What is the other 85% of V1 doing?

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Main Points

• There is still much that we do not understand about V1 function.

• Acknowledging this fact opens the door to new theories.
The “standard model”
V1 space-time receptive field

(Courtesy of Dario Ringach)
The problem

- Neurons are highly nonlinear
- Recurrent circuits of neurons are even more nonlinear
- There is no general method for characterizing nonlinear systems
Nonlinearities

• Action potentials

• Adaptation

• Dendritic trees
be difficult to achieve ([71]; see also Figure 7 in [72]). The precise lower limit on compartment size in the thin dendrites of pyramidal cells remains to be determined, perhaps through the use of voltage-sensitive dyes [73] and highly focal uncaging techniques [74].

Getting at the inner neuron

What are the implications of these findings for single-neuron computation? Could there be an underlying principle that permits the full complexity of a dendritic tree to be represented in highly simplified terms? The available data suggest that the thin terminal branches of the apical and basal trees of pyramidal cells provide a set of independent non-linear 'subunits' that sum up their synaptic inputs and then apply a sigmoidal thresholding non-linearity to the output. In this scenario, how should the outputs of multiple subunits be combined to influence the cell's overall response? In the few experimental studies that have addressed the question of location dependent synaptic summation, so far only involving simple spatial integration scenarios, the data are most consistent with a linear or sublinear summation rule for signals that originate in different dendritic branches [30, 75–78]. Building on these findings, one can formulate a working model in which the thin branches are the integrative subunits of pyramidal neurons. According to this model, each thin-branch subunit sums up its synaptic drive and then applies a sigmoidal thresholding non-linearity to the result, and the subunit outputs are summed linearly within the main trunks and cell body before output spike generation. This hypothesis is interesting, in that it states that an individual pyramidal neuron functions something like a conventional two-layer abstract 'neural network' [12], in which the thin dendritic branches themselves act like classical point neurons (Figure 3b).

Poirazi and co-workers [79/C15/C15] used a detailed CA1 pyramidal cell model [80] to test the two-layer neural network hypothesis. The authors used a complex set of

Figure 3

Current Opinion in Neurobiology

**Simplified models of pyramidal cells.**

(a) CA1 pyramidal cell morphology [123]. A grey triangular soma was added for clarity.

(b) Two-layer sum-of-sigoids model as discussed by Poirazi et al. [79/C15/C15]. All thin branches are treated as independent subunits with sigmoidal thresholds whose outputs are summed linearly in the main trunks and cell body. Small grey circles labelled $\alpha_i$ represent subunit weights, which might vary as a function of location or branch order.

(c) A next generation single neuron model could include a multiplicative interaction between proximal and distal integrative regions of the cell. Overall output of such a three-layer model might be expressed using the form $y_1 + \alpha y_2$. 

The reductionist approach

- Use simple, “controlled” stimuli (bars, spots, gratings)
- Record from one neuron at a time
Five problems with the current view of V1

1. Biased sampling
2. Biased stimuli
3. Biased theories
4. Interdependence and context
5. Ecological deviance
1. Biased sampling

- Neurons with large (extracellular) action potentials
- “Visually responsive” neurons
- Neurons with high firing rates
Distribution of the Brain’s Energy Budget

- Activations
- Spontaneous Activity
- Vegetative Functions
Brain Signaling-Related Energy Expenditure

Distribution of ATP consumption for a mean action potential rate of 4 Hz

(Ignores the energy expenditure unrelated to signaling as well as glial glycolysis associated with transient increases in activity)

Adapted From Attwell & Laughlin
JCBF&M 21:1133-1145, 2001
**Extreme sparse coding**

- Gilles Laurent - mushroom body, insect
- Michael Fee - HVC, zebra finch
- Tony Zador - auditory cortex, mouse
- Bill Skaggs - hippocampus, primate
- Harvey Swadow - motor cortex, rabbit
- Michael Brecht - barrel cortex, rat
- Christof Koch - inferotemportal cortex, human
Exponential firing rate distribution

- Mean = 1 Hz
- Mean = 4 Hz

The graph shows the probability distribution of firing rates for two different mean values.
Sampling bias

![Graph showing the relationship between measured mean rate and threshold, and the fraction of the population as a function of threshold.](image)
Estimated fraction of population characterized

- Missed neurons due to small action potentials (5-10%)
- Missed neurons due to unresponsiveness (5-10%)
- Missed neurons due to low firing rates (50-60%)

Even allowing for some overlap among these populations would yield the generous estimate that **40% of the population has been adequately sampled.**
2. Biased stimuli
Searching the entire stimulus space is impossible

$8 \times 8$ patch with 6 bits of gray level $= 2^{384} > 10^{100}$ possible combinations.
3. Biased theories

• Emphasis on “telling a story” encourages investigators to demonstrate when a theory explains data, not when a theory provides a poor model.

