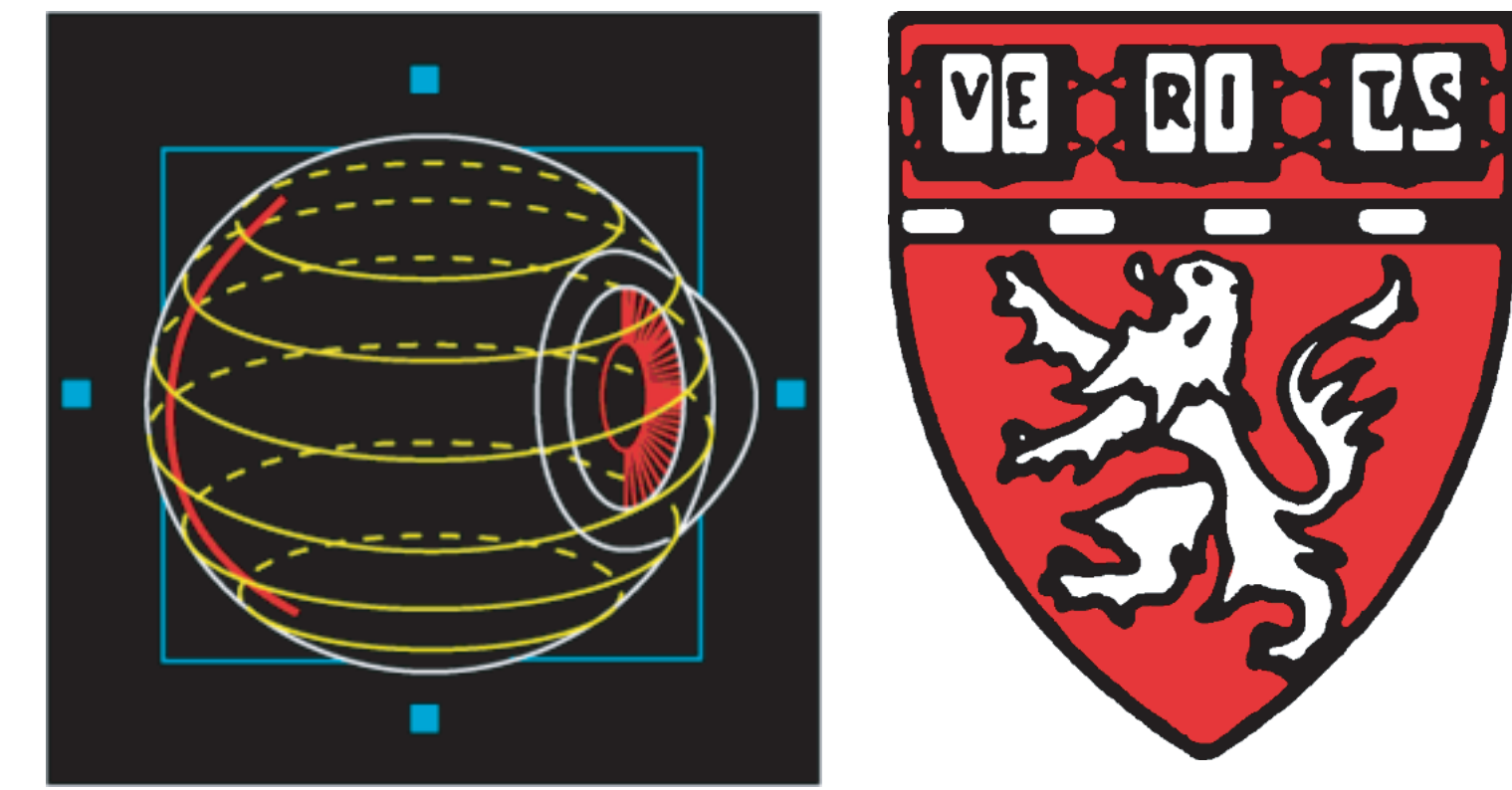


SA27 RESPONSES OF MACAQUE V1 NEURONS TO FIXATIONAL AND VOLUNTARY EYE MOVEMENTS CORRELATE WITH RECEPTIVE FIELD PROPERTIES

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INTRODUCTION

Natural viewing in primates consists of abrupt saccades followed by slower movements. Even during fixation, involuntary small saccades and drift still persist. In a previous study, we found that fixational eye movements differentially modulate activity of V1 neurons. The type of activation was related to basic receptive field properties, suggesting that distinct groups of neurons contribute differently to processing of the visual scene.

