Really more like: “multiple views of cortex”

1. What is cortex?
   a. uniformity
   b. canonical microcircuit

2. What should cortex do?
   a. theory (Barlow 1994)
   b. representations for learning

3. What can you do with more cortex?
   a. one area → acuity & computation
   b. many areas → maps
Why Cortex?

Lichtman & Sanes

Krubitzer & Kaas
Two Views of Cortex

early sensory cortex

Hubel & Wiesel 1962

frontal cortex

Mante, Sussillo et al. 2013
Uniformity of Cortex I: Modules

Hubel & Wiesel 1974

Hubel 1982

visual field

receptive fields
Uniformity of Cortex I: Modules

Hubel & Wiesel
“Thus the machinery may be roughly uniform over the whole striate cortex, the differences being in the inputs. A given region of cortex simply digests what is brought to it, and the process is the same everywhere. . . . It may be that there is a great developmental advantage in designing such a machinery once only, and repeating it over and over monotonously, like a crystal, for all parts of the visual field.”

### Uniformity of Cortex II: Anatomy

![Brain section image]

#### Table: Mean thickness of neocortical layers

<table>
<thead>
<tr>
<th></th>
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</thead>
<tbody>
<tr>
<td>Mouse</td>
<td>109.2 ± 6.7</td>
<td>111.9 ± 6.9</td>
<td>110.8 ± 7.1</td>
<td>110.5 ± 6.5</td>
<td>104.7 ± 7.2</td>
<td>112.2 ± 6.0</td>
<td>109.9 ± 6.8</td>
</tr>
<tr>
<td>Rat</td>
<td>108.2 ± 5.8</td>
<td>107.0 ± 6.7</td>
<td>104.3 ± 7.2</td>
<td>107.7 ± 9.2</td>
<td>105.2 ± 6.8</td>
<td>107.8 ± 7.9</td>
<td>106.7 ± 7.4</td>
</tr>
<tr>
<td>Cat</td>
<td>103.9 ± 7.6</td>
<td>106.6 ± 7.2</td>
<td>108.0 ± 6.2</td>
<td>113.8 ± 7.3</td>
<td>110.6 ± 7.4</td>
<td>109.8 ± 9.9</td>
<td>108.8 ± 7.7</td>
</tr>
<tr>
<td>Monkey</td>
<td>110.2 ± 9.4</td>
<td>109.4 ± 9.4</td>
<td>112.0 ± 11.1</td>
<td>109.8 ± 10.3</td>
<td>114.6 ± 9.9</td>
<td>----</td>
<td>----</td>
</tr>
<tr>
<td>Man</td>
<td>102.3 ± 9.5</td>
<td>103.7 ± 5.8</td>
<td>103.3 ± 8.6</td>
<td>107.7 ± 7.5</td>
<td>104.1 ± 12.5</td>
<td>----</td>
<td>----</td>
</tr>
</tbody>
</table>

Mean ± s.d.

---

Uniformity of Cortex II: Anatomy

Szentágothai 1975
Uniformity of Cortex II: Transcriptomics?

Glutamatergic: 19 cell types

GABAergic: 23 cell types

Tasic et al. 2016
Schlaggar & O’Leary 1991

Uniformity of Cortex III: Transplantation
Uniformity of Cortex III: Transplantation

Schlaggar & O’Leary 1991
Re-routing experiments (ferret)

lab of Mriganka Sur
Uniformity of Cortex IV: Re-routing

Roe et al. 1990
Uniformity of Cortex IV: Re-routing

Sur et al. 1988
RF structure learned from natural images

Olshausen & Field 1996
Uniformity of cortex V: Computation

- End-stopped
- Complex
- Simple
- LGN (center-surround)

Hubel & Wiesel

Remove known correlations:
- Curvature

Invariant:
- a) position
- b) sign of contrast

Represent "suspicious coincidences"

Remove known correlations:
- Contrast
Uniformity of cortex V: Computation

“Cardinal Cells”? (Barlow 1972)

- Selectivity
- Generalization

Selectivity
Generalization
Selectivity

Riesenhuber & Poggio 1999
A woman is throwing a **frisbee** in a park.

A little **girl** sitting on a bed with a teddy bear.

A group of people shopping at an outdoor market.

There are many vegetables at the fruit stand.

