatory vs inhibitory) in two hierarchically-related brain regions, V1 and V2, of the visual pathway.

Methods

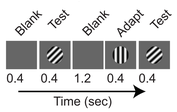
We performed multi-tetrode single-unit recordings to measure neural responses to drifting sinusoidal gratings before and after 400ms adaptation to preferred and non-preferred stimuli

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

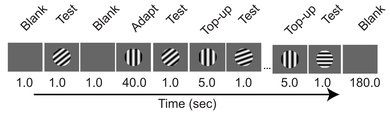
Recordings
6-tetrode array, each independently movable
Spike sorting(KlustaKwik and Klusters)
Lesions and histology performed post experiment

Adaptation Paradigms

Brief Adaptation

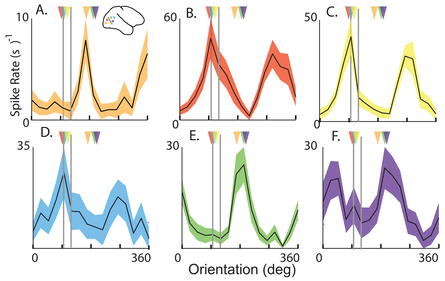


Prolonged Adaptation



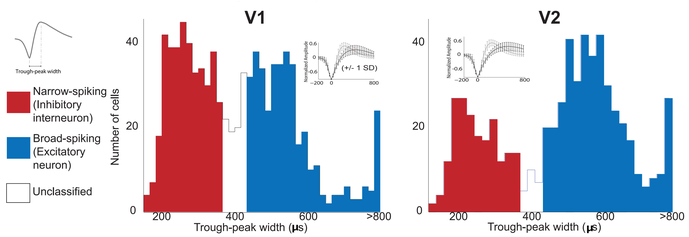
For each recording site, two adaptation experiments are performed, one at 0.4sec and another at 40 sec durations. These times are chosen known to demonstrate adaptation-induced effects in V1 (Patterson et al, 2013).

Selection of Adaptation Parameters



Based on online analysis of tuning measured at 6 tetrodes, the adapting orientations are chosen. In this example, neural activity at 3 of 6 tetrodes have peaks within 22.5 degrees of a common direction. The vertical bars (a 90 and 112.5) are therefore selectected for adaptation experiments. Stimuli are presented at the spatial frequency that is optimal for at least one of the six tetrodes.

Extracellular wave shape analysis



Based on the bimodality in the distribution of trough to peak widths ($p < 0.01$ by the Hartigan dip test), we classified 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. For the data collected in this study the same criteria were utilized to classify the two functionally distinct cell-types.