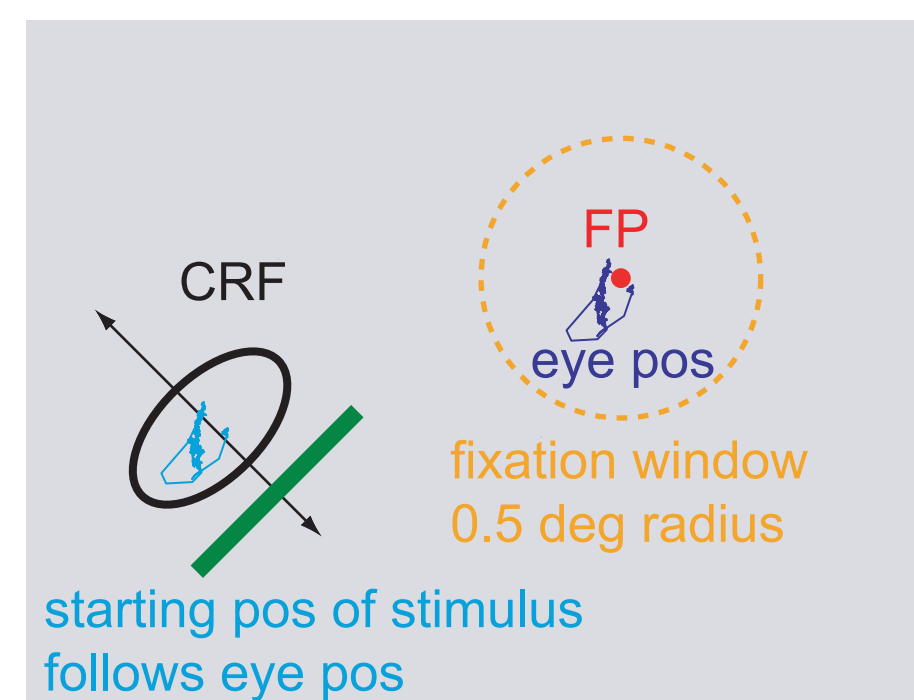
The goals of the present study are:

- (1) To gain better understanding of how eye movements modulate neuronal firing by studying controlled (evoked) voluntary saccades.
- (2) To compare effects of retinal motion and stimulus onset imposed by fixational saccades, voluntary saccades, and externally modulated stimuli.

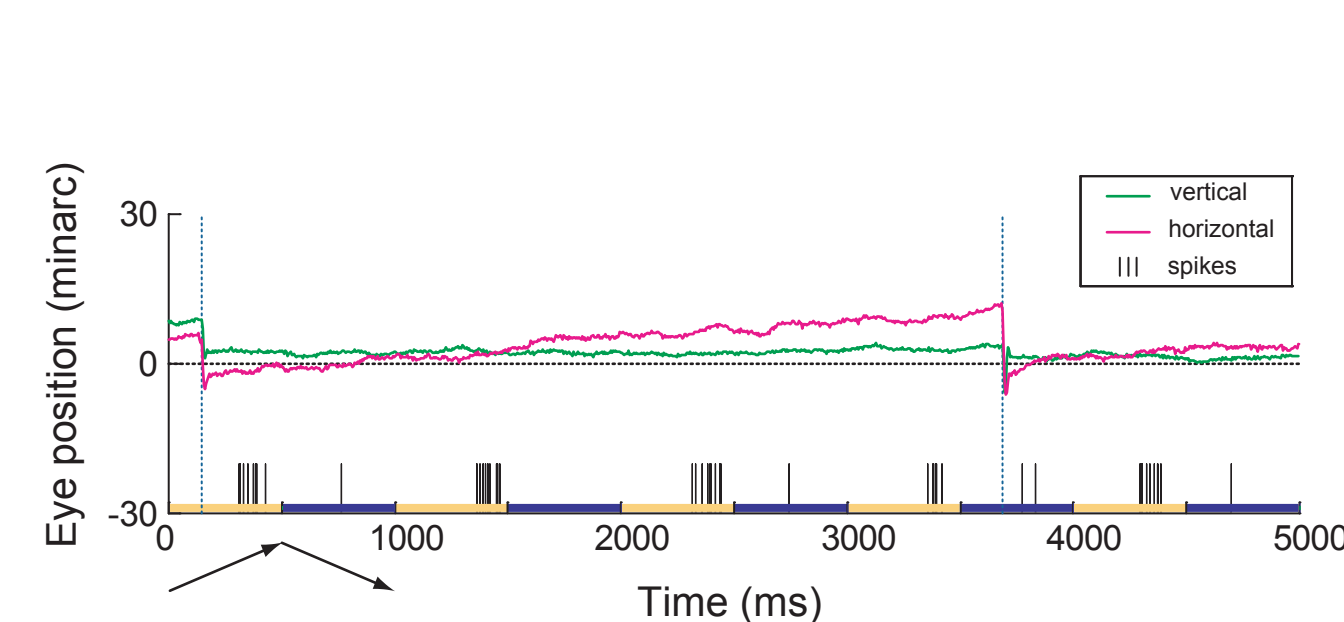
METHODS

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).

