

# MRI: Maps and models in the human visual brain

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QUANTITATIVE MEASUREMENTS

∞

COMPUTATIONAL MODELS

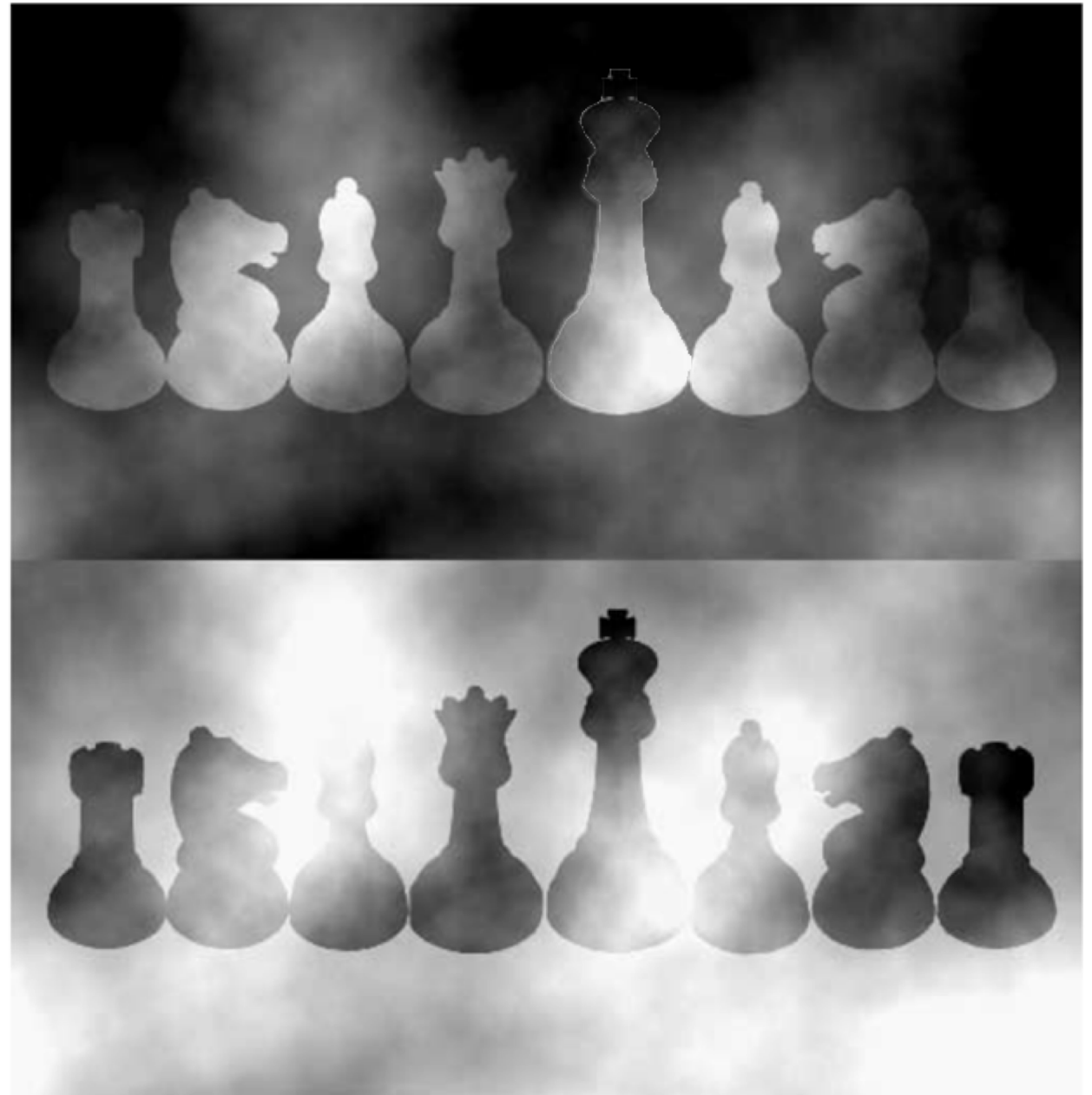
∞

CHECK AND SHARE

# Vision and computation

- Even simple perceptual judgments – such as lightness - depend on substantial interpretation carried out by brain circuits
- Vision science exploration of these computations has been influential in developing principles for other neuroscience fields and artificial intelligence
- Vision science fundamentals are important for the entire imaging industry

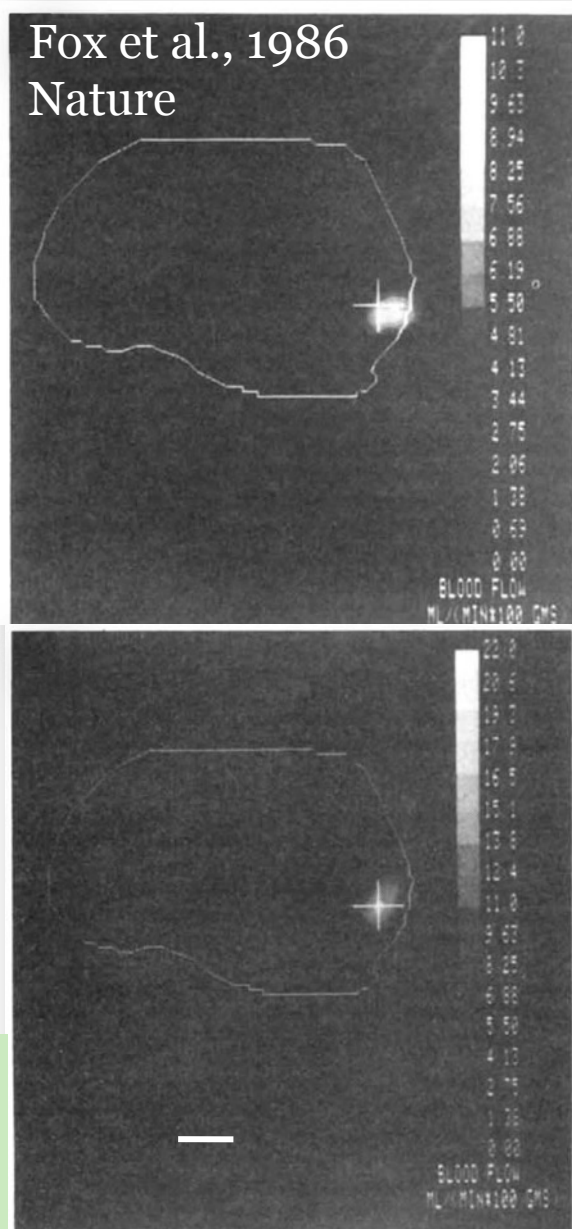
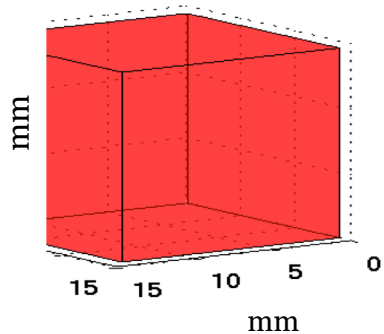
Image segmentation and lightness perception  
Anderson and Winawer - **Nature**, 2005



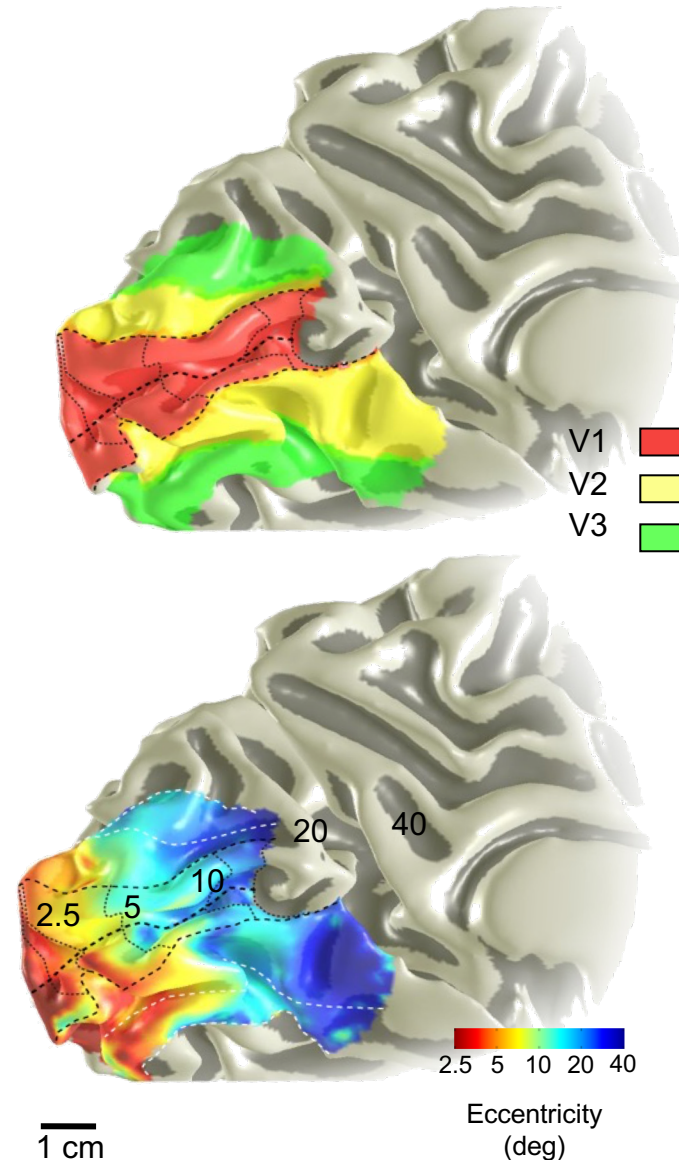
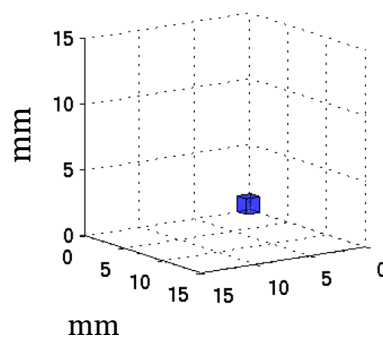
# Remarkable progress from PET to advanced MRI in 25 years

(Wandell and Winawer, 2011)

Voxel size  
1986



Voxel size  
2009

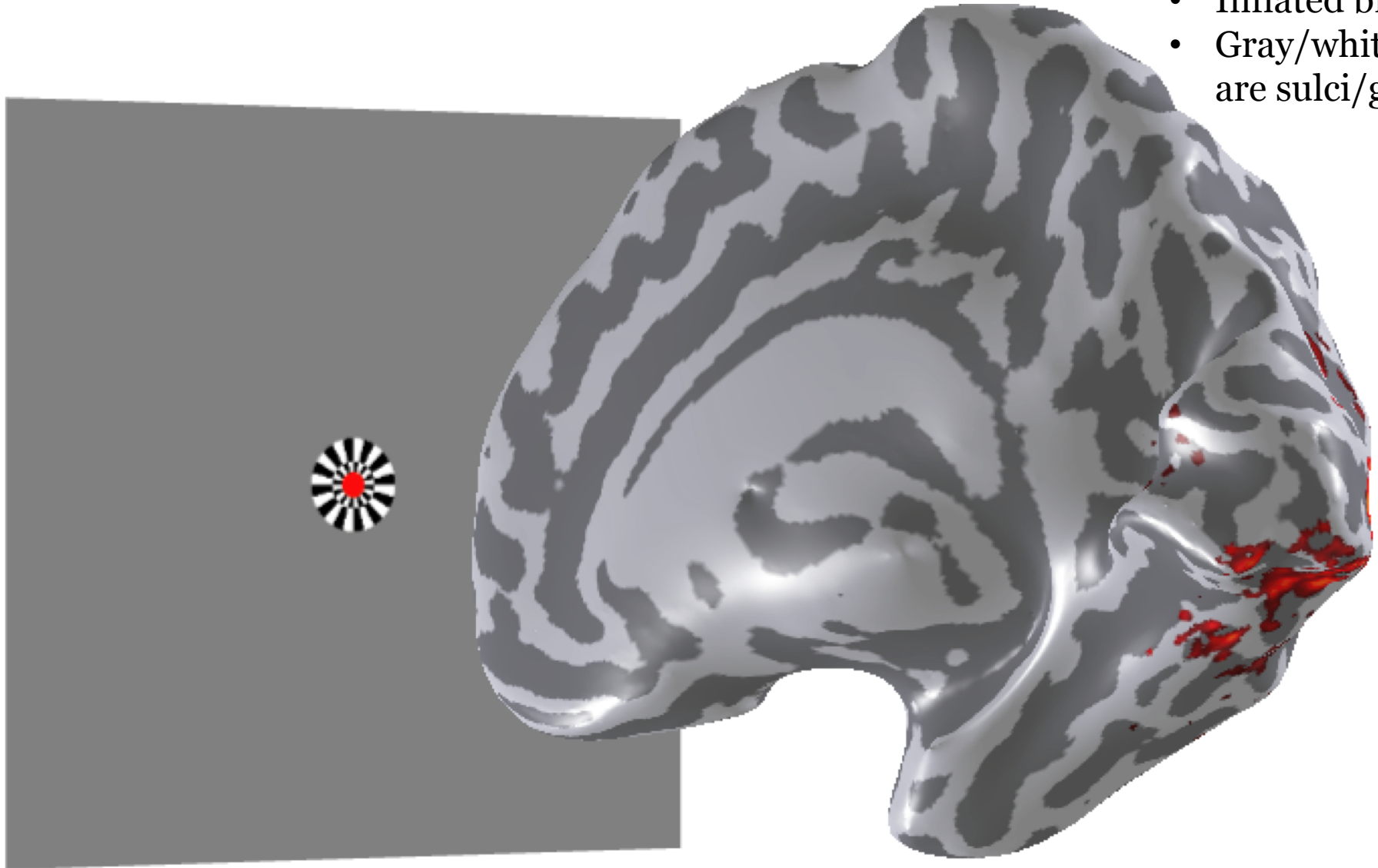


Mapping human visual cortex with positron emission tomography. Fox, Mintun, Raichle, Miezin, Allman & Van Essen (1986). **Nature**, v 323,

# Human eccentricity mapping with fMRI

(Engel et al., 1994,1997; Sereno; Tootell, DeYoe; Others)

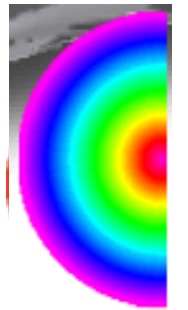
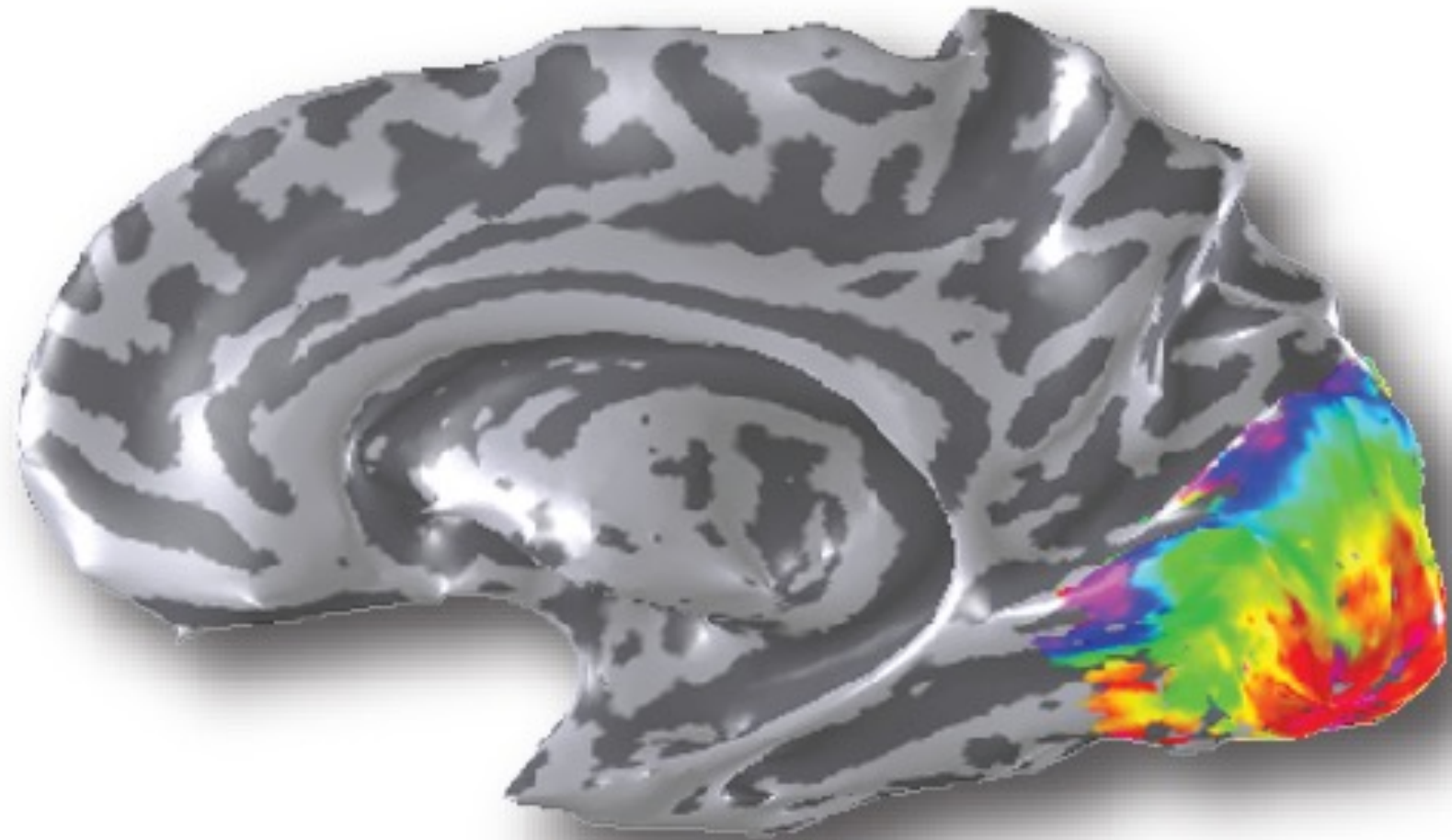
- Inflated brain
- Gray/white are sulci/gyri



