What Are All Those Neurons in Foveal V1 Doing?

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Fibers of Henle

ganglion cells
amacrine cells
bipolar cells
horizontal cells
photoreceptors

GCL
IPL
INL
OPL
HFL
ONL
PRs
RPE
Ch/CC
Sclera

SD-OCT Scan Angle

Measuring HFL Thickness

Horizontal frame-averaged B-scans acquired with Cirrus at the two extreme horizontal entrance positions were used to measure the contribution of this hyporeflective zone corresponding to HFL was reported as a percentage of the total distance between the ELM and the OPL.

The relative contribution of different zones of reflectivity between the external limiting membrane (ELM) and the hyporeflective layer was calculated using Bioptigen systems' commercial software (version 4.5), which averages 20 individual B-scans each consisting of 1024 A-scans where the nominal spacing between scans was set to zero. The rendered B-scans have an aspect ratio of 2:1 (i.e., the scale is doubled in the axial dimension), but this was corrected to 1:1 before data analysis described below.

Frame-averaged B-scans obtained with Bioptigen from each subject were exported to Image J, where a manual tool was used to segment the hyporeflective zone corresponding to HFL.

The position was documented using the pupil camera. At each entrance pupil location, a horizontal and vertical frame were placed at multiple intervals superiorly, inferiorly, temporally, and nasally. B-scans rendered in real time to obtain a beam entry position in which both the horizontal and the vertical B-scans appeared “flat” (i.e., symmetrical). The absolute beam entry position of the SD-OCT beam. This was used in conjunction with monitoring of the pupil position during scans and that indicates the entrance position from where the B-scan appeared flat was measured.

A headrest was used to stabilize subjects, and deviation of foveal fixation was confirmed by the midpoint position of the horizontal cells running in HFL. GCL, ganglion cells.

Revealing Henle’s Fiber Layer using SD-OCT 1487

Mammalian foveal histology, showing the photoreceptors, horizontal cells, bipolar cells, amacrine cells, and ganglion cells.
Midget ganglion cells receive input from midget bipolar cells.

Ratio is 1:1 in fovea.
Retinal ganglion cell sampling array
(shown at one dot for every 20 ganglion cells)

\[ \Delta \approx 0.01(|E| + 1) \]

(from Anderson & Van Essen, 1995)
Letter size vs. eccentricity
(Anstis, 1974)
Fig. 3. All letters should be equally readable when centre of this chart is fixated, since each letter is ten times its threshold height.
‘Crowding’

From: Whitney & Levi (2011)
Foveal oversampling in LGN and Cortex
(Connolly & Van Essen, 1984)

“...despite the fact that the estimated total number of LGN cells is similar to the total number of retinal ganglion cells, their ratio must vary from many LGN cells per retinal ganglion cell for the fovea to fewer than one LGN cell per retinal ganglion cell in the periphery.”
Cortex:LGN cell ratio ranges from 1000:1 in fovea to 100:1 in periphery (Connolly & Van Essen, 1984)
Fixational eye movements
(drift)

(from Austin Roorda, UC Berkeley)
Bayesian model of dynamic image stabilization in the visual system

Yoram Burak, Uri Rokni, Markus Meister, and Haim Sompolinsky

C No Drift  Drift

D

Retina

\[ y \]

What

i

Where

x

\[ y \]

Retina

\[ i \]

What

x

Where
Traditional models compute motion and form independently
Motion and form must be estimated simultaneously
Retinal image motion helps pattern discrimination

Graphical model for separating form and motion
(Alex Anderson, Ph.D. thesis)

Eye position
Spikes
(from LGN afferents)
Pattern

\[ \hat{S} = \arg \max_S \log P(R|S) \]
Given current estimate of position (X), update S
Given current estimate of pattern \((S)\), update \(X\)

\[
P(X_t|R_{0:t}) \\
\downarrow \\
P(X_{t+1}|R_{0:t})
\]

\[
P(X_{t+1}|R_{0:t}) \xrightarrow{S^t} P(R_{t+1}|X_{t+1}, S = S^t)
\]

\[
P(X_{t+1}|R_{0:t+1})
\]
Joint estimation of form and motion
(Alex Anderson, Ph.D. thesis)

Image Projected on the Retina and Generated Spikes at $t = 0.05$ ms
Motion helps estimation of pattern S
Motion restores acuity in the case of cone loss

Figure 3:

a, Tumbling E with a retinal cone lattice that has 30 percent of the cones dropped out randomly.

b, SNR as a function of time for a moving and a stationary retina plus or minus half a standard deviation \( p = 0.003 \) at \( t = 700 \text{ ms} \).

c, d, An example reconstructed E in the motion and no motion cases.
Including a prior over $S$

$$S = D A$$

$$\hat{A} = \arg \max_A \log P(R|A) + \log P(A)$$

Sparse prior

Eye position

Spikes (from LGN afferents)

Pattern
Natural image pattern may be inferred with a sparse prior using a Gabor-like basis similar to V1 receptive fields.

- **Figure 4:** Neurons with structured receptive fields improve inference: a, A natural scene patch projected onto a retina that moves according to a random walk. The generated spikes are decoded using three pattern priors (IND: independent pixel prior, PCA: gaussian prior, SP: dictionary trained with sparse coding with both a L1 and L2 prior).
  - **b,** SNR at $t = 600$ ms relative to PCA averaged over 15 trials (different patches and eye trajectories). Error bars show 95\% confidence intervals.
  - **c,** A random set of 25 elements from the sparse coding dictionary.
  - **d,** **e,** **f,** Example reconstructed patterns for each method after 600 ms.

- **IND:** SNR = 2.48
- **PCA:** SNR = 8.06
- **SP:** SNR = 11.97
Main points

• The foveal representation in LGN, and again in cortex, is highly oversampled, *in terms of number of neurons per ganglion cell*, with respect to the periphery.

• Phenomena such as crowding and shape adaptation suggest a looser representation of shape in the periphery that is more subject to grouping or contextual influences than in the fovea.

• Neural circuits in the foveal portion of V1 *must* take into account estimates of eye position or motion in order to properly integrate spatial information.

• One possibility is separate populations of neurons that interact multiplicatively in order to explicitly disentangle form and motion.