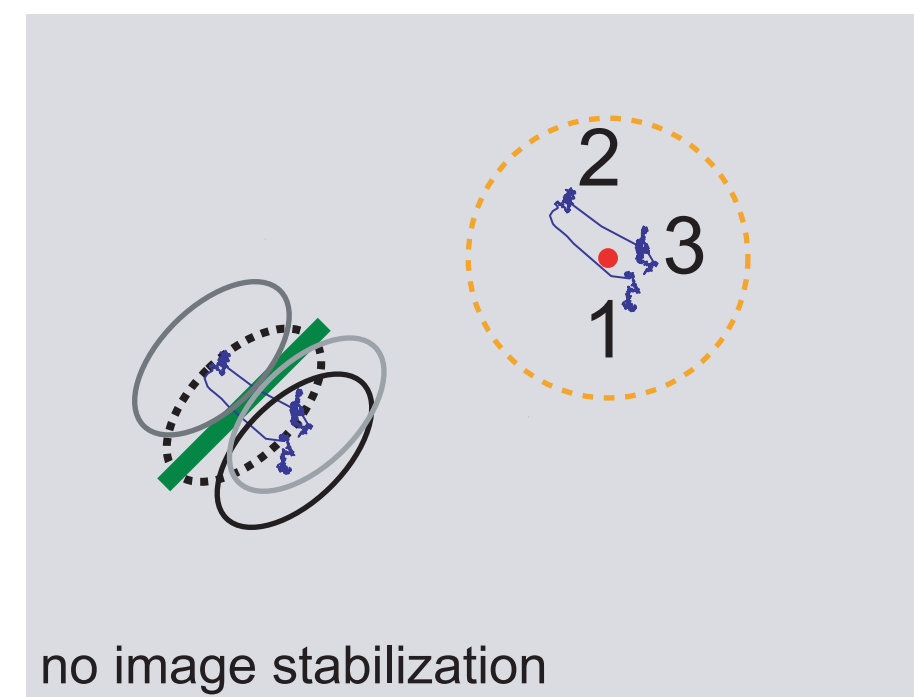
The **extent** of classical receptive fields (CRFs), **velocity tuning**, **direction selectivity** (DS) and response **transiency** (TI) tested with moving and flashing bars while compensating for fixational shifts and drift ("image stabilization"):



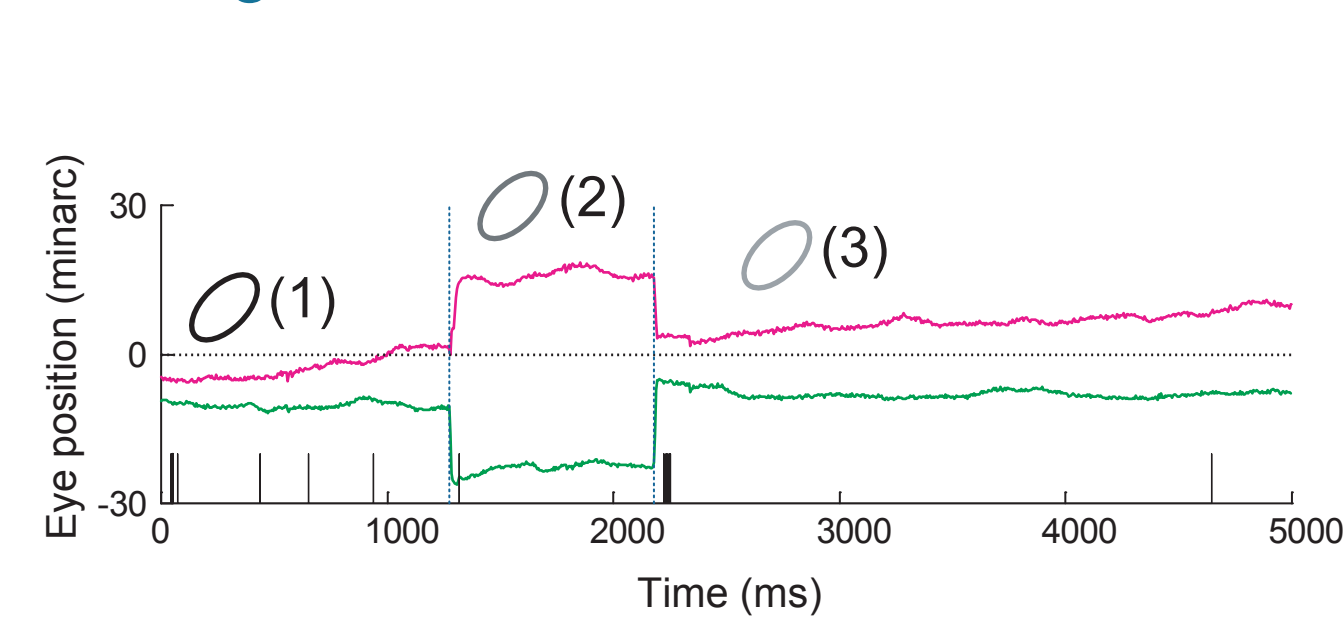
mapping with moving bar



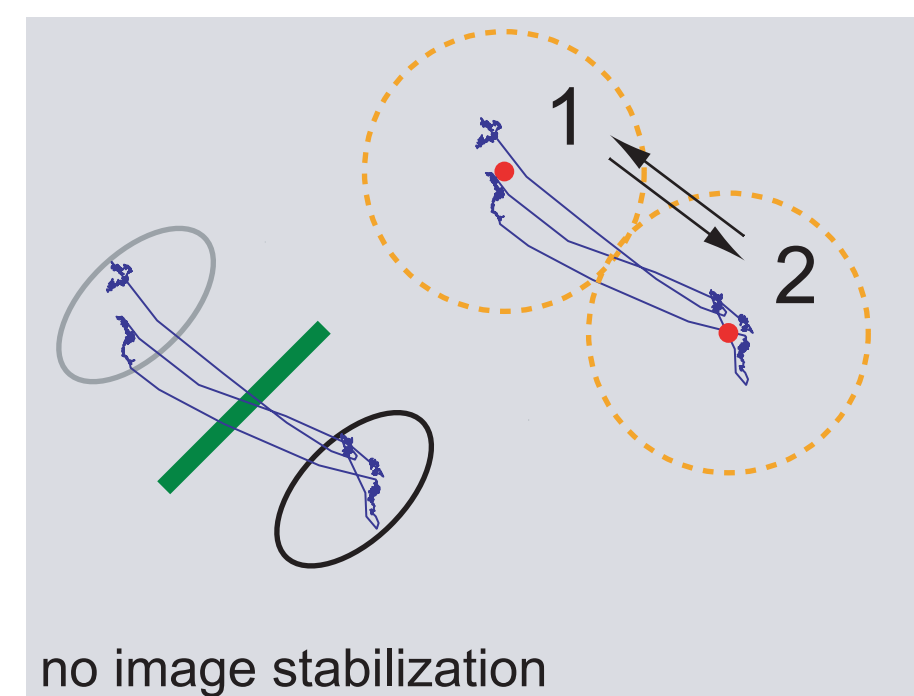
To study effects of fixational eye movements, an optimal **stationary** bar was placed within the CRF and position compensation was **turned off**:



