Complementary functions of saccadic, position/drift, and extraretinal responses to eye movements in V1 neurons

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introduction

Natural viewing in primates consists of abrupt saccades followed by fixation periods comprising involuntary small (fixational) saccades and drifts. We found that fixational eye movements differentially modulate activity of V1 neurons. The type of eye movement activation was related to basic receptive field properties, suggesting that distinct groups of neurons contribute differently to the processing and perceptions of visual scenes.

Here we also used voluntary saccades in order to:

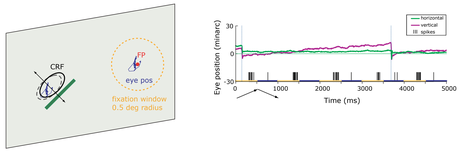
1) Elicit carefully controlled receptive field - stimulus interactions and different saccade amplitudes.

2) Compare effects of fixational and voluntary saccades in individual cells and at the population level.

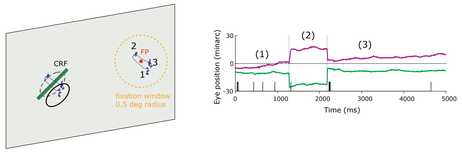
methods

We recorded extracellular activity of single V1 neurons while monkeys performed a fixation task or made voluntary saccades of different sizes. Eye position was monitored by a double Purkinje image eye tracker (2-3 minarc resolution; 100 Hz sampling rate) or a magnetic field search coil (1-2 minarc resolution, 200 Hz sampling rate).

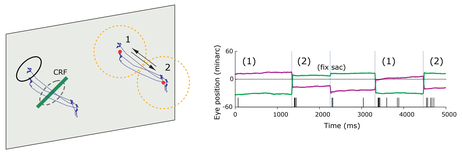
The size of classical receptive fields (CRFs), velocity tuning, direction selectivity (DS) and response transiency (TI) were tested with moving and flashing bars while compensating for fixational shifts and slow drift ("image stabilization"):



To study effects of fixational eye movements, an optimal stationary bar was placed within the CRF and image stabilization was turned off:



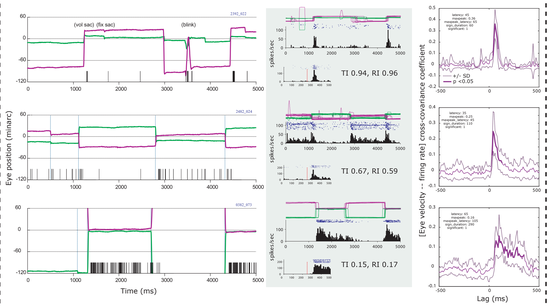
Voluntary saccades were elicited by transition between fixation targets so that the CRF would cross the bar, land on it, or leave it:



results

Saccadic and position/drift responses to eye movements

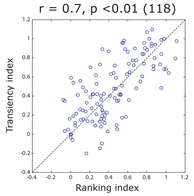
Voluntary saccades: "land/leave" single trials and analysis:

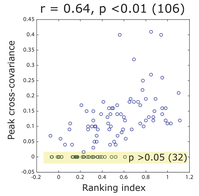


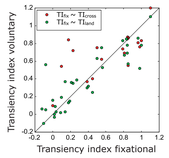
Transiency Index: $TI = (FR_{peak} - FR_{tail}) / |FR_{peak} + FR_{tail} - 2FR_{base}|$ (local)

Ranking Index: $RI = (FR_{postsac} - FR_{drift}) / |FR_{postsac} + FR_{drift} - 2FR_{base}|$ (global)

Strong correlation between TI, RI, and [eye velocity -- firing rate] cross-covariance peak, both for fixational (below) and voluntary (not shown) eye movements:





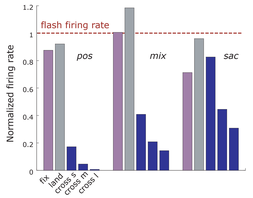


$TI_{fix} \sim TI_{cross}$: r=0.62 (18)

$TI_{fix} \sim TI_{land}$: r =0.84 (34)

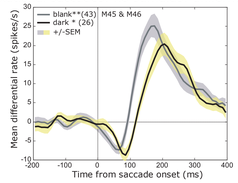
p<0.01

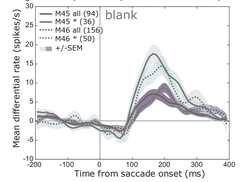
Comparison of peak firing rates for "enhancing" fixational and voluntary landing and crossing saccades of different amplitudes, normalized by the response to flash:



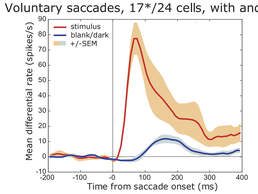
Extraretinal modulation of ongoing activity

Fixational saccades: no stimulus: uniform background ("blank") or in the dark ("**dark**").





