

Human visual cortex: circuitry for vision and reading

Brian A. Wandell

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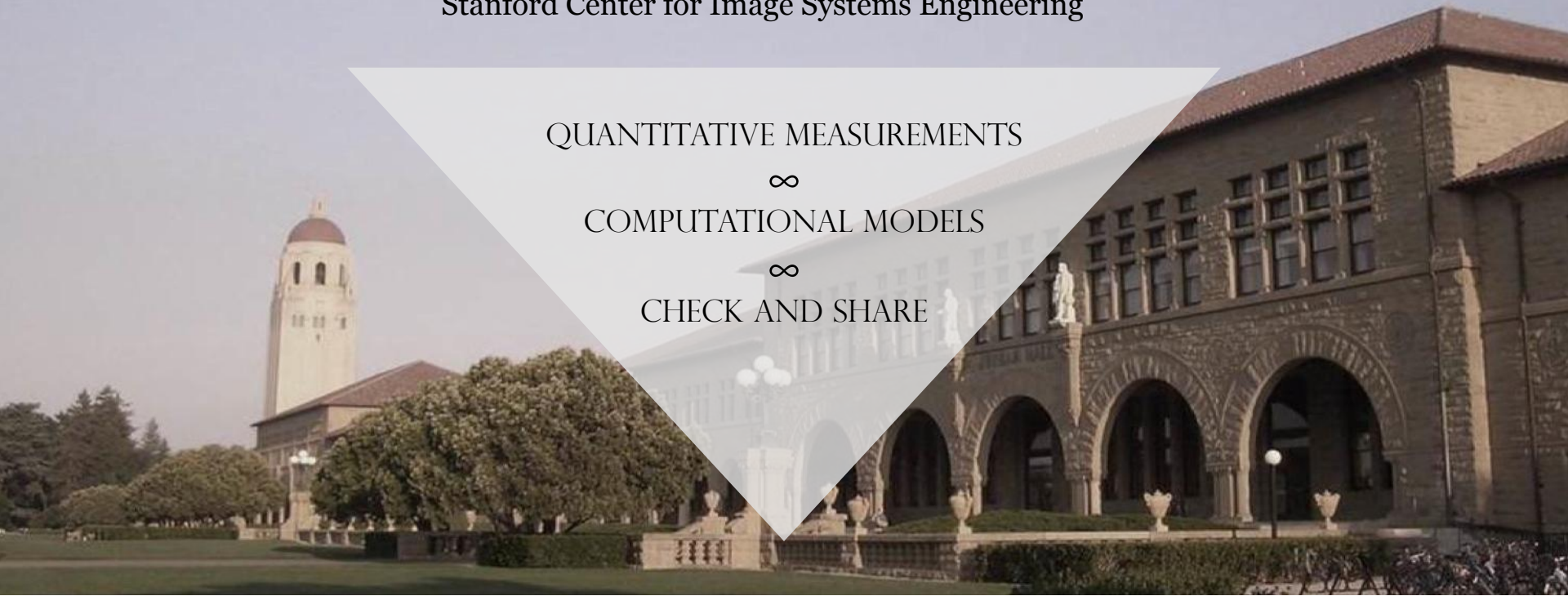
QUANTITATIVE MEASUREMENTS

∞

COMPUTATIONAL MODELS

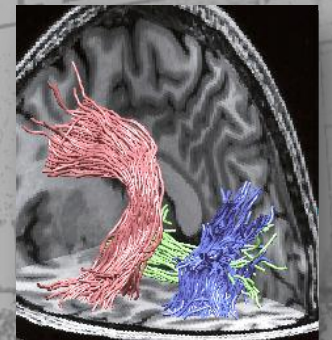
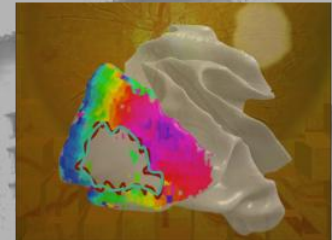
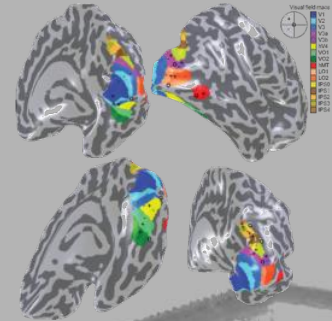
∞

CHECK AND SHARE



Human visual cortex: circuitry for vision and reading

- Human visual field maps and clusters
- Plasticity and stability of human visual cortex
- Seeing words – connecting vision to cognition



1880-1920 Identifying human V1 and retinotopic mapping



Henschen



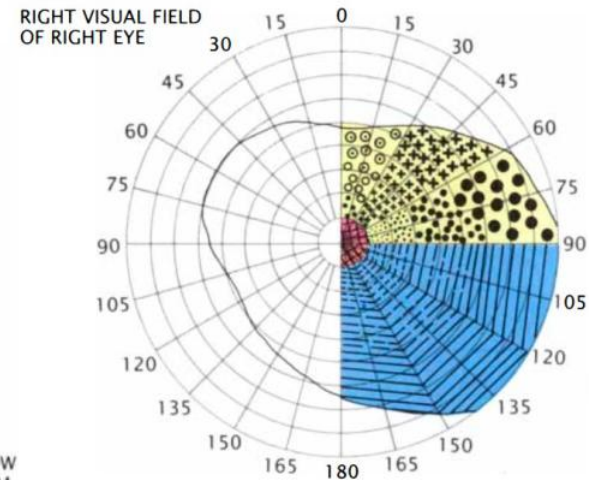
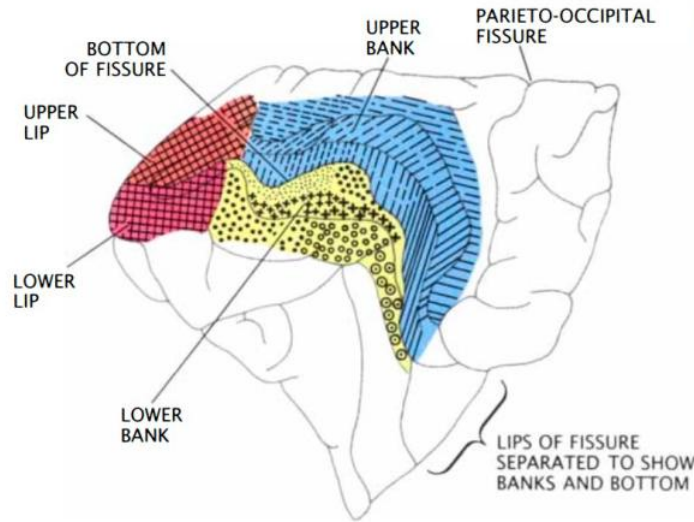
Munk



Inouye



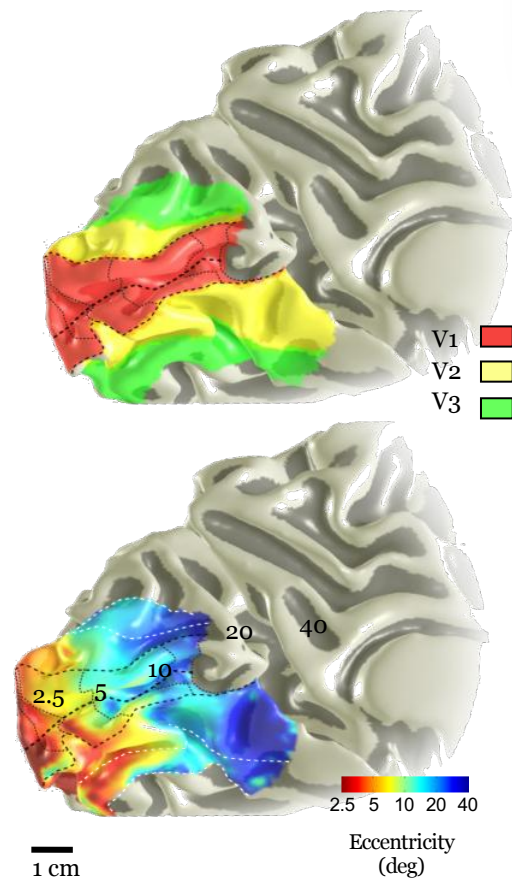
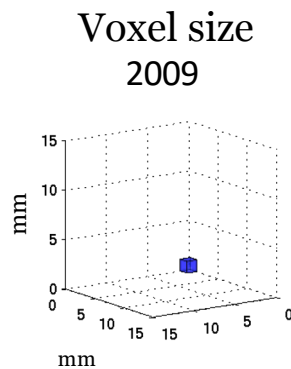
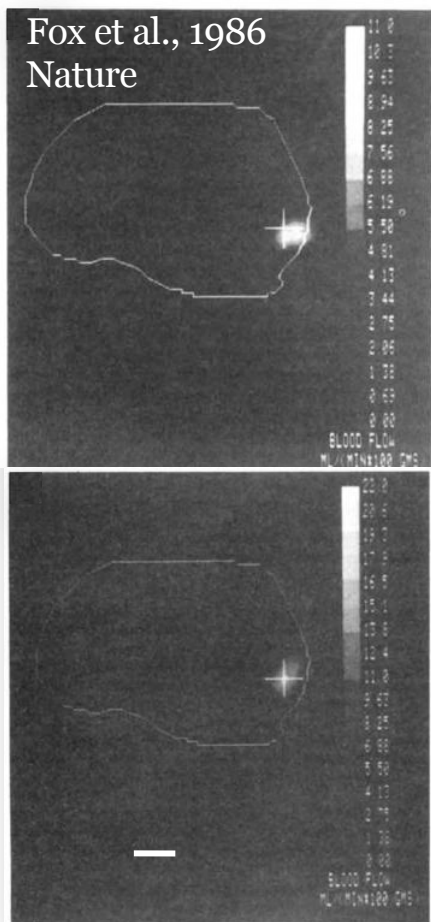
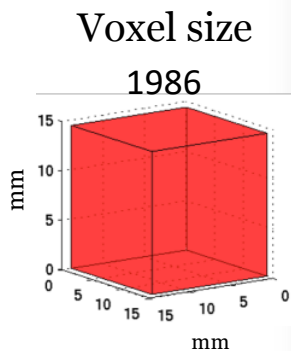
Holmes