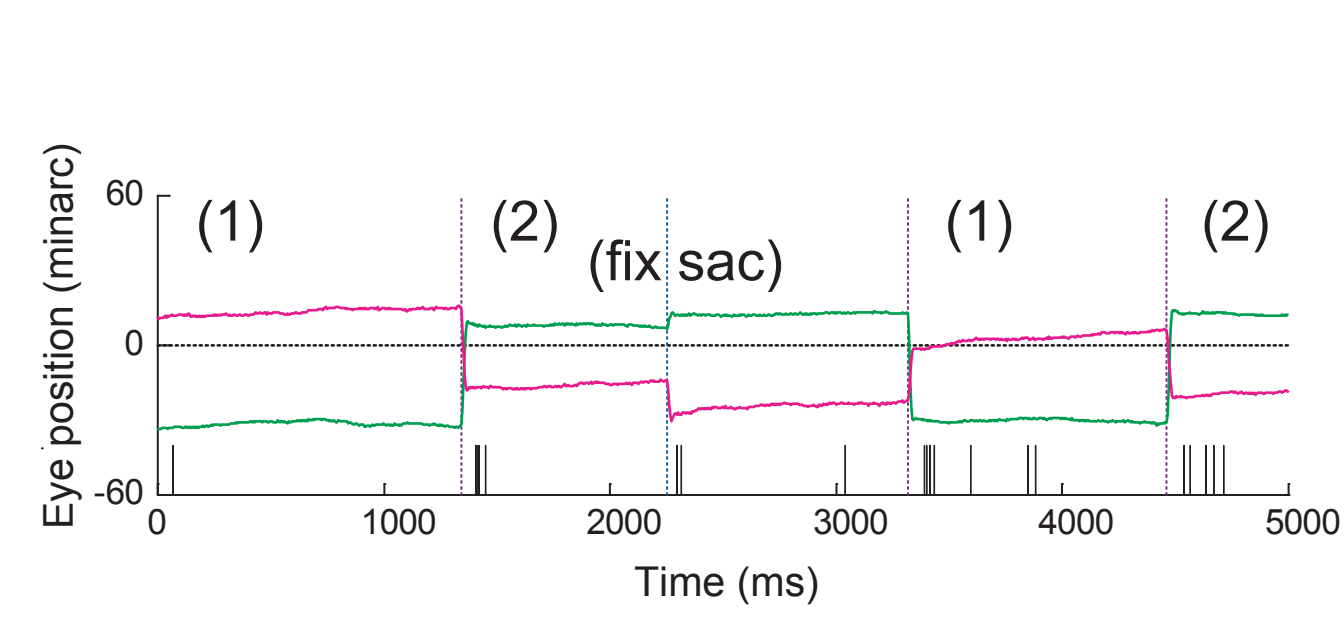
testing fixational movements



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



testing voluntary (evoked) saccades

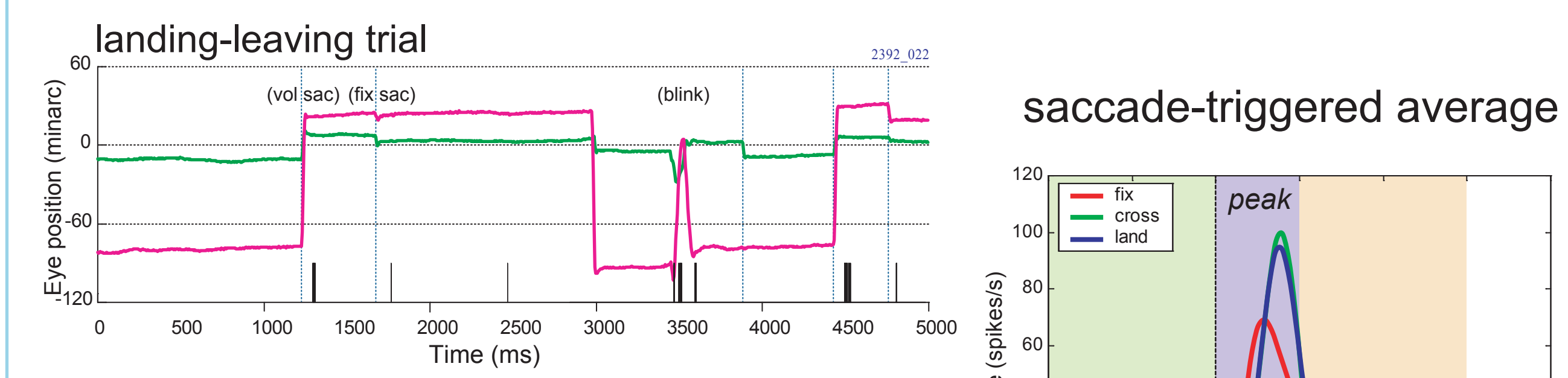


RESULTS

Different patterns of activation induced by eye movements

Three types of activation were found in responses to fixational and voluntary saccades:

- (1) **"Saccade-activated"** cells discharged a transient burst when a saccade moved the CRF onto the stimulus, off the stimulus, or across the stimulus.

