Input diversity in the synaptic receptive field of V1 cells

Fournier Julien, Monier Cyril and Frégnac Yves

CA: J.F. and Y.F
Unit of Neuroscience, Information and Complexity (UNIC)
CNRS, Gif-sur-Yvette, 91 198, France
Email: julien.fournier@unic.cnrs-gif.fr, yves.fregnac@unic.cnrs-gif.fr

We have read with interest and pleasure the review made by Sedigh-Sarvestani et al based on our original paper on "Hidden complexity of synaptic receptive fields in cat V1" (Fournier et al., 2014). We would like to further discuss here two particular issues they raised, since our own work suggests a different interpretation.

1. Receptive field subunits recovered from spiking responses

Sedigh-Sarvestani et al. summarize the consensus that studies using spike-triggered covariance (STC) techniques "generally *indicate[d] that simple and complex cells are not purely linear and nonlinear operators but instead form a continuum*". Previous STC analyses performed in macaque V1 indeed showed that the second-order components of spiking receptive fields (RFs) generally cover up multiple subunits, tuned to distinct stimulus features, in both Simple and Complex cells (Rust et al., 2005; Chen et al., 2007). But in cats, STC methods suggested that the second-order nonlinearities of V1 RFs are consistent with the LN model for Simple cells and the energy model for Complex cells (Touryan et al., 2002, 2005; Felsen et al., 2005). Our combined analysis on spiking and subthreshold responses solve this apparent controversy: by mapping the selectivity of the spiking response in the stimulus subspace identified at the subthreshold level, we showed that the diversity of RF subunits observed in the subthreshold response is actually represented in the spike train, although it is not readily accessible from the spiking response with classical STC techniques (see Figure 10 in Fournier et al., 2014). The apparent discrepancy between previous STC reports in cat and macaque V1 is therefore most likely due to the sensitivity of STC methods to the number of recorded spikes relative to the dimensionality of the input stimulus (Rust et al., 2005; Levy et al. 2013) rather than to interspecies differences. More generally, our intracellular approach shows that subthreshold responses are much more appropriate than spike records to infer the diversity of the synaptic input map and assess the functional continuity between Simple and Complex receptive fields (also see Priebe et al., 2004).

2. Diversity in the tuning of excitatory and inhibitory synaptic inputs

As reviewed by Sedigh-Sarvestani et al., our intracellular work revealed Complex-like subunits with a wide variety of orientation preferences and with no systematic relationship to the selectivity of the linear RF (Fournier et al., 2014, Fig. 7). Sedigh-Sarvestani et al. underline quite rightly the interest of combining covariance-based techniques with direct conductance measurements. Nevertheless, while they relay the view that existing conductance studies are not supportive of such diversity of synaptic inputs, they limit their review to reports arguing for

iso-oriented excitation and inhibition (Anderson et al., 2000; Tan et al., 2011) and overlook several other in-depth studies which clearly showed a much larger diversity of configuration of orientation selectivity between excitation and inhibition (Martinez et al., 2002; Schummers et al., 2002; Monier et al., 2003, 2008; Mariño et al., 2005). We already demonstrated (Monier et al., 2003) that the apparent discrepancy between those different reports stems from methodological issues related to the way the tuning curves were fitted and that the diversity in the selectivity of the conductance inputs seems equally present in the raw data. A consensual view would be to acknowledge, once and for all, that while excitation and inhibition are often tuned to the same orientation (~60% in Monier et al., 2003), a significant proportion of cells also reveal cross-oriented inhibition (~40% in Monier et al., 2003).

One should keep in mind that all these conductance studies measured global excitation and inhibition, pooling the contributions from many different presynaptic cells which might individually have different selectivity. Therefore, these studies could only look at the tip of the iceberg of the functional diversity conveyed by the synaptic afferents. Sedigh-Sarvestani et al. also emphasize that while we found non-oriented inhibitory RF subunits, there has been no clear evidence of untuned inhibition in previous conductance studies or earlier STC reports. This finding is furthermore interesting, because untuned inhibition was proposed first as a mechanism necessary to account for contrast invariance of V1 cells (Lauritzen and Miller, 2003) before being confirmed experimentally (Hirsch et al., 2003; Lauritzen and Miller, 2003; Nowak et al., 2008; Liu et al., 2009).