1990-2010 Excellent progress in human measurements



Winawer

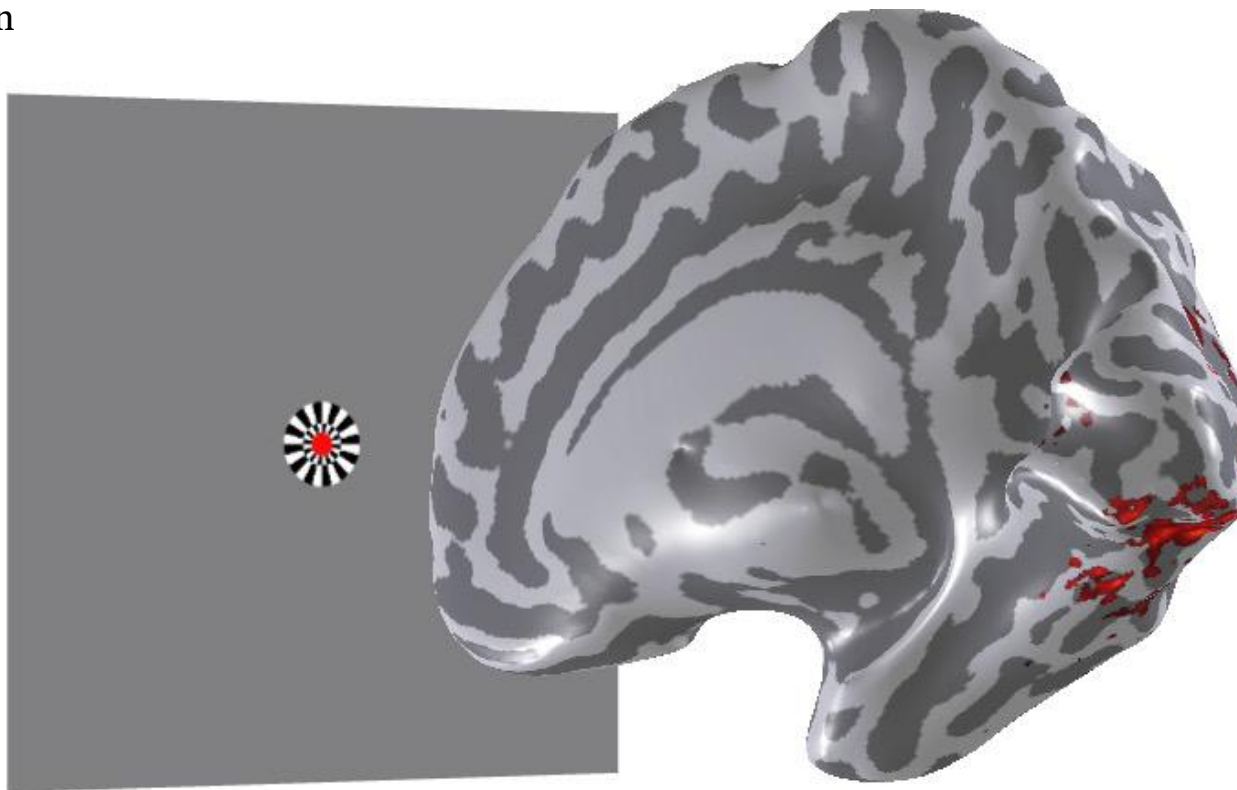


Human eccentricity mapping with fMRI

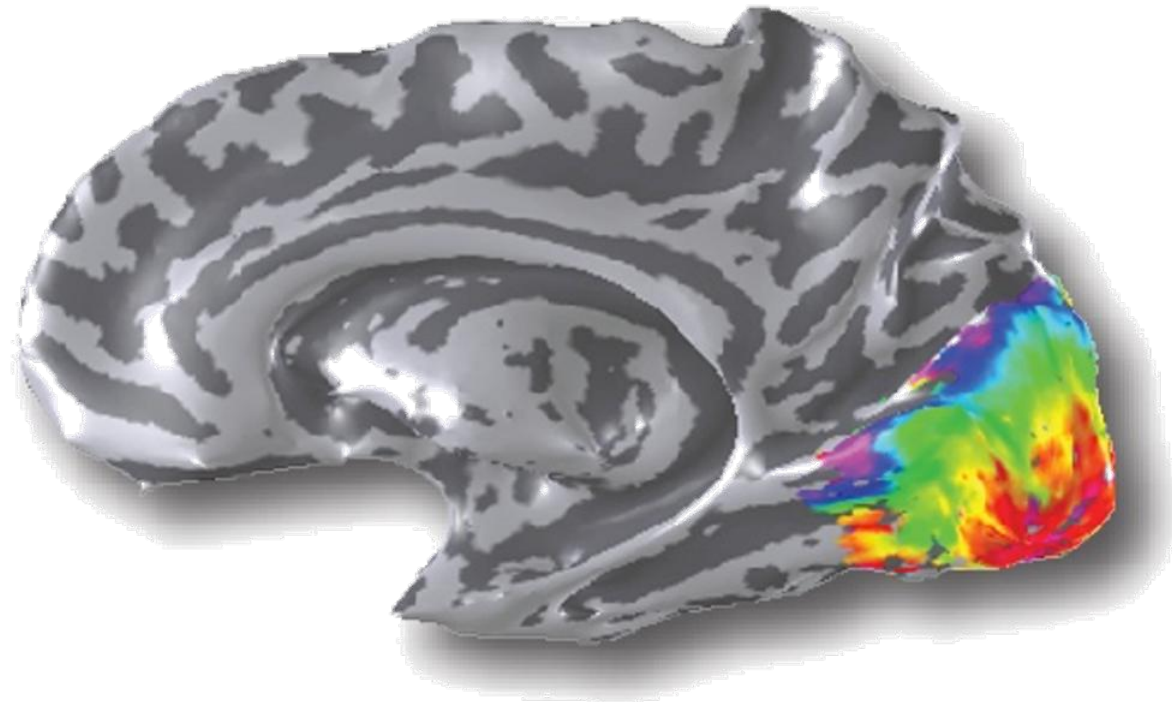


Engel

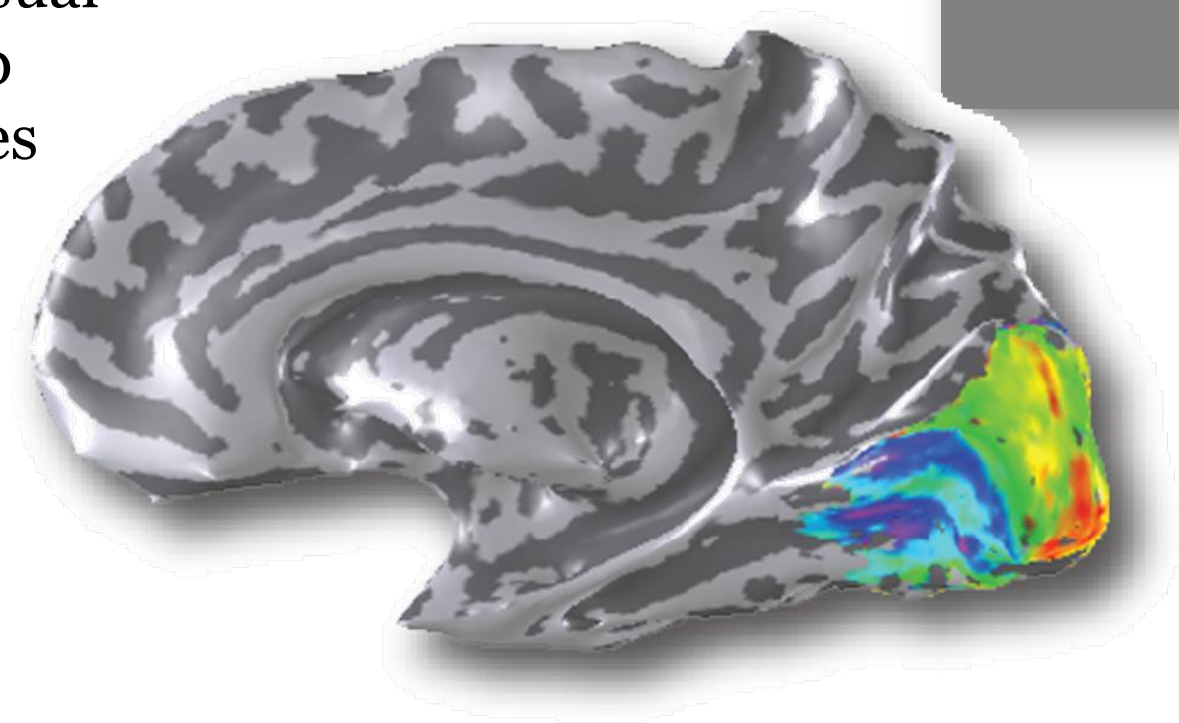
- Segmented brain surface
- Inflated brain
- Gray/white are sulci/gyri



Pseudo-color representation of visual field map



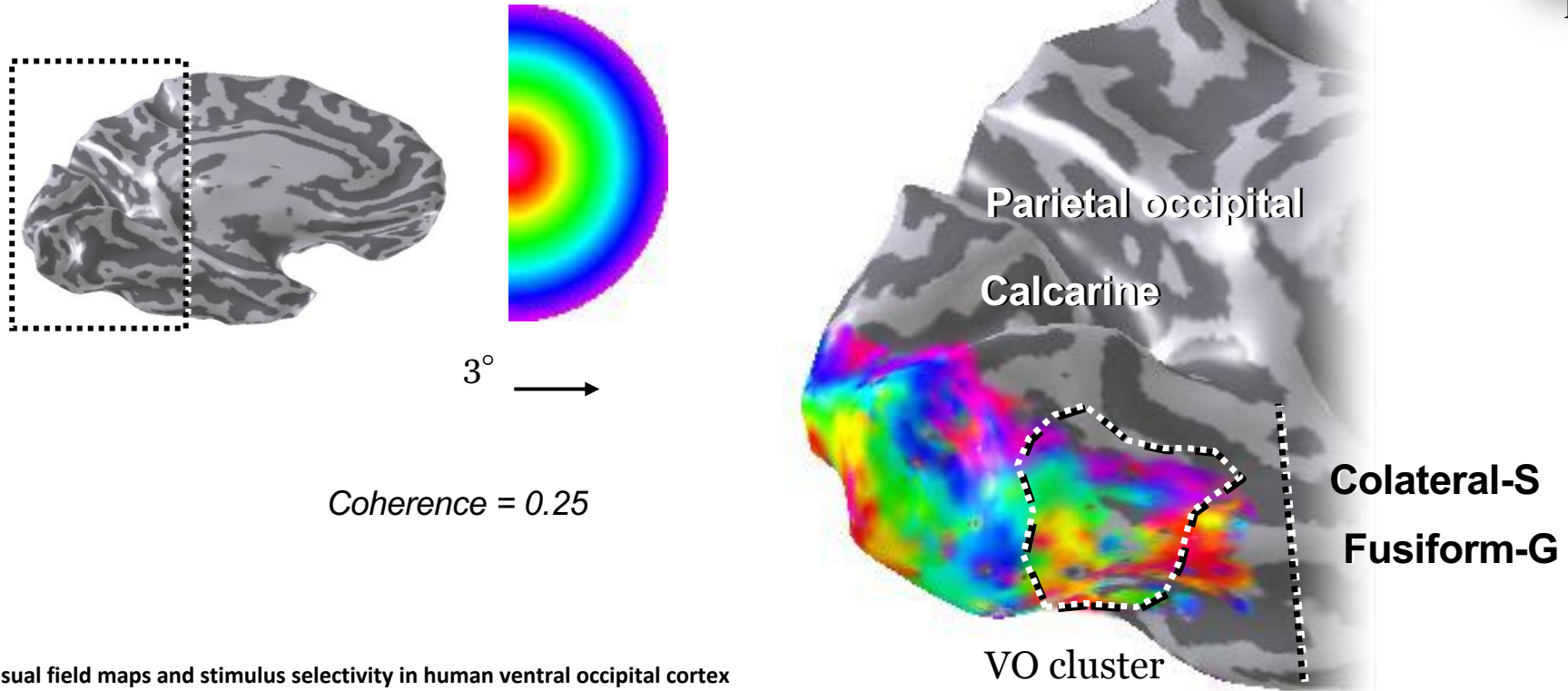
Angular
measurements
delineate visual
field map
boundaries



Visual field map clusters



Brewer



Visual field maps and stimulus selectivity in human ventral occipital cortex (2005) . A.A. Brewer, J. Liu, A.R. Wade, B.A. Wandell, Nat Neurosci.

Visual field map clusters

Left hemisphere

Lateral view

Medial view

Clusters

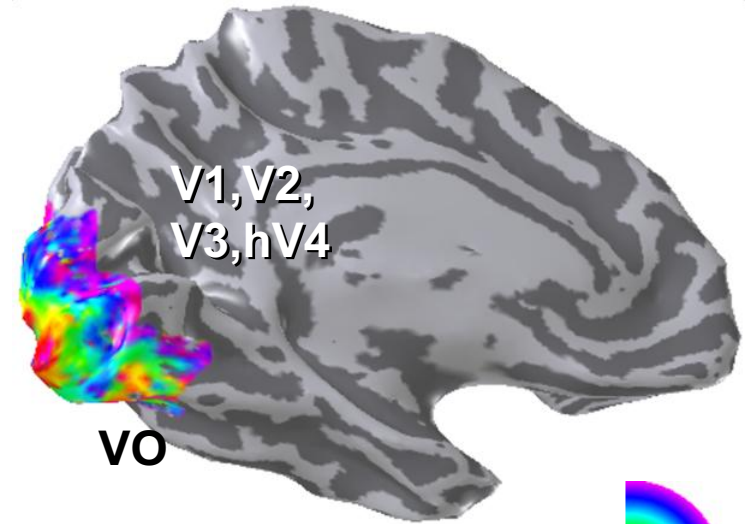
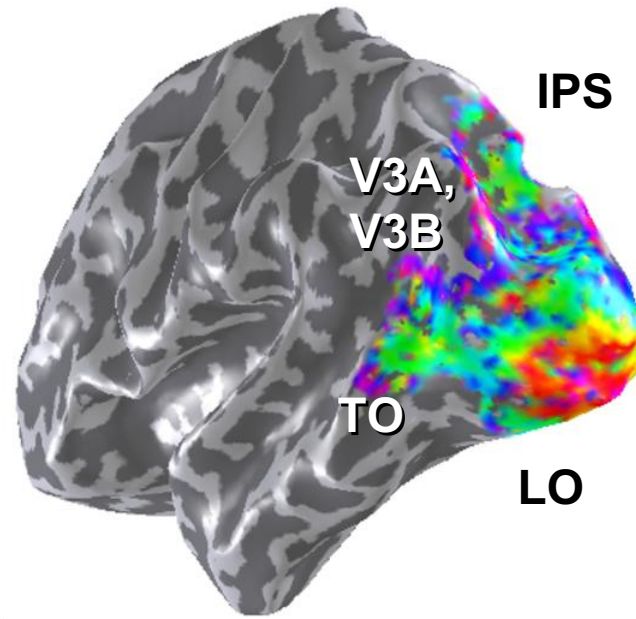
Early - V1, V2, V3, hV4

LO - Lateral occipital

VO - Ventral occipital

TO - Temporal occipital

IPS - Intraparietal sulcus

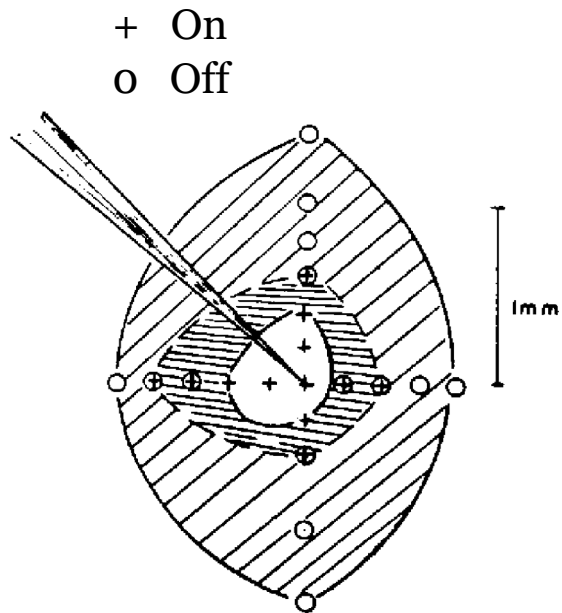


Coherence ≥ 0.20

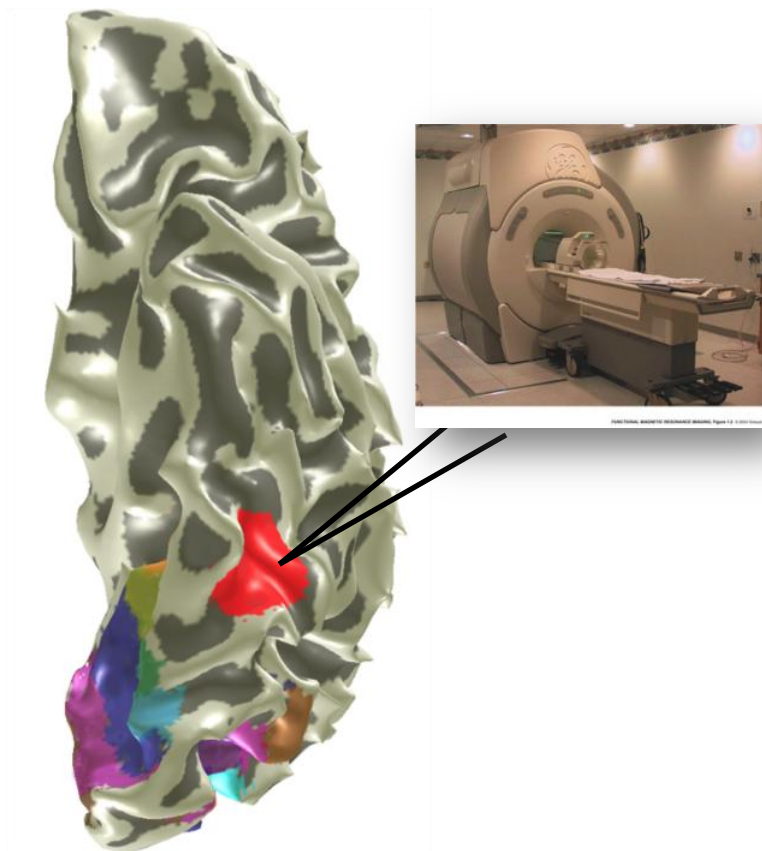


Quantitative modeling: the population receptive field (pRF)

‘Responses can be obtained in a given optic nerve fiber only upon illumination of a certain restricted region of the retina, termed the receptive field of the fiber (Hartline, 1936)’.



Sherrington, 1910
Kuffler, 1953

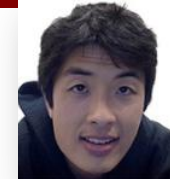


PRF size varies substantially and regularly across visual cortex

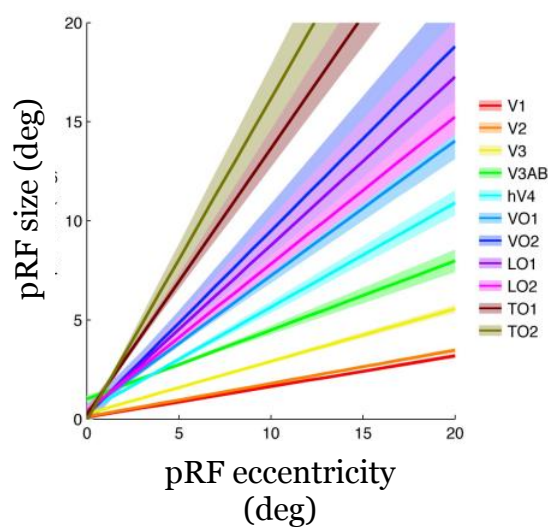
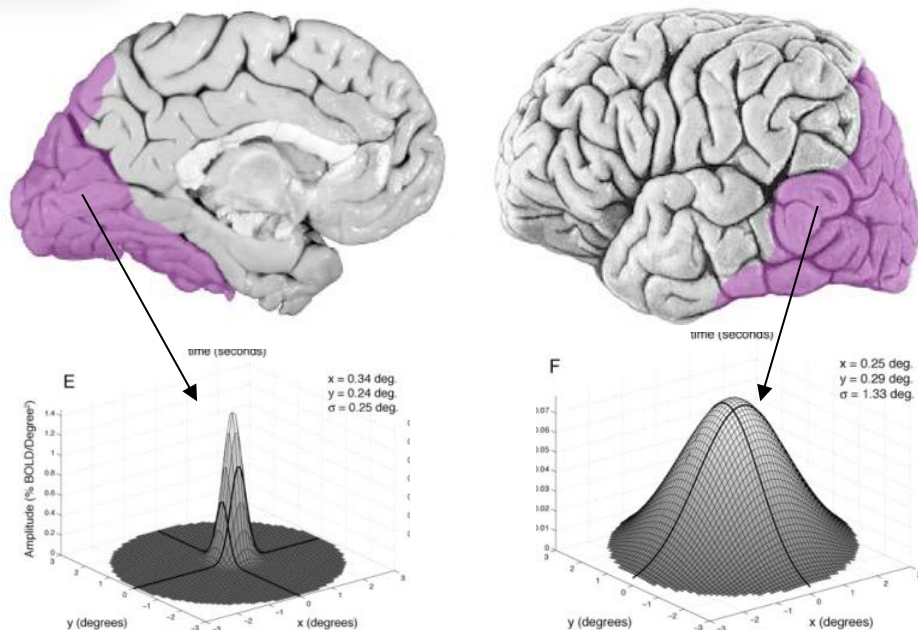
- PRF size increases with eccentricity for all maps
- At equal eccentricity, different maps have different pRF sizes