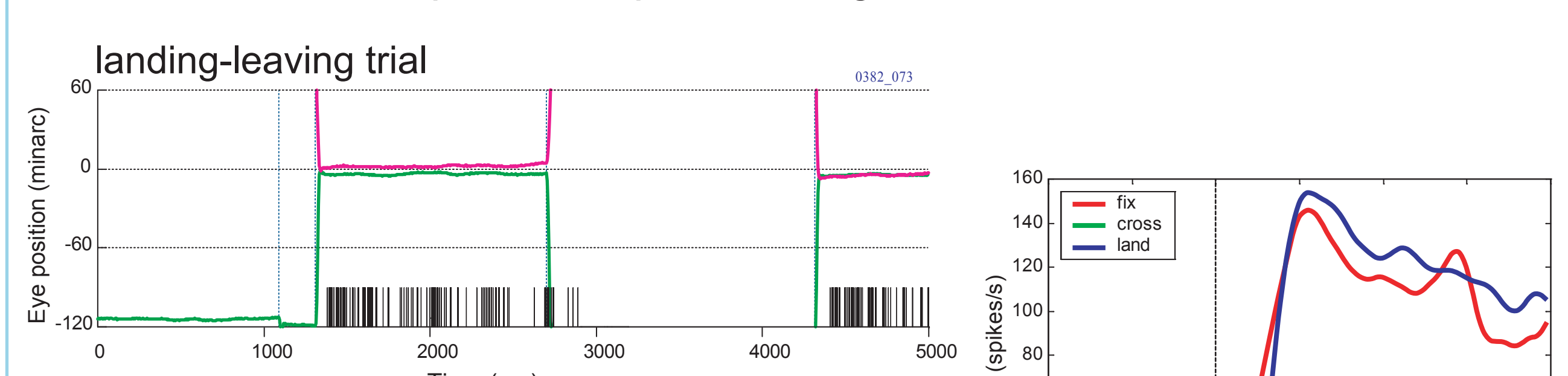


Transiency Index

$$TI = (peak - tail) / |peak + tail - 2base|$$

TI is near unity for transient responses.

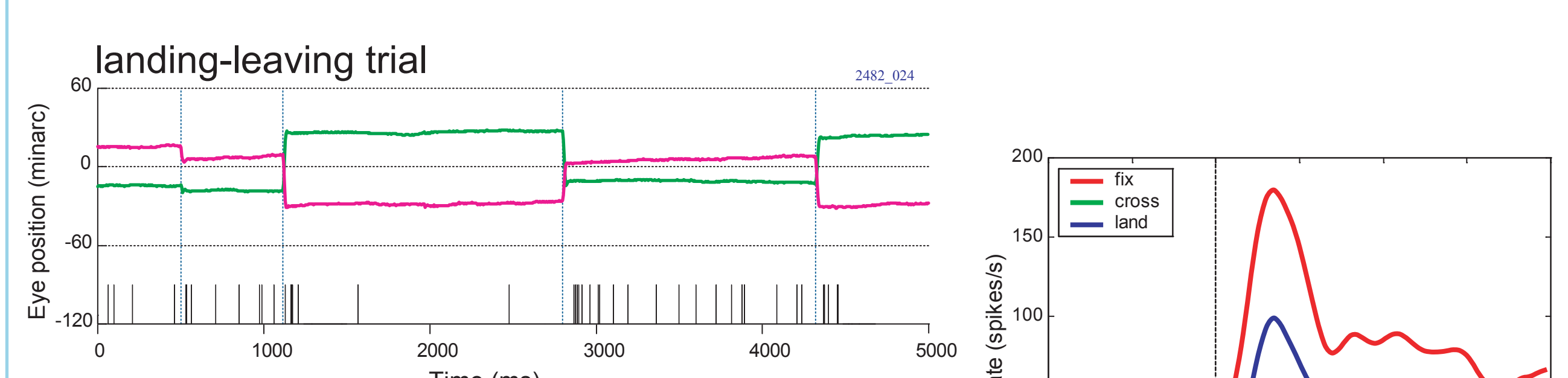
- (2) **"Position/drift"** cells fired continuously while the stimulus was within the CRF but did not respond to rapid crossings of the stimulus.



TI is near zero for sustained responses.

The "position/drift" activation was very pronounced. At least third of our sample (34/104 cells) had strong sustained firing in drift periods after **landing** saccades but no or weak responses to **crossing** saccades.

- (3) **"Mixed"** cells fired bursts of spikes following saccades but also continued to fire at a lower rate during intersaccadic intervals - if the CRF remained on the stimulus.

