Cortico-cortical long-range connectivity: Anatomical data from mouse and monkey

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Cortico-cortical long-range connections
Tracer methods

Square root compartments

Global connectivity in the mouse cortex

Patchy connections in large brains

Human cortical white matter
Tracer methods

Using axonal transport:

Slow transport: up to 30 mm/day
Fast transport: up to 40 cm/day
anterograde tracing

where to?
Anterograde: radioactive amino acids

phaseolus vulgaris (PHA-L)

WGA (wheet germ agglutinine)

biotinylated dextran amine (BDA)
Anterograde staining after Injection of the tracer BDA

From Schüz et al., 2005
retrograde tracing

where from?
Retrograde: fluorescent dyes (e.g. Rhodamin, Fast Blue, Fluorogold)

horse-radish peroxidase (HRP) (predominantly retrogr.)

Both directions: biocytin (biotin + Lysin)

neurotrophic viruses (e.g. Herpes simplex or Rabies) – also transsynaptically
Fluorescent dyes, retrograde staining, after injection in Area 17 (light blue) and 41 (greenish blue)
Retrograde Tracer, horseradisch peroxidase

Fig. 66. Correspondence, or lack of correspondence, of the areas defined by their projection and the areas of cortical architectonics. Frontal section through the dorsal part of the right cerebral hemisphere of the rat, at the level of areas 4 and 6. Injection of horseradish peroxidase into the spinal cord, which marks the cell bodies of the corticospinal neurons, the "giant pyramids" (g). The transition between areas 4 and 6 can be recognized because of the different level of the big cells in layer V, (cf. Fig. 63), but the corticospinal neurons are localized in both fields.

From Braitenberg and Schüz, 1998
Retrogradely stained pyramidal cells, mouse cortex (BDA)
Tracing in the human brain post-mortem

Superior frontal gyrus

Corp. call

left hemisphere

Gyrus precentralis

Gyrus postcentralis

premotor cortex

motor cortex

somatosensory cortex
Tracers usable in vivo in magnetic resonance imaging (MRI):

Manganese (activity dependent; transsynaptic)

Biocytin
Magnetic resonance imaging and histology of biocytin (type L3) tracer with Gd

From: Mishra et al. (2011) Biocytin-Derived MRI Contrast Agent for Longitudinal Brain Connectivity Studies
Surface area of the cortex (1 hemisphere)

mouse – monkey – human

~ x 1000

1 cm
An abstract scheme for a full set of cortico-cortical connections:

Parcellation into „square root compartments“
(Braitenberg, 1978)
An abstract scheme for a full set of cortico-cortical connections:

Parcellation into „square root compartments“
(Braitenberg, 1978)

N total number of neurons

$\sqrt{N}$ compartments

Each containing $\sqrt{N}$ neurons
Mouse cortex:

\[ N \approx 8-9 \times 10^6 / \text{hemisphere} \]

\[ \sqrt{N} \approx 3000 \text{ compartments, diameter about } 0.17 \text{ mm} \]

Human cortex:

\[ N \approx 10^{10} / \text{hemisphere} \]

\[ \sqrt{N} \approx 100 000 \text{ compartments, diameter ca. } 1 \text{ mm} \]
Mouse, Nissl-stain, Coronal section
Global connectivity of the cortex, a tracer study in the mouse

Together with Daniel Liewald, Denis Chaimow and Monika Dortenmann
Anterograde staining after Injection of the tracer BDA

From Schüz et al., 2005
Mouse

The neurons under
≈0.1 mm² reach    ≈15 mm²

Total neocortex   71 mm²

% of neocortical
surface area      20 %

From Schüz et al., 2005
<table>
<thead>
<tr>
<th></th>
<th>Mouse</th>
<th>Monkey</th>
</tr>
</thead>
<tbody>
<tr>
<td>The neurons under ≈0.1 mm² reach</td>
<td>≈15 mm²</td>
<td>≈120 - 240 mm²</td>
</tr>
<tr>
<td>Total neocortex</td>
<td>71 mm²</td>
<td>6400 mm²</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(Filimonov)</td>
</tr>
<tr>
<td>% of neocortical surface area</td>
<td>20 %</td>
<td>2 – 4 %</td>
</tr>
</tbody>
</table>