Functional magnetic resonance imaging of human visual cortex Engel, et al. (1994). **Nature**

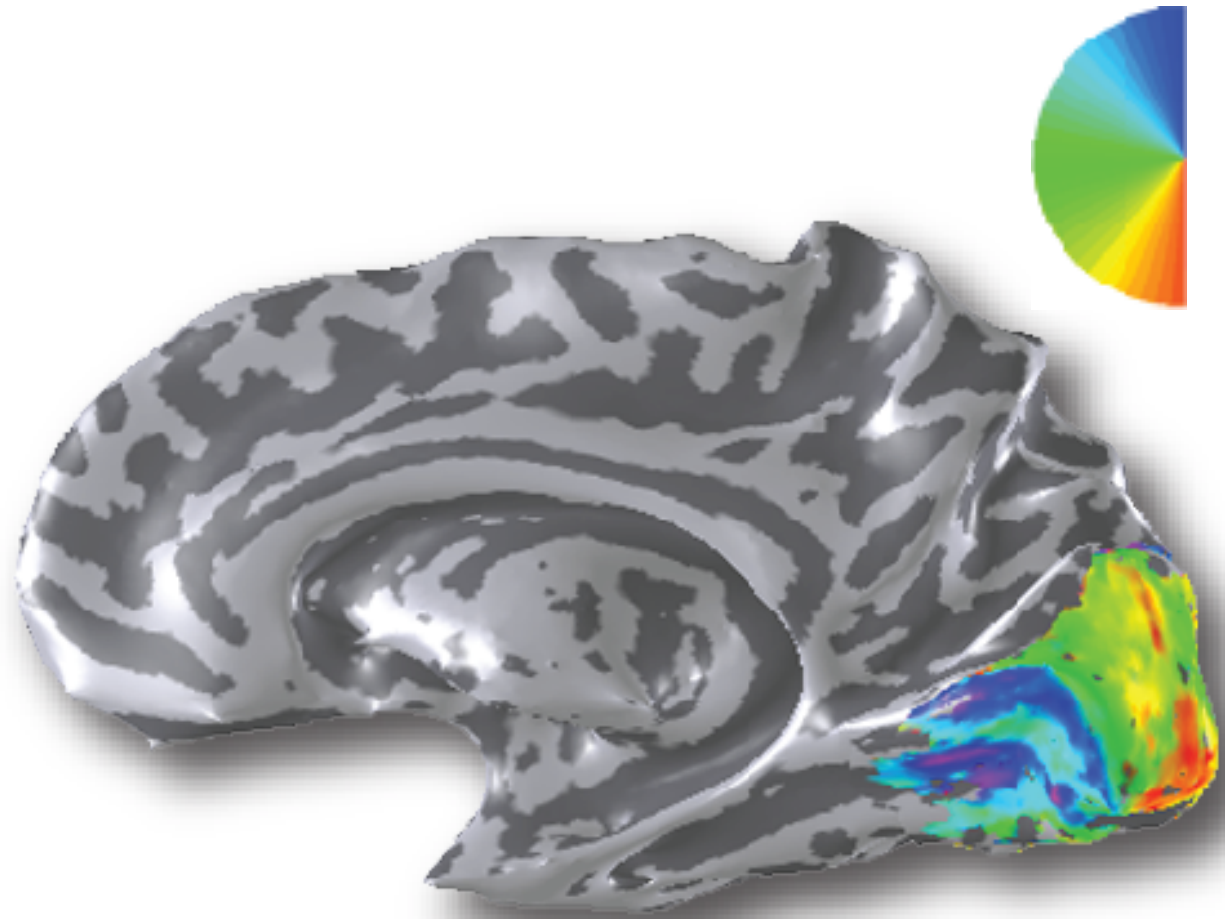
Retinotopic organization in human visual cortex and the spatial precision of functional MRI Engel, et al. (1997). **Cerebral Cortex**

# Pseudo-color representation of visual field map

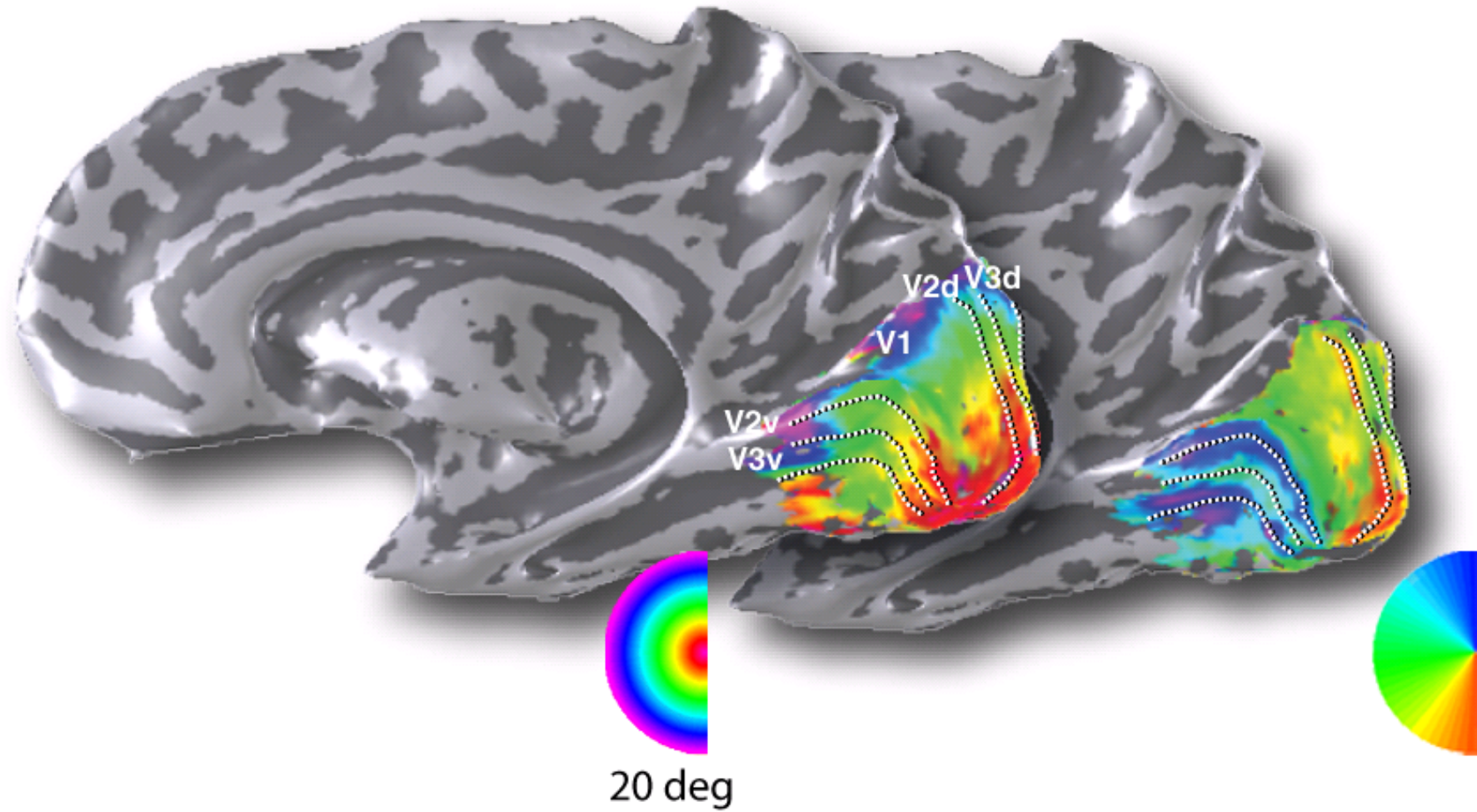


20 deg

# Angular measurements delineate visual field map boundaries

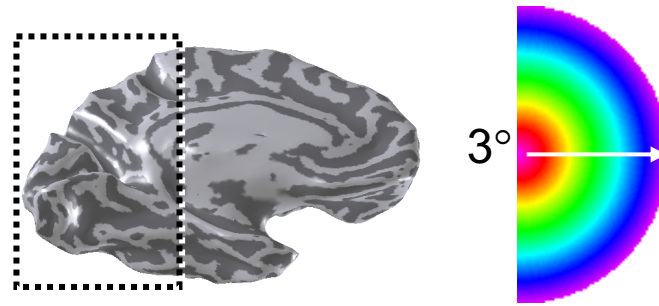


# Combining eccentricity and angle data yields maps

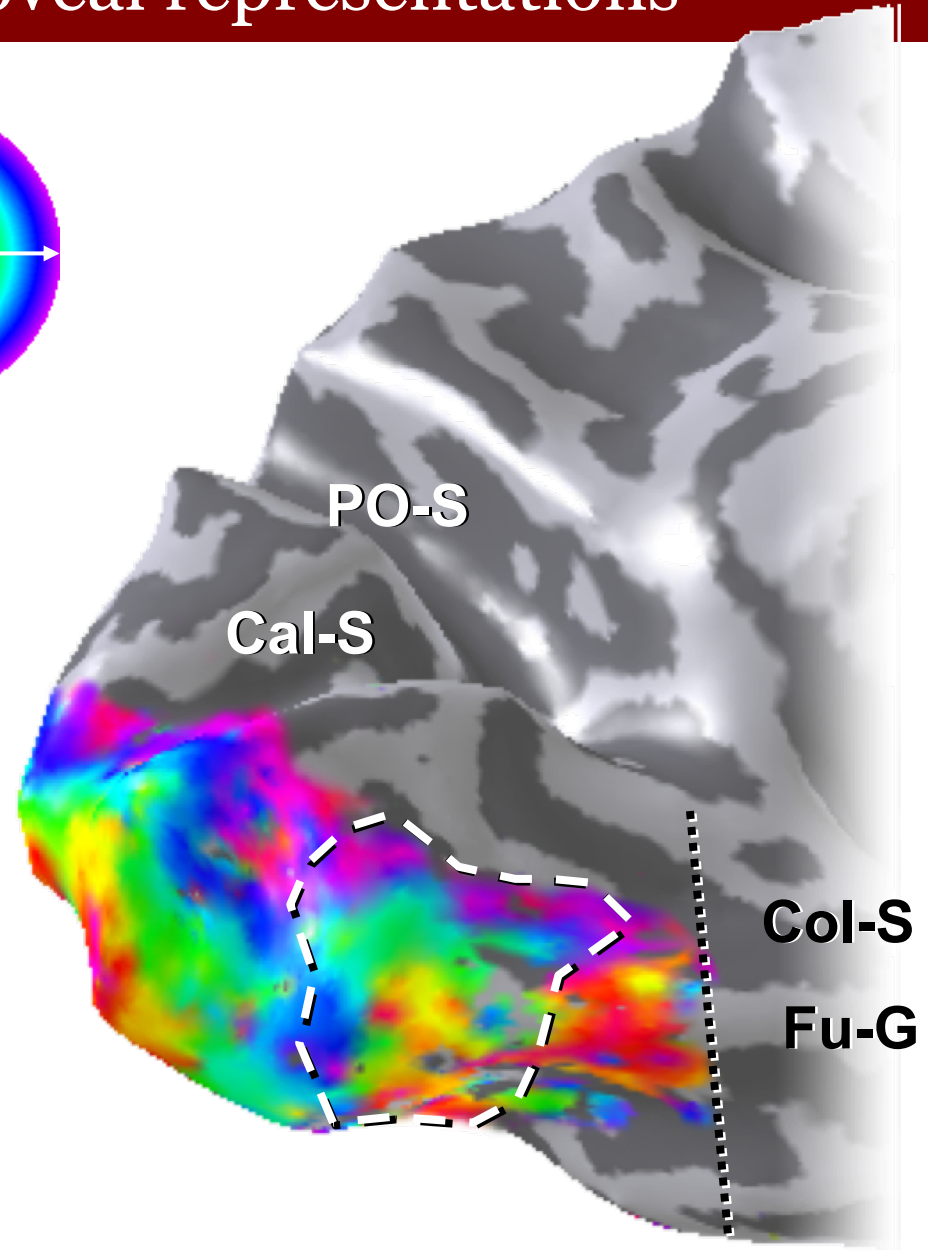


# Visual field map clusters: Distinct foveal representations

- Distinct foveal representations can be easily identified
- These are often confluent with multiple eccentricity maps
- The areas are separated by multiple angle maps within the shared eccentricity representation.



*Coherence > 0.25*

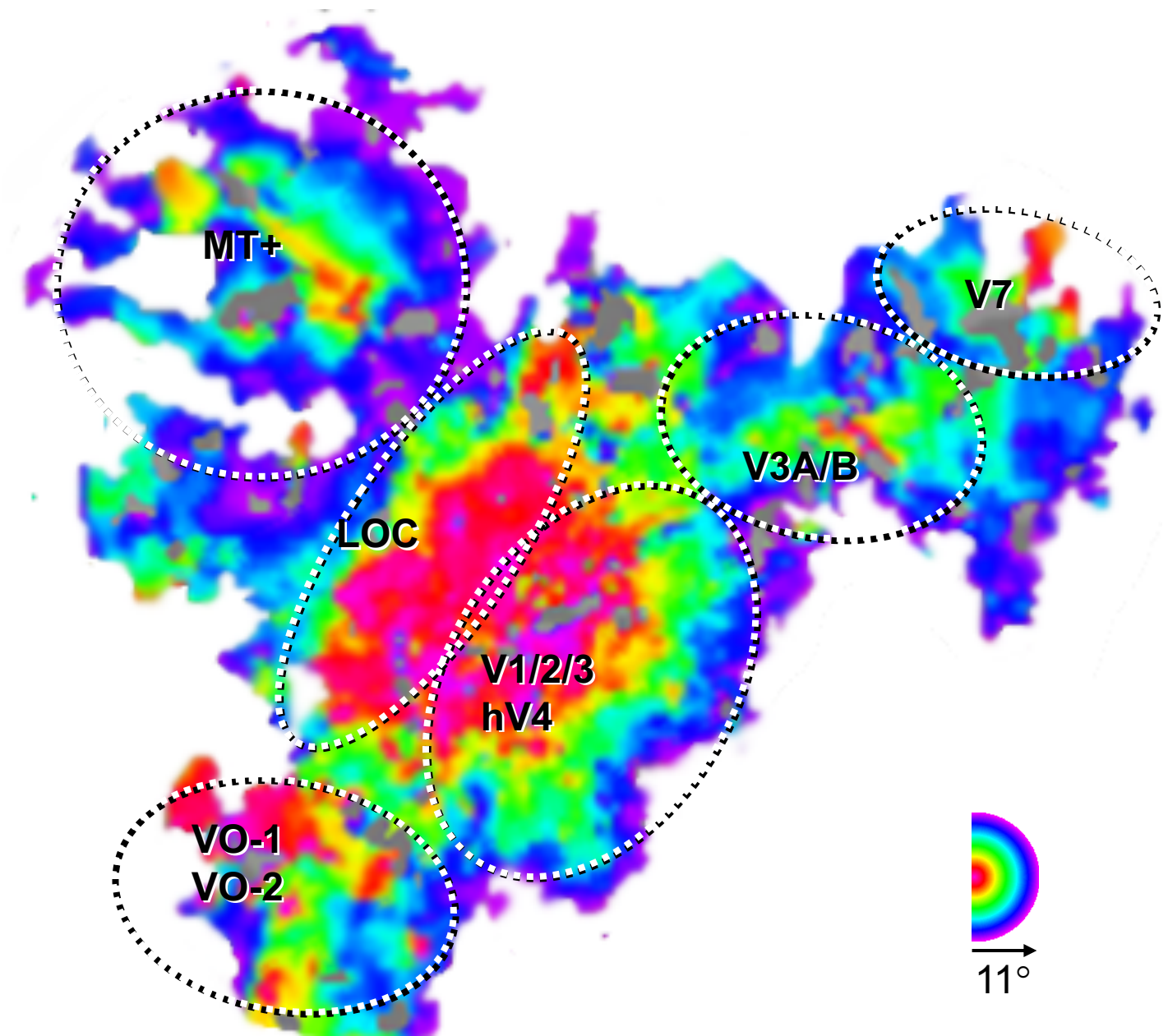


Brewer

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.*, vol. 8 no. 8, pp. 1102-9

# Visual field map clusters

- Share a common circular or semi-circular eccentricity map.
- Contain multiple angle maps within the eccentricity representation.