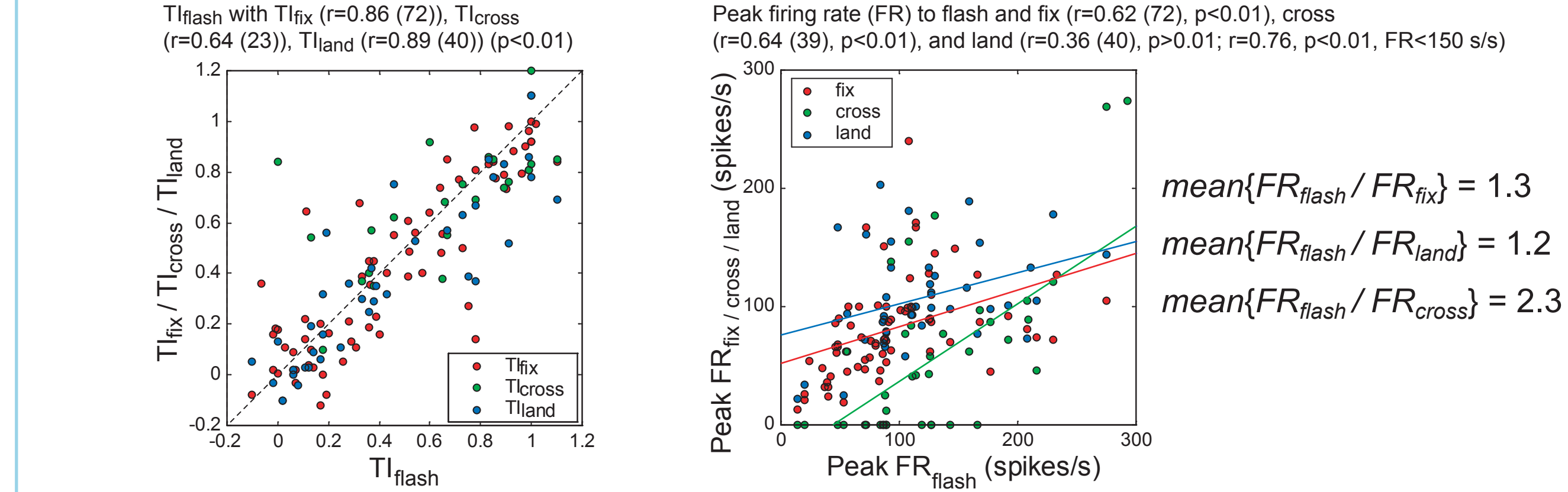


TI is around 0.5 for intermediate responses.

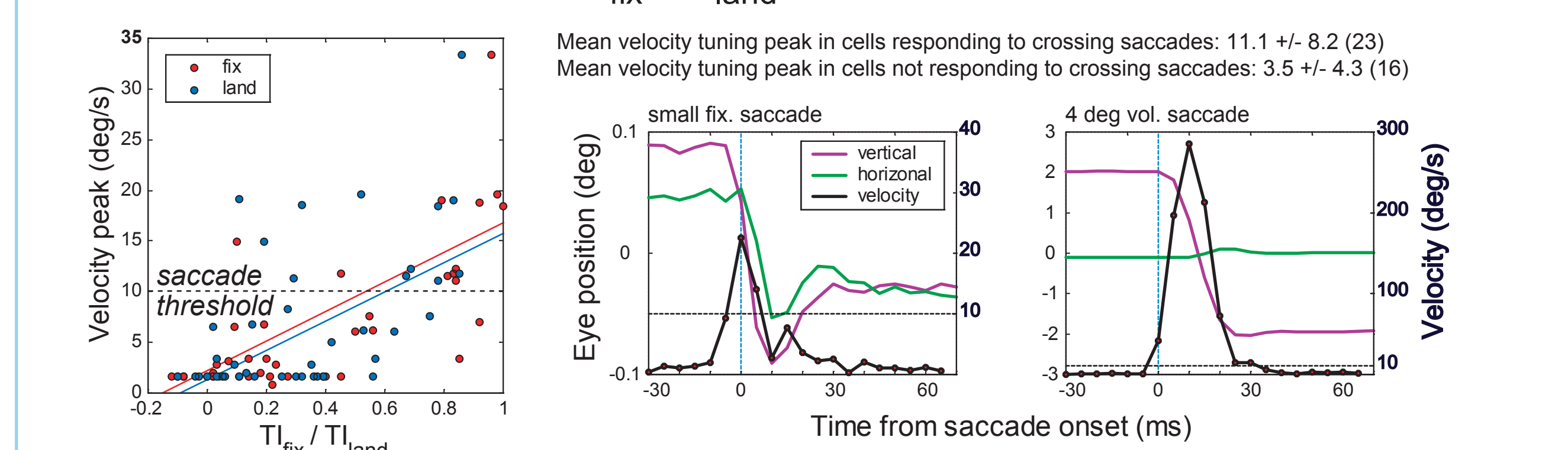
In most cases, various firing patterns can be predicted from information about RF movement relative to the stimulus, and RF properties.

Correlation of activation patterns and RF properties

- Correlation of responses to flashes and saccades (fix, land, cross):



- Correlation (with few exceptions) of velocity preference to moving bars (velocity tuning peak) and TI_{fix} / TI_{land} ($r=0.70$ (41); $r=0.56$ (40); $p<0.01$):



- Weak correlation of DS and TI_{fix} / TI_{land} ($r=0.29$ (93), 0.52 (39); $p<0.01$).