From Schüz et al., 2005
From Denis Chaimow
From Denis Chaimow
Fibre length per area

\[ L_A = \frac{\rho}{2} \cdot \frac{N}{l_{\text{testline}}} \]

(Buffon, 1777; Smith and Guttmann, 1953)
Figure 9. A 3-dimensional orientation can be represented by a vector $v$ on a sphere that is parametrized by an angle of elevation $\alpha$ and an azimuthal angle $\theta$. For a uniform distribution of 3-dimensional orientations, the probability density for finding a vector $v$ is equal at any place on the sphere. Given a specific elevation $\alpha$, $v$ is constrained to lie on the circle $c$, which is the horizontal section of the sphere at the elevation $\alpha$. The probability density for any vector to lie on that circle is proportional to its circumference, which is proportional to $\cos \alpha$. Therefore the probability density of finding a vector $v$ with an elevation $\alpha$ in a uniform distribution of orientations is proportional to $\cos \alpha$. 
\[
\left\langle \frac{l_{2D}}{l_{3D}} \right\rangle = \frac{\pi}{2} \int_0^\infty \cos(\alpha) P(\alpha) d\alpha = \int_0^\infty \cos^2(\alpha) d\alpha
\]

\[
= \frac{\pi}{4}
\]

\[
L_A = \frac{\pi}{2} \times \frac{N}{l_{testline}}
\]

\[
L_V = \frac{L_A}{d} \times \left\langle \frac{l_{2D}}{l_{3D}} \right\rangle^{-1} = \frac{1}{d} \times \frac{\pi}{2} \times \frac{N}{l_{testline}} \times \frac{4}{\pi}
\]

\[
= \frac{2N}{l \times 50 \mu m}
\]

From: Denis Chaimow

N = number of intersections  
l = length of test line  
d = diameter of section (50 mm)
Low density: 3 m/mm$^3$

High density: 25 m/mm$^3$
Low density: 3 m/mm$^3$

High density: 25 m/mm$^3$

Total density of axons in the neuropil:

4 km/mm$^3$

25 m/mm$^3$ are 0.6 % of 4 km
Fibre density in the local (=black) field
Procedure:

1) Estimating the total length of stained fibres (assuming 35 mm of axon per neuron)
2) Estimating the fibre length in the hatched regions
3) Subtracting (2) from (1)
Area 4

\[ \text{density up to 5 m/mm}^3 \]

\(|\text{230 input fibres}\)

Area 41

\[ \text{density up to 14 m/mm}^3 \]

\(|\text{540 input fibres}\)

\[ 7700 \text{ py-cells} \]

\[ 2900 \text{ py-cells} \]

\[ \text{density up to 4.6 m/mm}^3 \]

\[ 14 \text{ input fibres} \]

\[ \text{density up to 21 m/mm}^3 \]

\(|\text{890 input fibres}\)
Density in the vicinity of the injection site:

38 - 141 m/mm$^3$ (1 - 3.5% of 4 km)
Connectivity in the horizontal plain

**Measurements**

- **mouse**
  - 0.07 mm² project onto about 12 mm²
  - Density of distant proj. 3 – 25 m/mm³

**Deduced numbers**

- (factor of > 100)
- < 1% of 4 km/mm³
- a few percent of 4 km/mm³

**Conclusions**

- Great spatial divergence
- Projections very weak
- Great spatial convergence
- Great mixing of inputs at any given place
- Short-range input dominating

Most projections within an area and between neighbouring areas.

Diagram showing the distribution of connectivity.
Main conclusions on horizontal connectivity:

1) Great spatial divergence of projections (> x 100 in mouse)

2) A high degree of convergence at any place

3) The largest part of the terminal field (~ 2/3) connects neurons within the same area and in neighbouring areas
Patchy connections in large brains

Together with Nicole Voges, Ad Aertsen, Stefan Rotter
From: Voges, Schüz, Aertsen, Rotter; Progress in Neurobiology (2010)
What is the variability of these patches?