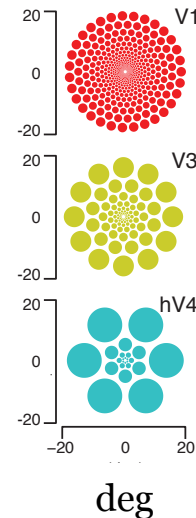
Dumoulin



Kay



From J. Freeman



Visual field maps and pRF reviews



Winawer



Brewer



Dumoulin

Cell PRESS

Neuron 2007,

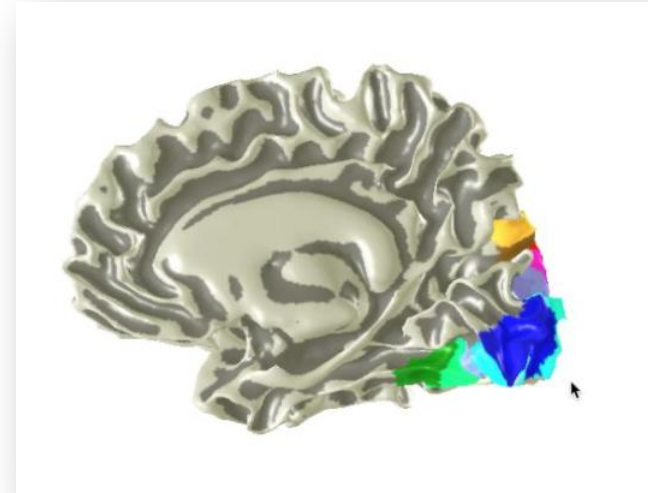
Neuron Review

Visual Field Maps in Human Cortex

Brian A. Wandell,^{1*} Serge O. Dumoulin,¹ and Ayssa A. Brewer²

¹Psychology Department, Stanford University, Stanford, CA 94305-2130, USA
²Department of Cognitive Sciences, University of California, Irvine, Irvine, CA 92697, USA
*Correspondence: wandell@stanford.edu
DOI 10.1016/j.neuron.2007.10.012

Much of the visual cortex is organized into visual field maps: nearby neurons have receptive fields at nearby locations in the image. Mammalian species generally have multiple visual field maps with each species having similar, but not identical, maps. The introduction of functional magnetic resonance imaging made it possible to identify visual field maps in human cortex, including several near (1) medial occipital (V1, V2, V3), (2) lateral occipital (LO-1, LO-2, hMT+), (3) ventral occipital (hV4, VO-1, VO-2), (4) dorsal occipital (V3A, V3B), and (5) posterior parietal cortex (IPS-0 to IPS-4). Evidence is accumulating for additional maps, including some in the frontal lobe. Cortical maps are arranged into clusters in which several maps have parallel eccentricity representations, while the angular representations within a cluster alternate in visual field sign. Visual field maps have been linked to functional and perceptual properties of the visual system at various spatial scales, ranging from the level of individual maps to map clusters to dorsal-ventral streams. We survey recent measurements of human visual field maps, describe hypotheses about the function and relationships between maps, and consider methods to improve map measurements and characterize the response properties of neurons comprising these maps.



Vision Research (2011)

ELSEVIER VISION RESEARCH journal homepage: www.elsevier.com/locate/vires

Review

Imaging retinotopic maps in the human brain

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Psychology Department, Stanford University, Stanford, CA 94305, United States

ARTICLE INFO

ABSTRACT

A quarter-century ago visual neuroscientists had little information about the number and organization of retinotopic maps in human visual cortex. The advent of functional magnetic resonance imaging (fMRI), a non-invasive, spatially-resolved technique for measuring brain activity, provided a wealth of data about human retinotopic maps. Just as there are differences amongst non-human primate maps, the human maps have their own unique properties. Many human maps can be measured reliably in individual sub-

Review

Trends in Cognitive Sciences, 2015,

CellPress

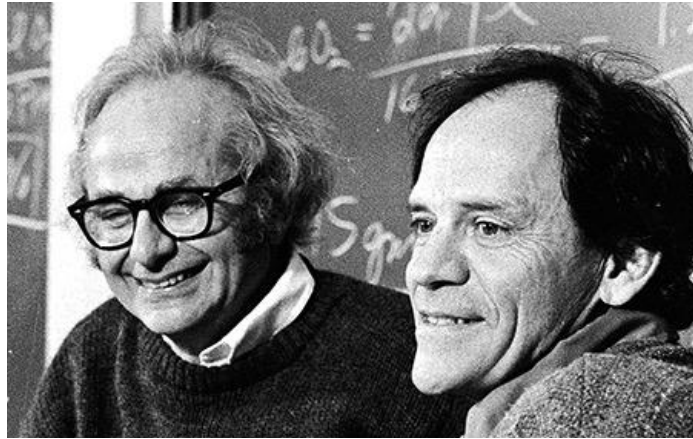
Computational neuroimaging and population receptive fields

Brian A. Wandell¹ and Jonathan Winawer²

¹ Psychology Department and Neuroscience Institute, Stanford University, Stanford, CA, USA

² Psychology Department and Center for Neural Science, New York University, New York, NY, USA

Plasticity and stability in primate cortex



David Hubel

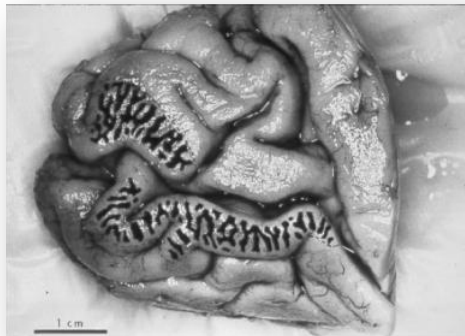
Torsten Wiesel



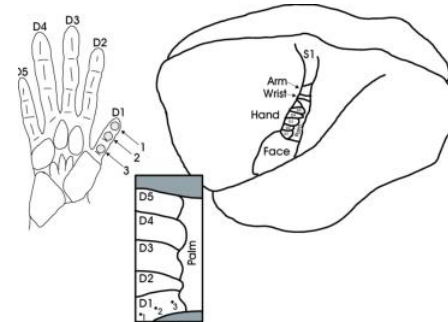
Michael Merzenich



Jon Kaas



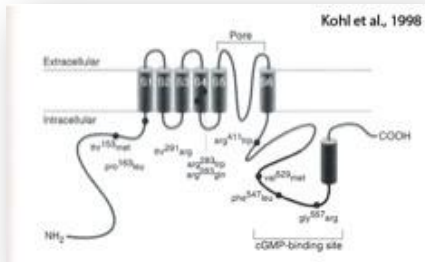
Thanks to Jonathan Horton



Thanks to A. Das (adapted from Kaas 1991)

Developmental plasticity

Congenital complete achromatopsia (Rod monochromats)



Baseler



Morland



Brewer

Achromatopsia.info

Journey through the Light!

Achromatopsia.info

The Island of the Color Blind

Many individuals first learned of achromatopsia in 1997, when Oliver Sacks published his classic book, *Island of the Color Blind*. This story beautifully chronicles Oliver Sack's 1994 quest with

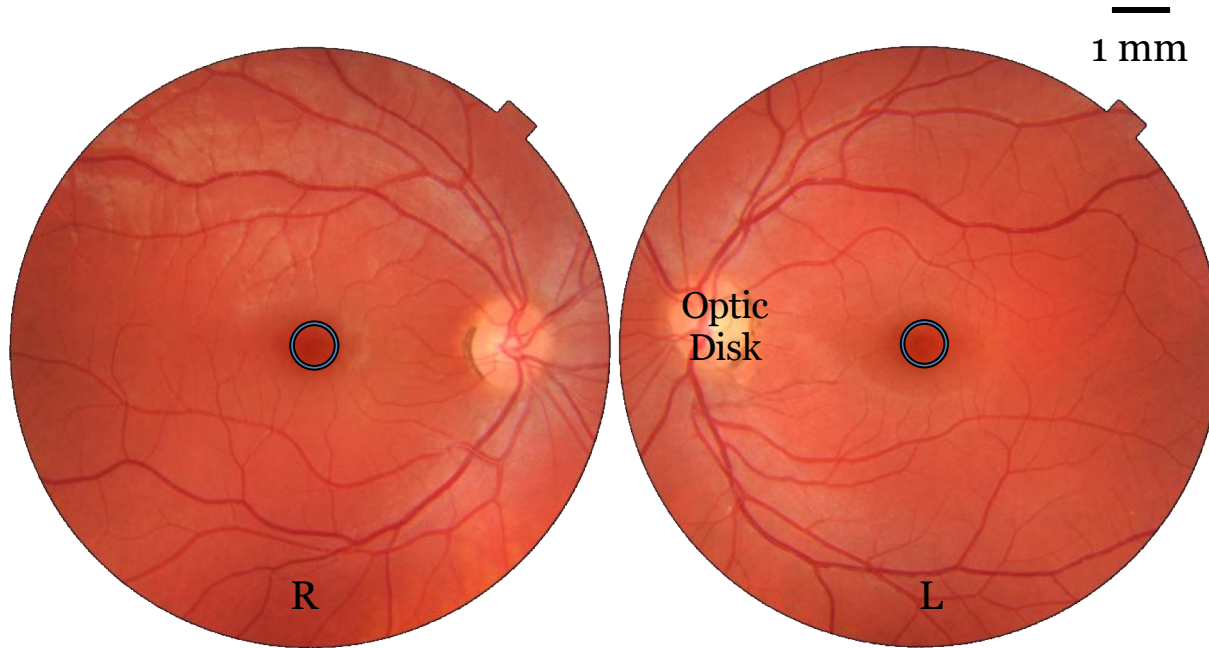
Navigation

- Home
- Achromat Vision
- Debilitating Glare
- Colorblindness

Reorganization of human cortical maps caused by inherited photoreceptor abnormalities (2002). Baseler, Brewer, Sharpe, Jägle and Wandell. Nature Neuroscience

The rod-free zone in the retina

Rod free zone (1.25 deg, ~ 400 μm)



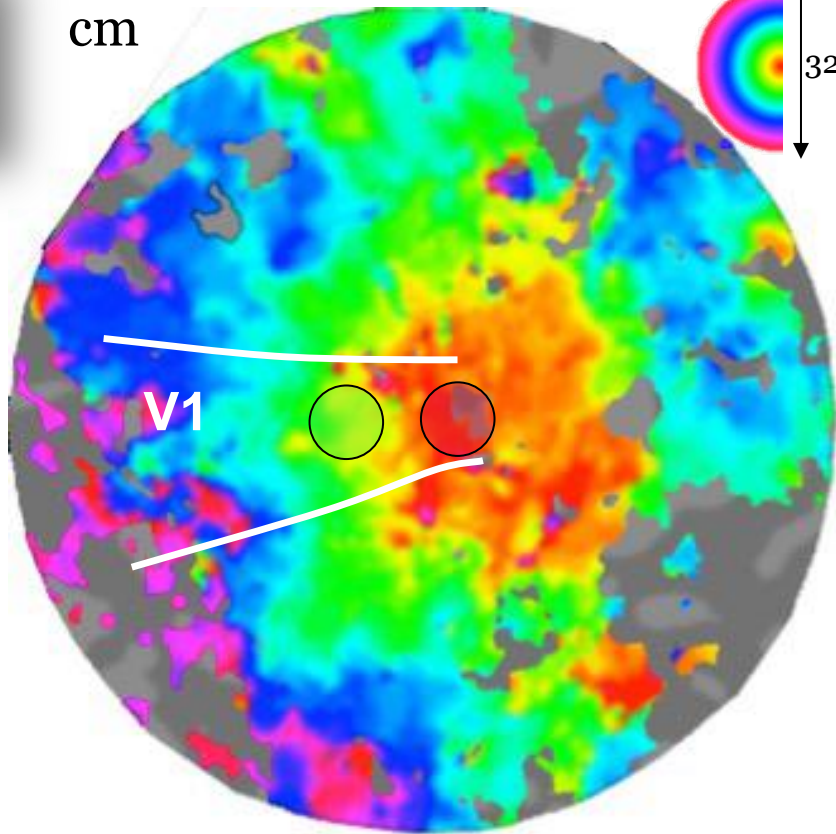
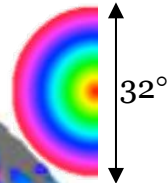
Typical cone-driven to expanding ring stimulus

