Relationship of contextual modulations in V1 and V2 revealed by nonlinear receptive field mapping

Weill Cornell Medical College

Anita M. Schmid, Jonathan D. Victor

Department of Neurology & Neuroscience, Weill Cornell Medical College, New York, NY

3-96

INTRODUCTION

Responses of neurons in primary visual cortex (V1) are modulated by context, due to processes such as surround suppression and facilitation. These modulations may serve as a mechanism for detecting texture borders. Neurons in secondary visual cortex (V2), on the other hand, respond more directly to texture borders. It is as yet unclear how these processes relate to each other: are they independent of each other and serve different purposes or are they connected and jointly serve the purpose of detecting texture borders? To gain more insight into this relationship, we investigated the dynamics of both types of nonlinearities.

How does changing stimulus duration affect the dynamics of contextual modulations in V1 and V2?

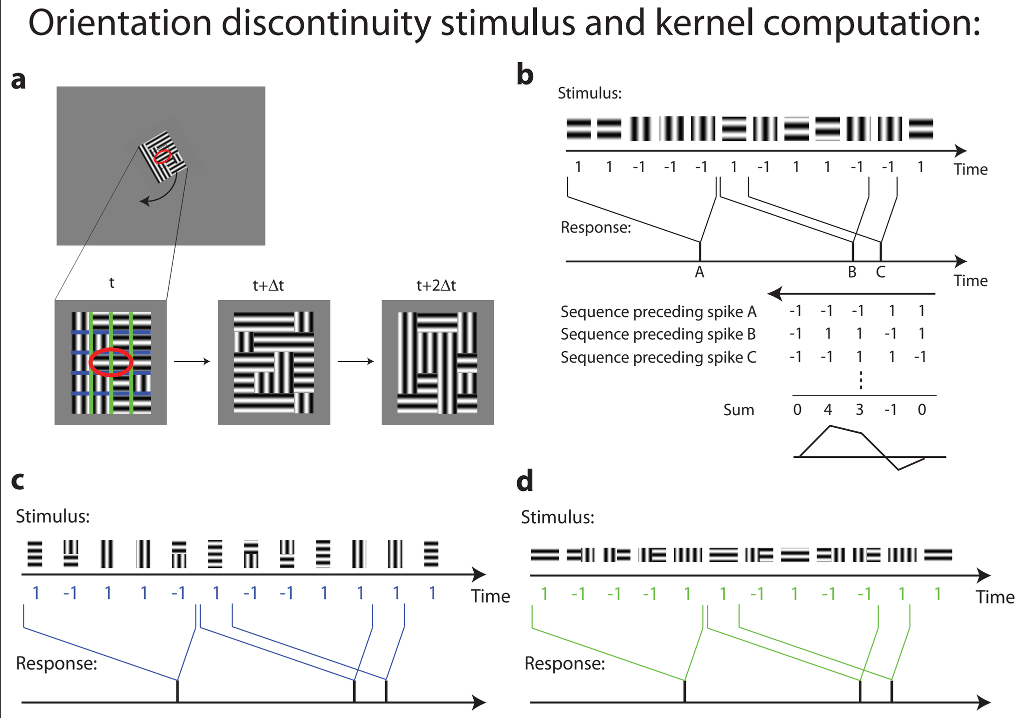
METHODS

Physiology:
- Anesthetized and paralyzed macaques
- Extracellular single unit recordings using tetrodes

Stimulus:
- Grid of rectangles containing static sinusoidal gratings (4 x 5 or 6 x 6)
- Preferred orientation or orthogonal orientation
- Grid aligned with receptive field (RF), covering surround
- Pseudo-random sequences (m-sequences)
- Frame durations of either 20 or 40 ms

Analysis:
- First-order as well as second-order responses
- Reverse correlation

Orientation discontinuity stimulus and kernel computation:

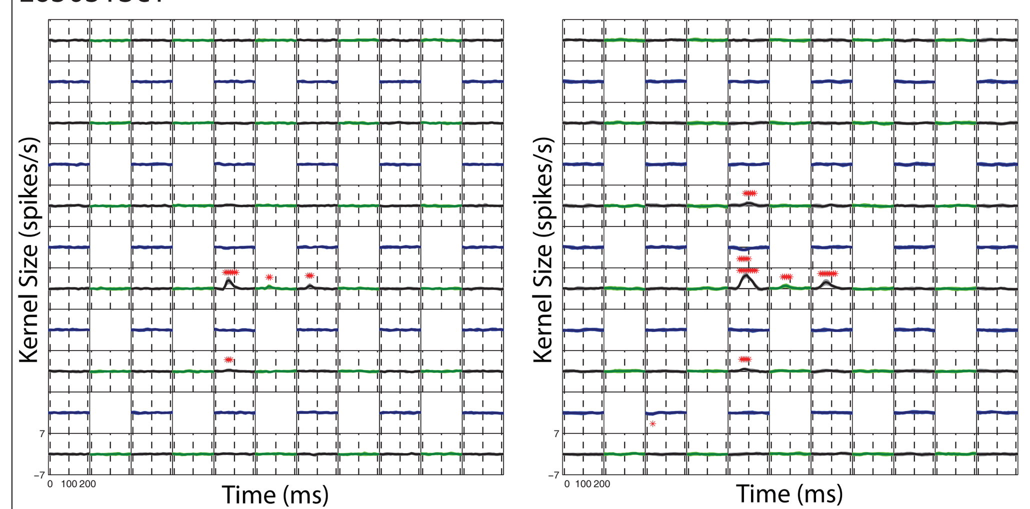


(a) Stimulus setup. Blue and green lines show the region boundaries parallel (blue) and orthogonal (green) to the receptive field; these lines were not part of the stimulus. (b) Computation of a first-order kernel. The sign convention is such that **when the response to the preferred grating is larger, the first-order kernel is positive.** (c) Computation of the spatial second-order kernel across boundaries parallel to the receptive field. (d) Analogous computation of the spatial second-order kernel across boundaries orthogonal to the receptive field. (c) and (d) The sign convention is such that **when the response is larger when the adjacent regions have the same orientation, than when their orientation is different, the second-order kernel is positive.**

Example Neurons in V1

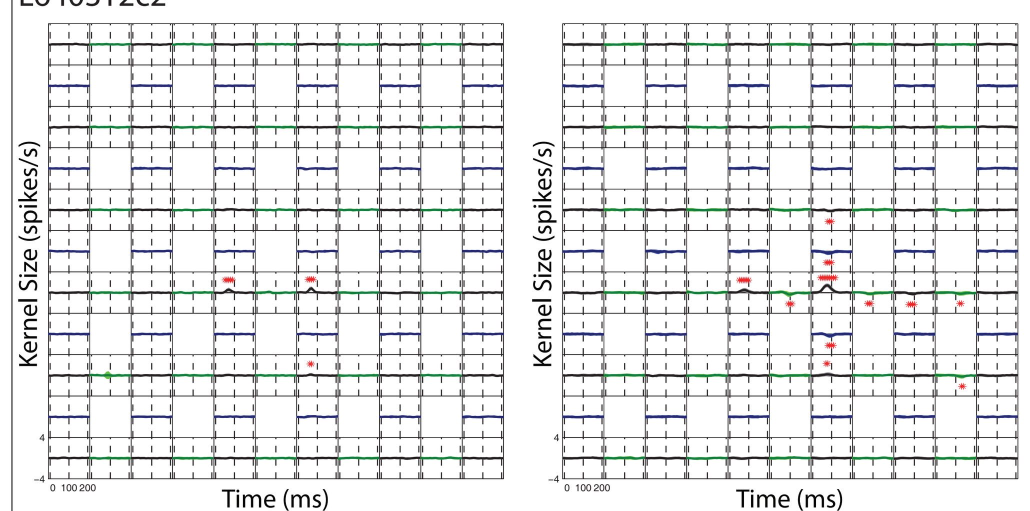
Responses to individual regions (black) and interactions between neighboring regions (green and blue). In V1, for frame durations of 20 ms, only positive interactions are observed. For frame durations of 40 ms, positive as well as negative interactions are observed in V1.