Is it possible to make a generalized model?
<table>
<thead>
<tr>
<th>Literature</th>
<th>Species</th>
<th>cortical area</th>
<th>$\sigma$</th>
<th>$N_p$</th>
<th>$\varphi_p$</th>
<th>$d_p$</th>
<th>$d_{p,\text{max}}$</th>
<th>$d_{cc}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gilbert &amp; Wiesel (1989)</td>
<td>cat</td>
<td>V1</td>
<td>0.2</td>
<td></td>
<td></td>
<td></td>
<td>2 (6-8)</td>
<td></td>
</tr>
<tr>
<td>Buzas et al. (2006)</td>
<td>cat</td>
<td>vis.</td>
<td>0.15</td>
<td></td>
<td>0.25</td>
<td>1.2</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>Read et al. (2001)</td>
<td>cat</td>
<td>A1 (intr.)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Wallace et al. (1991)</td>
<td>cat</td>
<td>A1</td>
<td>3.8</td>
<td>0.8</td>
<td>0.5</td>
<td></td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>Burkhalter &amp; Bernado (1989)</td>
<td>human</td>
<td>V1, V2</td>
<td>0.25</td>
<td>0.3</td>
<td>0.5</td>
<td></td>
<td>6</td>
<td>0.6-1</td>
</tr>
<tr>
<td>Galuske et al. (2000)</td>
<td>human</td>
<td>22, A1 (intr.)</td>
<td>0.4</td>
<td>10-56</td>
<td>0.56-0.86</td>
<td></td>
<td>7, 5</td>
<td>1-1.5,</td>
</tr>
<tr>
<td>Bosking et al. (1997)</td>
<td>shrew</td>
<td>V1 (intr.)</td>
<td>0.2</td>
<td></td>
<td>0.2x</td>
<td>&gt;0.5</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 1: List of publications on patchy projections resulting from extracellular tracer injections ("group data"), ordered according to the analyzed species and cortical areas. Listed are the injection size $\sigma$, the average number of patches per cell/axon $N_p$, the average patch diameter $\varphi_p$, the average and maximum lateral distance between the cell body and the patches $d_p, d_{p,\text{max}}$, the maximum lateral axonal spread $\Sigma$, and the average distance between the patches $d_{cc}$ (all length measurements in millimeters).

<table>
<thead>
<tr>
<th>Literature</th>
<th>Species</th>
<th>cortical area</th>
<th>$\sigma$</th>
<th>$N_p$</th>
<th>$\varphi_p$</th>
<th>$d_p$</th>
<th>$d_{p,\text{max}}$</th>
<th>$d_{cc}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Burkhalter &amp; Charles (1990)</td>
<td>rat</td>
<td>V1, V2</td>
<td>0.1-0.25</td>
<td></td>
<td>0.15-0.25</td>
<td>1.8</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rumberger et al. (2001)</td>
<td>rat</td>
<td>V1, V2 (intr.)</td>
<td>0.3-1</td>
<td></td>
<td>0.37-0.43</td>
<td>0.75</td>
<td></td>
<td>0.9</td>
</tr>
<tr>
<td>Malach et al. (1997)</td>
<td>owl</td>
<td>V5</td>
<td>0.15-3</td>
<td>&gt;29</td>
<td>0.3</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pucak et al. (1996)</td>
<td>monkey</td>
<td>PFC</td>
<td>0.35</td>
<td>12</td>
<td>0.25</td>
<td>2.8</td>
<td>7.5</td>
<td></td>
</tr>
<tr>
<td>Levitt et al. (1993)</td>
<td>macaque</td>
<td>PFC (intr.)</td>
<td>0.2</td>
<td></td>
<td>0.27</td>
<td>7.8</td>
<td>0.5</td>
<td>0.6</td>
</tr>
<tr>
<td>Lund et al. (1993)</td>
<td>macaque</td>
<td>PFC (intr.)</td>
<td>0.2</td>
<td></td>
<td>0.27</td>
<td>1.5</td>
<td>9.4x3</td>
<td>0.54</td>
</tr>
<tr>
<td>Amir et al. (1993)</td>
<td>macaque</td>
<td>V1,2,4 (intr.)</td>
<td>0.2</td>
<td></td>
<td>0.23</td>
<td>4-6</td>
<td>0.43</td>
<td></td>
</tr>
<tr>
<td>Amir et al. (1993)</td>
<td>macaque</td>
<td>V4,7a (intr.)</td>
<td>0.9</td>
<td>15-33</td>
<td>0.31</td>
<td>2.14</td>
<td>8.98</td>
<td>1.56</td>
</tr>
</tbody>
</table>