Baseler et al., (2002) Nature Neuroscience



—
cm

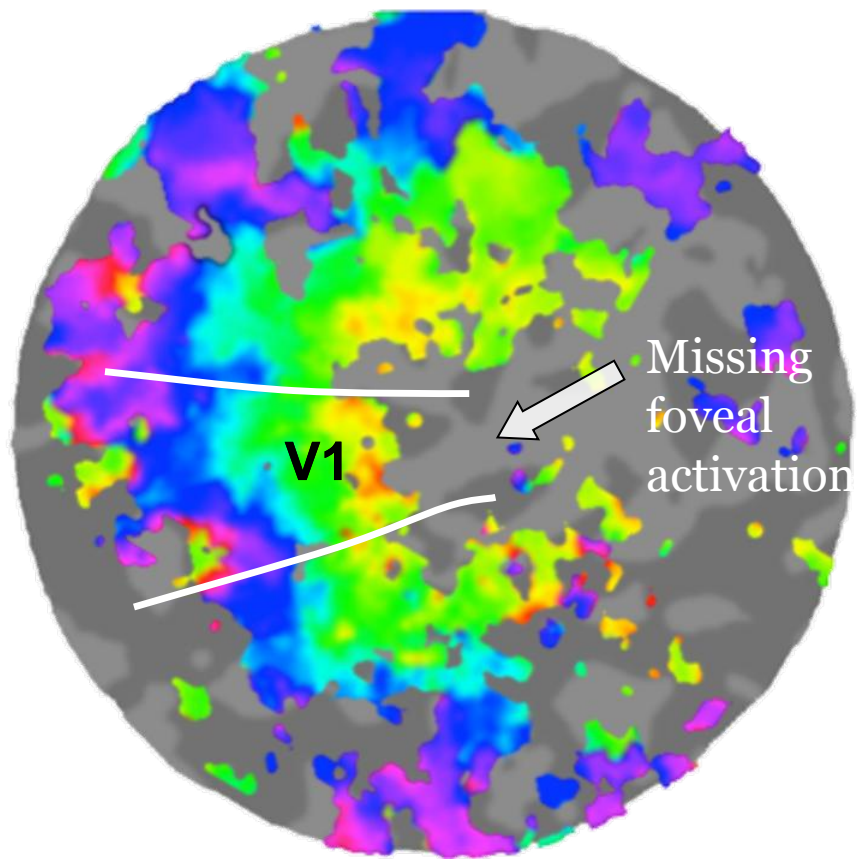
Cone vision



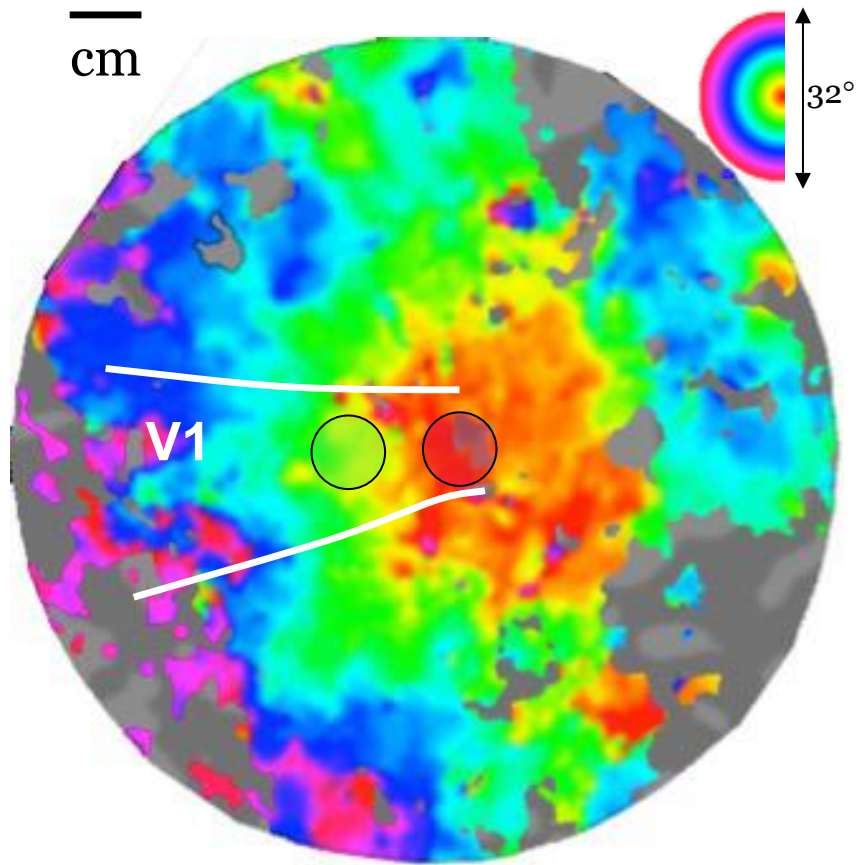
V1

Rod-driven response: missing central representation

Rod vision



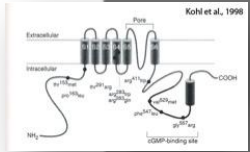
Trichromat



Rod monochromats: a visual response in the central representation

Baseler et al., (2002) Nature Neuroscience

Rod
monochromat



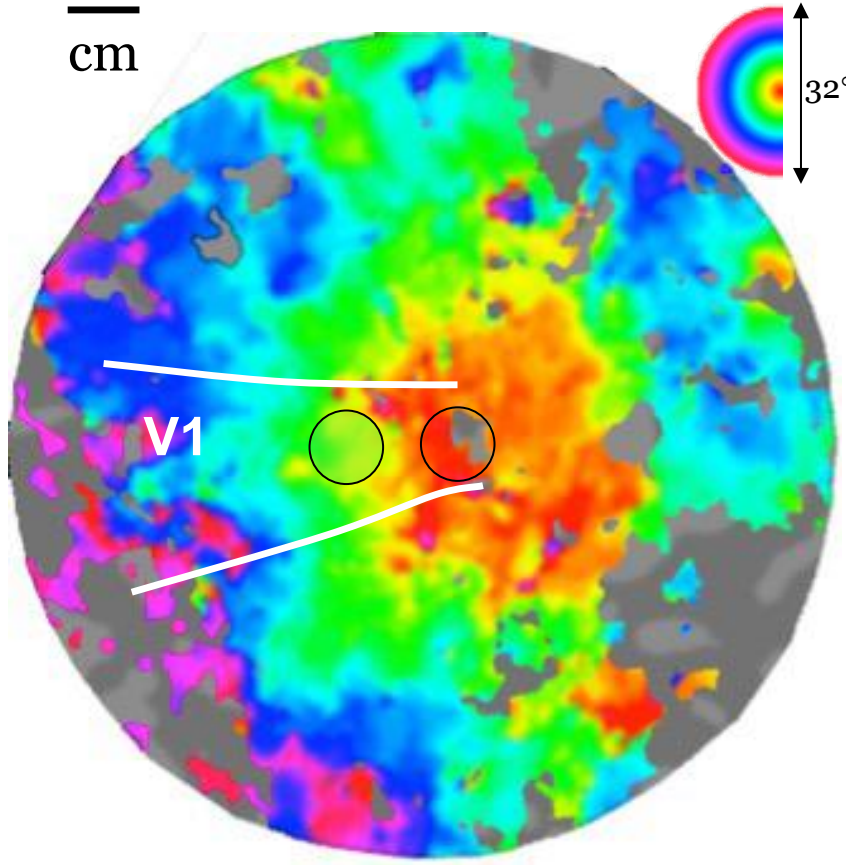
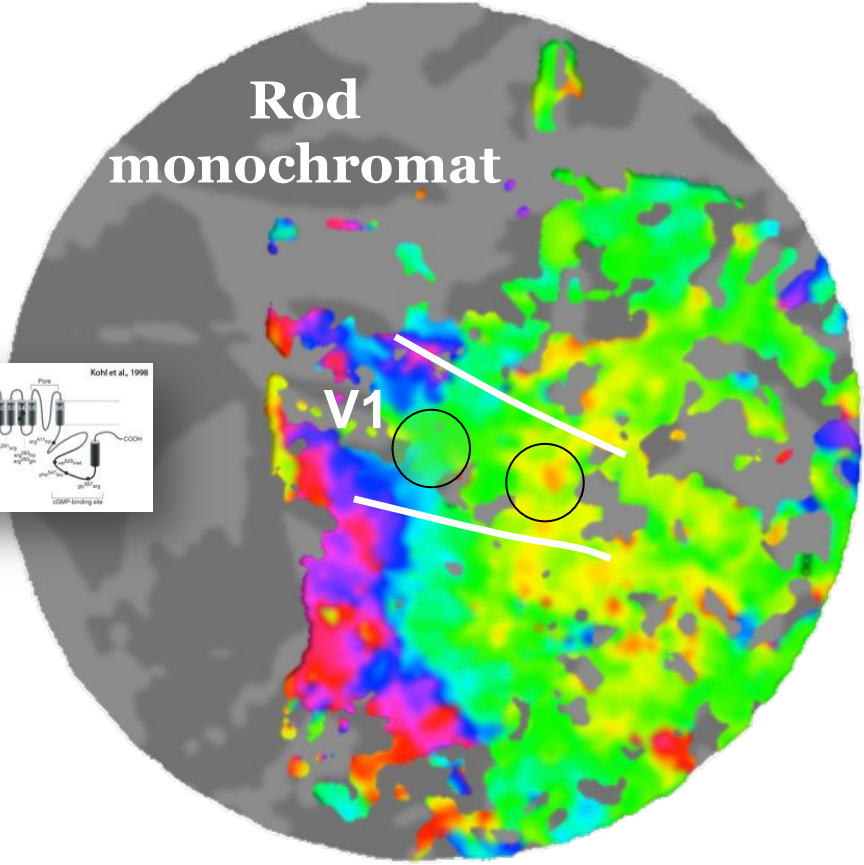
V1

cm

Trichromat

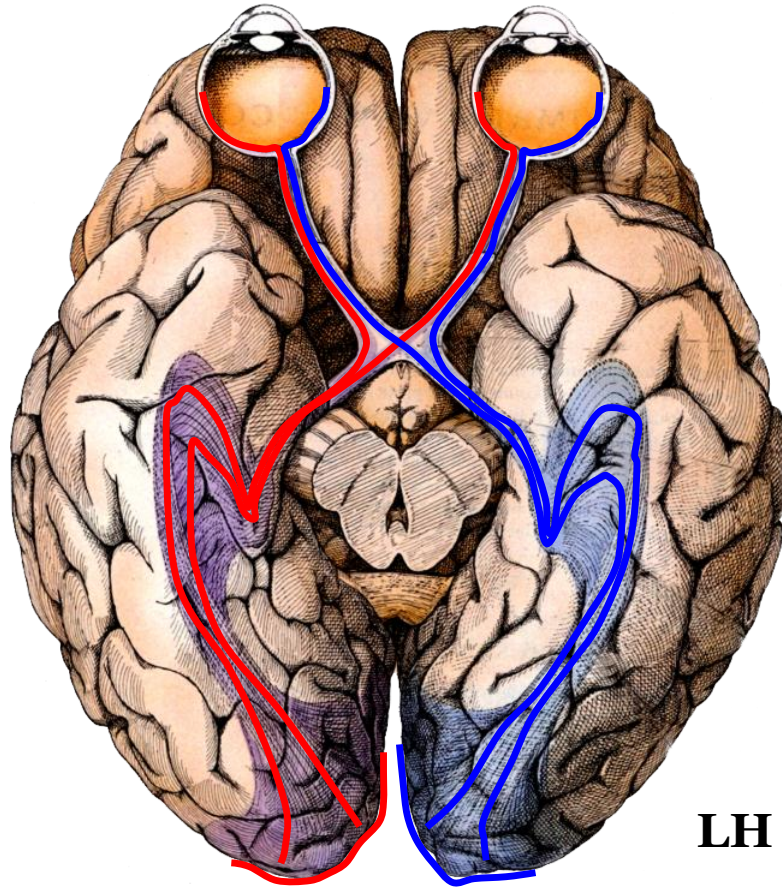
32°

V1



An achiasmatic subject: Major projections from retina to V1

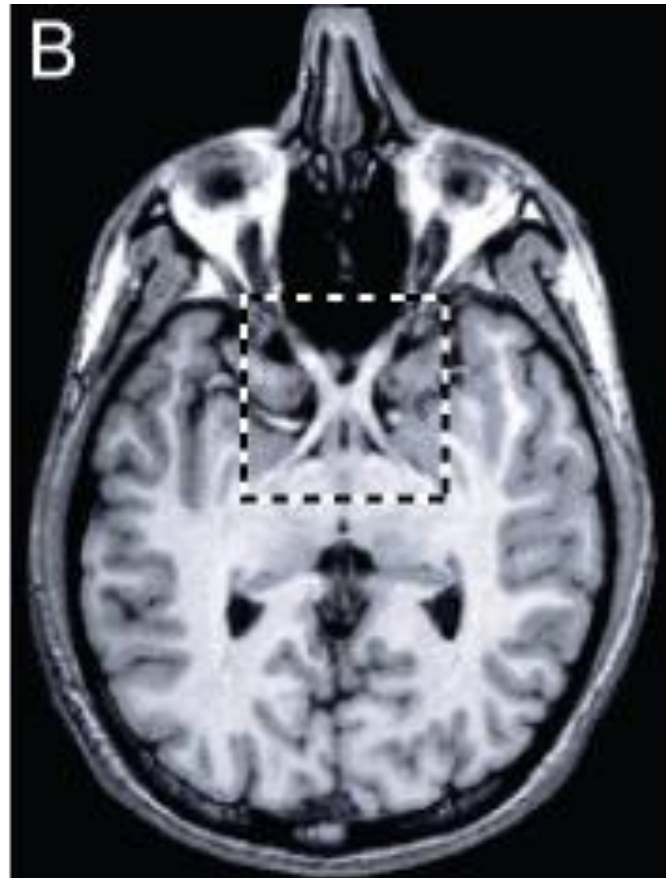
Molecular guidance at chiasm mediated by Ephrin-B2 and EphB1 (Williams et al., 2003, Neuron)



- **Right visual field**
 - left temporal retina
 - right nasal retina
 - **Left visual field**
 - right temporal retina
 - left nasal retina
- Right visual field
— Left visual field

LH

The optic chiasm is easy to see in a T1-weighted MRI

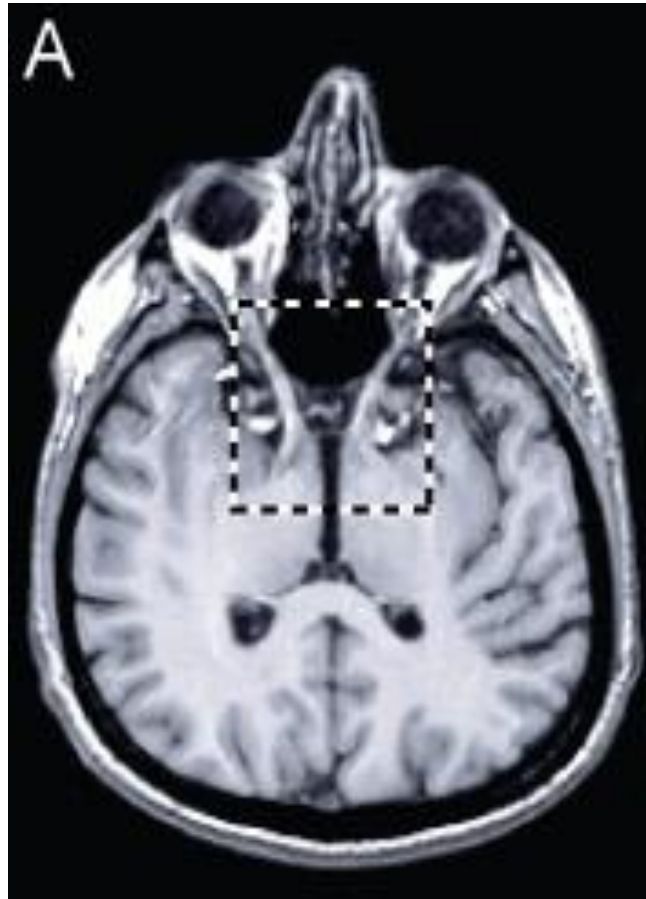


Conventional
optic chiasm

Control



This subject doesn't have an optic chiasm

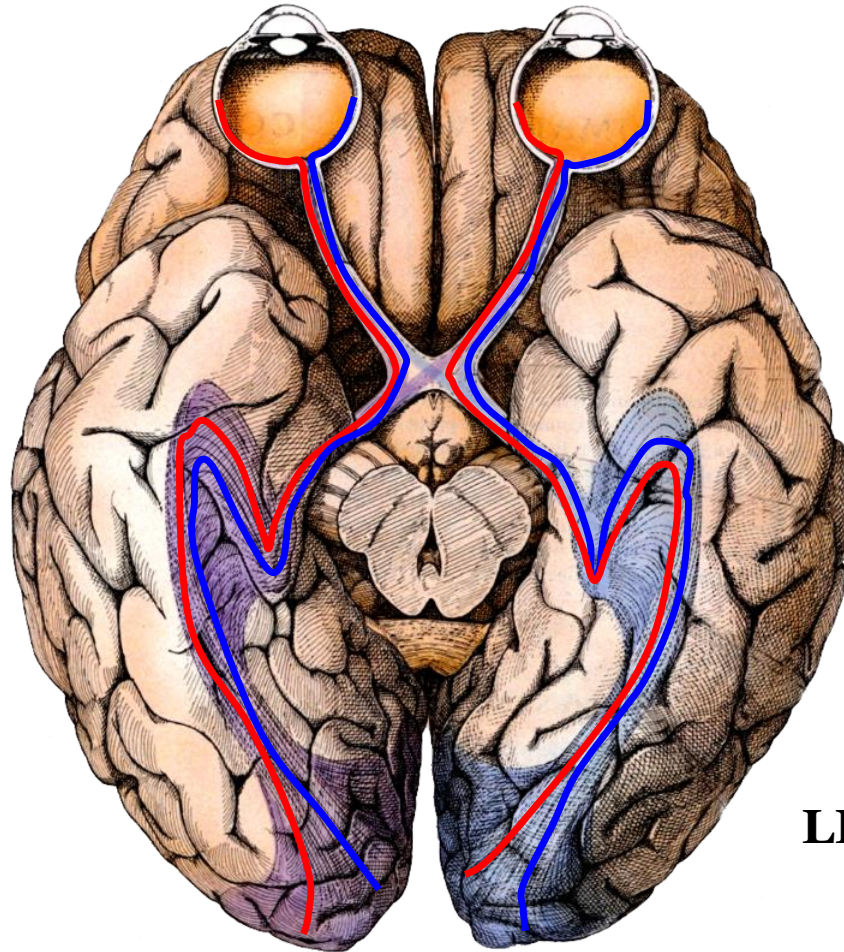


Missing
optic
chiasm

Achiasma



In the achiasmatic subject, each eye maps to ipsilateral cortex

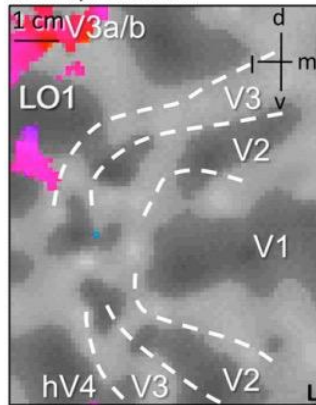
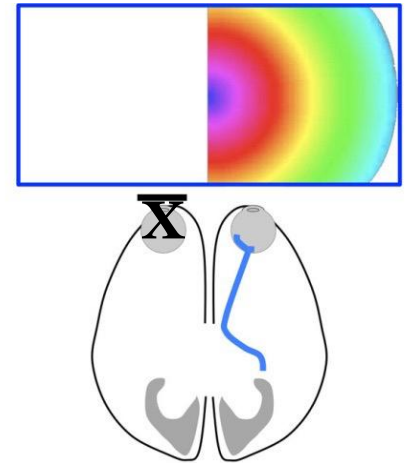
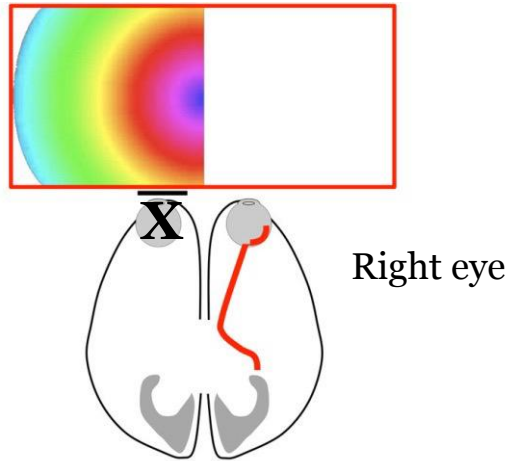