Uniformity of cortex V: Computation

Douglas & Martin 1991
"Canonical Cortical Circuit"

- Smooth cells
- P2 & 3 (4)
- P5 & 6

Thalamus

- L1
- L2/3
- L4
- L5
- L6

Numbers represent the proportion of all area 17 synapses that are E→E

Douglas & Martin 1991

Binzegger, Douglas & Martin 2004
Dynamical models using recurrent connectivity
A puzzling feature of surround suppression

Ozeki et al 2009
Uniformity of Cortex V: Connectomics

Bock et al. 2011
A connectivity matrix for cortex

slices cut from C2 of mouse barrel cortex

Lefort et al. 2009
tested 8895 possible synaptic connections and found 909 functional synaptic connections (10.2%)

A connectivity matrix for cortex
Logic of intra-cortical connections

Natural images

Time

Ca$^{2+}$ signal

Ca$^{2+}$ imaging

Reverse correlation

Linear receptive field (RF)

20°

Example Layer 2/3 volume

50 μm

Cossell et al. 2015
Cossell et al. 2015

Logic of intra-cortical connections

50% of total connection wgt.
12% of most correlated pairs

Cumulative distribution of pairs

Spatial RF correlation

Cumulative synaptic weight
Logic of intra-cortical connections

50% of total connection wgt.
12% of most correlated pairs

Cumulative synaptic weight

Spatial RF correlation

50% of total connection wgt.
12% of most correlated pairs

Prediction performance

0.4
0.2
0
Prediction of connection strength

Response correlation
ON+OFF overlap
OFF overlap
RF correlation
ON overlap
\( \Delta \) Orientation
Cortical distance
Shuffled resp. corr.

Cossell et al. 2015
Cortical inhibition: theme and variations

Optogenetic mapping of inhibitory connectivity

Kätzel et al. 2011
The strength of a connection is expressed as the average percentage of inhibitory charge flow arising from identified inputs in a layer. (s.d. in parentheses)

Kätzel et al. 2011
Cortical inhibition: theme and variations: role of plasticity?
Macroscopic view of cortex
Scaling laws: More cortex = smarter?

\[ E = 0.07 \times P^{2/3} \]

Body weight (Kilograms)

Brain weight (grams)

- Primates
- Bony Fish
- Mammals
- Reptiles
- Birds

Crile & Quiring
Half of area V1 represents the central 10° (2% of the visual field)
See better?

A

B
1.5°

C
3°

D
6°

E
9°

F
12°

G
Inferior vertical meridian

H
Superior vertical meridian

I
Right horizontal meridian

Duncan & Boynton 2003
Two tests of visual acuity

- Grating acuity
- Vernier acuity

Contrast:
- Low
- High

Spatial frequency:
- Low
- High
Acuity scales with cortical magnification factor.
Subjects with larger cortical magnification factors have better vernier acuity.

---

A

\[ R = -0.46 \]

\( \text{Vernier } \beta \text{ parameter} \)

\( \text{Cortical } \beta \text{ parameter} \)

B

\[ R = -0.16 \]

\( \text{Gragting } \beta \text{ parameter} \)

\( \text{Cortical } \beta \text{ parameter} \)
What can you do with more cortex?
More areas = more maps

Lateral view of monkey brain

Medial view of monkey brain

Cortex unfolded

Felleman and Van Essen 1991
The perfect map?
Abstract maps for rapid search

Space

Feature

Streets
Aberdeen Rd ........C7
Academy St ..........D9
Acorn Pk ............F9
Acton St ............C7
Adamian Pk ..........C9
Adams St ..........D9
Addison St ..........D9
Aerial St ............C8
Albermarle St ........D8
Alfred Rd ..........E9
Allen St ..........D9
Alpine St ............C7

Longwood Ave ........L12
The desired map depends on what it will be used for.
Problem of detecting common surfaces

Guzmann 1968
V1 as a map sorted by orientation

after Hubel & Wiesel 1962
V1: Abstract maps for rapid search

Space

Feature

Tootell et al. 1982
Abstract maps for rapid search

Streets
Aberdeen Rd ........C7
Academy St ..........D9
Acorn Pk ............F9
Acton St .............C7
Adamian Pk ..........C9
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Aerial St ..........C8
Albermarle St ........D8
Alfred Rd ............E9
Allen St ............D9
Alpine St ..........C7

Longwood Ave ......L12
Intrinsic connectivity of V1 is not random.

“like-to-like” ellipse of patches

Bosking et al. 1997
Anisotropy for co-linearity?
Guzman’s linking via intrinsic connectivity in V1

Guzmann 1968
More areas = more maps

Felleman and Van Essen 1991