L6505T3c1 Δt = 20 ms Δt = 40 ms



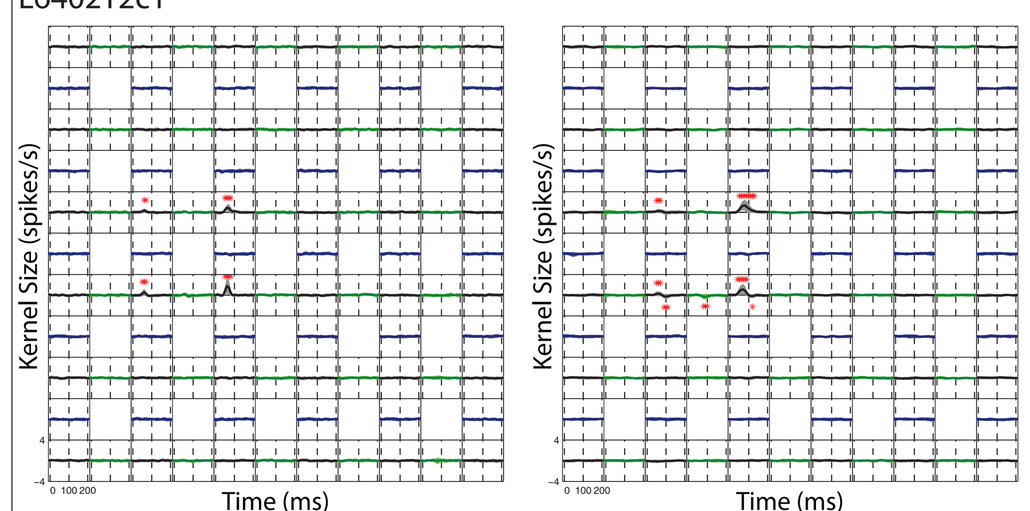
For 20 ms, this neuron shows a positive interaction within the receptive field, across a boundary orthogonal (green) to the RF indicating that the response is larger when neighboring patches have the same orientation, compared to when they differ. For 40 ms, the neuron shows an additional negative interaction across a boundary parallel (blue) to the RF indicating that responses are larger when neighboring patches have different orientation, compared to when they are the same.

L6403T2c2 Δt = 20 ms Δt = 40 ms



For 20 ms, this neuron shows no significant interactions. For 40 ms, the neuron shows negative interactions across boundaries parallel (blue) as well as orthogonal (green) to the RF. There are also additional responses in the surround of the RF to individual patches (black) of negative sign indicating that responses are larger when an orientation orthogonal to the preferred is displayed in these regions.

L6402T2c1 Δt = 20 ms Δt = 40 ms

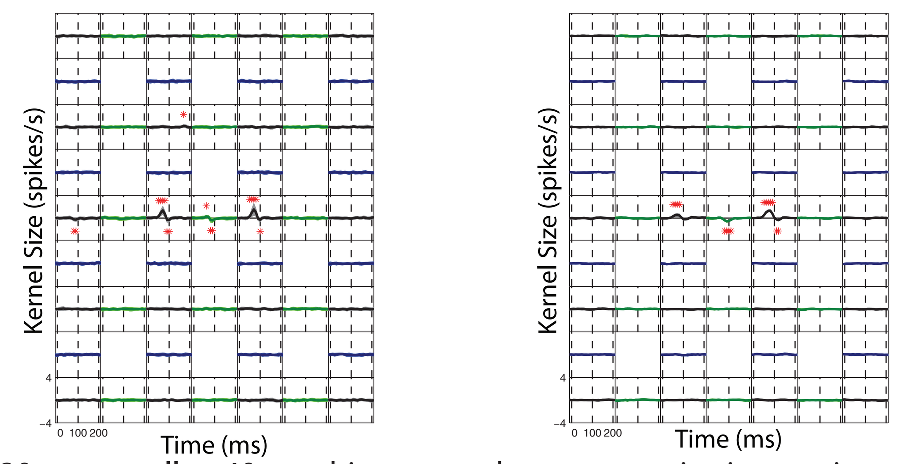


For 20 ms, this neuron shows no interactions, and the responses to individual regions are monophasic. For 40 ms, the neuron shows a negative interaction (green). In addition, some responses to individual patches (black) are now biphasic indicating that at a longer latency, responses are larger when an orientation orthogonal to the preferred has been displayed in these regions.