References

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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.
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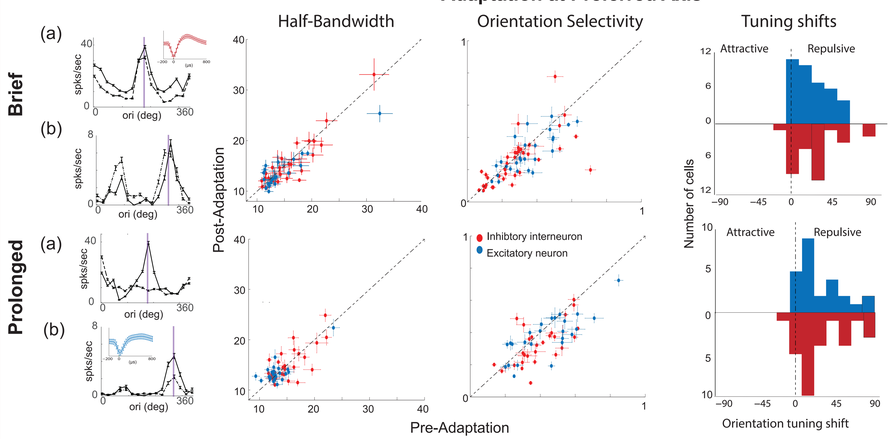
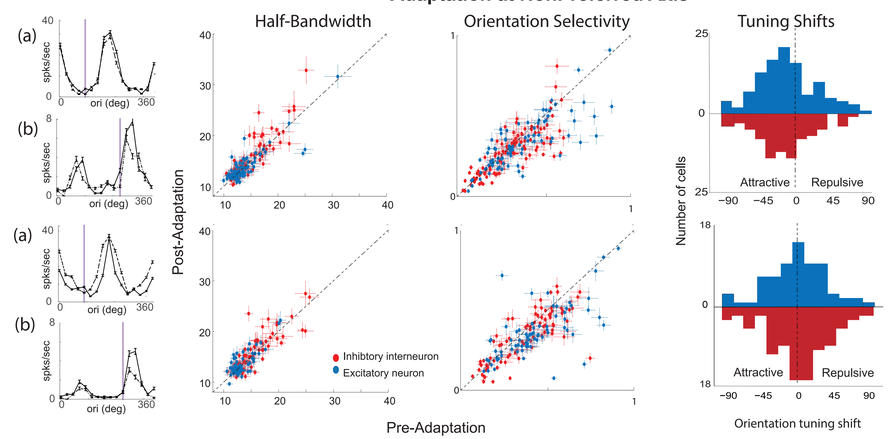
Population Results

Cortical Area V1 Supragranular Layers

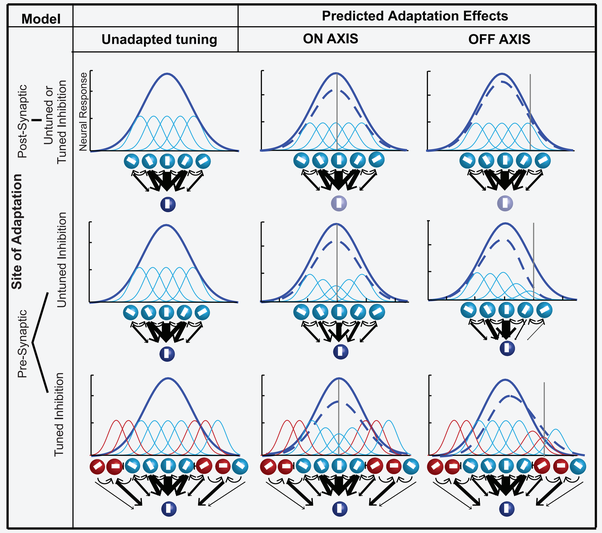


Both brief and prolonged adaptation at the preferred axis induces changes in orientation selectivity and half-bandwidth in excitatory (blue) and inhibitory (red) cells. In most cases, tuning shifted away from the adapter (i.e a "repulsive" tuning shift).



In contrast to adaptation at the preferred axis, both brief and prolonged adaptation at a non- preferred orientation axis induces attractive shifts (towards the adapter) in excitatory and inhibitory units.

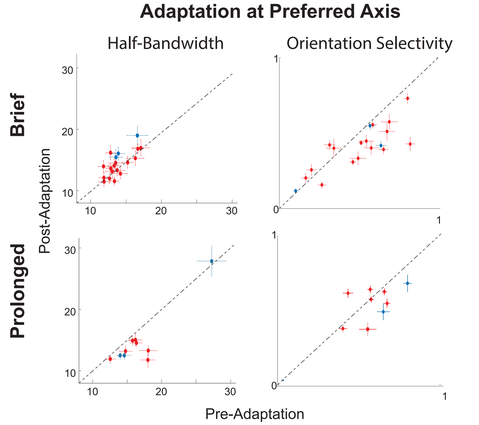
Adaptation-induced tuning shifts in models of orientaton selectivity