• Data-driven vs. functional theories (e.g., spatial-frequency tuning).

• Simple/complex/hypercomplex - are these categories real, or the result of the way neurons were stimulated with bars of light?
How do you classify simple vs. complex?

Skottun et al. (1991)  
Kagan et al. (2002)
Mata & Ringach (2004)

\( \alpha = +1.00 \)
\( \rho = -0.91 \)
\( \delta = +0.94 \)
\( \omega = -0.36 \)
\( \Delta \phi = +3.00 \)

\( \alpha = +0.99 \)
\( \rho = -0.80 \)
\( \delta = +1.05 \)
\( \omega = -0.38 \)
\( \Delta \phi = +0.37 \)

\( \alpha = +0.92 \)
\( \rho = -0.59 \)
\( \delta = +0.59 \)
\( \omega = -0.21 \)
\( \Delta \phi = +2.75 \)

\( \alpha = +0.99 \)
\( \rho = -0.94 \)
\( \delta = NA \)
\( \omega = NA \)
\( \Delta \phi = +3.02 \)

\( \alpha = +1.00 \)
\( \rho = -0.83 \)
\( \delta = NA \)
\( \omega = NA \)
\( \Delta \phi = +2.99 \)

\( \alpha = +0.95 \)
\( \rho = -0.56 \)
\( \delta = NA \)
\( \omega = NA \)
\( \Delta \phi = +2.79 \)

\( \alpha = +0.64 \)
\( \rho = +0.18 \)
\( \delta = +0.37 \)
\( \omega = +0.26 \)
\( \Delta \phi = +1.11 \)

\( \alpha = +0.70 \)
\( \rho = -0.30 \)
\( \delta = +0.44 \)
\( \omega = +0.01 \)
\( \Delta \phi = +2.16 \)

\( \alpha = +0.88 \)
\( \rho = -0.60 \)
\( \delta = +0.71 \)
\( \omega = -0.16 \)
\( \Delta \phi = +0.28 \)

\( \alpha = +0.13 \)
\( \rho = +0.93 \)
\( \delta = +0.01 \)
\( \omega = +0.89 \)
\( \Delta \phi = +0.15 \)
Do V1 neurons act as feature detectors?
Vision is a difficult problem.

Good theories need to be functionally driven as well as data driven.
Surface representation

- We live in a three-dimensional world.
- The fundamental causes of images are surfaces reflecting light, not two-dimensional features such as spots, bars, edges or gratings.
- We rarely see the surface of an object in its entirety.

Example: ‘Mooney faces’
Example: ‘Mooney faces’
Completion depends upon occlusion
4. Interdependence and context

• < 5% of the excitatory input in layer 4 arises from LGN (Peters & Payne, 1993).

• Geniculate input is responsible for < 35% of a V1 neuron’s response (Chung & Ferster, 1998).

• Ongoing population activity can account for 80% of an individual V1 neuron’s response variance (Arieli et al., 1996).
How to study effects of context?

Knierim & Van Essen (1992)

Sillito et al. (1995)
Context in natural scenes sparsifies responses

Vinje & Gallant (2000, 2002)
Synchrony
Contour integration

Models of contour integration


Figure 8: Illustration of connection fields for curves (top, based on co-circularity, Parent & Zucker, 1989) and textures (bottom, based on right helicoidal model, Ben-Shahar & Zucker, 2003b). Each position in these fields represents one orientation hypercolumn, while individual bars represent the orientation preference of single neurons, all of which are connected to the central cell in each field. Multiple bars at any given point represent multiple neurons in the same hypercolumn that are connected to the central cell, a result of the dilation of the compatible structure due to broad RF tuning (see the caption of Figure 7). All fields assume that orientation tuning is quantized to 10 degrees and their radius of influence is set to four to five nonoverlapping hypercolumns to reflect a cortical range of horizontal connections (Gilbert & Wiesel, 1989) and hypercolumn diameter of 1.5 mm (to account for ocular dominance domains). (a–d) Examples of co-circularity projection fields (Parent & Zucker, 1989) for cells with orientation preference of 150 degrees (center bars) and different values of curvature tuning based on the implementation by Iverson (1994). (a) $\kappa = 0.0$ (curvature in units of pixels$^{-1}$). (b) $\kappa = 0.08$. (c) $\kappa = 0.16$. (d) $\kappa = 0.24$. (e) The union of all projection fields of all cells with same orientation preference (0 degrees in this case) but different curvature tuning. Note the similarity to the schematic association field in Figure 6b. (f–j) Examples of the texture flow projection fields (Ben-Shahar & Zucker, 2003b) for cells with horizontal orientation preference (center bars) and different curvature tuning. Note the intrinsic dependency on curvatures and the qualitatively different connectivity patterns that they induce. (f) $(\kappa_T, \kappa_N) = (0.0, 0.0)$. (g) $(\kappa_T, \kappa_N) = (0.2, 0.0)$. (h) $(\kappa_T, \kappa_N) = (0.0, 0.2)$. (i) $(\kappa_T, \kappa_N) = (0.1, 0.1)$. (j) $(\kappa_T, \kappa_N) = (0.2, 0.2)$. Note that while the majority of connections link cells of roughly similar orientation, some connect cells of large orientation differences. The fields shown are just a few examples sampled from the models, both of which contain similar (rotated) connection fields for each of the possible orientation preferences in the central hypercolumn. The circles superimposed on d and i are used to characterize retinotopic distance zones for the predictions made in Figure 15.
5. Ecological deviance