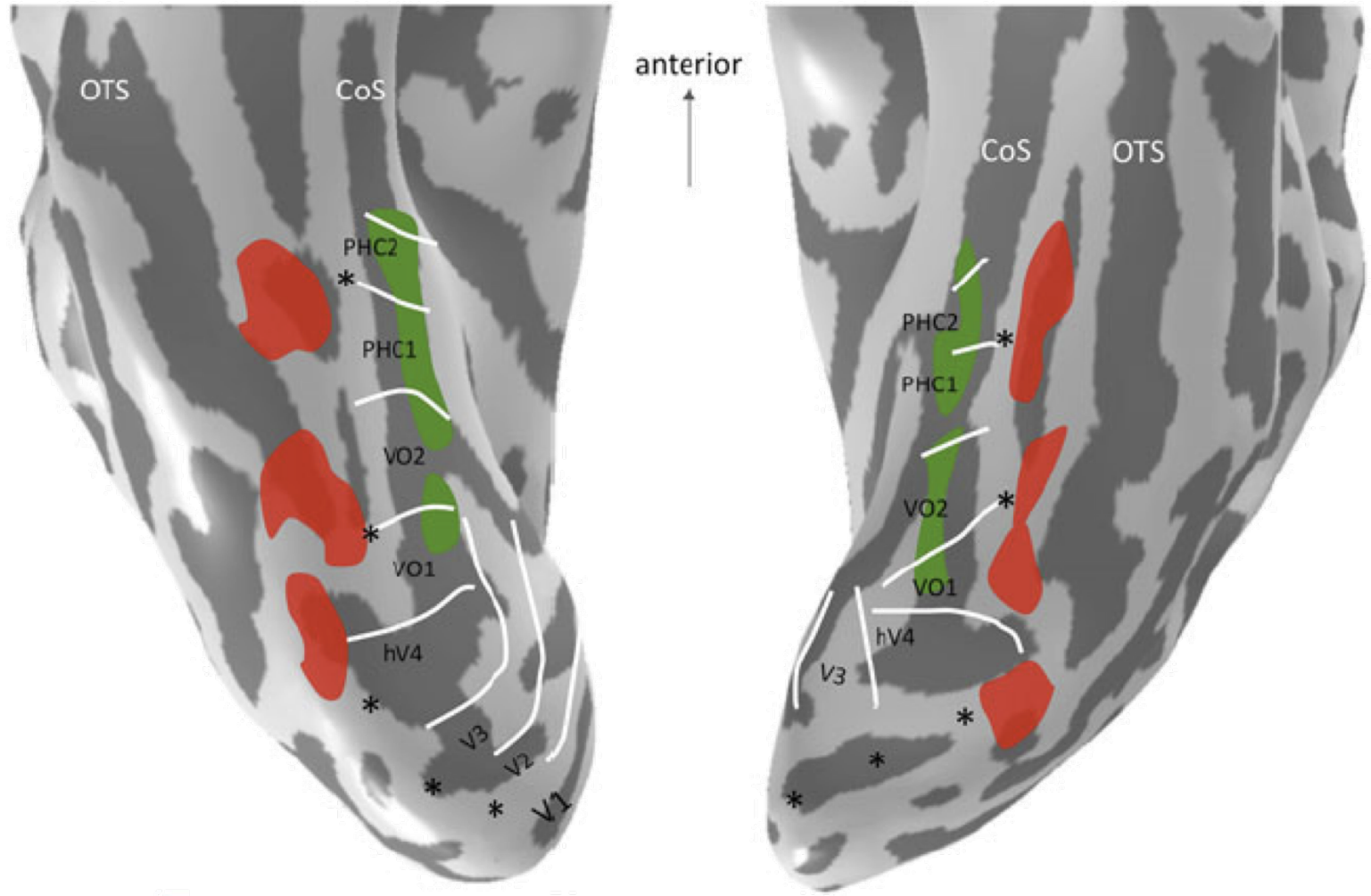


Visual Field Map Clusters in Human Cortex. B. Wandell, A. A. Brewer and R.F. Dougherty (2005). **Phil. Trans. of the Royal Society London**, vol. 360, pp. 693-707

Visual field maps and stimulus selectivity in human ventral occipital cortex. A.A. Brewer, J. Liu, A.R. Wade, B.A. Wandell (2005). **Nat Neurosci.**, vol. 8 no. 8, pp. 1102-9

# Relationship between maps and functional specializations

- Face-selective
- Place-selective



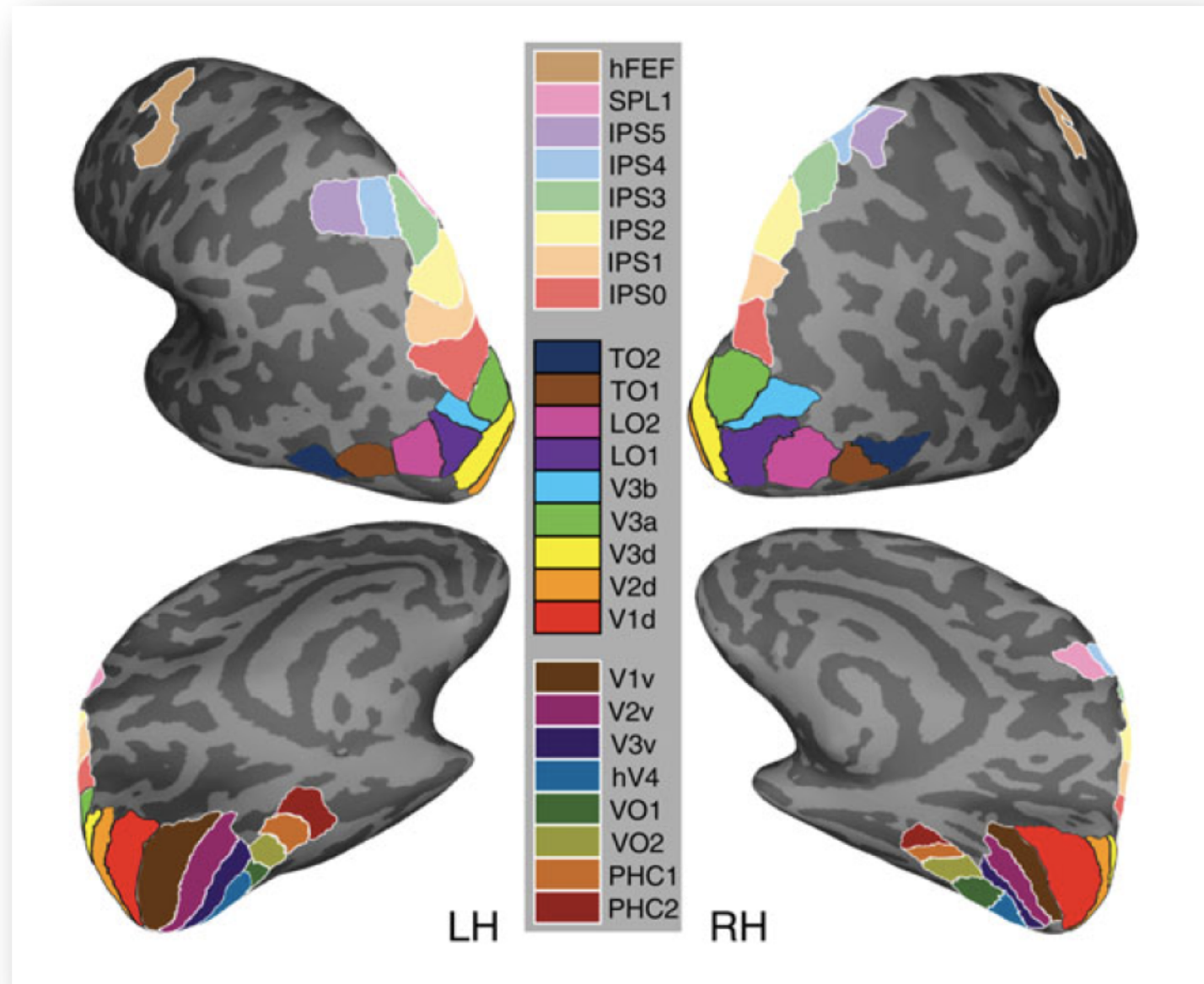
The functional architecture of the ventral temporal cortex and its role in categorization  
Grill-Spector and Weiner (2014) **Nature Reviews Neuroscience**

# Atlas fitting is automated in a number of ways

- The Benson et al. methods and Wang et al. (2015) atlas are very valuable and practical contributions
- There are several public routines that automatically estimate the positions of atlases on T1w anatomical data

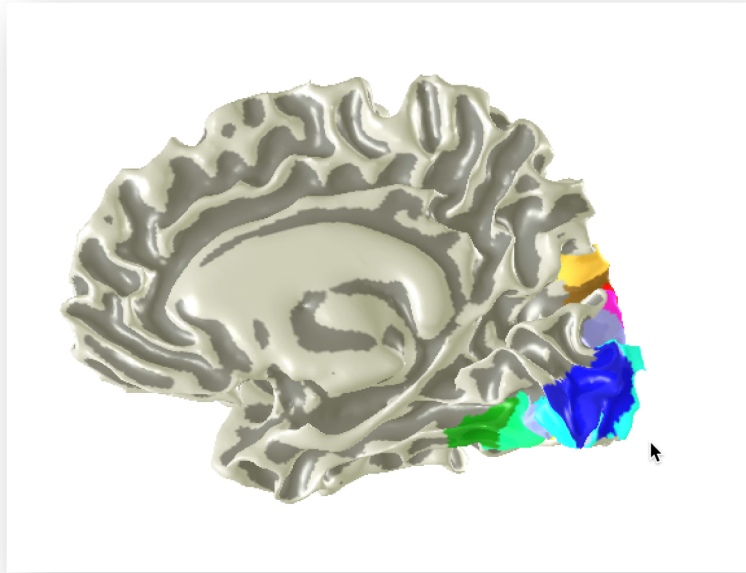
The retinotopic organization of striate cortex is well predicted by surface topology. Benson, et al. (2012) **Current Biology**

Probabilistic maps of visual topography in human cortex. Wang et al. (2015). **Cerebral Cortex**





# Visual field map reviews



- Maps tile the occipital lobe
- Extend into IPS and VOT
- Response properties differ
- Identification from gross anatomy

**Cell PRESS** 366 Neuron 56, October 25, 2007 Neuron Review

## Visual Field Maps in Human Cortex



Brian A. Wandell,<sup>1,\*</sup> Serge O. Dumoulin,<sup>1</sup> and Alyssa A. Brewer<sup>2</sup>

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<sup>2</sup>Department 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 51 (2011) 718-737

Contents lists available at ScienceDirect

**Vision Research**

journal homepage: [www.elsevier.com/locate/visres](http://www.elsevier.com/locate/visres)

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Review

### Imaging retinotopic maps in the human brain

Brian A. Wandell\*, Jonathan Winawer

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

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**ARTICLE INFO**

Article history:  
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**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-

# Additional references

## Forthcoming from Winawer and Benson Gazzaniga Cognitive Neuroscience volume

**Title:** Population Receptive Field Models in Human Visual Cortex

**Authors:** Jonathan Winawer and Noah C. Benson

**Affiliations:** Department of Psychology and Center for Neural Science, New York University, New York, NY, 10003

**Abbreviated title:** Population Receptive Fields Models

bioRxiv preprint first posted online Apr. 25, 2018; doi: <http://dx.doi.org/10.1101/308247>. The copyright holder for this preprint (which was not peer-reviewed) is the author/funder. It is made available under a [CC-BY 4.0 International license](#).

## The HCP 7T Retinotopy Dataset

Noah Benson<sup>1</sup>, Keith W. Jamison<sup>2,\*</sup>, Michael J. Arcaro<sup>3</sup>,  
An Vu<sup>2,#</sup>, Matthew F. Glasser<sup>4,5</sup>, Timothy S. Coalson<sup>4</sup>, David Van Essen<sup>4</sup>,  
Essa Yacoub<sup>2</sup>, Kamil Ugurbil<sup>2</sup>, Jonathan Winawer<sup>1,\*</sup>, Kendrick Kay<sup>2,\*</sup>

ORIGINAL ARTICLE

## Probabilistic Maps of Visual Topography in Human Cortex

Liang Wang<sup>1,2,3,†</sup>, Ryan E.B. Mrcuzek<sup>1,2,4,†</sup>, Michael J. Arcaro<sup>1,2</sup>,  
and Sabine Kastner<sup>1,2</sup>

<sup>1</sup>Princeton Neuroscience Institute and, <sup>2</sup>Department of Psychology, Princeton University, Princeton, NJ 08544, USA, <sup>3</sup>Key Laboratory of Mental Health, Institute of Psychology, Chinese Academy of Sciences, Beijing 100101, China, and <sup>4</sup>Department of Psychology, Swarthmore College, Swarthmore, PA 19081, USA

*Cerebral Cortex*, October 2015;25: 3911–3931

*Visual Neuroscience* (2015), 32, e020, 13 pages.  
Copyright © Cambridge University Press, 2015 0952-5238/15  
doi:10.1017/S0952523815000176

SPECIAL COLLECTION

Controversial Issues in  
Visual Cortex Mapping

REVIEW ARTICLE

## Human V4 and ventral occipital retinotopic maps

JONATHAN WINAWER<sup>1</sup> AND NATHAN WITTHOFT<sup>2</sup>

<sup>1</sup>Department of Psychology and Center for Neural Science, New York University, New York, New York 10003

<sup>2</sup>Department of Psychology, Stanford University, Stanford, California 94305

(RECEIVED February 3, 2015; ACCEPTED June 3, 2015)

F1000Research

F1000Research 2017, 6:1526 Last updated: 07 NOV 2017



METHOD ARTICLE

## Identification of the ventral occipital visual field maps in the human brain [version 1; referees: 2 approved, 1 approved with reservations]

Jonathan Winawer <sup>1</sup>, Nathan Witthoft<sup>2</sup>

<sup>1</sup>Psychology and Center for Neural Science, New York University, New York, NY, 10003, USA

<sup>2</sup>Department of Psychology, Stanford University, Stanford, CA, 94305, USA

# Modeling visual cortex responses

- Population receptive fields

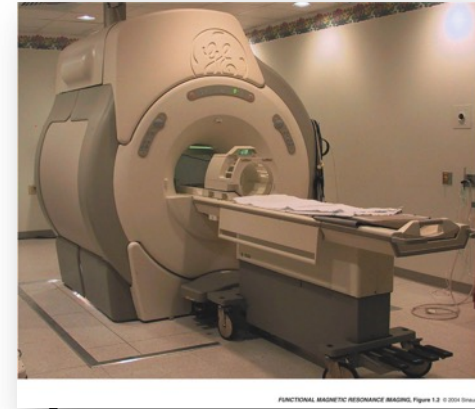
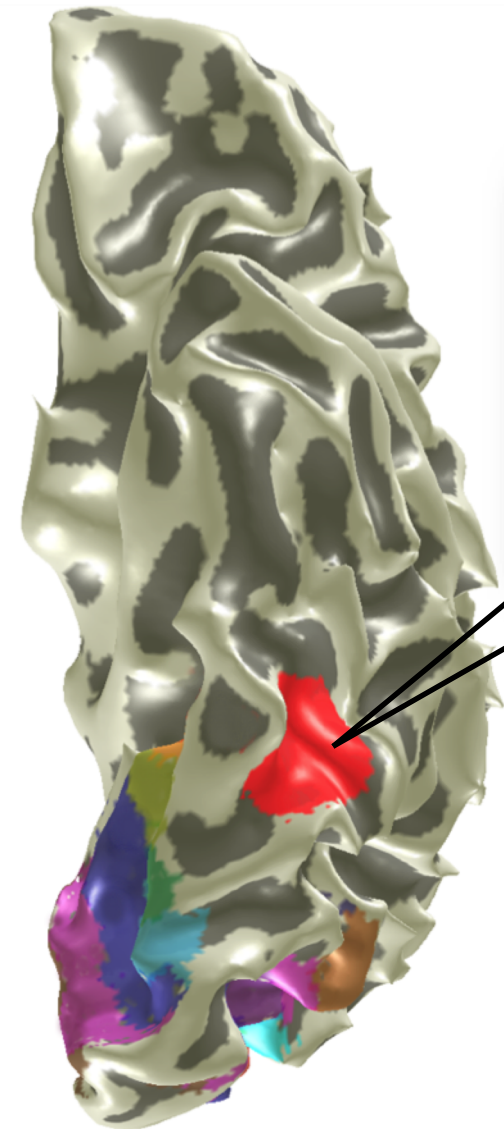
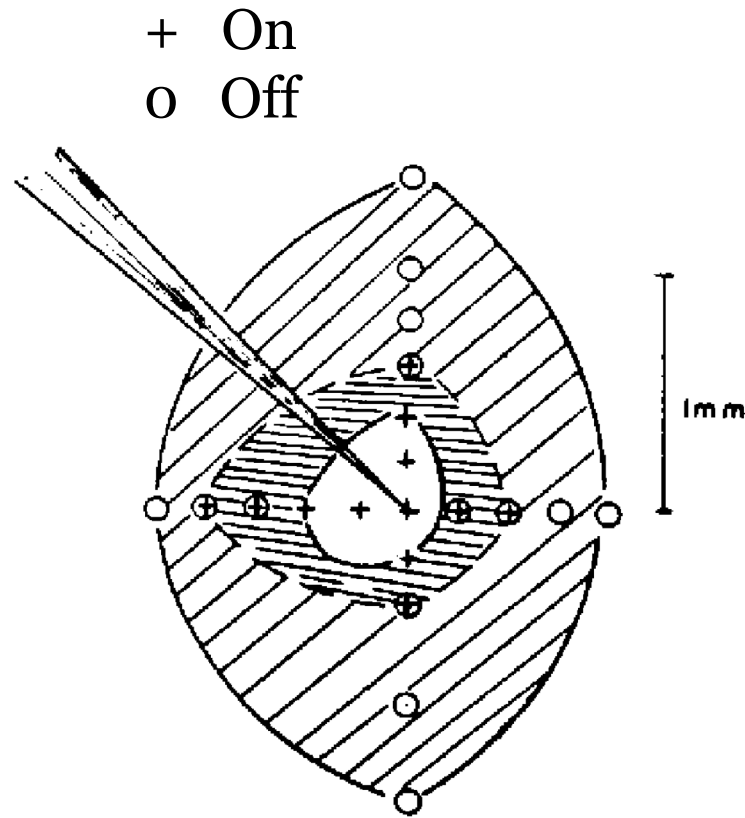