- "Position/drift" cells had sustained responses, preferred low velocity, tended to have small CRFs, often selective for sign-of-contrast (*monoccontrast* and *simple* cells) and non-directional.
- "Saccade" cells had transient responses, were tuned for relatively high velocity and were frequently directional.
- "Mixed" cells' properties were intermediate between "saccade" and "position/drift" cells.

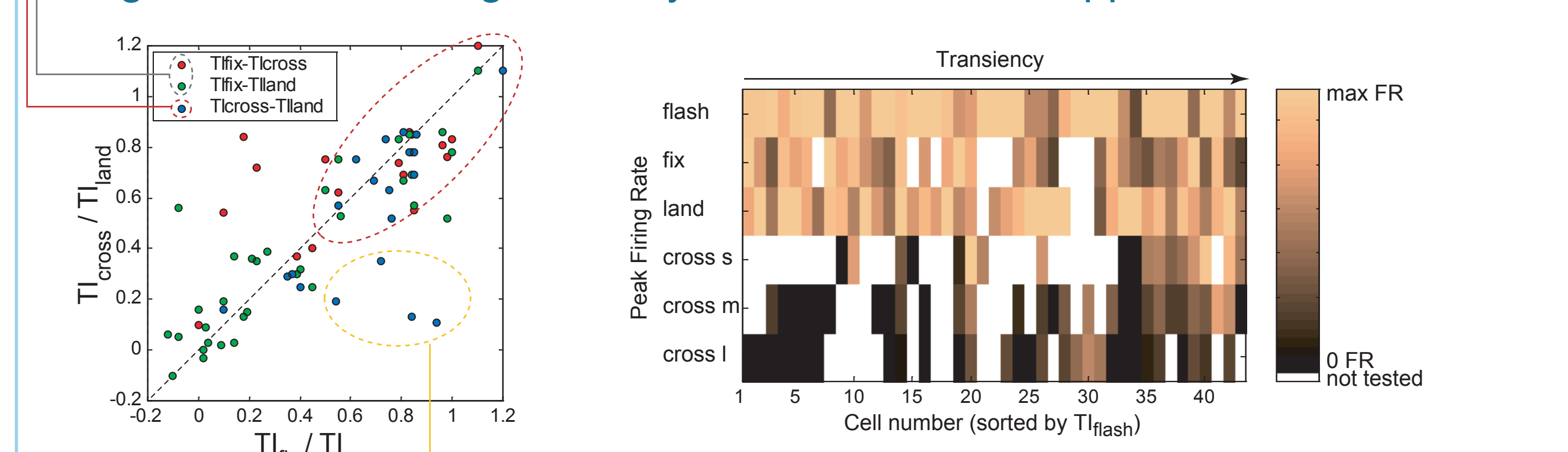
Comparison of fixational and voluntary saccades' effects

Correlation between TIs for **fixational** saccades and **voluntary** crossing and landing saccades ($r=0.62$ (18) and $r=0.84$ (34), $p<0.01$).

In "saccade" and transient "mixed" cells responses to **landing** and **crossing** saccades were **qualitatively similar**. But often responses to larger crossing saccades were weaker than to smaller saccades.

In most "position/drift" cells and some "mixed" cells, there was either no response at all to crossing saccades of all amplitudes (16/39 cells), or there was only a weak response to small crossing saccades (5/39 cells).

It remains an open question what causes the decrease of response to "large" saccades: a high velocity cut-off, an active suppression, or both.



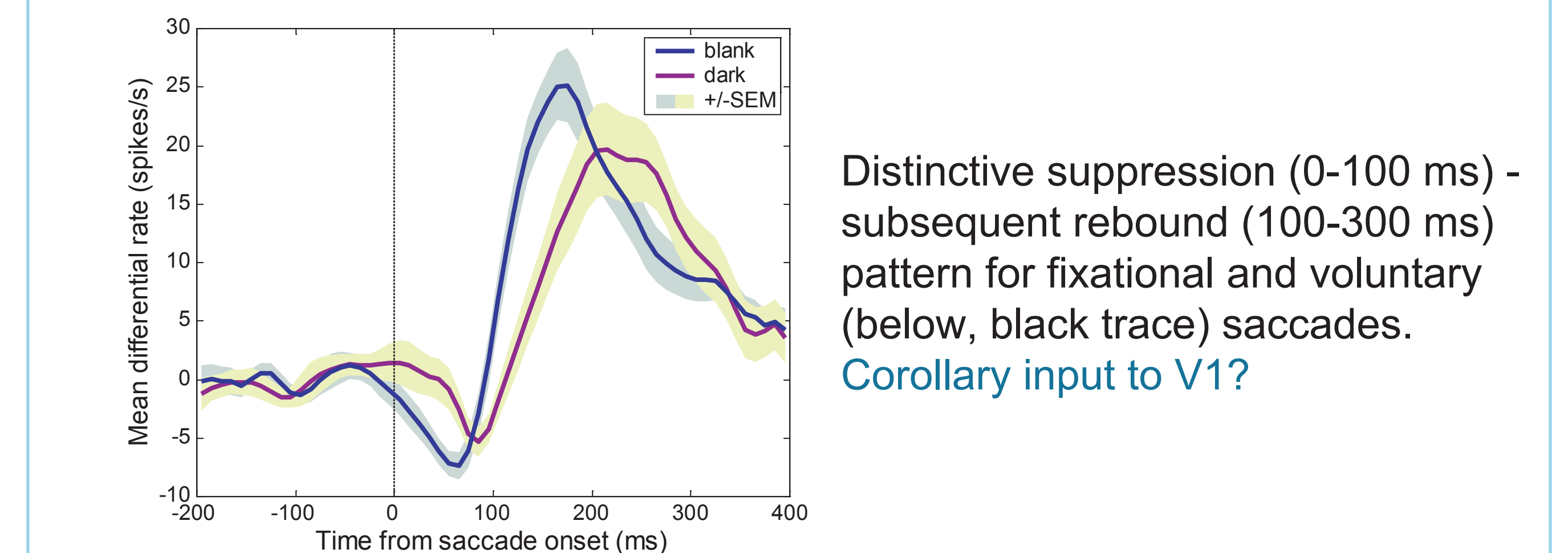
A few **exceptional sustained cells** ($TI_{land} < 0.4$) gave relatively strong and brisk response to crossing saccades. This resulted in a weak correlation between TIs for crossing and landing saccades ($r=0.46$ (20), $r>0.01$).