Neural responses to time-varying natural scenes deviate significantly from the predictions of current models.

- David, Vinje & Gallant (1999) - can account for 20-30% of response variance with current models.

- Gray & Baker (unpublished observations) - responses to natural movies are often not predicted by simple receptive field models.

V1 neural responses to natural scenes deviate from predictions of simple receptive field models

Data from Gray lab (J. Baker)
Qualitative characterization of the failures

The widespread failure of the linear model to predict responses for many but not all complex stimuli indicates a high but stimulus-dependent degree of nonlinearity. By comparing the predicted and actual responses, we can characterize the different failure modes of the STRF model.

Three sample predictions are shown in Figure 7, A–C, for the same data as in Figures 2, D and E, and 3, A and B. Although the predicted trace (red line) in Figure 7 A accounts for the approximate times at which PSPs occur, it does not capture their precise shape. This observation can be quantified by spectrally resolving the prediction success. For that purpose, we again use the coherence function as a measure of the correlation at each frequency (in this case, between actual and predicted response) (Fig. 7 D, solid line). Clearly, this particular STRF does not predict any response fluctuations faster than /H11015 10 Hz. As a comparison, recall that the response is reliable up to at least 20 Hz (Fig. 7 D, dashed line).

Figure 7 B shows a natural stimulus that elicited a highly reliable response that the STRF predicted only poorly. The example uses the same data as in Figure 2, D and E (central panel). Although the STRF predicts the timing of the PSPs, it underestimates their amplitudes (Fig. 7 B, arrows).

As demonstrated by Figure 7 C, the linear model can sometimes fail completely in predicting PSPs. The arrows point to PSPs that occurred reliably in the actual response but were not predicted by the STRF. Such failures lead to a correspondingly weak coherence (Fig. 7 F) and a small prediction success (in this case, 8%).

The inability of the STRF to predict the correct size of the PSPs and its occasional failure to predict the occurrence of PSPs can be visualized in a calibration plot in which the actual response is plotted against the predicted response (Fig. 7 G–I). In Figure 7 G, most dots cluster around the identity line, suggesting an overall match between actual and predicted response. In Figure 7, H and I, however, most of the dots fall clearly above the identity line, corresponding to underestimated PSP amplitudes or PSPs that were missed by the STRF.

Ruling out trivial nonlinearities

Although the failure to predict PSPs suggests the existence of complex nonlinearities, the incorrect size of predicted PSPs could...
Single unit recording
## Summary

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<th>Biased sampling</th>
<th>Biased stimuli</th>
<th>Biased theories</th>
<th>Interdep. &amp; context</th>
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<tr>
<td><strong>Problem</strong></td>
<td>large neurons; visually responsive neurons; neurons with high firing-rates</td>
<td>use of reduced stimuli such as bars, spots, &amp; gratings</td>
<td>simple/complex cells; data-driven theories</td>
<td>influence of intra-cortical input; effect of context; synchrony</td>
<td>responses to natural scenes deviate from predictions of standard models</td>
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<td><strong>Solution</strong></td>
<td>chronically implanted electrodes; parallel recording arrays</td>
<td>use natural scenes, ecologically relevant stimuli</td>
<td>consider more functional/computational theories that solve problems of vision</td>
<td>examine how context affects responses in natural scenes</td>
<td>develop models that can account for responses to natural images</td>
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Bottom line

- Variance explained: 0.3-0.4
- Proportion of cells studied: 0 to 1
- Approximately 85% of V1 function not understood
Conclusions

• We still do not understand the vast majority of what V1 is doing under natural conditions.

• What is needed:
  – Natural scenes, surfaces
  – Simultaneous recordings from large populations of neurons

• We should be prepared for some surprises.