- **Right visual field**
 - left temporal retina
 - right nasal retina
- **Left visual field**
 - right temporal retina
 - left nasal retina

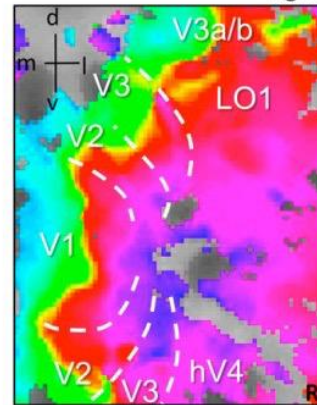
— Right visual field
— Left visual field

We confirmed this using fMRI measurements

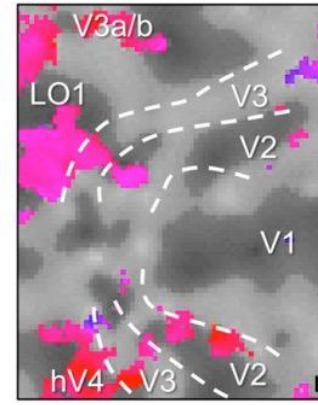
Signals from the right eye stay in the right hemisphere, unlike controls



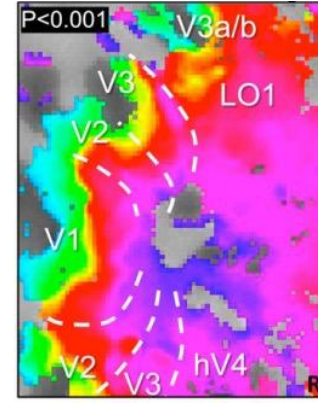
Left hemisphere



Right hemisphere



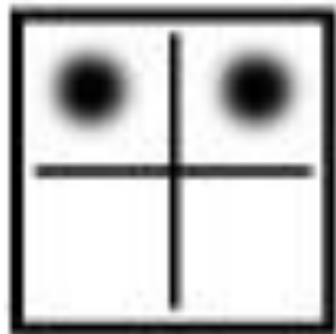
Left hemisphere



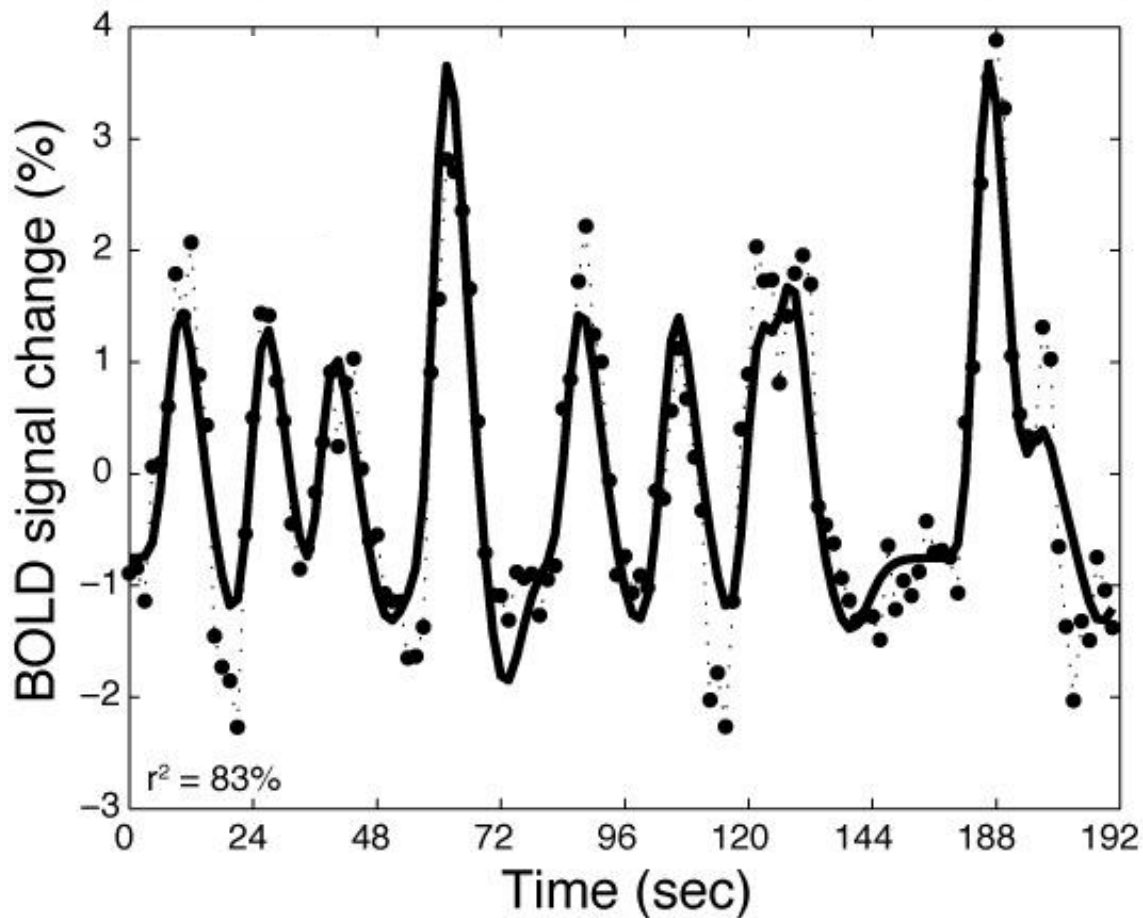
Right hemisphere

The population receptive fields are symmetric around the midline

Dual pRF model, with regions symmetric across the midline, fit the subject's data



we
sh
man
al
take
tu
wa
it
gav
fre
s
w
f



Non-human primate measurements



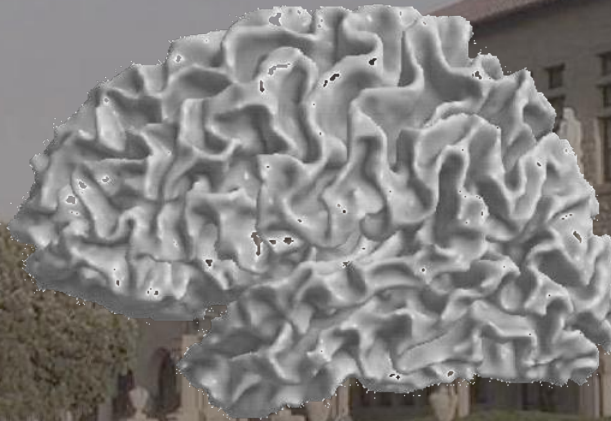
Smirnakis



Logothetis

Potential for molecular and pharmacological studies of cortical plasticity

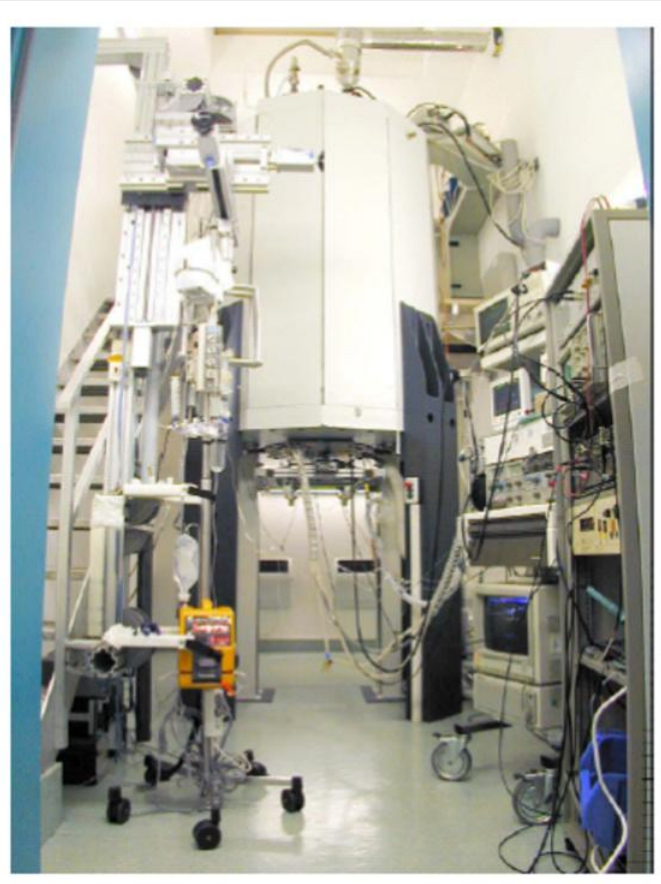
Human



Macaque

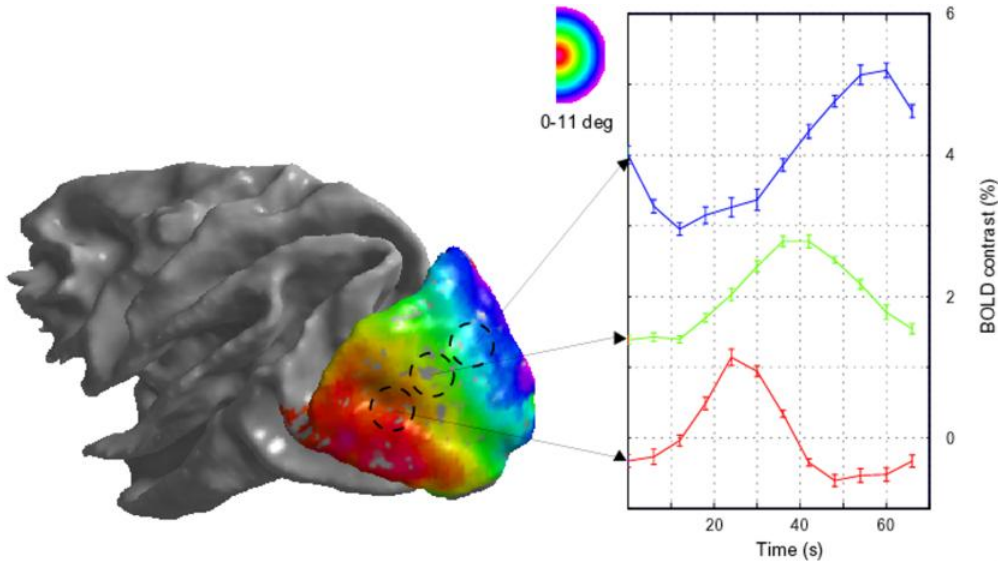


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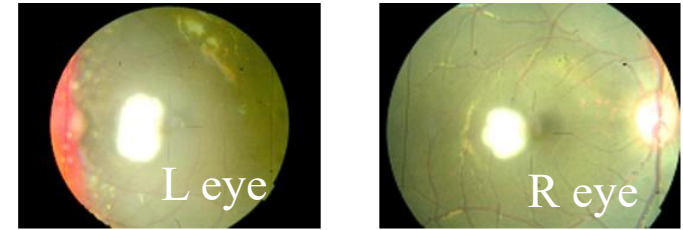


FMRI visual field mapping in macaque

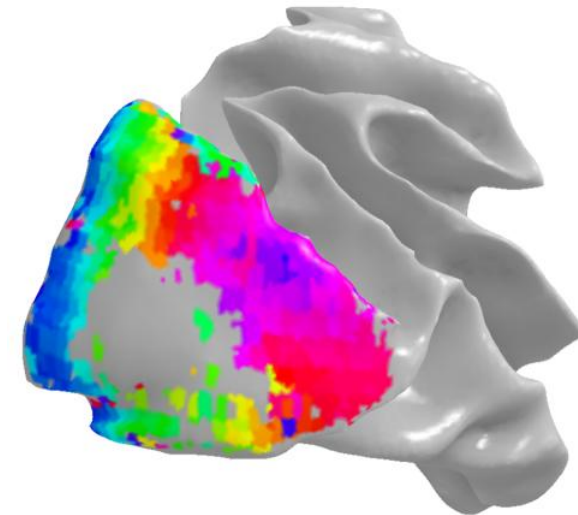
(a)



(b)



4° - 12° eccentricity



"Visual Areas in Macaque Cortex Measured Using Functional Magnetic Resonance Imaging." Brewer, Alyssa A., William A. Press, Nikos K. Logothetis, and Brian A. Wandell. 2002. *The Journal of Neuroscience*.

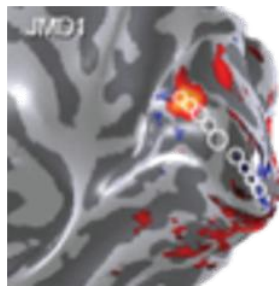
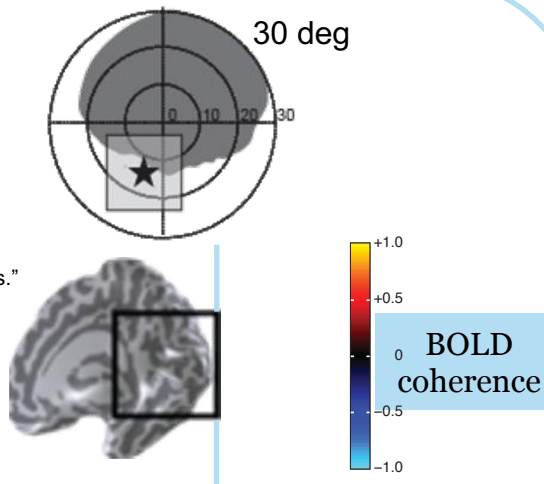
"Lack of Long-Term Cortical Reorganization after Macaque Retinal Lesions." Smirnakis, Stelios M., Alyssa A. Brewer, Michael C. Schmid, Andreas S. Tolias, Almut Schüz, Mark Augath, Werner Inhoffen, Brian A. Wandell, and Nikos K. Logothetis. 2005. *Nature*.

Human adult cortical plasticity in cases of retinal scotomas

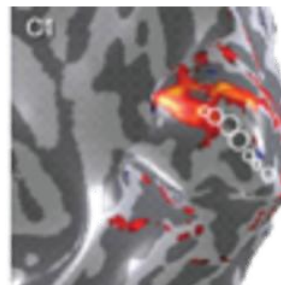
Juvenile Macular Degeneration

Masuda et al. 2008. "V1 Projection Zone Signals in Human Macular Degeneration Depend on Task, Not Stimulus." *Cerebral Cortex*.

Masuda, et al. 2021. "V1 Projection Zone Signals in Human Macular Degeneration Depend on Task Despite Absence of Visual Stimulus." *Current Biology*.