Modulation of response with a blank screen / in the dark

In a subset of neurons, fixational and voluntary saccades also modulated *ongoing* (spontaneous) firing in the absence of a visual stimulus (either in the **dark** or with **uniform illumination**).

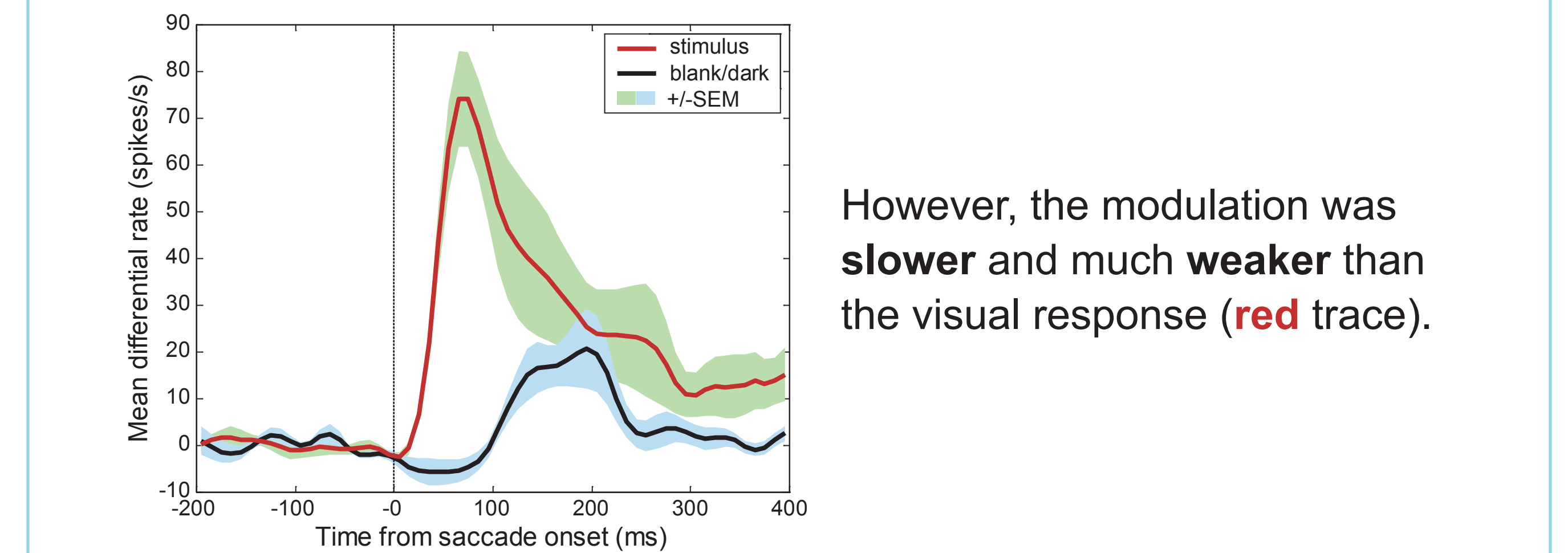
$$Mean\ differential\ rate = mean\{rate(i)_{\text{perisaccadic}} - rate(i)_{\text{presaccadic}}\}, i=1...n$$

Fixational saccades, blank: 43 cells, dark: 20 cells



Distinctive suppression (0-100 ms) - subsequent rebound (100-300 ms) pattern for fixational and voluntary (below, black trace) saccades. Corollary input to V1?

Voluntary saccades, 10 cells, with and without stimulus



However, the modulation was **slower** and much **weaker** than the visual response (red trace).

CONCLUSIONS

The effects of both fixational and voluntary eye movements on neuronal activity are diverse, but can be mostly explained by interactions of receptive field properties with visual stimulation induced by these movements.

Different groups of V1 neurons selectively extract information about motion, change, position and visual detail.

An extraretinal input to V1 is detectable, even for the small saccades, but it is small compared to stimulus-driven responses.

Future work

Study interactions of eye movements with stimulus attributes and non-classical surround using sub-optimal and extended stimuli.

Introduce temporal and spatial conditions experienced during viewing of natural scenes.