Example Neurons in V2

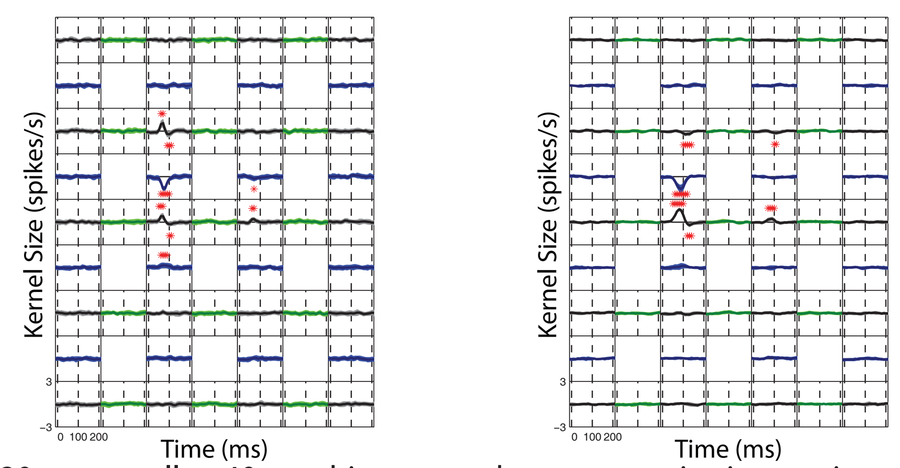
In V2 transient neurons (Schmid et al., 2009), responses to individual regions (plotted in black) are consistently biphasic for frame durations of 20 ms a well as 40 ms. Also, there are robust negative interactions (green and blue). Sustained V2 neurons (Schmid et al., 2009) show almost no interactions for either frame duration and therefore no examples are shown here.

L5706T2c2 Δt = 20 ms Δt = 40 ms



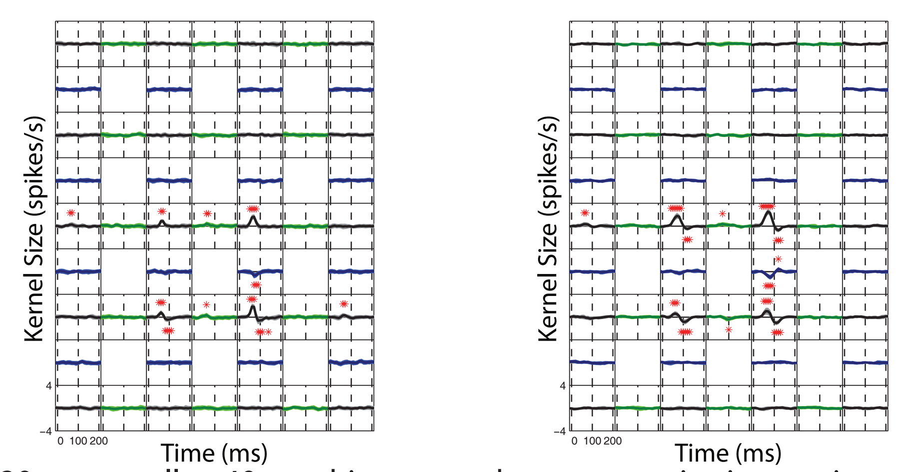
For 20 ms as well as 40 ms, this neuron shows a negative interaction, across a boundary orthogonal (green) to the RF indicating that responses are larger for an orientation texture border orthogonal to the RF than for continuous gratings. In addition, the responses to individual patches (black) are biphasic for both frame durations indicating that responses are larger when the orientation switches from orthogonal to preferred, compared to when it stays preferred.

L5604T3c2 Δt = 20 ms Δt = 40 ms



For 20 ms as well as 40 ms, this neuron shows a negative interaction, across a boundary parallel (blue) to the RF indicating that responses are larger for an orientation texture border parallel to the RF than for continous orientation. One positive and one negative interaction (blue) vanishes for 40 ms. The response to one individual patch (black) is biphasic for both frame duration and the response to another region switches from biphasic to negative for one region, while the third one only emerges for 40 ms and is negative.