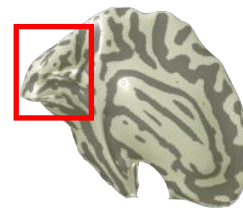
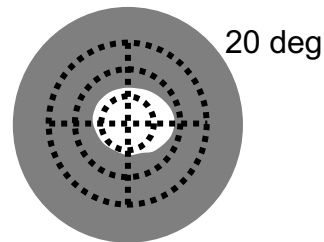
JMD



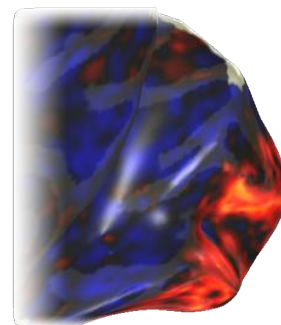
Control

Retinitis Pigmentosa

Masuda, et al. 2010. "Task-Dependent V1 Responses in Human Retinitis Pigmentosa." *IOVS*.



RP

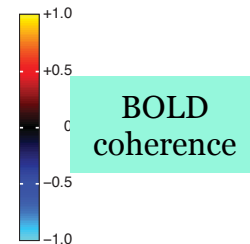


Control



Masuda

Horiguchi

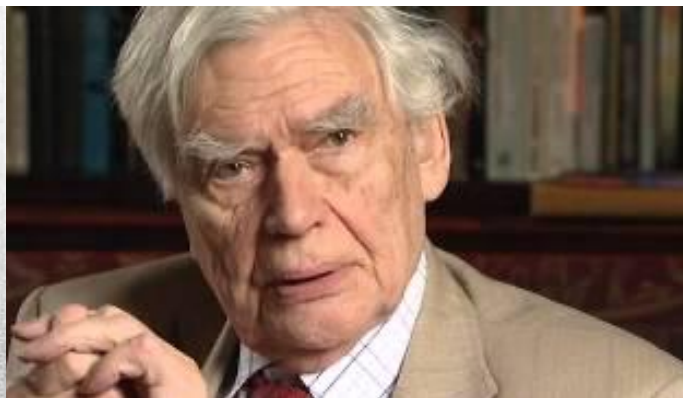


BOLD coherence

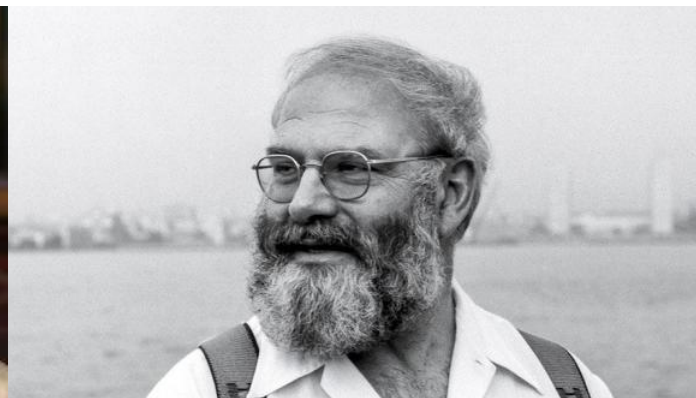
Miracle cures in vision



Chesselden, 1728



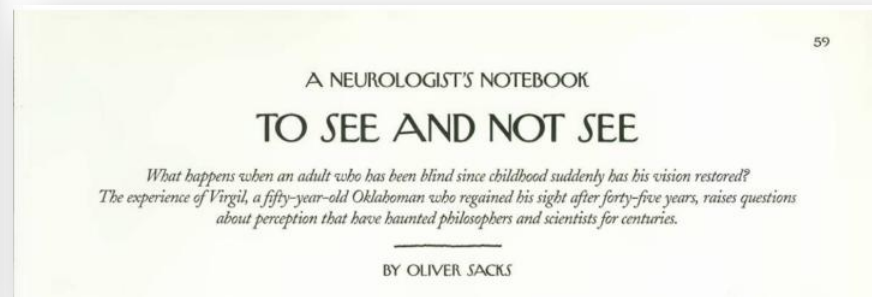
Gregory, 1960



Sacks, 1990

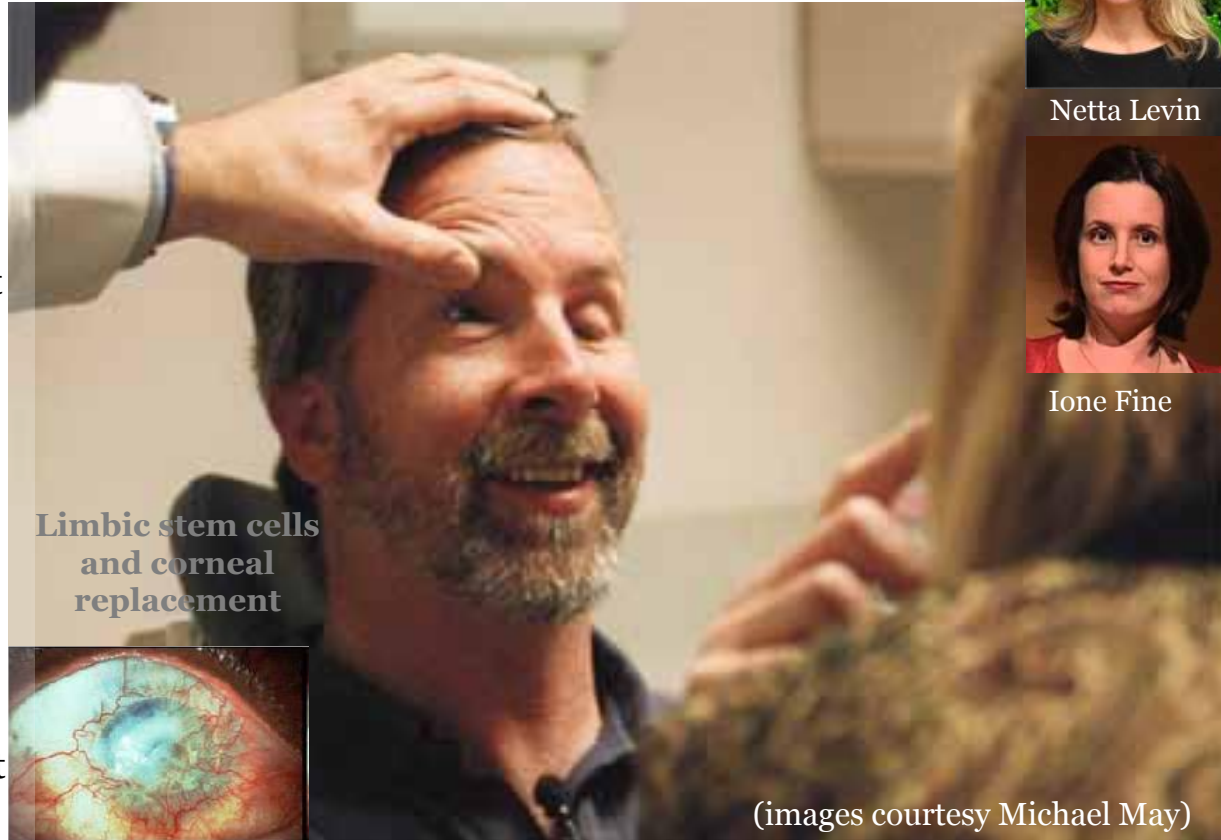


Alberto
Valvo, 1970



Human contrast deprivation from 3-46 years of age

- At three and a half years of age, MM lost one eye and was blinded in the other (chemical and thermal damage to his corneas).
- One unsuccessful corneal replacement in childhood
- For the next 43 years he had some light perception, but no experience of contrast or form; he reports no visual memories or imagery.
- At age 46, MM received a corneal and limbal stem-cell transplant in his right eye; this restored his retinal image

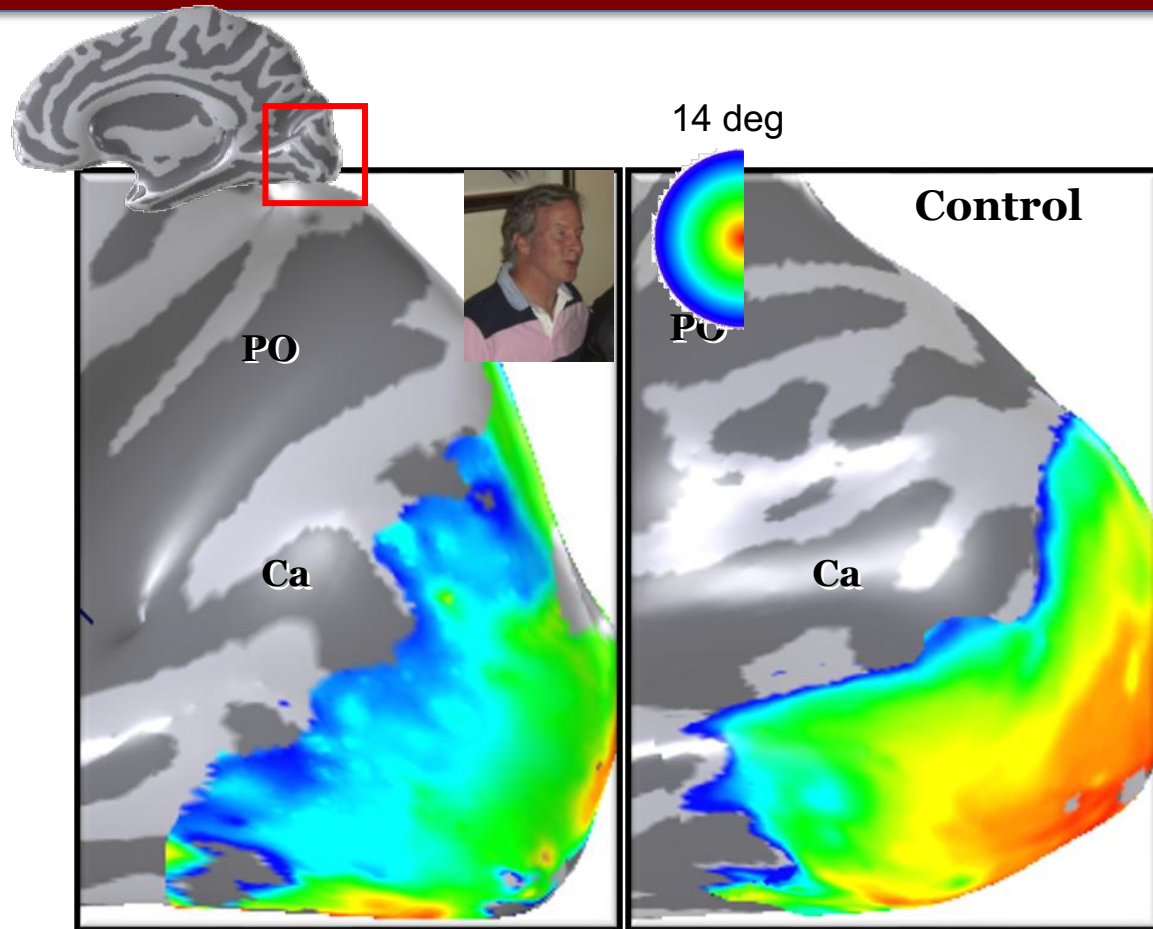


Limbic stem cells
and corneal
replacement

(images courtesy Michael May)

Levin, Dumoulin, Winawer, Dougherty, and Wandell. 2010. "Cortical Maps and White Matter Tracts Following Long Period of Visual Deprivation and Retinal Image Restoration." *Neuron* 65 (1): 21–31.

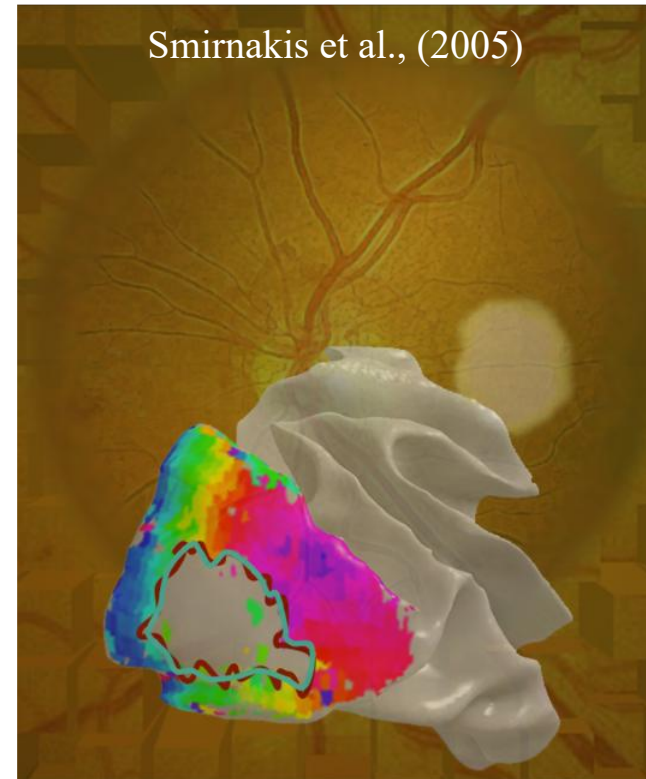
Missing foveal signals in visual cortex



Levin et al.,
2010

Summary: Plasticity and stability in early visual cortex

- Plasticity easily demonstrable in development
- In adult early visual cortex, stability is dominant
- Which parts of visual cortex remain plastic to support visual learning, such as **enabling kids to learn to see words rapidly?**



Functional specializations in ventral occipital temporal cortex

- Achromatopsia
- Prosopagnosia
- Akinetopsia
- Alexia

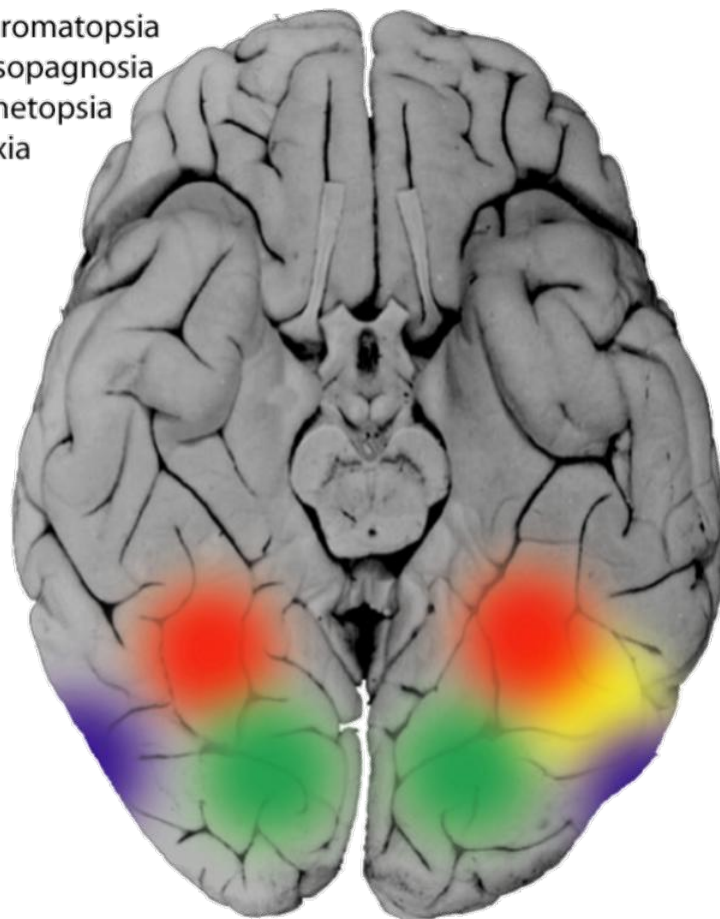
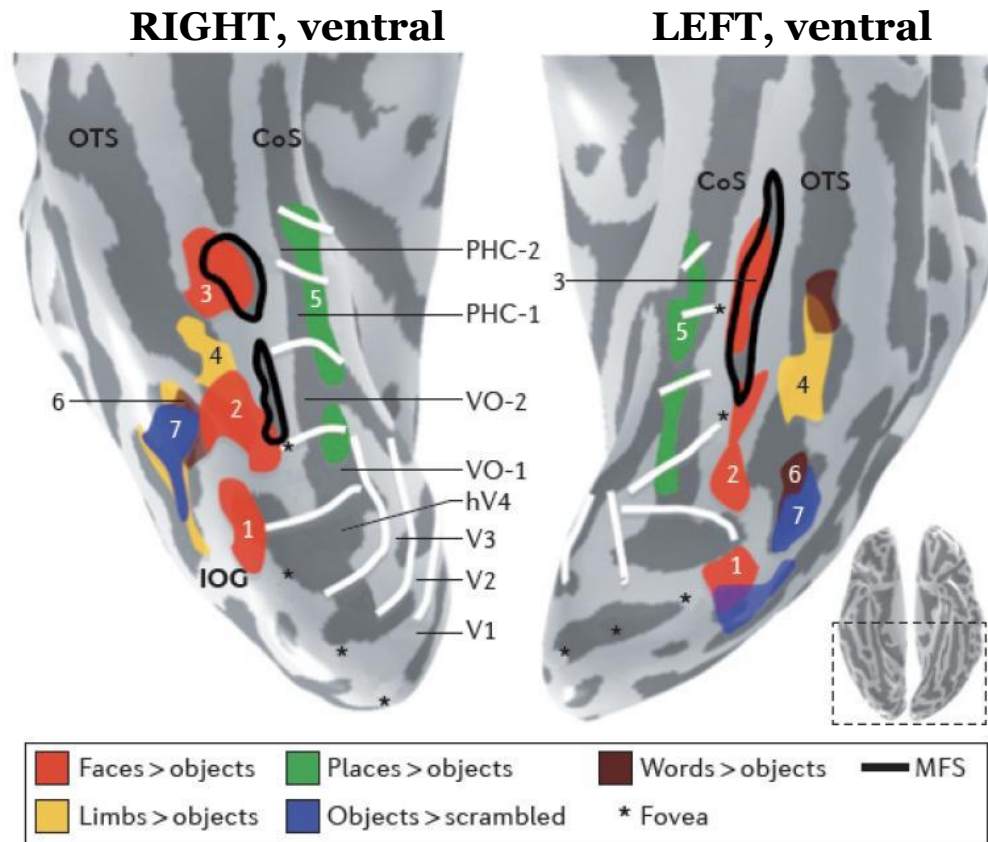