# Quantitative modeling: the population receptive field (pRF)

‘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

- Functional description
- Stimulus-referred



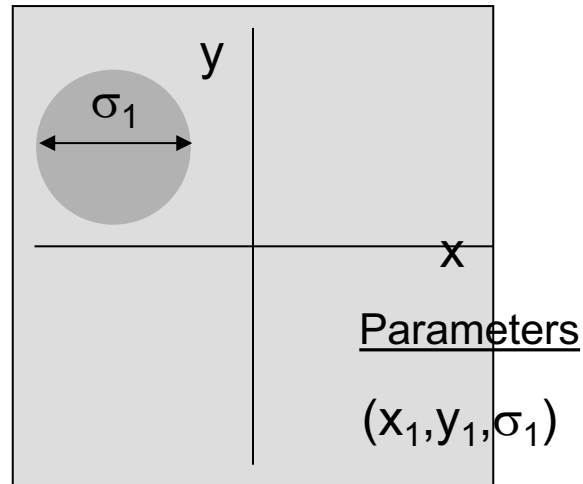
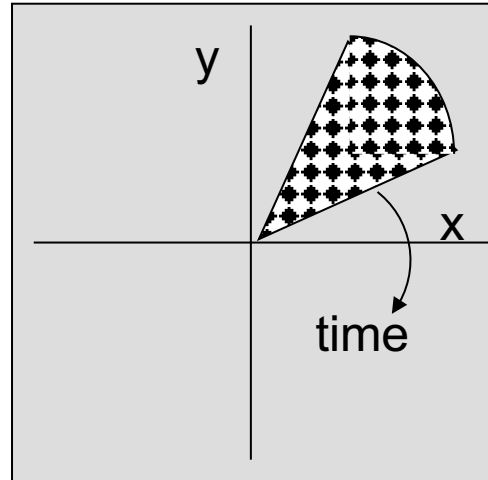
FUNCTIONAL MAGNETIC RESONANCE IMAGING, Figure 1.3 © 2004 Elsevier



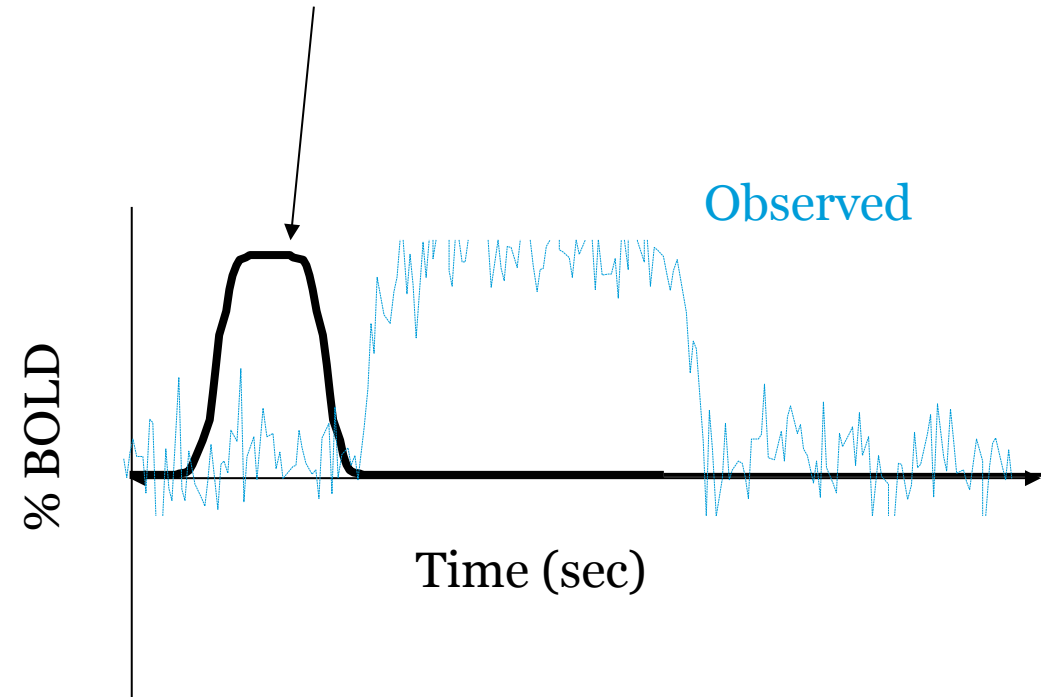
# Population receptive field idea

- For each voxel, find a spatial receptive field that explains the fMRI measurement.
- The spatial RF model is the object of interest
- Minimally, the model is linear in space and has an  $(x,y)$  location in the visual field and a spread

Stimulus



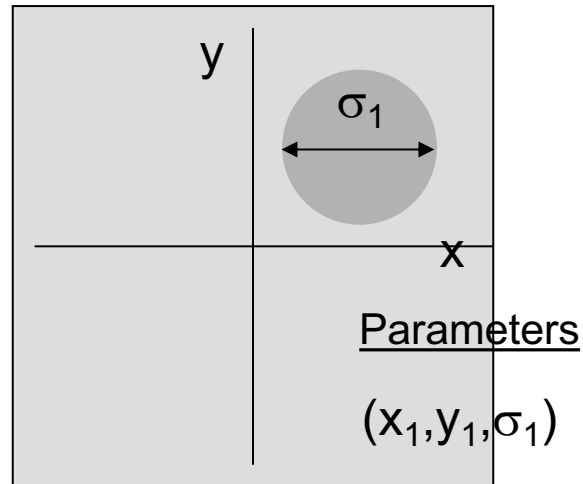
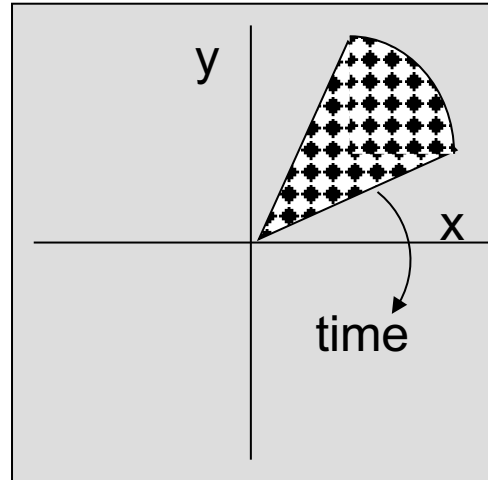
Predicted BOLD (including HRF)



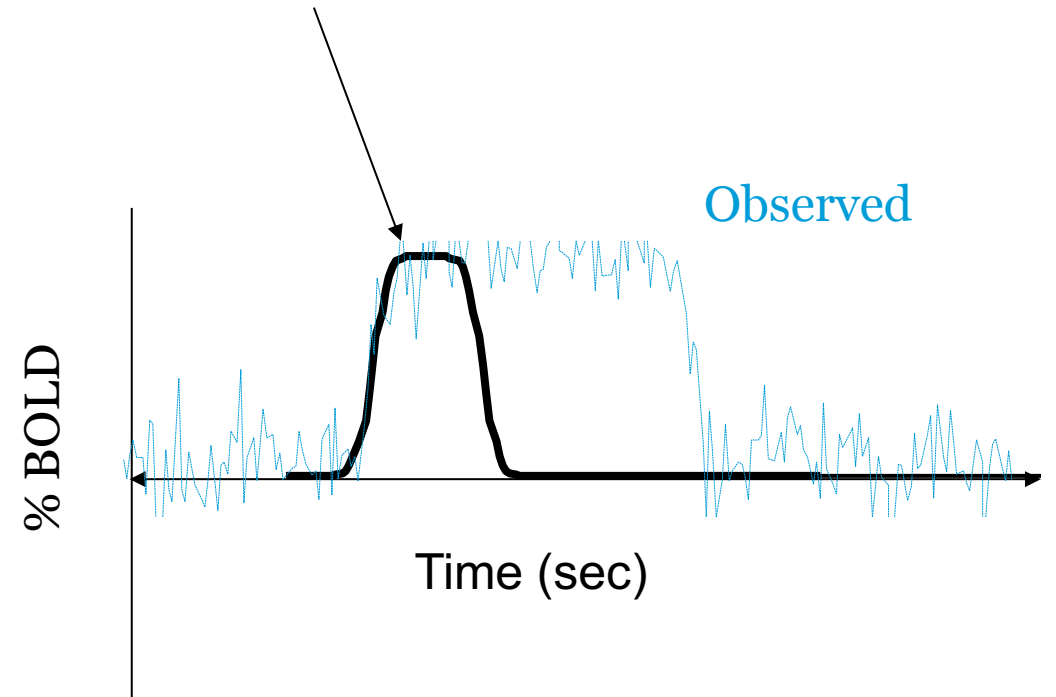
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Stimulus



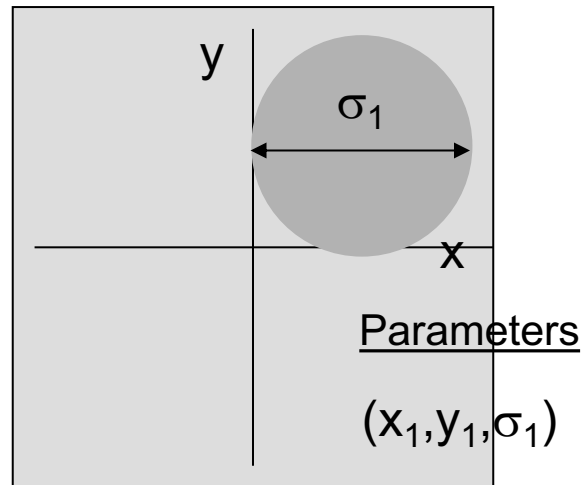
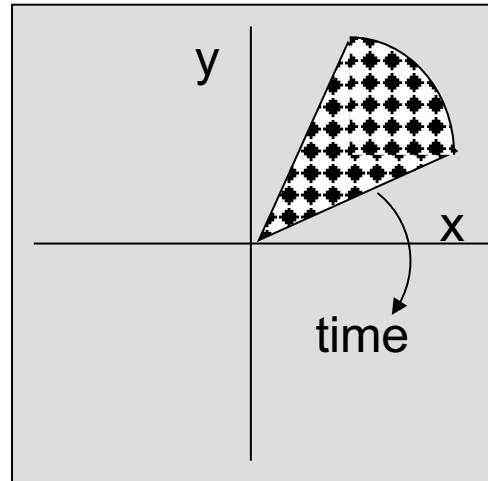
Predicted BOLD (including HRF)



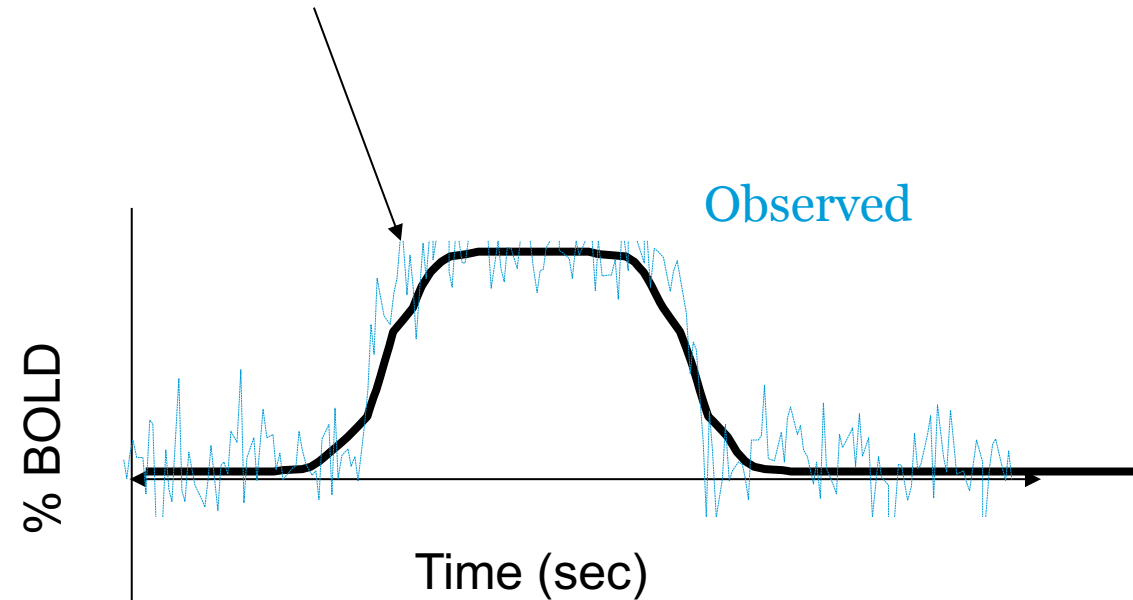
# Stimulus Population receptive field idea

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Stimulus

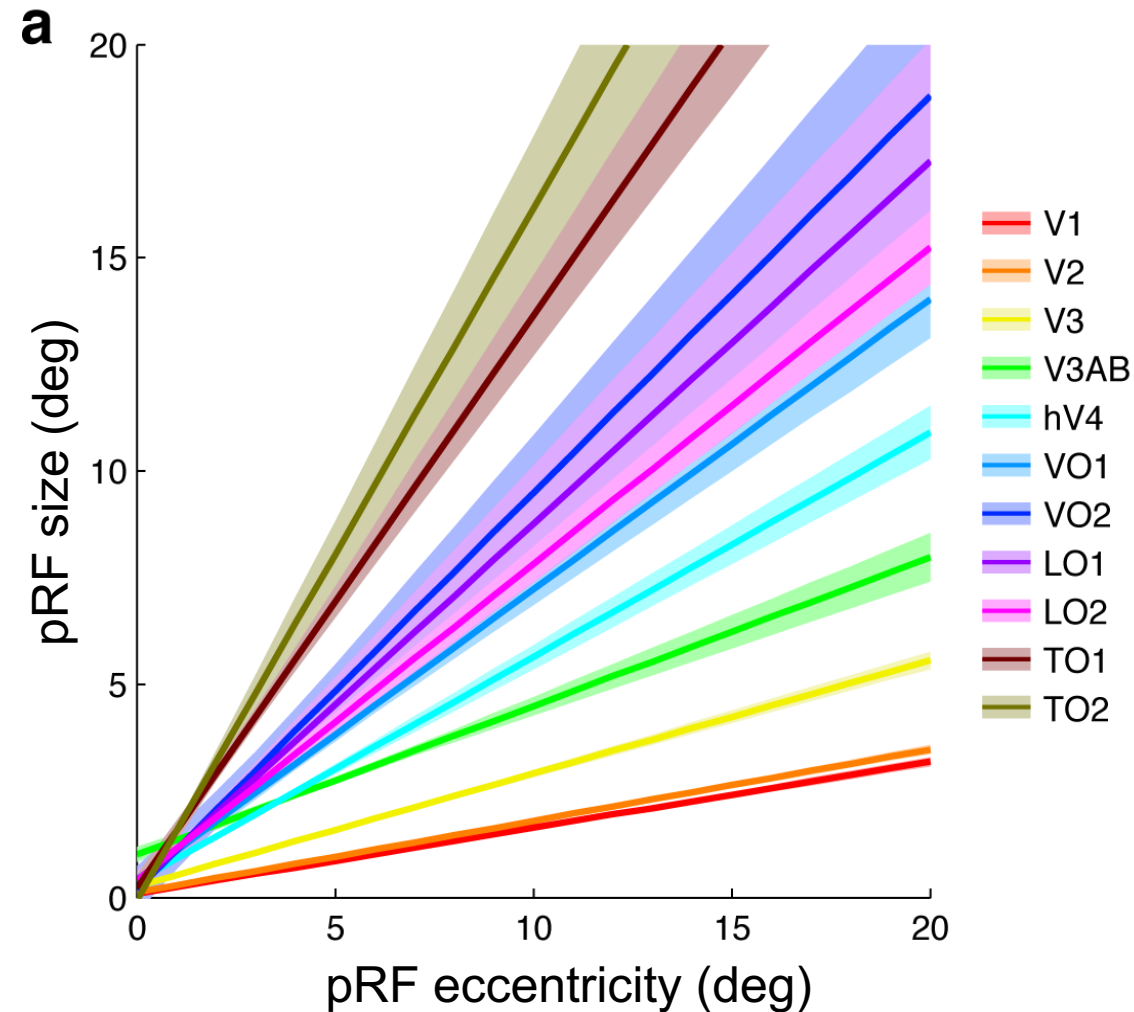
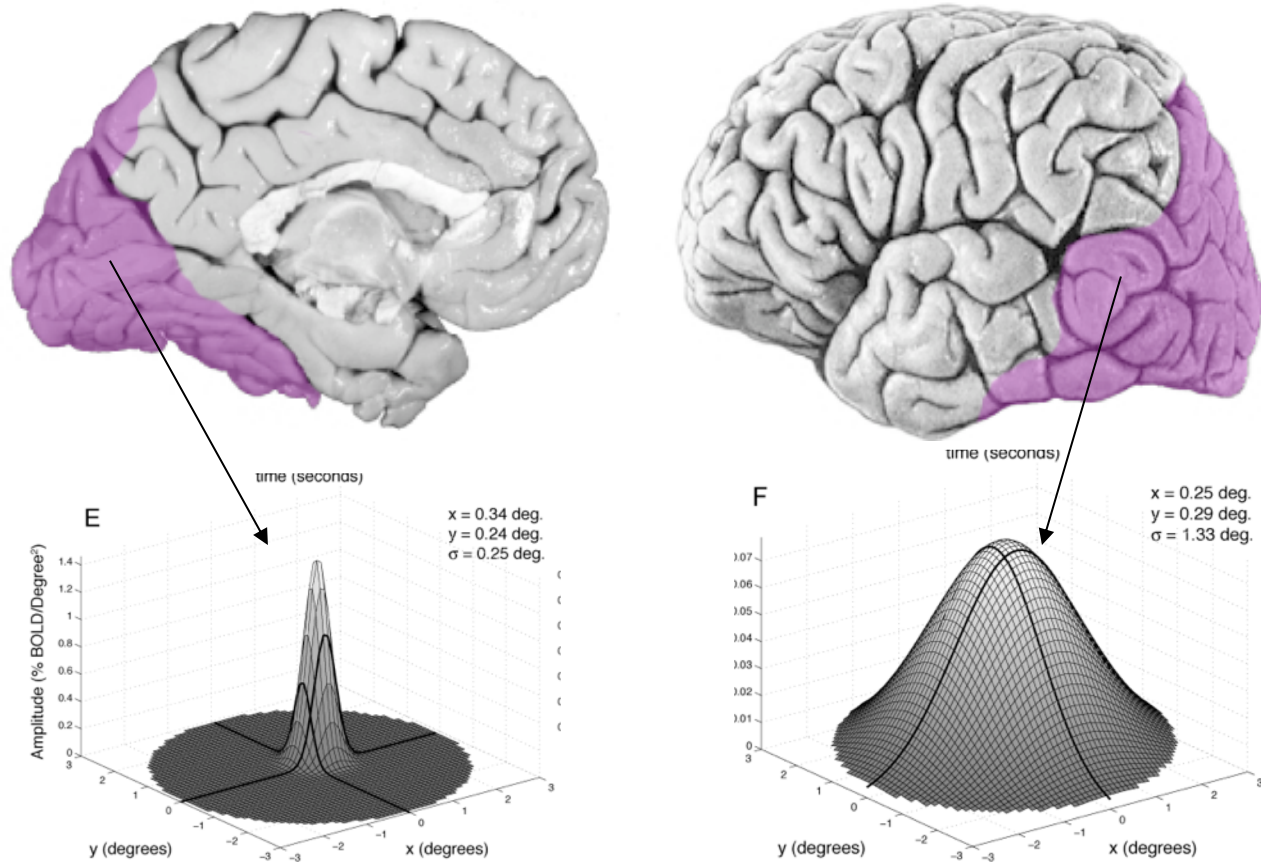