We agree that further conductance measurements would definitely help clarifying the synaptic nature of the RF subunits identified with covariance-based methods. The similarity between the distributions of orientation selectivity we reported lately (Fournier et al., 2014) and in our previous conductance measurements (Monier et al., 2003, 2008) suggests that one should expect at least a comparable functional diversity of RF subunits at the conductance level to what we described at the membrane potential level.

Our reviewed work has been supported by the CNRS, the National Agency of Research (ANR) and European FET initiatives (Facets, BrainSales and the Human Brain Project).

References

Chen X, Han F, Poo M-M, Dan Y (2007) Excitatory and suppressive receptive field subunits in awake monkey primary visual cortex (V1). PNAS 104:19120–19125.

Felsen G, Touryan J, Han F, Dan Y (2005) Cortical sensitivity to visual features in natural scenes. PLoS Biol 3, e342.

Fournier J, Monier C, Levy M, Marre O, Sári K, Kisvárday ZF, Frégnac Y (2014) Hidden complexity of synaptic receptive fields in cat V1. The Journal of neuroscience 34:5515–5528.

Hirsch J, Martinez L, Pillai C, Alonso J, Wang Q, Sommer F (2003) Functionally distinct inhibitory neurons at the first stage of visual cortical processing. Nature neuroscience 6:1300–1308.

Lauritzen TZ, Miller KD (2003) Different roles for simple-cell and complex-cell inhibition in V1. The Journal of neuroscience 23:10201–10213.

Liu BH, Li P, Li Y, Sun YJ, Yanagawa Y, Obata K, Zhang LI, Tao HW (2009) Visual receptive field structure of cortical inhibitory neurons revealed by two-photon imaging guided recording. The Journal of neuroscience 29:10520–10532.

Mariño J, Schummers J, Lyon DC, Schwabe L, Beck O, Wiesing P, Obermayer K, Sur M (2005) Invariant computations in local cortical networks with balanced excitation and inhibition. Nature Neuroscience 8:194–201.

Martinez L, Alonso J, Reid R, Hirsch J (2002) Laminar processing of stimulus orientation in cat visual cortex. Journal of Physiology 540:321–333.

Monier C, Chavane F, Baudot P, Graham L, Fregnac Y (2003) Orientation and direction selectivity of synaptic inputs in visual cortical neurons: a diversity of combinations produces spike tuning. Neuron 37:663–680.

Monier C, Fournier J, Frégnac Y (2008) In vitro and in vivo measures of evoked excitatory and inhibitory conductance dynamics in sensory cortices. Journal of Neuroscience Methods 169:323–365.

Nowak LG, Sanchez-Vives M V, McCormick DA (2008) Lack of orientation and direction selectivity in a subgroup of fast-spiking inhibitory interneurons: cellular and synaptic mechanisms and comparison with other electrophysiological cell types. Cerebral Cortex 18:1058–1078.

Priebe NJ, Mechler F, Carandini M, Ferster D (2004) The contribution of spike threshold to the dichotomy of cortical simple and complex cells. Nature neuroscience 7:1113–1122.

Rust NC, Schwartz O, Movshon JA, Simoncelli EP (2005) Spatiotemporal elements of macaque v1 receptive fields. Neuron 46:945–956.

Schummers J, Marino J, Sur M (2002) Synaptic integration by V1 neurons depends on location within the orientation map. Neuron 36:969–978.

Touryan J, Felsen G, Dan Y (2005) Spatial structure of complex cell receptive fields measured with natural images. Neuron 45:781–791.

Touryan J, Lau B, Dan Y (2002) Isolation of relevant visual features from random stimuli for cortical complex cells. The Journal of neuroscience 22:10811–10818.