Image courtesy of S. Zeki

- Ventral occipito-temporal cortex (VOT) includes many regions that appear to play a special role in visual object recognition
- Neurological studies from the 70s on show that these regions play an essential role in perceiving color, faces, motion, word recognition (**Zeki**, Meadows, Geschwind, Greenblatt, Nobre, McCarthy, Cohen, Dehaene)

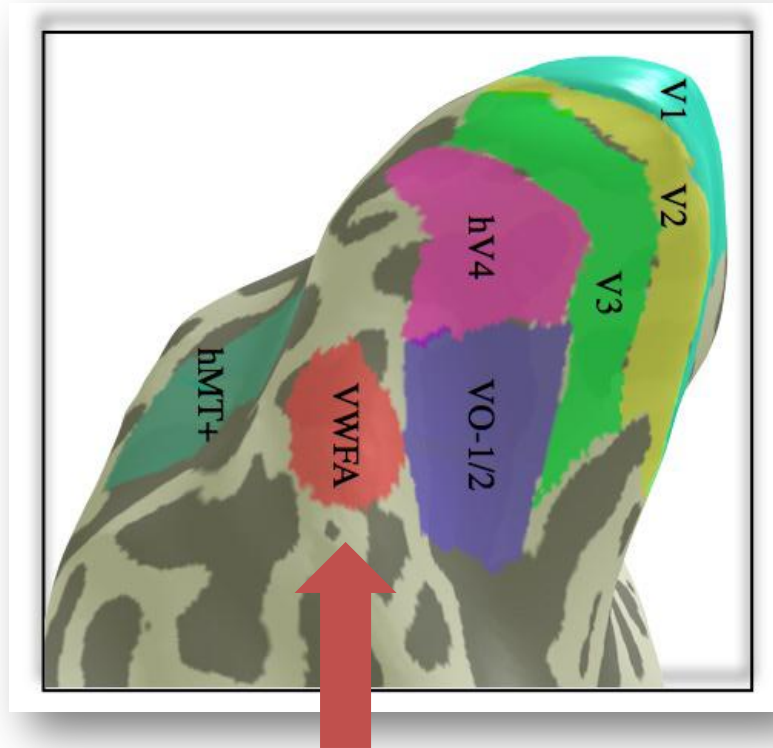
Specializations in ventral occipital temporal cortex

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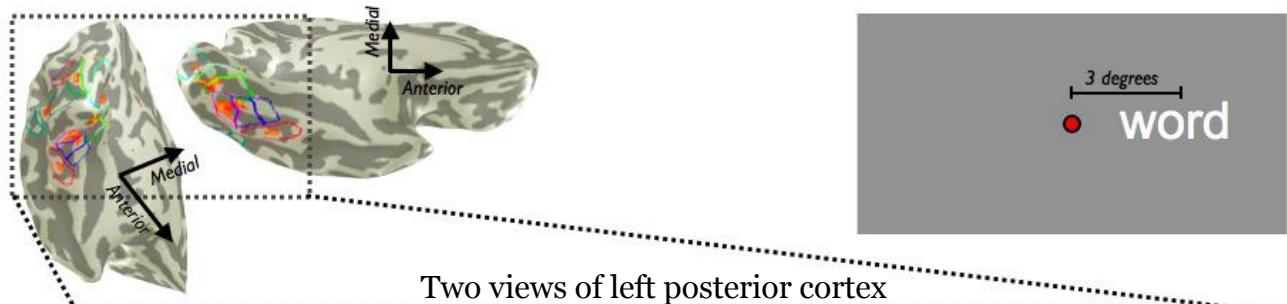


Specializations in ventral occipital temporal cortex

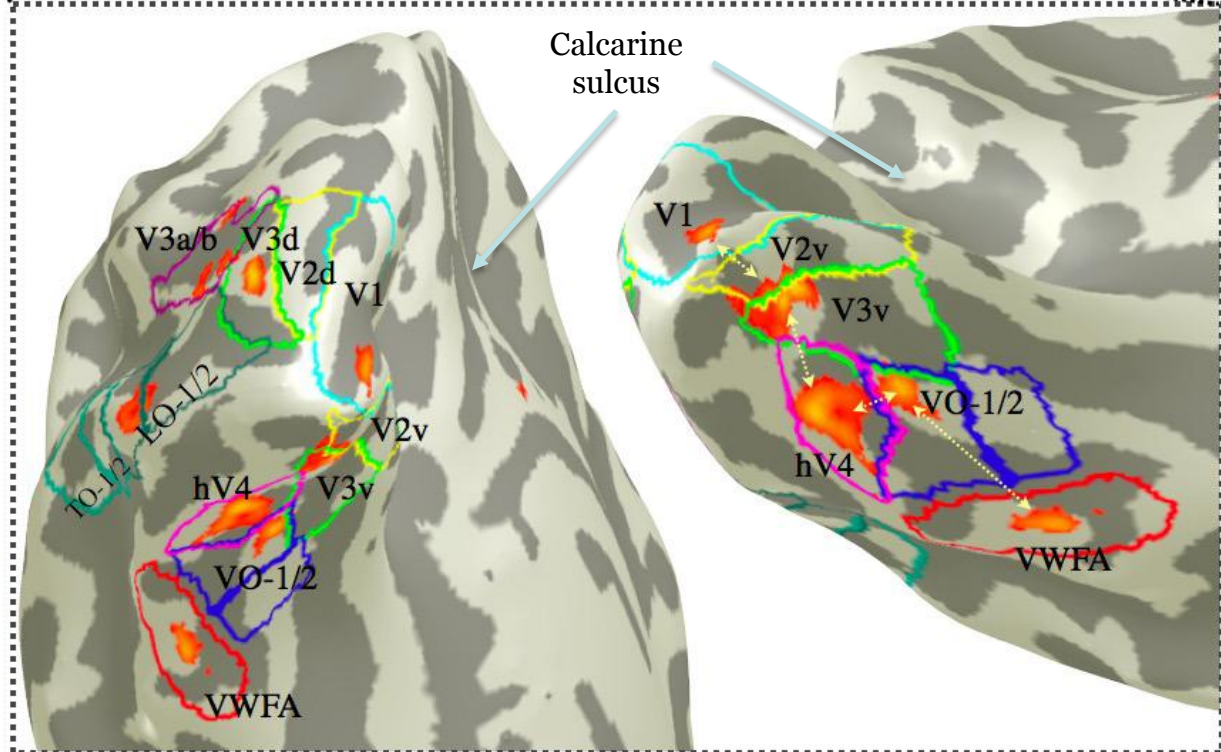
Ventral view, posterior left cortex



- Can we trace the signals and field of view from cortex into VOT, and particularly the reading circuitry?

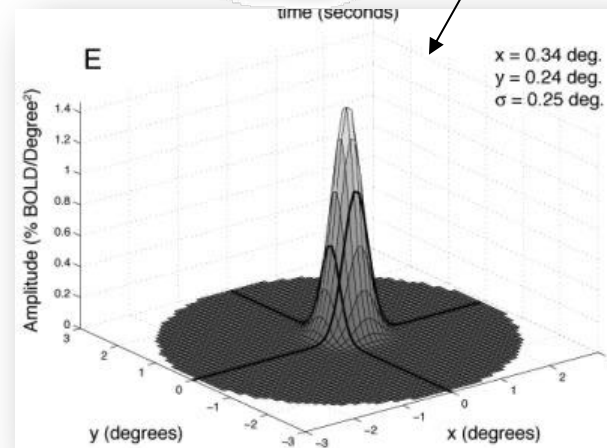
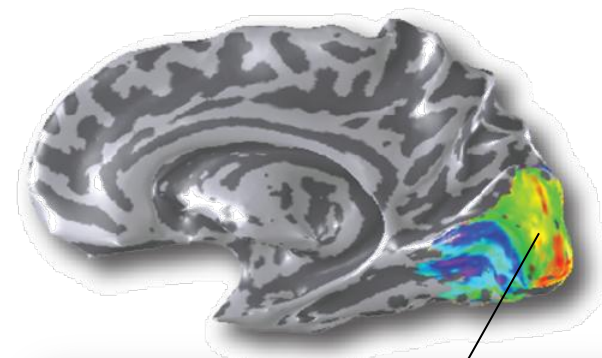


- Comparing a word to just fixation, fMRI measures the activity in the specialized circuitry (VWFA) as well as the visual field maps in individual participants



Measuring the field of view of a cortical region

- A single voxel within, say V1, responds to a small part of the visual field and thus has a small **field of view**
- Combining the pRFs from the voxels in a region tells us about its field of view
- In early visual field maps, the population receptive fields tile large portions of the visual field



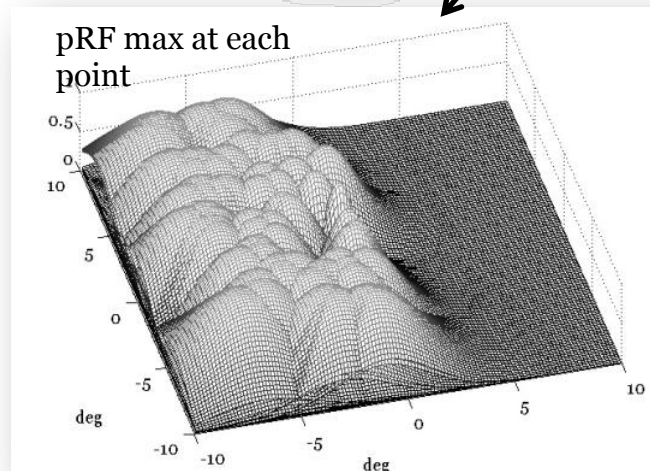
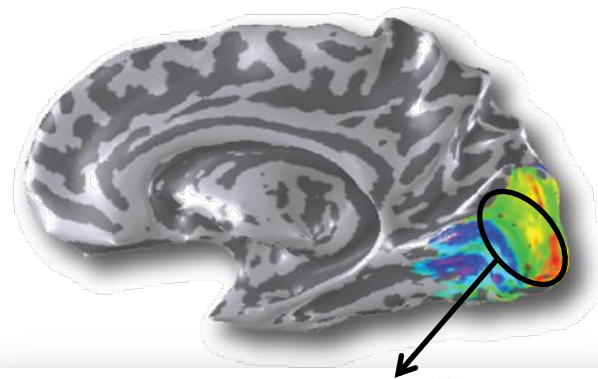
Amano



Dumoulin

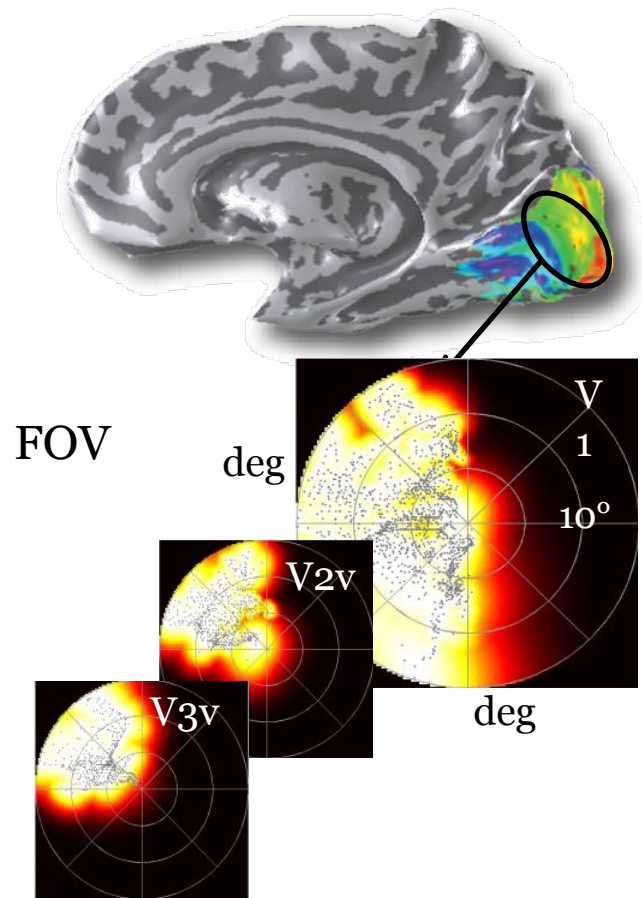
Measuring the field of view of a cortical region

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- In early visual field maps (V1, V2, ...), the field of view covers a large portion of the visual field; by hV4 the coverage is reduced



Measuring the field of view of cortical regions

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The reading circuitry field of view of a single subject

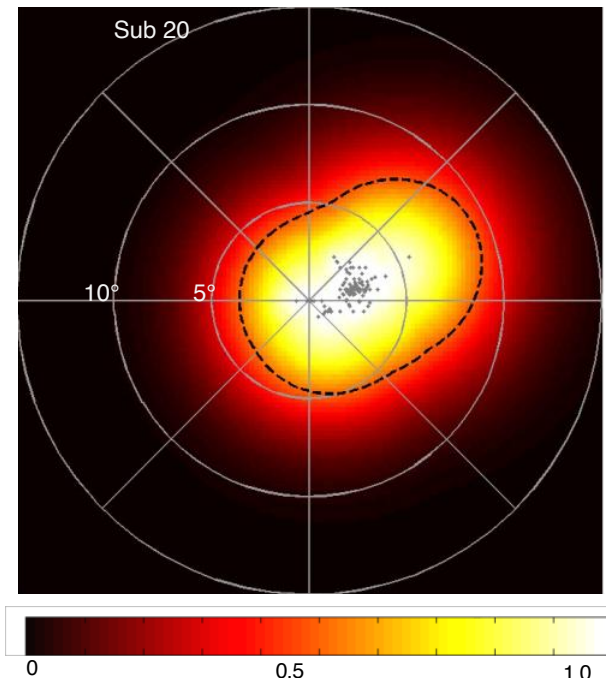
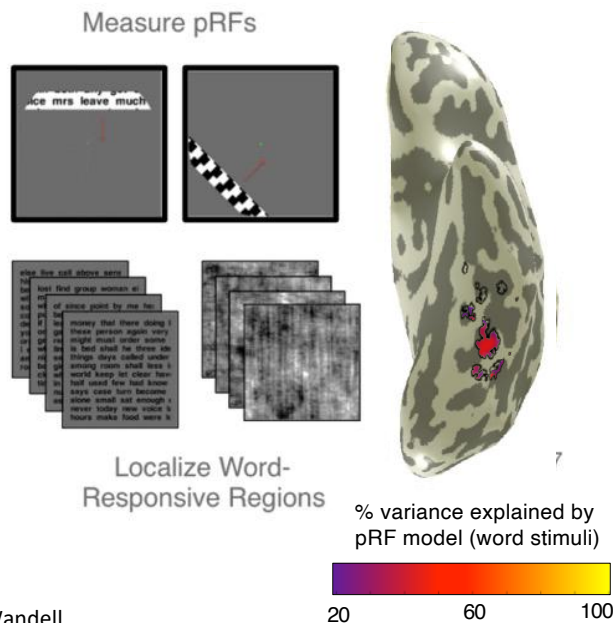