L5603T3c3 Δt = 20 ms Δt = 40 ms

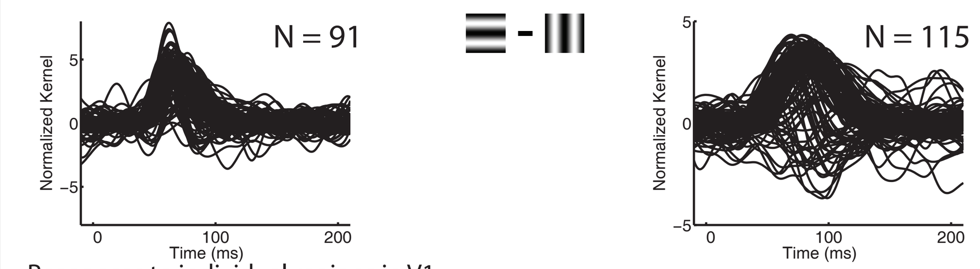


For 20 ms as well as 40 ms, this neuron shows a negative interaction, across a boundary parallel (blue) to the RF. The responses to two individual patches (black) are biphasic for both frame durations and the responses to two other regions switch from monophasic to biphasic for two regions, while the positive response to one region vanishes for 40 ms.

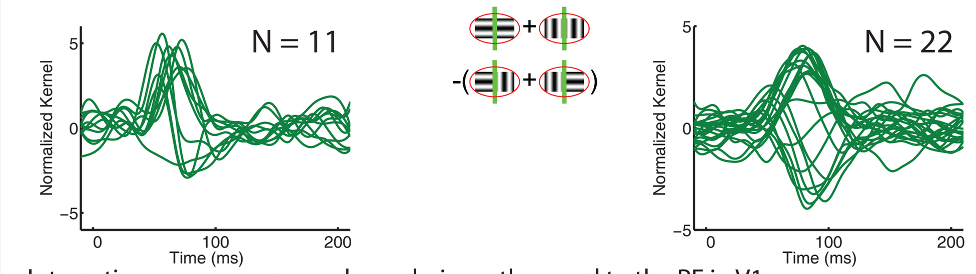
V1: 31 neurons

N = number of significant responses

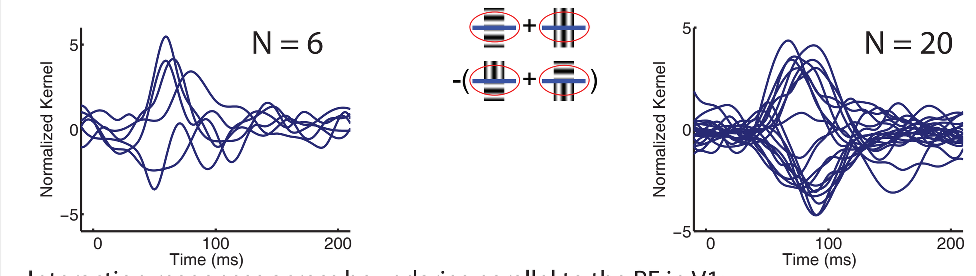
Δt = 20 ms Δt = 40 ms



Responses to individual regions in V1:
- 20 ms: only few biphasic (6) and negative (2) responses
- 40 ms : few more biphasic (8) and many more negative responses (16)



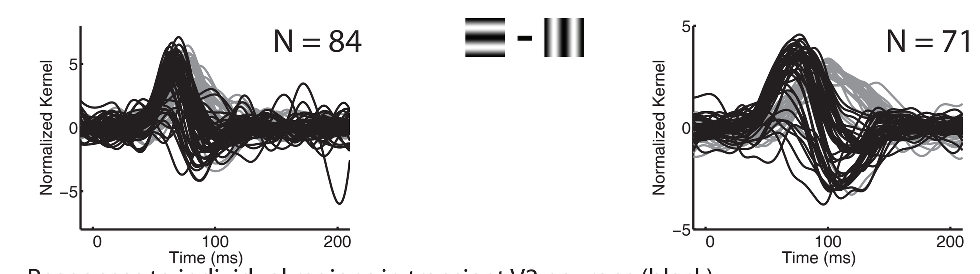
Interaction responses across boundaries orthogonal to the RF in V1:
- 20 ms: only one biphasic and 2 negative responses
- 40 ms : few more biphasic (3) and more negative responses (6)



Interaction responses across boundaries parallel to the RF in V1:
- 20 ms: only one biphasic and 2 negative responses
- 40 ms : no biphasic and many more negative responses (13)