Predicted BOLD (including HRF)



# PRF size varies substantially and regularly across visual cortex

- At common eccentricities, different maps have different pRF sizes
- PRF size increases with eccentricity for all maps
- Bands are bootstrap estimates of the standard error



# Population receptive field modeling is now widely used

- Attention
- Stability and Plasticity
- Prosopagnosia
- Development and aging
- Autism
- Alzheimer's disease

Review

Trends in Cognitive Sciences, June 2015, CellPress  
Vol. 19, No. 6 349

## Computational neuroimaging and population receptive fields

Brian A. Wandell<sup>1</sup> and Jonathan Winawer<sup>2</sup>

<sup>1</sup>Psychology Department and Neurosciences Institute, Stanford University, Stanford, CA, USA

<sup>2</sup>Psychology Department and Center for Neural Science, New York University, New York, NY, USA

Functional magnetic resonance imaging (fMRI) noninvasively measures human brain activity at millimeter resolution. Scientists use different approaches to take advantage of the remarkable opportunities presented by fMRI. Here, we describe progress using the computational neuroimaging approach in human visual cortex, which aims to build models that predict the neural responses from the stimulus and task. We focus on a particularly active area of research, the use of population receptive field (pRF) models to characterize human visual cortex responses to a range of stimuli, in a variety of tasks and different subject populations.

### Understanding sensory circuits

A mark of understanding a sensory system is the ability to predict how it will respond to stimulation. In the case of human visual cortex, we would like to accurately predict how each part of the system responds to any visual input. Such predictions are beyond current capabilities, but progress has

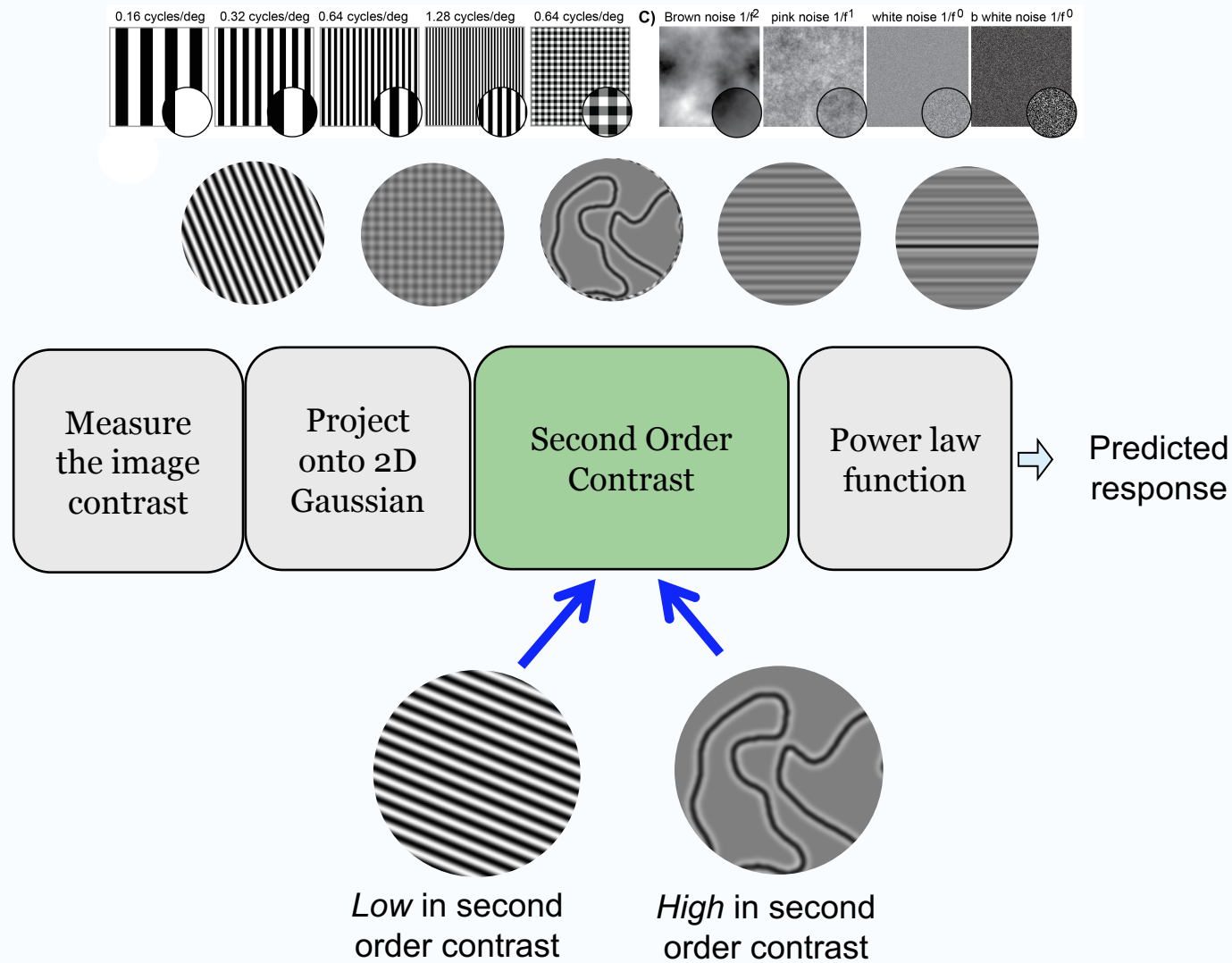
### Receptive field models

For more than 75 years, visual neuroscientists have relied on the receptive field concept to make progress in the face of limited knowledge of the neural circuitry [3]. Sherrington [4] coined the phrase 'receptive field' to describe the region of skin from which a scratch reflex could be elicited: 'The "receptive field" may be conveniently applied to designate the total assemblage of receptive points whence by suitable stimuli a particular reflex movement can be evoked' ([4], p. 32). Hartline applied the concept to visual neurons [5]. Hartline's initial definition, similar to Sherrington's, emphasized the spatial extent of the receptive field: 'No description of the optic responses in single fibers would be complete without a description of the region of the retina which must be illuminated in order to obtain a response in any given fiber. This region will be termed the receptive field of the fiber' ([5], p. 410). Over the years, the receptive field concept has expanded to include stimulus features (e.g., orientation, motion, or contrast) and to be based on explicit



# Compressive spatial summation model and SOC model

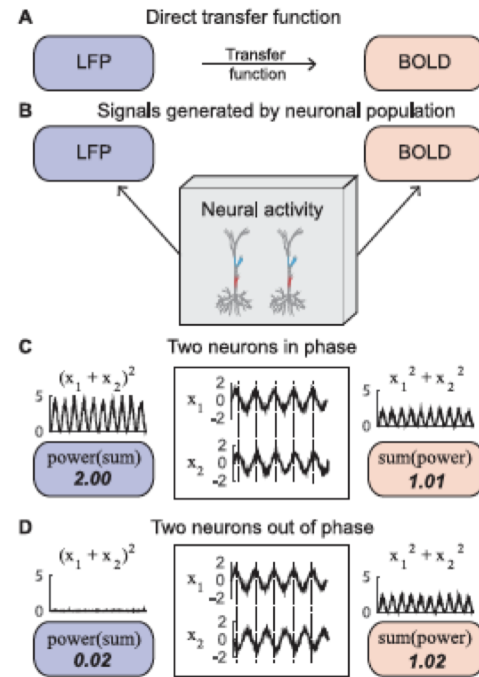
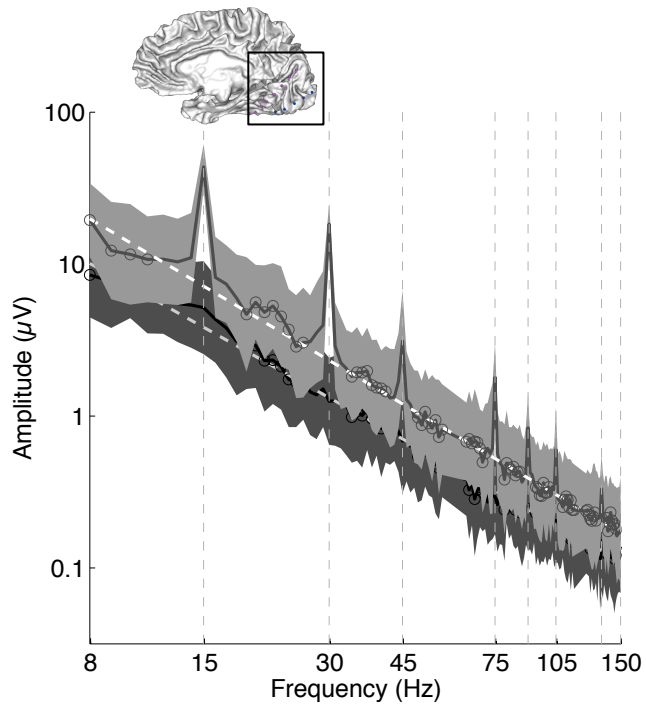
- **Prediction:** Start with image and produce BOLD time series and produce BOLD time series
- Greatly extended range of stimuli
- For achromatic, bandpass stimuli, **the model accounts for about 80-90% of the explainable variance** (cross-validation) in V1, V2, V3, hV4



Kay, Winawer, Mezer, Wandell, **J Neurophys** 2013

Kay et al., 2013, **PLoS Computational Bio**

# ECoG: PRF modeling and stimulus-referred modeling



Please cite this article in press as: Winawer et al., Asynchronous Broadband Signals Are the Principal Source of the BOLD Response in Human Visual Cortex, *Current Biology* (2013), <http://dx.doi.org/10.1016/j.cub.2013.05.001>

*Current Biology* 23, 1–9, July 8, 2013 ©2013 Elsevier Ltd All rights reserved <http://dx.doi.org/10.1016/j.cub.2013.05.001>

## Article

### Asynchronous Broadband Signals Are the Principal Source of the BOLD Response in Human Visual Cortex

Jonathan Winawer,<sup>1,2,\*</sup> Kendrick N. Kay,<sup>1</sup> Brett L. Foster,<sup>2,3</sup> Andreas M. Rauschecker,<sup>1,2,4</sup> Josef Parvizi,<sup>2,3</sup> and Brian A. Wandell<sup>1,2</sup>

<sup>1</sup>Department of Psychology  
<sup>2</sup>Stanford Human Intracranial Cognitive Electrophysiology Program (SHICEP)  
<sup>3</sup>Department of Neurology & Neurological Sciences, School of Medicine  
<sup>4</sup>Medical Scientist Training Program and Neurosciences Program  
Stanford University, Stanford, CA 94305, USA

signaling is captured by each modality. In this paper, we consider the relationship between two different modalities, electrocorticography (ECoG) and functional magnetic resonance imaging (fMRI).

ECoG and fMRI measure neural activity in different ways and cannot be directly compared: the ECoG signal measures the electric field potential on the cortical surface [1], whereas fMRI measures the hemodynamic blood oxygen level-dependent (BOLD) response associated with neural activity [2]. To compare such different signals, we use a stimulus-referred approach. Specifically, we compare how the ECoG and fMRI

## RESEARCH ARTICLE

### Neuronal synchrony and the relation between the blood-oxygen-level dependent response and the local field potential

Dora Hermes<sup>1,2,3,\*</sup>, Mai Nguyen<sup>4</sup>, Jonathan Winawer<sup>1,\*</sup>

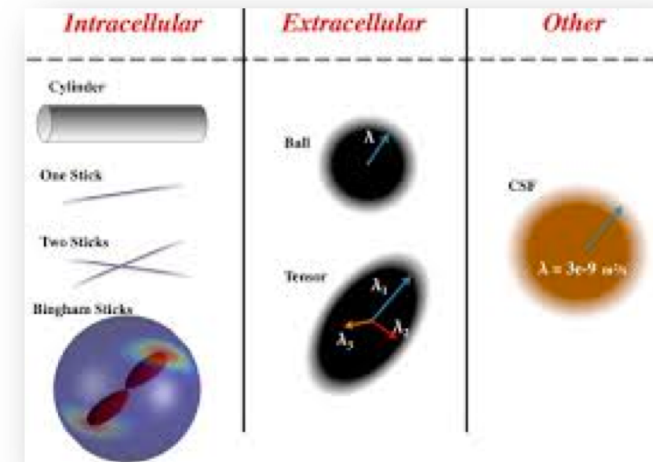
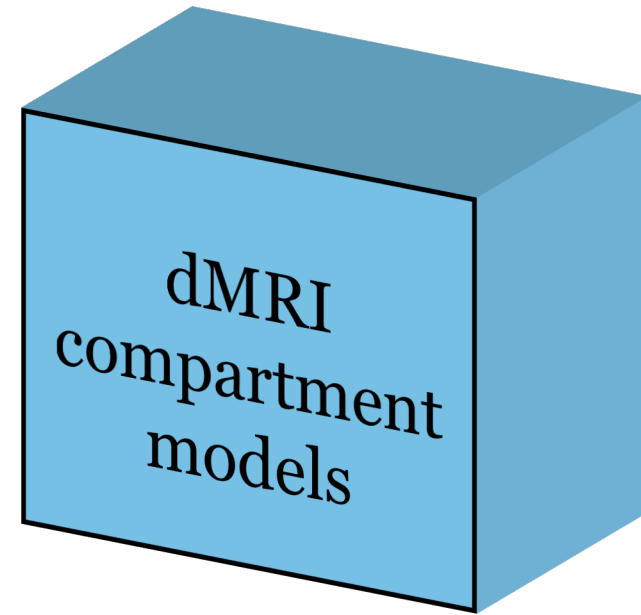
1 Department of Psychology, New York University, New York, New York, United States of America, 2 Brain Center Rudolf Magnus, Department of Neurology & Neurosurgery, University Medical Center Utrecht, Utrecht, the Netherlands, 3 Department of Psychology, Stanford University, Stanford, California, United States of America, 4 Department of Psychology, Princeton University, Princeton, New Jersey, United States of America



# Two temporal channels in human V1 identified using fMRI

- As we use a larger range of stimuli, the model of the response in each voxel will need to become more complex
- We think of these as compartment models

Diffusion compartment models are already in widespread use



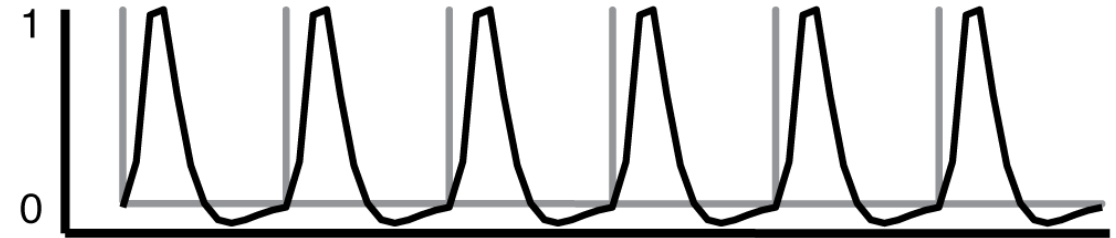
Two temporal channels in human V1 identified using fMRI . Horiguchi, Nakadomari, Misaki, Wandell (2009). **NeuroImage**



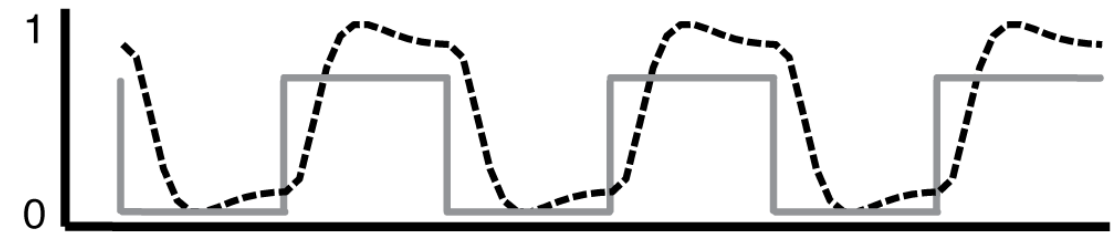
# Two temporal channels in human V1 identified using fMRI

- We developed a model that included two temporal channels in each voxel
- These are a sustained and transient channel, as expected from psychophysics
- The number of (testable) channels a model can support will depend on the number of different measurements that are made