Model		Predicted Adaptation Effects	
Site of Adaptation	Type of Inhibition	Adaptation Preferred Axis	Adaptation NonPreferred Axis
Post-Synaptic	Tuned or Untuned	Gain reduction	Less gain reduction; **No Orientation Shifts**
Pre-Synaptic	Untuned	Gain reduction Bandwidth Narrowing	Less gain reduction; Bandwidth Narrowing; **Repulsive shifts only**
	Tuned	Gain reduction Bandwidth Narrowing or Broadening	Less gain reduction; Bandwidth Narrowing; **Attractive or Repulsive shifts**

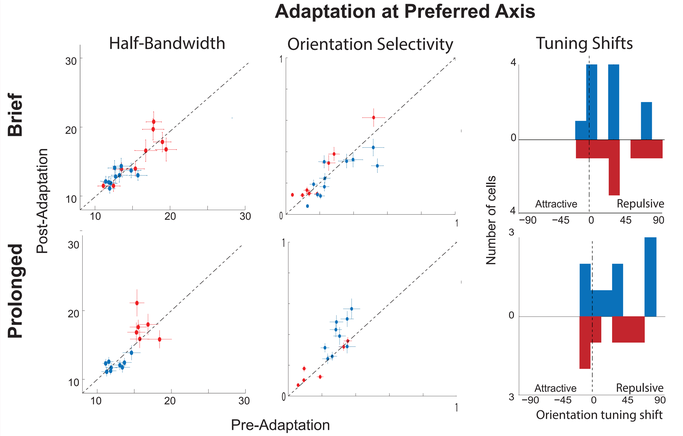
Three models for adaptation effects on orientation tuning. Arrows indicate the strength of connections from pre- to post-synaptic neurons. Row 1: postsynaptic adaptation. Adaptation reduces all connection strengths by the same factor, but no change in the tuning curve shape . Row 2: presynaptic adaptation of excitatory inputs. Adaptation modulates the connection strengths in proportion to the activity of the presynaptic neuron. Off-axis adaptation shifts the tuning curve, but only in a repulsive manner. Row 3, presynaptic adaptation and tuned inhibition: Off-axis adaptation can lead to attractive shifts in the tuning curve .

Cortical Area V1 Granular Layer



Brief adaptation induces broadening of half-bandwidth and decreases in orientation selectivity. However prolonged adaptation induces narrowing of half-bandwidth with decreases in orientation selectivity.

Cortical Area V2

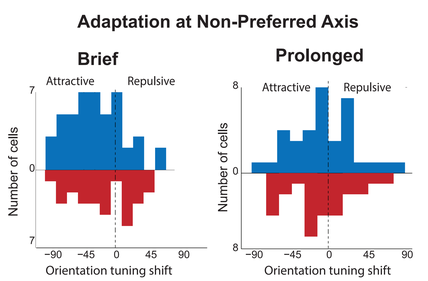


In area V2, adaptation at the preferred axis induces both broadening and narrowing of half-bandwidth in the inhibitory units, while the excitatory units mostly narrow their half-bandwidths and increase their orientation selectivity. Orientation tuning in the two cell types mostly shifts away from the adapter with brief or prolonged stimulation.

Summary

- Excitatory and inhibitory neurons both show adaptive shifts of their orientation tuning curves, for brief and prolonged presentations of the adapting stimulus.
- In the supragranular layer of V1, adaptation to non-preferred orientations induces strong attractive shifts (towards the adapter), in contrast to adaptation at the preferred axis.
- In the granular layer of V1, prelimiary evidence suggest that brief adaptation at the preferred axis induces mostly broadening of the half-bandwidth, while prolonged adaptation induces predominantly narrowing of the half-bandwidth
- In visual cortical area V2, adaptation induces mostly narrowing of orientation tuning in excitatory cells, but tends to increase or decrease the inhibitory interneurons based on their selectivity at baseline. Both repulsive and attractive shifts in tuning are observed in the two cell types with adaptation.

Adaptation at Non-Preferred Axis



Both attractive and repulsive shifts with brief and prolonged stimulation, are observed in V2, similar to visual cortical area V1.

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