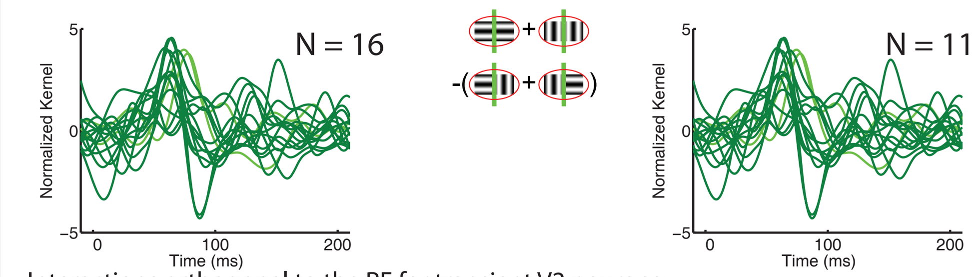
V2: 22 neurons: 13 transient, 9 sustained

Δt = 20 ms Δt = 40 ms



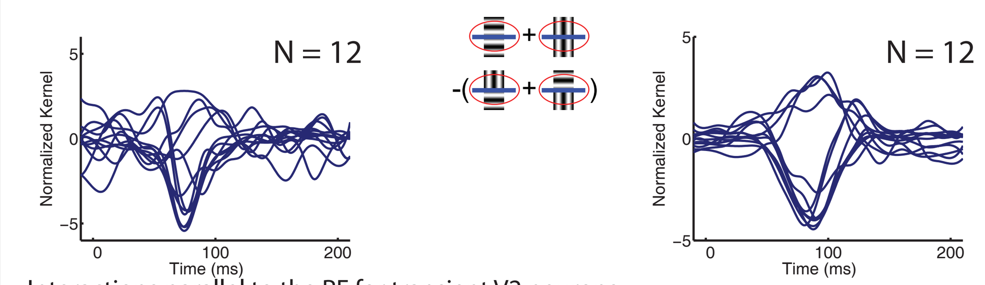
Responses to individual regions in transient V2 neurons (black):
- 20 ms: biphasic (20) and negative (7) responses
- 40 ms: biphasic (23) and negative (7) responses

Sustained V2 neurons (gray) mainly show slower positive responses



Interactions orthogonal to the RF for transient V2 neurons:
- 20 ms: few biphasic (3) and few negative (2) responses
- 40 ms : one biphasic and few negative responses (4)

There are 2 positive interactions from sustained V2 neurons (light green)



Interactions parallel to the RF for transient V2 neurons:
- 20 ms: only few biphasic (2) and some negative (6) responses
- 40 ms : no biphasic and some negative responses (8)

There are no interactions from sustained V2 neurons

SUMMARY

V1 neurons:

20 ms frame duration:
- positive responses to individual regions
- positive interaction responses

40 ms frame duration:
- positive and negative responses to individual regions
- positive and negative interaction responses

- **For V1, the longer stimulus frame duration activates surround suppression and contextual modulations favoring orientation texture borders.**
- **The interactions often occur between regions that individually elicit a positive response and therefore can be considered within the "center" of the receptive field.**
- **Positive interactions, which indicate preference for continuous orientations, occur with a shorter latency than negative interactions, which yield larger responses for orientation texture borders.**

V2 neurons:

20 ms and 40 ms frame duration:
- positive, biphasic and negative responses to individual regions
- biphasic and negative interaction responses

- **In V2, for the longer stimulus frame duration the responses stay qualitatively the same.**
- **Biphasic and negative responses to individual regions as well as negative interactions lead to robust responses to orientation texture borders.**
- **These interactions in V2, which are consistent with a spatial differentiation operation, started with the same latency as the contextual interactions in V1.**

CONCLUSIONS

This study shows, firstly, that contextual modulations in V1 are dynamic processes and do not merely take place between a static receptive field "center" and "surround". Interestingly, very short frame durations of 20 milliseconds do not elicit negative interactions in V1, suggesting that they need more time to build up, whereas the positive interactions act faster. Most strikingly, nonlinear interactions in V2 are more prominent for the shorter frame duration. **We conclude that the fast V2 responses to texture borders arise independent of the slower contextual modulations in V1.**

References:

Schmid AM, Purpura KP, Ohiorhenuan IE, Mechler F and Victor JD (2009) Subpopulations of neurons in visual area V2 perform differentiation and integration operations in space and time. Front. Syst. Neurosci. 3:15.

Acknowledgment:

This study was supported by grant NIH EY09314.