Table 2: List of publications on patchy projections resulting from extracellular injections, continuation of Table 1.
<table>
<thead>
<tr>
<th>Literature</th>
<th>Species</th>
<th>cortical area</th>
<th>$\sigma$</th>
<th>$N_p$</th>
<th>$\varnothing_p$</th>
<th>$d_p$</th>
<th>$d_{p,max}$</th>
<th>$d_{cc}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Levitt et al.</td>
<td>macaque</td>
<td>V2 (intr.)</td>
<td>0.2-0.3</td>
<td>10-15</td>
<td>0.25-0.3</td>
<td>2</td>
<td>4</td>
<td>0.25-2.2</td>
</tr>
<tr>
<td>(1994)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rockland &amp; Knutson</td>
<td>macaque</td>
<td>V1 (intr.)</td>
<td>0.1</td>
<td></td>
<td></td>
<td>8</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(2001)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stettler et al.</td>
<td>macaque</td>
<td>V1, V2</td>
<td>0.2</td>
<td></td>
<td></td>
<td>(7)</td>
<td></td>
<td>0.75</td>
</tr>
<tr>
<td>(2002)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tanigawa et al.</td>
<td>macaque</td>
<td>V1, TE</td>
<td>0.23-0.54</td>
<td>5-21,</td>
<td>0.25x0.39, 0.9-2,</td>
<td>2.5-7.7</td>
<td></td>
<td>1.3</td>
</tr>
<tr>
<td>(2005)</td>
<td></td>
<td></td>
<td></td>
<td>9-43,</td>
<td>0.35x0.55, 2.5-7.7</td>
<td></td>
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<td></td>
</tr>
</tbody>
</table>

Table 3: List of publications on patchy projections resulting from extracellular injections, continuation of Tables 1 and 2.
Table 4: List of publications on 2D or 3D reconstructions of single patchy PC projections, ordered according to the species and the cortical area they refer to. Listed are the layers, the average number of patches per cell/axon $N_p$, the average patch diameter $\varphi_p$, the average and maximum lateral distance between the cell body and the patches $d_p, d_{p,max}$, the maximum lateral axonal spread $\Sigma$, and the average distance between the patches $d_{cc}$. All measurements are given in millimeters. Part one: intracellular injections.