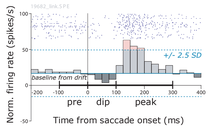
Voluntary saccades, 17*/24 cells, with and without stimulus

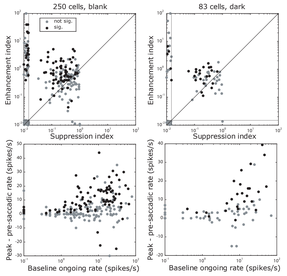


Extraretinal post-saccadic modulation of ongoing firing has biphasic time course: initial weak suppression followed by stronger enhancement peaking in between 100-200 ms after the saccade onset.

Extraretinal modulation is slower and weaker than the visual response (*cf.* blue and red trace).

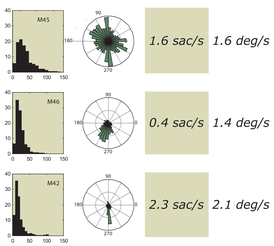
Normalized suppression (SI) and enhancement (EI) indices and significance of the modulation for each neuron: 34% (86/250 cells, blank) and 31% (26/83 cells, dark) are significantly modulated (denoted by * above).





Significant correlation between the ongoing rate and the enhancement strength expressed as the difference between mean firing rates in "peak" and pre-saccadic periods:

Metrics of eye movements in the *blank* for 3 monkeys:



show effect

1.6 sac/s 1.6 deg/s

0.4 sac/s 1.4 deg/s

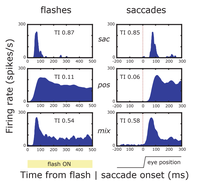
does not show effect

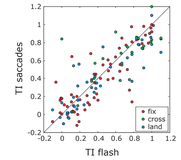
2.3 sac/s 2.1 deg/s

The detection of the extraretinal modulation may depend on the individual patterns of fixational eye movements:

Correlation of eye movement activation patterns and responses to external stimuli

Correlation between transiency of response to saccades and flashing bars:





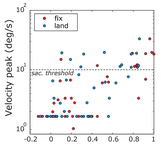
$TI_{flash} \sim TI_{fix}$: r=0.86 (72)

$TI_{flash} \sim TI_{cross}$: r=0.64 (23)

$TI_{flash} \sim TI_{land}$: r=0.89 (40)

(p<0.01)

Correlation between transiency of response to saccades and velocity tuning to moving bars:



Peak velocity ~ TI_{fix} : r=0.70 (41)

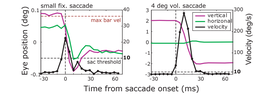
Peak velocity ~ TI_{land} : r=0.56 (40)

p<0.01

Mean velocity tuning peak in cells

- responding to crossing saccades:
  11.1 +/- 8.2 deg/s (23)
- not responding to crossing saccades:
  3.5 +/- 4.3 deg/s (16)

Comparison was not direct because of stimulus presentation limitations:



Saccade transiency index and directional selectivity (r : 0.3 - 0.5, p<0.01)

Saccade transiency index and CRF size (r : 0.33, p<0.01)

- Low TI "position/drift"-activated cells often small and selective for sign-of-contrast (monocontrast or simple cells).

summary

Our results suggest complementary functions for the two types of visual activation by eye movements in V1 neurons:

Post-saccadic bursts signal abrupt change/motion in the CRF and can be utilized to detect salient stimulus features like edges irrespective of the current spatial position, and to maintain perceptual stability during saccades.

Inter-saccadic discharge encodes stimulus position and conveys information about spatial details of a visual scene.

In addition to visual activation, weaker extraretinal modulation by eye movements in the absence of direct visual stimulation is present. This modulation may serve as substrate for saccadic suppression, or/and enhance stimulus visibility and discrimination following the saccades.

References and additional info: igor@vis.caltech.edu

http://igoresha.virtualave.net/Work/FixVolEyeMov