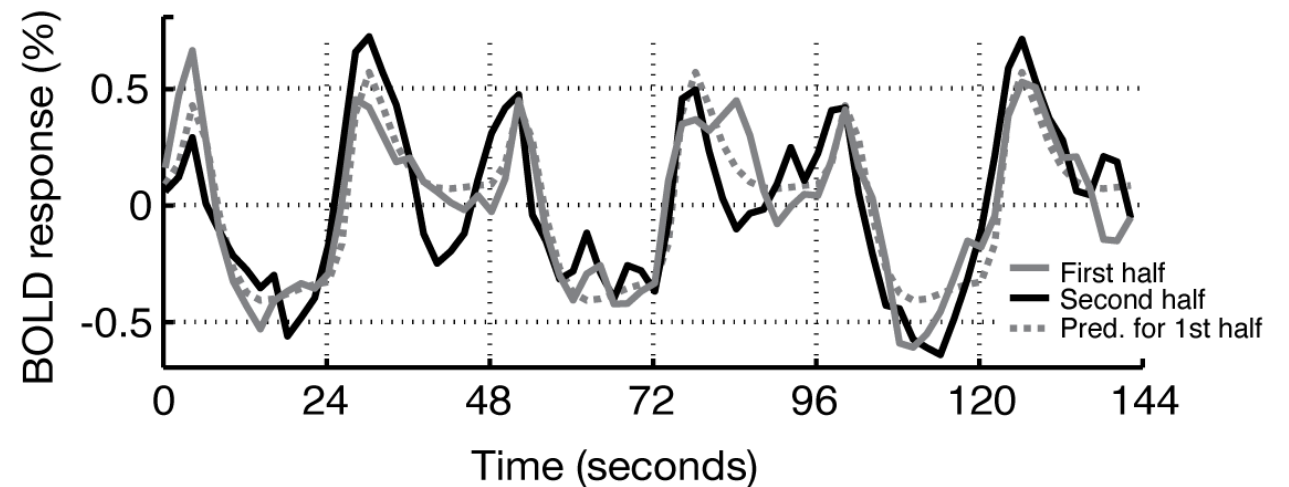
(a) Transient Predictor (  $T(t)$  )



(b) Sustained Predictor (  $S(t)$  )

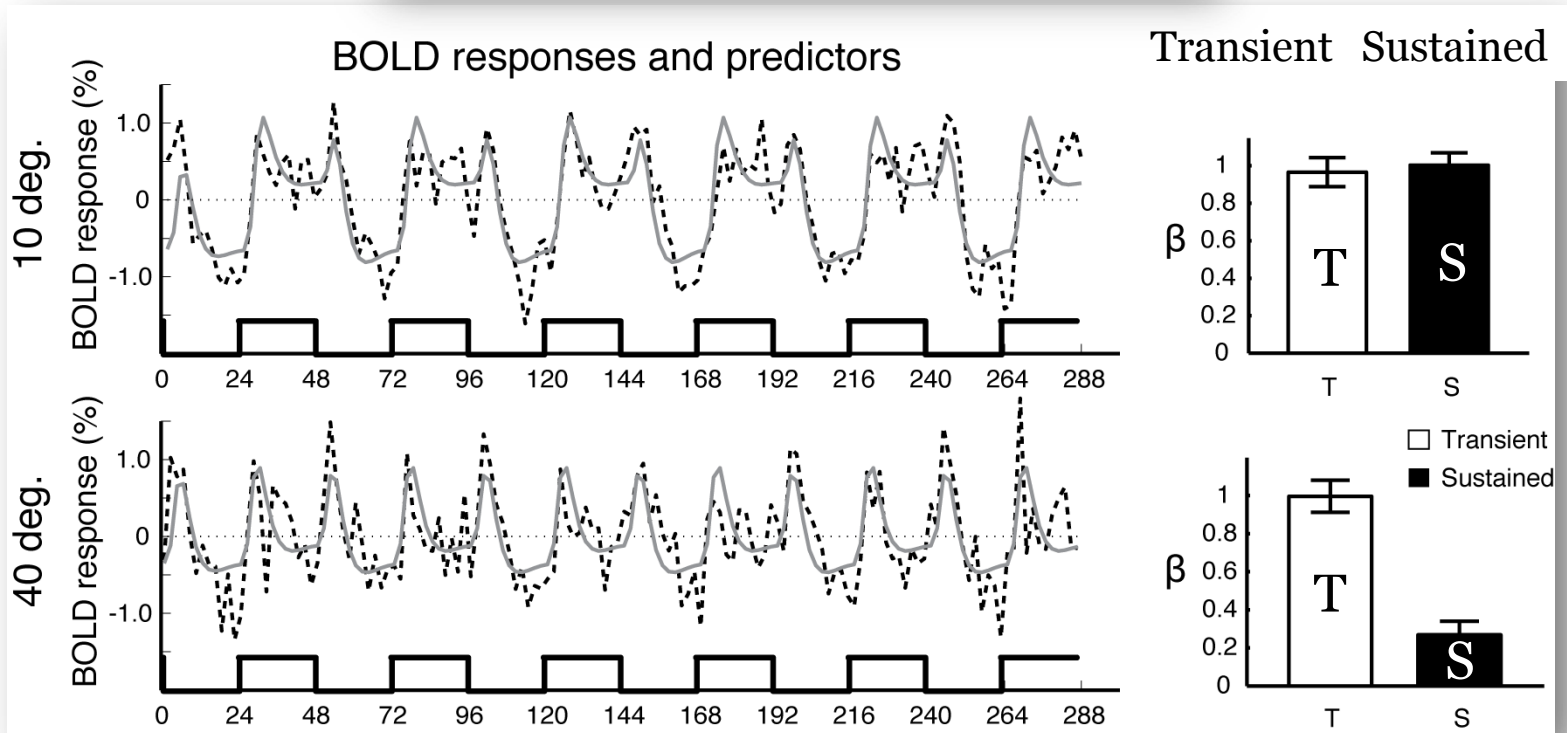
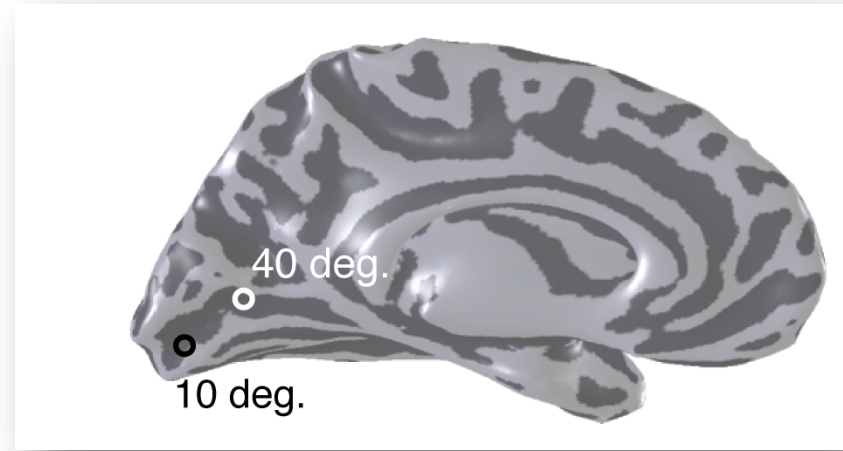


(c) First and second half time series in V1



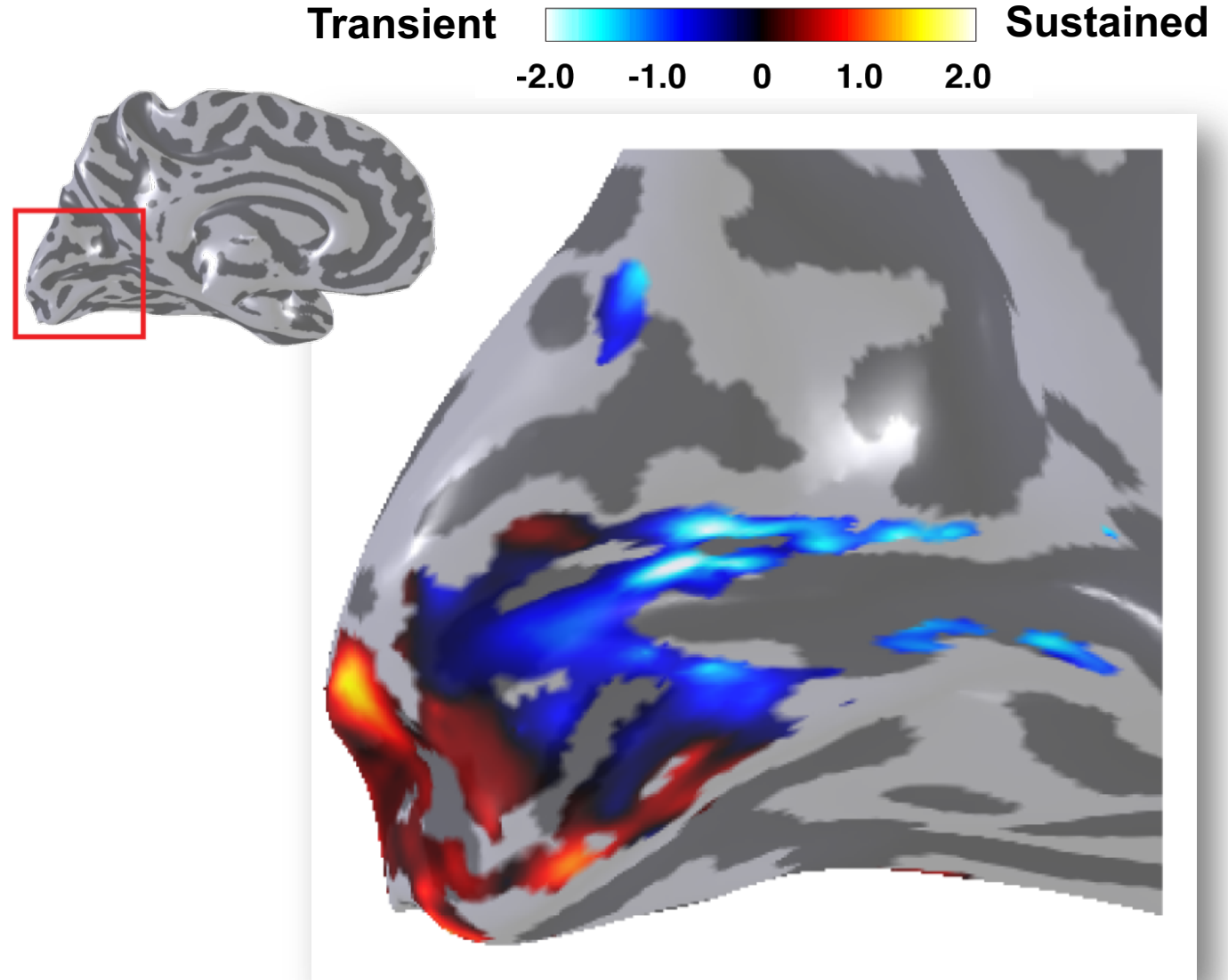
# Different temporal response functions at different eccentricities

- Responses at different eccentricities have very different time course
- These differences are modeled by assuming each voxel has as different amount of the two compartments



# Spatial distribution of sustained and transient changes

- Sustained channel is localized to the central 10 deg representation
- The transient channel extended out to 60 deg (ping pong ball ganzfeld)



# Additional papers extending and confirming the findings

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*Research Articles: Systems/Circuits*

## **Compressive Temporal Summation in Human Visual Cortex**

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## **Encoding model of temporal processing in human visual cortex**

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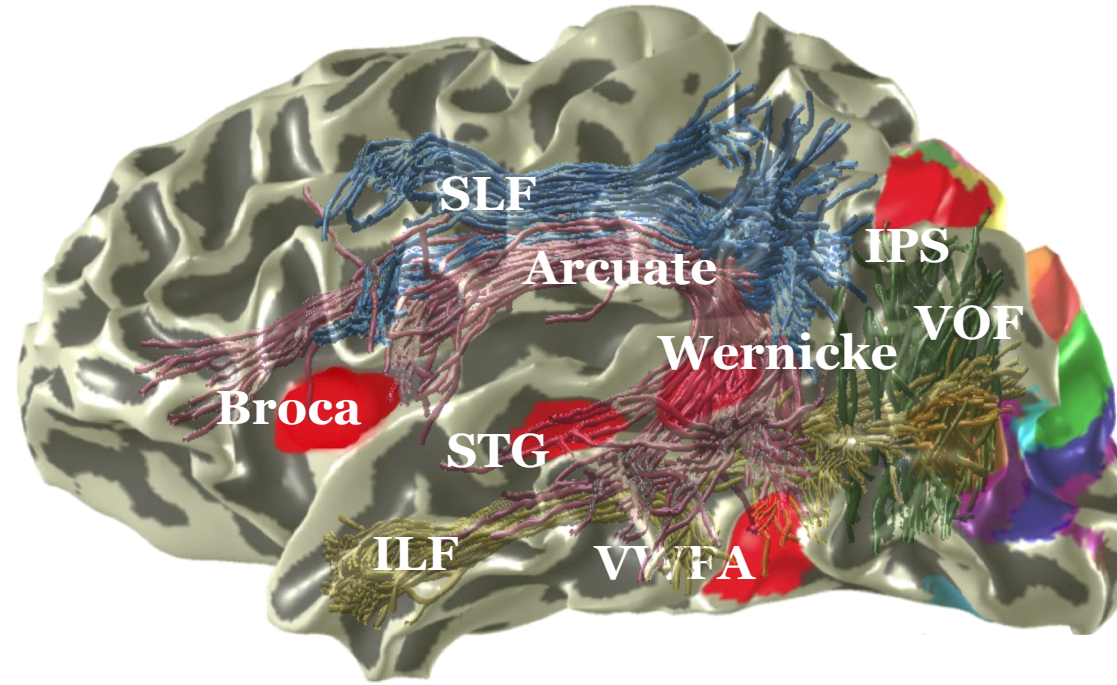
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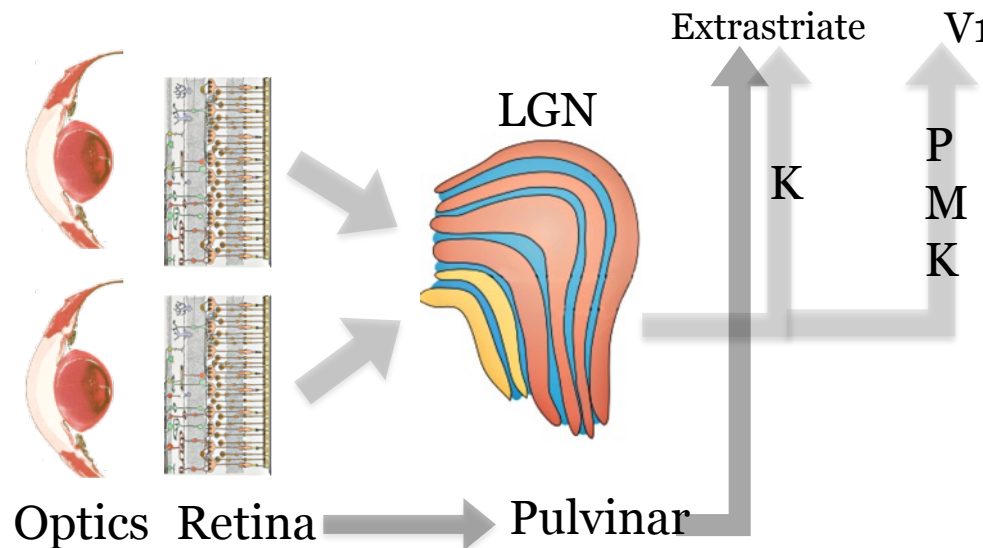
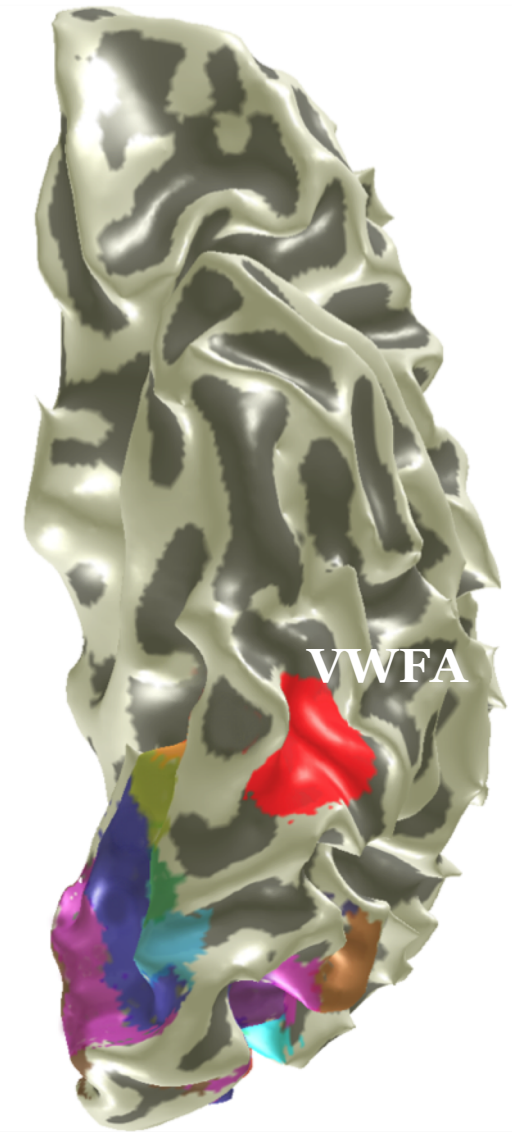
# Major components of the reading pathway

## The goal: Diagnosis

Identifying the locations and responses in a poor reader that differ significantly from measurements in good readers