<table>
<thead>
<tr>
<th>Literature</th>
<th>Species</th>
<th>cortical area</th>
<th>layer</th>
<th>$N_p$</th>
<th>$\varphi_p$</th>
<th>$d_p$</th>
<th>$d_{p,max}$</th>
<th>$d_{cc}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gilbert &amp; Wiesel (1983)</td>
<td>cat</td>
<td>vis. (intr.)</td>
<td>2-6</td>
<td>0.2-0.3</td>
<td>2</td>
<td>4</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Martin &amp; Whitteridge (1984)</td>
<td>cat</td>
<td>V1 (intr.)</td>
<td>2-5</td>
<td>0.1</td>
<td>0.2-2.2</td>
<td>1</td>
<td></td>
<td></td>
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<tr>
<td>Kisvarday et al. (1986)</td>
<td>cat</td>
<td>V1 (intr.)</td>
<td>3</td>
<td>0.3-0.4</td>
<td>0.5-1</td>
<td>2</td>
<td></td>
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</tr>
<tr>
<td>Gabbott et al. (1987)</td>
<td>cat</td>
<td>V1</td>
<td>5/6</td>
<td>3</td>
<td>1.1-1.5</td>
<td>2.6</td>
<td></td>
<td></td>
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<tr>
<td>Binzegger et al. (2007)</td>
<td>cat</td>
<td>V1</td>
<td>2-6</td>
<td>0-5</td>
<td>0.35-0.6</td>
<td>0.1-1</td>
<td>0.21</td>
<td></td>
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<tr>
<td>Ghosh et al. (1988)</td>
<td>cat</td>
<td>4/ (intr.)</td>
<td>2/3, 5</td>
<td>3-8</td>
<td>1.5</td>
<td></td>
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<td></td>
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<tr>
<td>Ojima et al. (1991)</td>
<td>cat</td>
<td>A1 (intr.)</td>
<td>2/3</td>
<td>2-4</td>
<td>0.5-1.5</td>
<td>2.5</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ojima et al. (1992)</td>
<td>cat</td>
<td>A1</td>
<td>5/6</td>
<td>4.5</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>McGaigre et al. (1991)</td>
<td>macaque</td>
<td>V1 (intr.)</td>
<td>3</td>
<td>4</td>
<td>2</td>
<td>0.4</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lohmann &amp; Rössig (1994)</td>
<td>rat</td>
<td>V2 (intr.)</td>
<td>2/3</td>
<td>0.18</td>
<td>1.2</td>
<td>0.2</td>
<td></td>
<td></td>
</tr>
<tr>
<td>DeFelipe et al. (1986)</td>
<td>macaque</td>
<td>SI, motor cortex</td>
<td>WM</td>
<td>1-5</td>
<td>6</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rockland &amp; Virga (1989)</td>
<td>macaque</td>
<td>V2 to V1</td>
<td>1-3</td>
<td>0.3-0.5</td>
<td>0.5-4.3</td>
<td>0.36-0.65</td>
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</tr>
<tr>
<td>Rockland &amp; Virga (1990)</td>
<td>macaque</td>
<td>V1 to V2</td>
<td>1-3</td>
<td>0.2-0.35</td>
<td>0.5</td>
<td>0.2-0.5</td>
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</tr>
<tr>
<td>Rockland (1995)</td>
<td>macaque</td>
<td>V2 to V5</td>
<td>1-3</td>
<td>0.2</td>
<td>0.4</td>
<td>0.2-0.6</td>
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</tr>
<tr>
<td>Tyler et al. (1998)</td>
<td>macaque</td>
<td>V1 (intr.)</td>
<td>2/3</td>
<td>0.32</td>
<td>0.35, 0.55,</td>
<td>0.05, 0.4</td>
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<td></td>
</tr>
<tr>
<td>Kisvarday &amp; Eysel (1992)</td>
<td>cat</td>
<td>V1 (intr.)</td>
<td>3</td>
<td>4-8</td>
<td>0.4</td>
<td>0.5-2.8</td>
<td>1.1</td>
<td></td>
</tr>
<tr>
<td>Clarke et al. (1993)</td>
<td>cat</td>
<td>A1</td>
<td></td>
<td>2</td>
<td>1.4</td>
<td>2.8</td>
<td>(4.9)</td>
<td></td>
</tr>
<tr>
<td>Wallace et al. (1991)</td>
<td>ferret</td>
<td>A1</td>
<td>2/3</td>
<td>6</td>
<td>0.3-1.4</td>
<td>0.8</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 5: List of publications on 2D or 3D reconstructions of single patchy PC projections, continuation of Table 4. Part two: extracellular injections with single axon reconstructions.
Results for single neurons (i.e. from intracellular injections):

- Number of patches: 1 – 5 (8)
- Radius of local spread: 300 – 500 mm
- Diameter of patches: 200 – 400 (800) mm
- Distance of patches to cell body: 0.4 – 5 (7) mm
- Shared patches of closely located neurons: 2 – 5
Results from extracellular injections:

Number of patches: usually 10 – 20 (total range: 1 – 58) depends on injection size and brain size, somewhat on areal hierarchy

Size of patches: comparable to those of single neurons

Distance of patches to cell body and between each other: similar as in single neurons, depending strongly on cortical hierarchy
Numbers for a model

Extracellular injections (groups of neurons):
in large brains usually 10 – 20 patches (total range: 1 – 58)
nr. depends mainly on brain size and injection size, somewhat on area

<table>
<thead>
<tr>
<th>Intracellular injections</th>
<th>our model</th>
<th>average</th>
<th>max</th>
<th>comments</th>
</tr>
</thead>
<tbody>
<tr>
<td>single neurons:</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>- Number of patches</td>
<td>3</td>
<td>1 - 5</td>
<td>8</td>
<td></td>
</tr>
<tr>
<td>- Radius of local links</td>
<td>0.5</td>
<td>0.3 - 0.5 mm</td>
<td>0.5</td>
<td></td>
</tr>
<tr>
<td>- Radius of patches</td>
<td>0.25</td>
<td>0.1 - 0.2</td>
<td>0.4</td>
<td>rather stable</td>
</tr>
<tr>
<td>- Distance of patches to cell body</td>
<td>0.75-3.75</td>
<td>0.4 - 5</td>
<td>7</td>
<td>dep. on brain size and area</td>
</tr>
<tr>
<td>- shared patches of closely located neurons</td>
<td>3 out of 6</td>
<td>10 neurons shared</td>
<td>2 - 5 of their patches</td>
<td></td>
</tr>
</tbody>
</table>
Result:

It is possible to make a generalized model, which can be easily adapted to particular areas:

The size of the patches is relatively constant

The number of patches depends mainly on
- the size of the injection
- somewhat also on hierarchical level

The spread of patches depends mainly on areal hierarchy
Fig. 20. Intrinsic connections produced by small vs. large biocytin injections in areas V1 and V4. A: Effects of enlarging the injection site on patch width. Note that patch width is barely affected by the increased injection site both in area V1 (left bars) and V4 (right bars).

B: Effects on number of patches. Here increasing the size of injections had a marked affect. Patch number both in areas V1 and V4 more than doubled due to the increased in size of injection sites.
Role of patches?
Fig. 2. Dendritic sampling from axonal patches: macaque area V1. (A) A scheme depicting how dendritic arbors of upper-layer pyramidal neurons sample from incoming inputs clustered into patches (red). Only a few representative neurons are shown (yellow), whereas in the real tissue the area is densely packed with pyramidal neurons having highly overlapping dendritic fields. The neurons and patches were generated from examples revealed by anterograde and retrograde transport of biocytin in area V1 of the macaque monkey. Note the similarity in size of the dendritic spread of individual neurons and the width of axonal patches. In this case, only a few neurons at the center of a patch or interpatch will receive ‘pure’ inputs while all the others will sample different mixes of patch–interpatch inputs. Below is the population sampling profile which shows the mix of patch–interpatch inputs to each neuron along the white line. The x-axis corresponds to position along the white line, while the y-axis shows the ratio of patch–interpatch inputs. Note that the population sampling profile oscillates smoothly between pure interpatch inputs and pure patch inputs, thus generating maximum neuronal diversity. Scale bar, 100 μm. (B) Dendritic sampling from oversized axonal patches. A depiction of a hypothetical case in which the size of the axonal patches greatly exceeds the spread of dendritic arbors. Note that, in this case, most dendritic arbors will be confined either to the patch or to the interpatch compartments. Only a small fraction of the neuronal population will integrate information from both compartments. The graph below shows the population sampling profile for this case. Note that, unlike the case shown in (A), here the peaks of the population sampling profile are flattened leading to redundant sampling by neighboring neurons. (C) Dendritic sampling from undersized axonal patches. Depiction of a hypothetical case in which the size of dendritic spread greatly exceeds the width of axonal patches. Note that in this case all neurons receive mixed patch–interpatch inputs so that the range of possible mix ratios is reduced. This is reflected in the shallow population sampling profile.
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