Rosemary Le



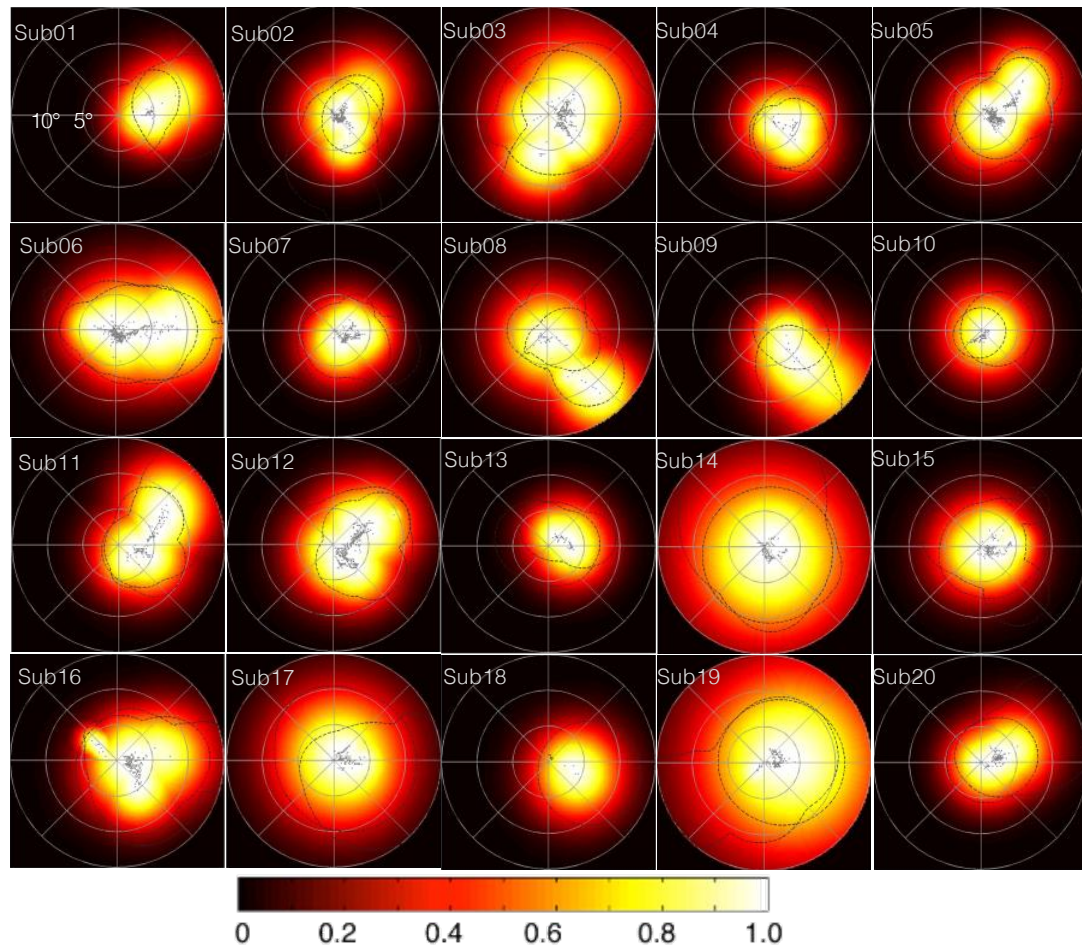
Gari Lerma-Usabiaga

- In the reading circuitry within the VOT, the field of view is quite small

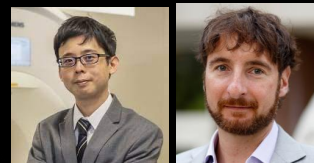


Field of view of the VOT reading circuitry

- There are significant differences between individuals
- It remains to show an impact on seeing words, but there is a reported correlations with eye movements measured using texture patterns (Gomez et al., 2018)



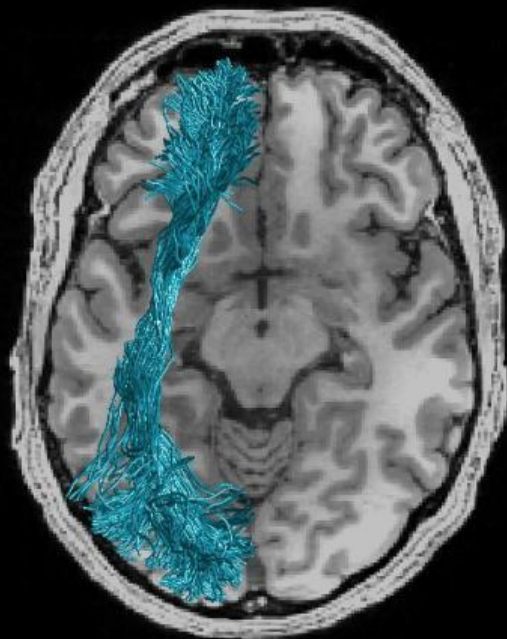
What's Next: Systems modeling



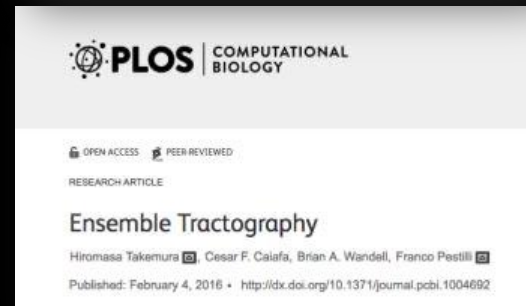
Takemura

Pestilli

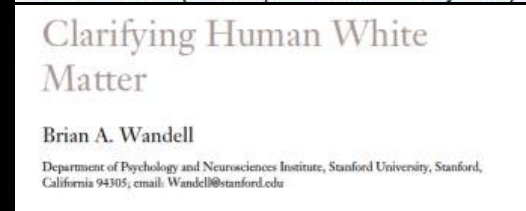
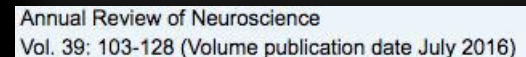
Left
IFOF



Introduction
to LiFE



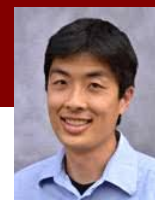
Extension to
ensemble
method



Review of
diffusion
imaging

150 Directions, 2 mm³, B=2000 projected on a 1 mm³ T1 anatomical image

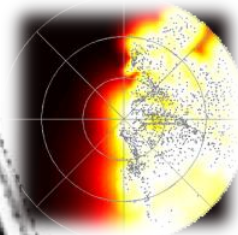
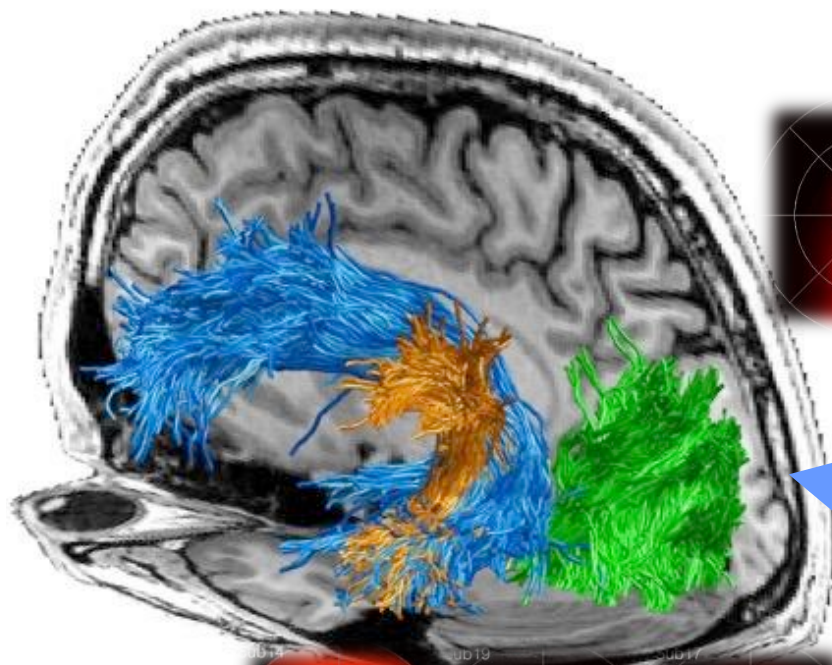
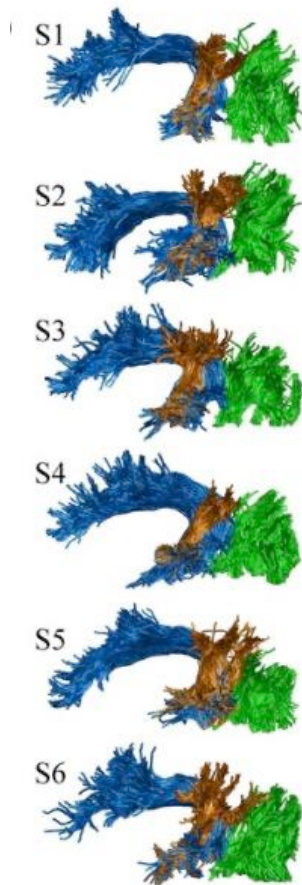
What's next: Systems modeling



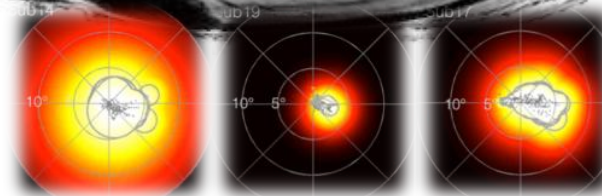
Kay



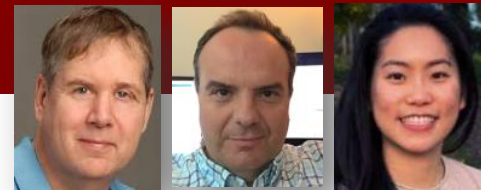
Yeatman



V1 inputs



VOT
Specialized processing
for faces, words, ...

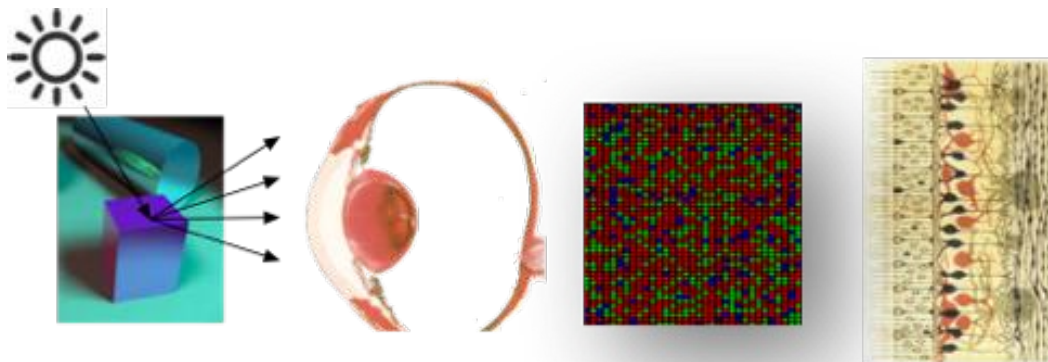


Brainard

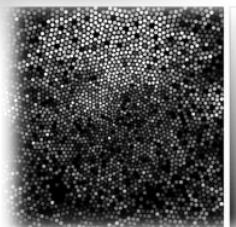
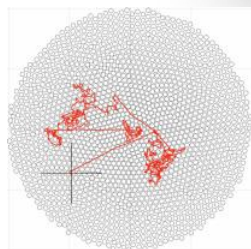
Cottaris

Lian

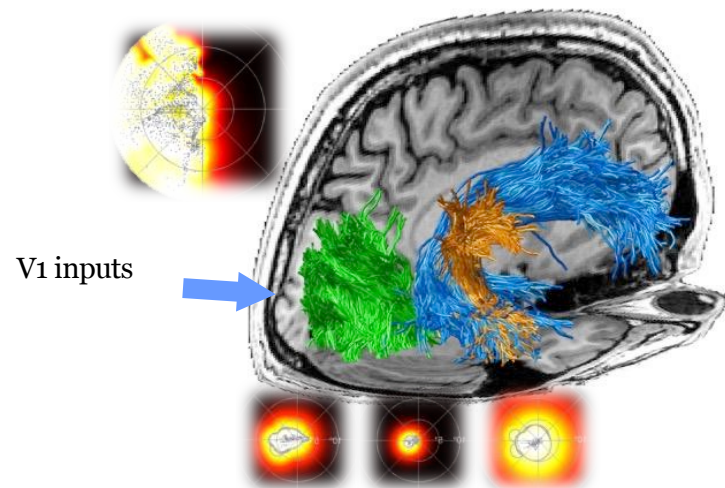
Image Systems Engineering Tools for Biology (ISETBio)



Cottaris, Wandell, Rieke, and Brainard. 2020. "A Computational Observer Model of Spatial Contrast Sensitivity: Effects of Photocurrent Encoding, Fixational Eye Movements, and Inference Engine." *Journal of Vision*



Lian, MacKenzie, Brainard, Cottaris, and Wandell. 2019. "Ray Tracing 3D Spectral Scenes through Human Optics Models." *J. Vis.*



VOT
Specialized processing for
faces, words, ...

Thanks to many students and postdocs!

David Brainard



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Steve Engel



Alyssa Brewer



Bob Dougherty



Heidi Baseler



Tony Morland



Alex Wade



Bill Press



Reno Bowen



Thanks to my many students and postdocs!

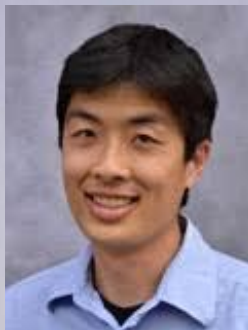
Jon Winawer



Ariel Rokem



Kendrick Kay



Aviv Mezer



A. Rauschecker



Netta Levin



Rory Sayres



Junjie Liu



Tony Sherbondy



Dora Hermes



Franco Pestilli



Hiromasa Takemura



Michael Perry



Thanks to my many students and postdocs!

Kaoru Amano



Michal Ben-Shachar



Jason Yeatman



Serge Dumoulin



Rosemary Le

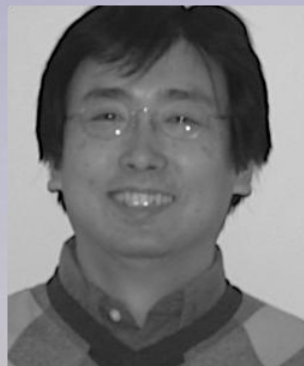


Gari Lerma-Usabiaga



And a special thanks to my ophthalmology collaborators who took career risks to come to the US and work with me!

Satoshi
Nakadomari



Hiroshi Horiguchi



Yoichiro Masuda



Shumpei Ogawa