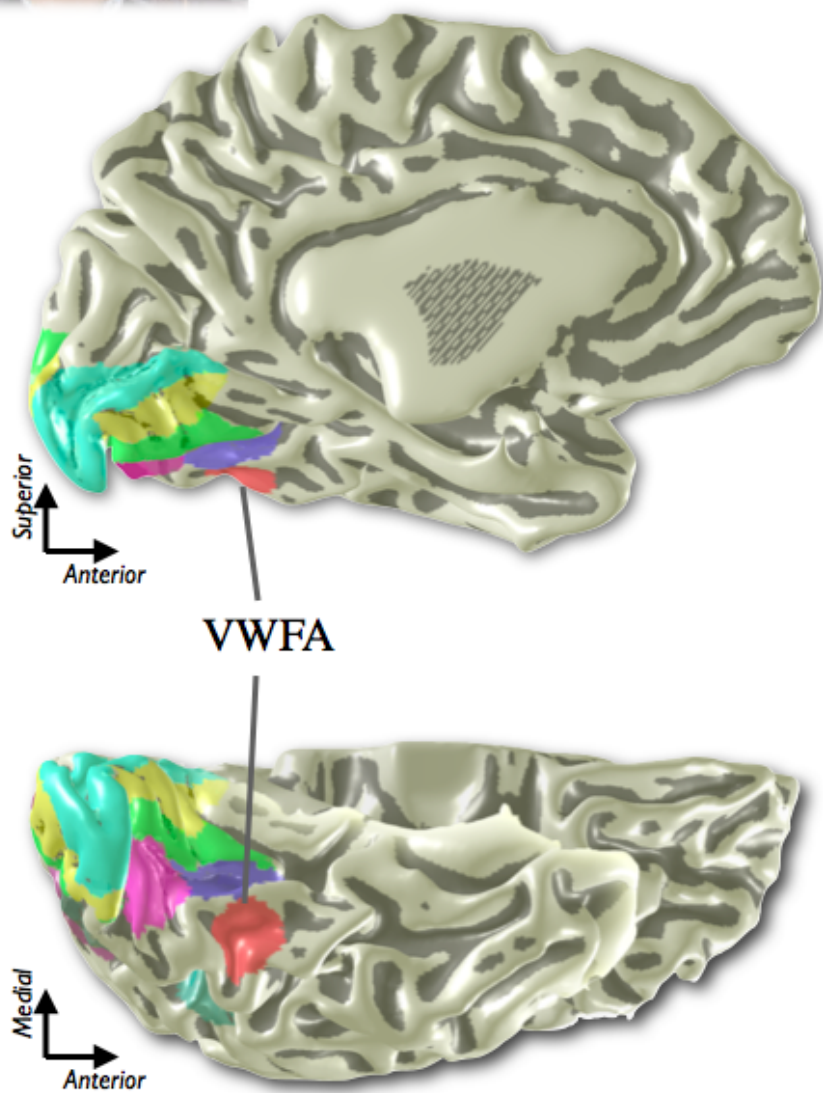
Wandell and Le (2017)



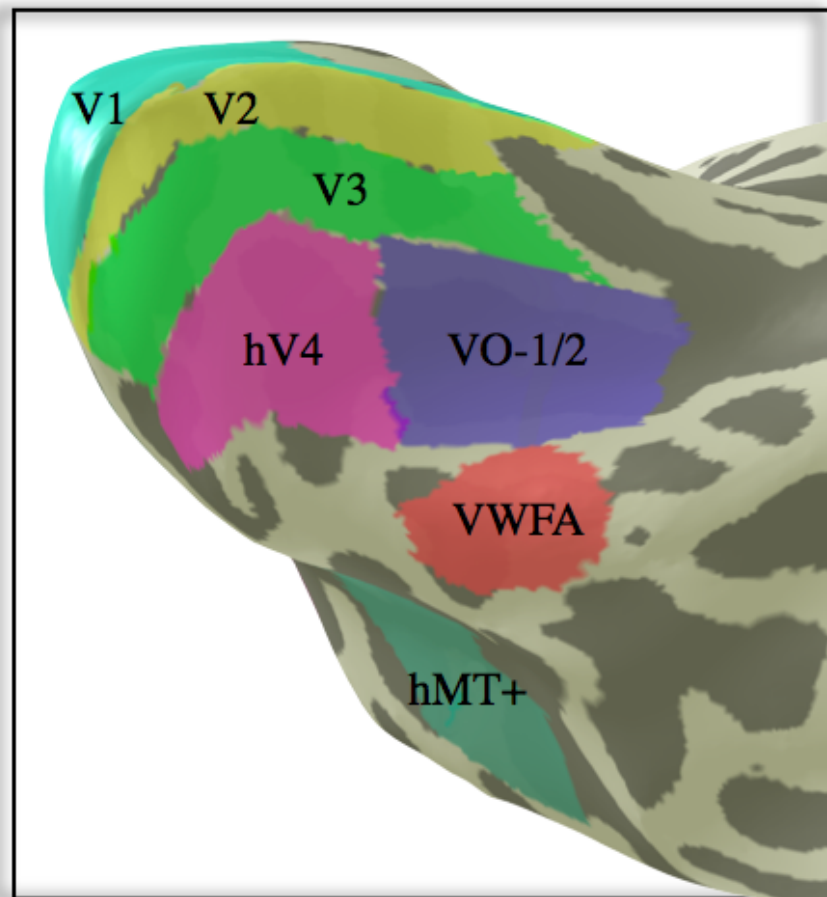
Diagnosing the Neural Circuitry of Reading (2017) Brian A. Wandell and Rosemary K. Le *Neuron* V. 96, Issue 2, October 11, 2017

Learning to See Words B.A. Wandell, A. Rauschecker and J. Yeatman (2012). *Annual Review of Psychology* Vol. 63, pp.31-53.

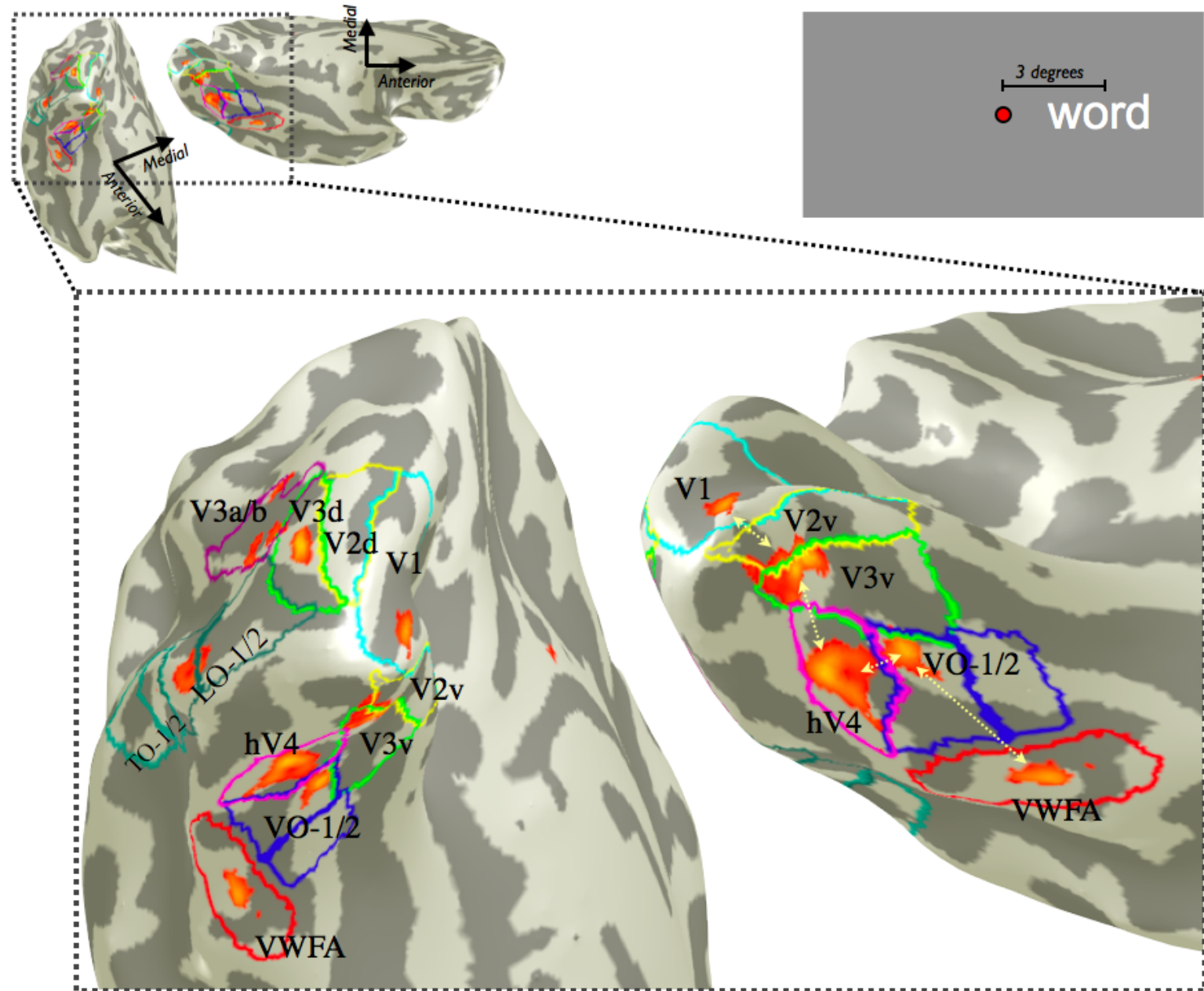
# Locating reading circuits and maps



VWFA - essential for reading, but not unique to reading



# Measuring the activity while reading (fMRI)



- We can see the locations of the cortical activations during reading
- Through the maps and on to the VWFA

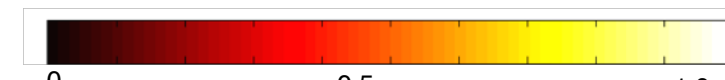
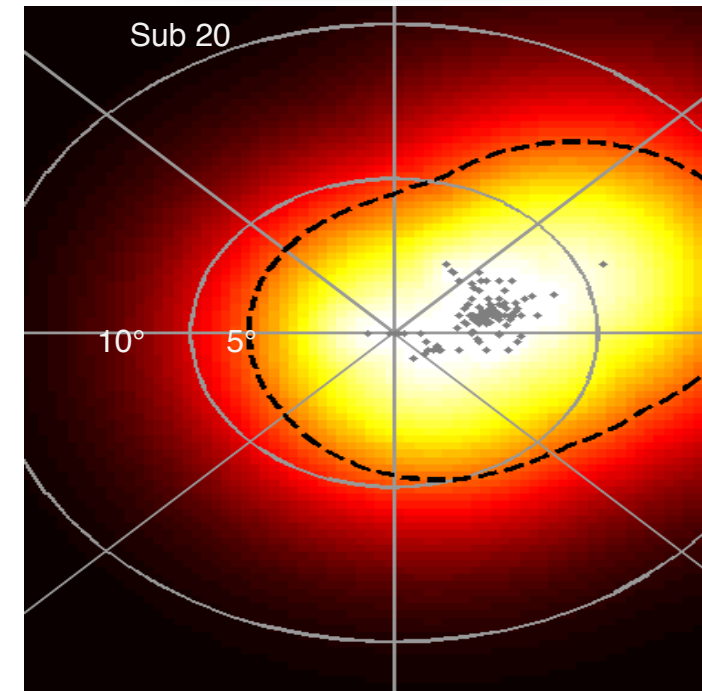
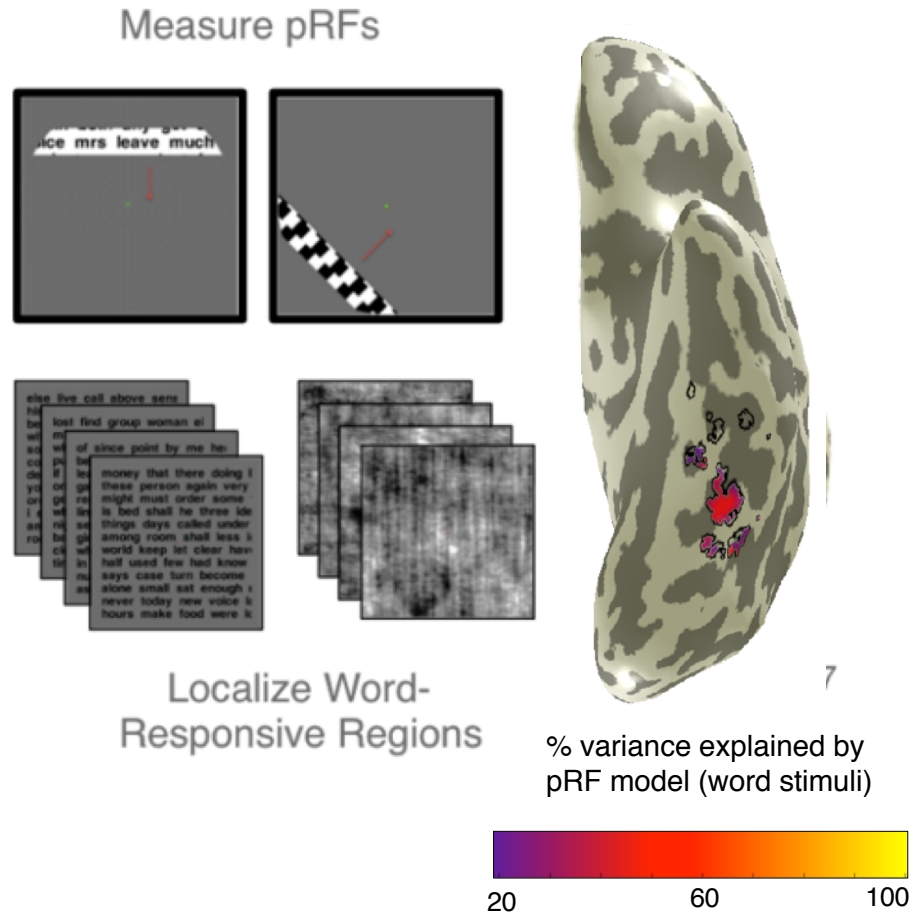


# Field of view in reading circuitry of a single subject

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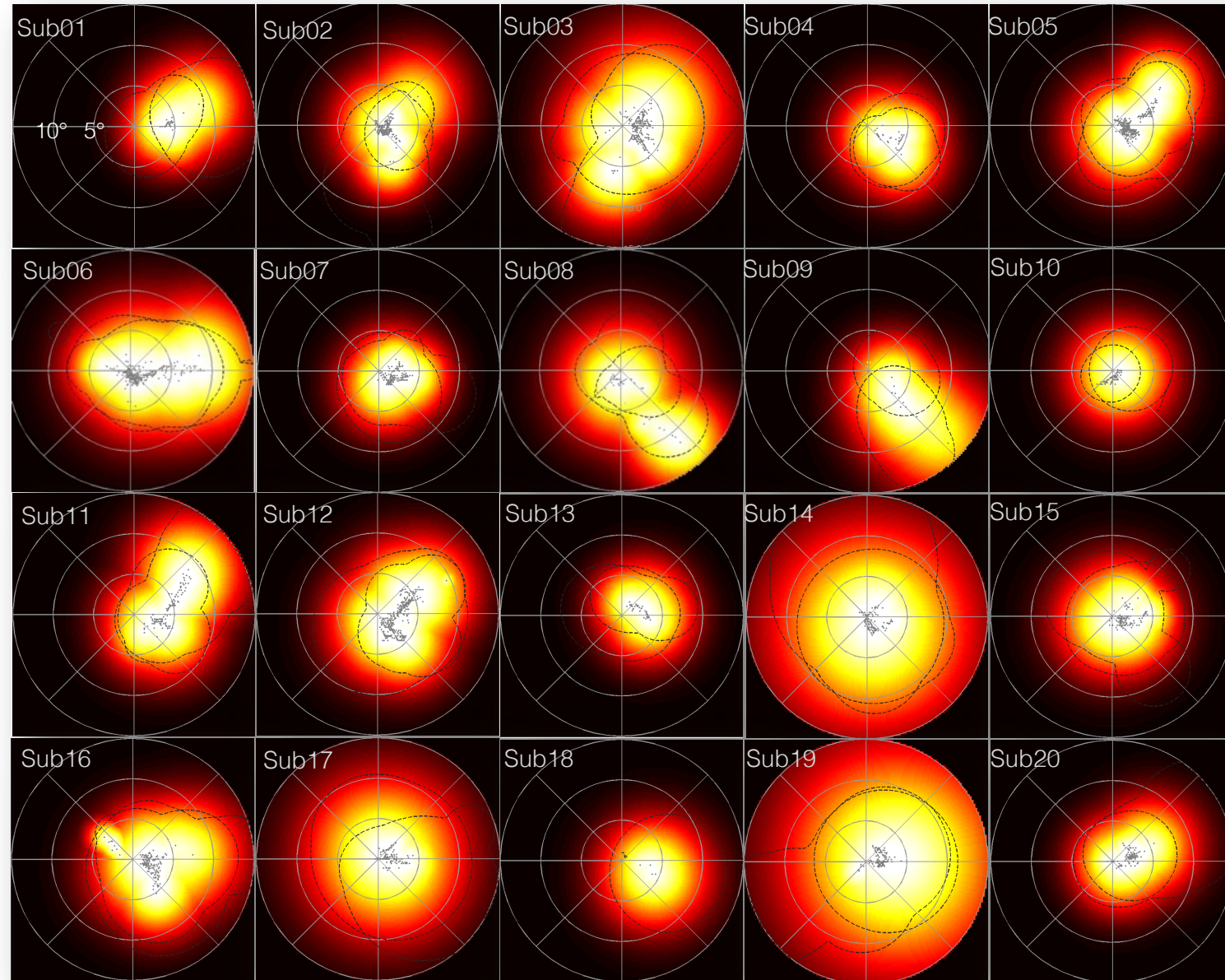
Using pRF methods, we have learned that the portion of cortex engaged in reading only sees a small part of the visual field

This may be why it is very hard to read in the peripheral field



# Field of view of the VOT reading reading circuitry

Left hemisphere only



- There are significant differences between participants
- We are correlating these differences with measures of word recognition
- With colleagues we are studying how the FOV in Israeli readers

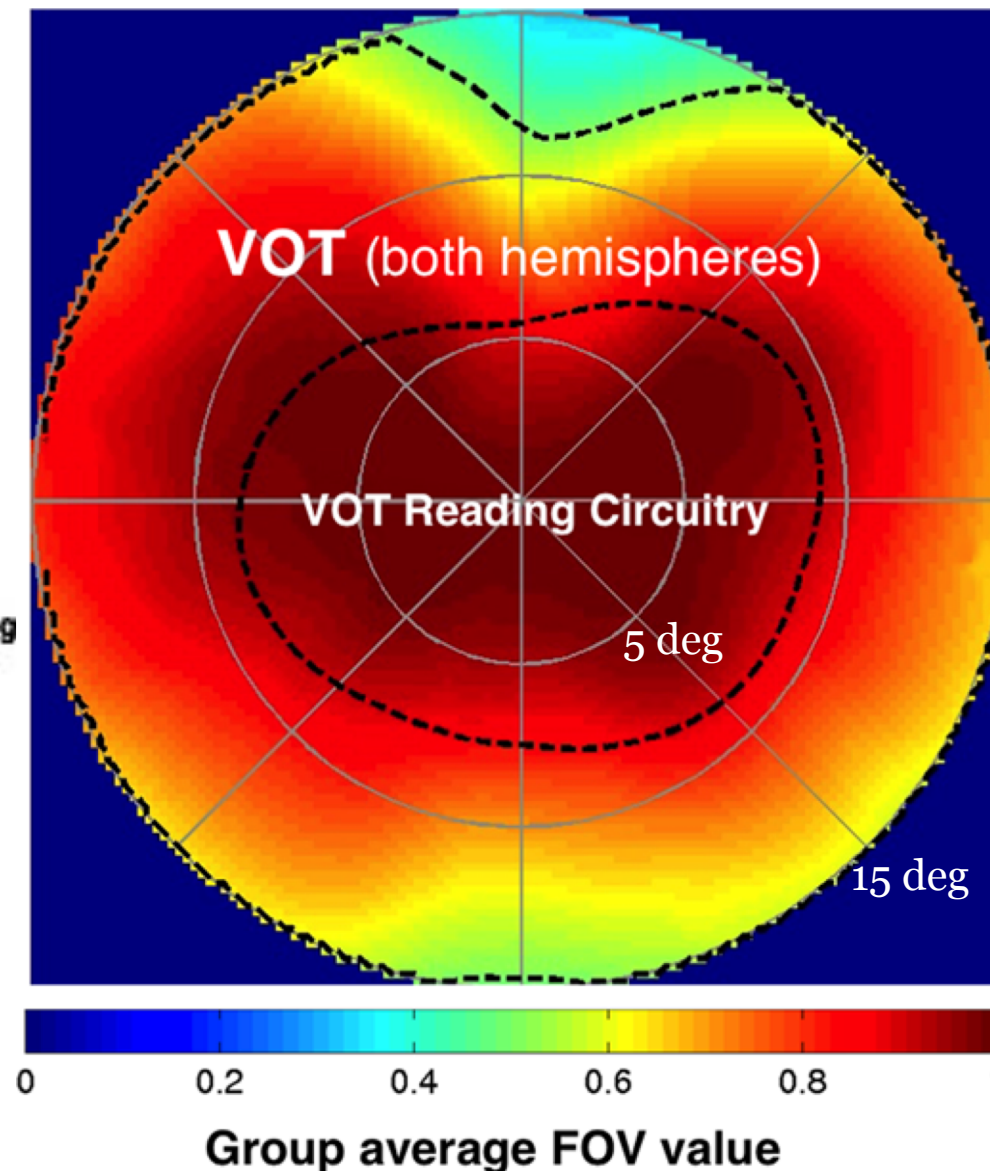
# Within the VOT the reading circuitry sees only a limited FOV

Le et al. 2017  
Journal of Vision

- The VOT as a whole receives input from much of the visual field
- When measured with words, the reading circuitry receives only a small part of the field available in VOT
- This may be why it is very hard to read in the peripheral field



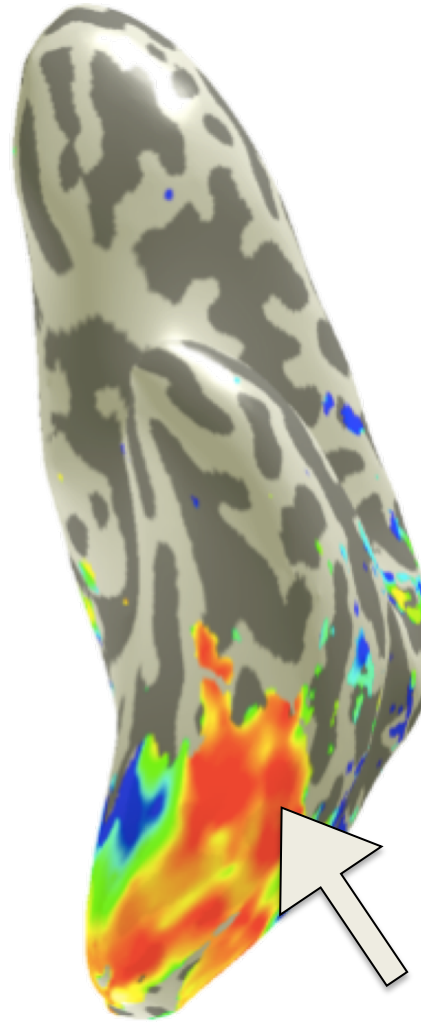
Left and right hemispheres



# VOTRC: pRF center estimates are stimulus dependent (adult)

- The shift is substantial (2-3 deg) throughout the fusiform and OTS region
- The pRF centers shift towards the central fovea along radial lines (not shown)

Words



Checkers



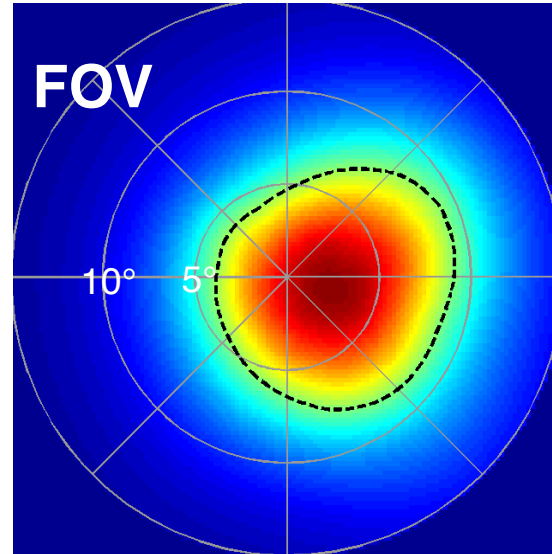
pRF eccentricity (°)



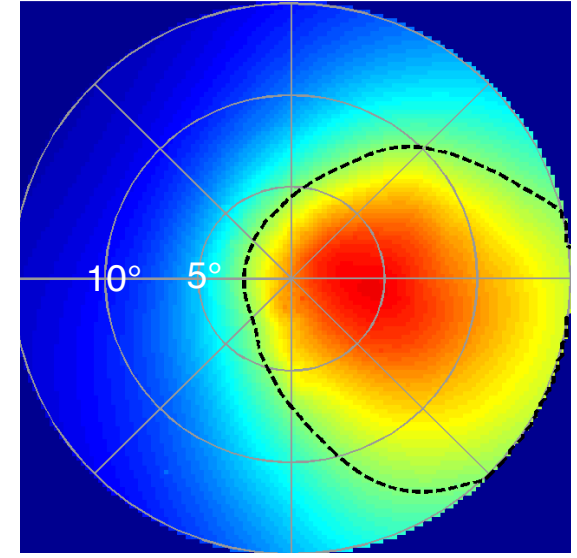
# VOT reading circuitry: FOV and pRF center positions depend on the stimulus

- The shift is substantial (2-3 deg) throughout the fusiform and OTS region
- The pRF centers shift towards the central fovea along radial lines (not shown)
- The shift causes a change in the FOV as well

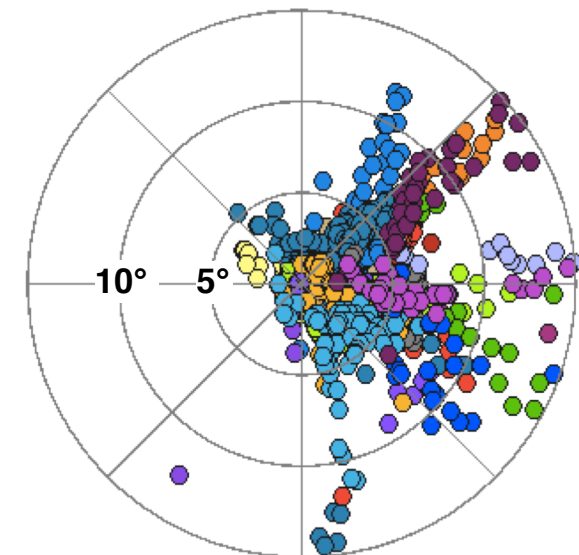
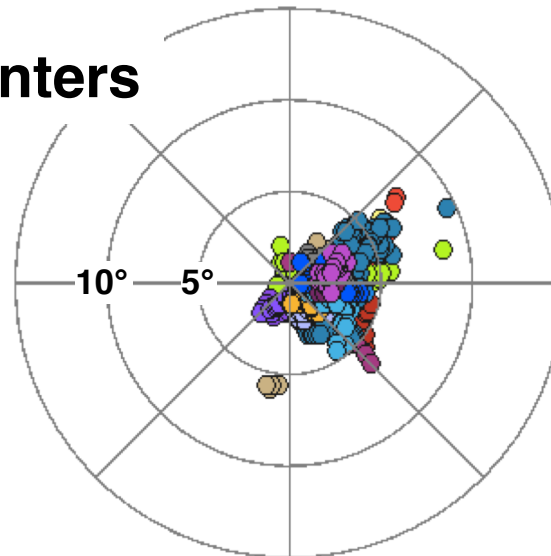
## Words



## Checkers

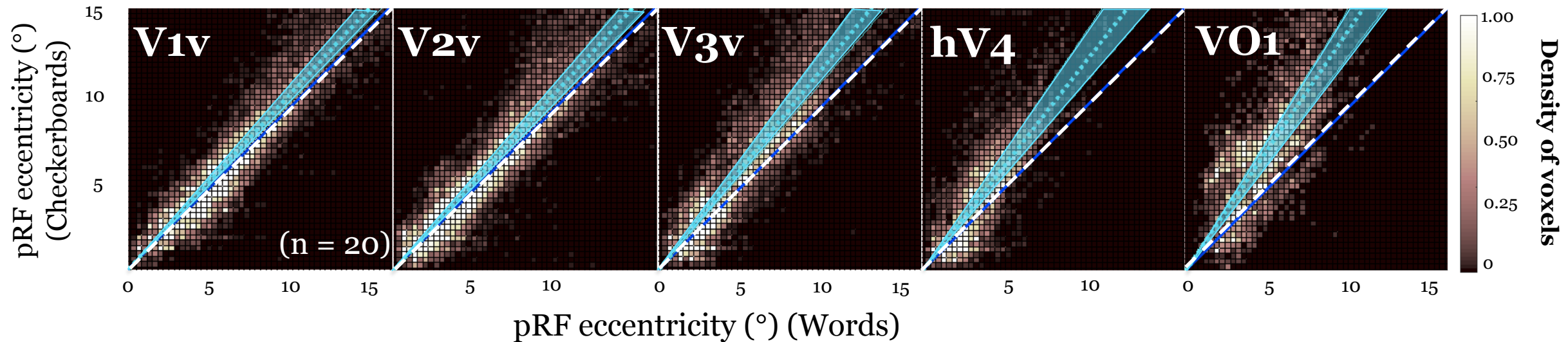


## pRF centers



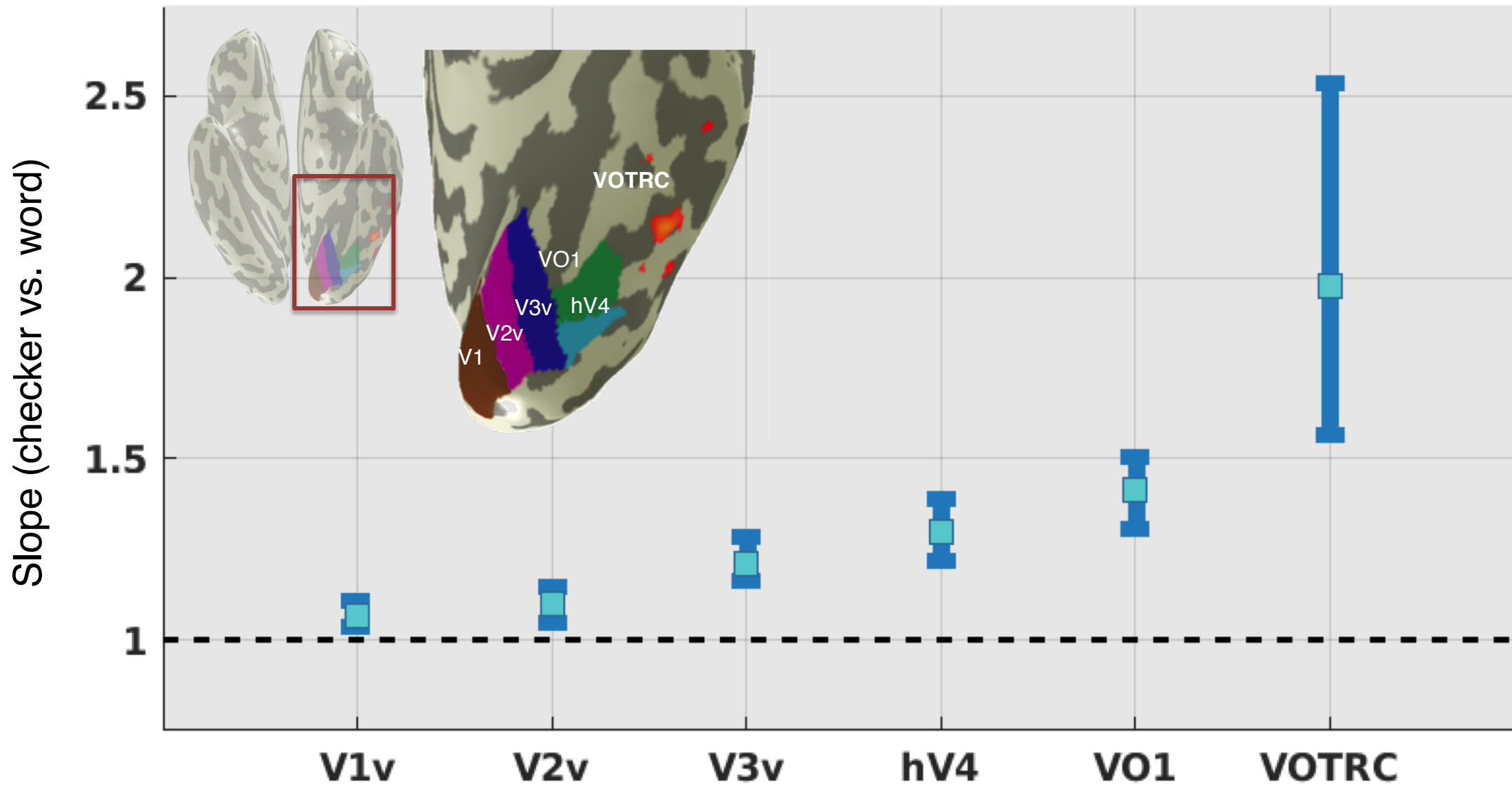
# The stimulus dependency emerges in V1-hV4-VO1

The pRF center of individual voxels shifts to larger eccentricities when measured with checkerboards than words



- **BLUE** - Linear fits to the data; bootstrapped 95% confidence intervals
- **DASHED WHITE** - The identity line

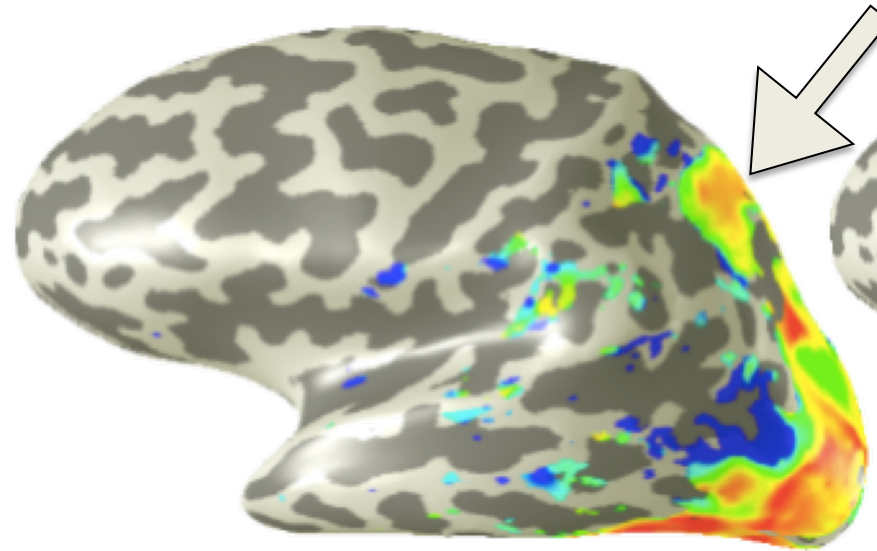
# The stimulus dependency can be observed emerging in V1-hV4-VO1



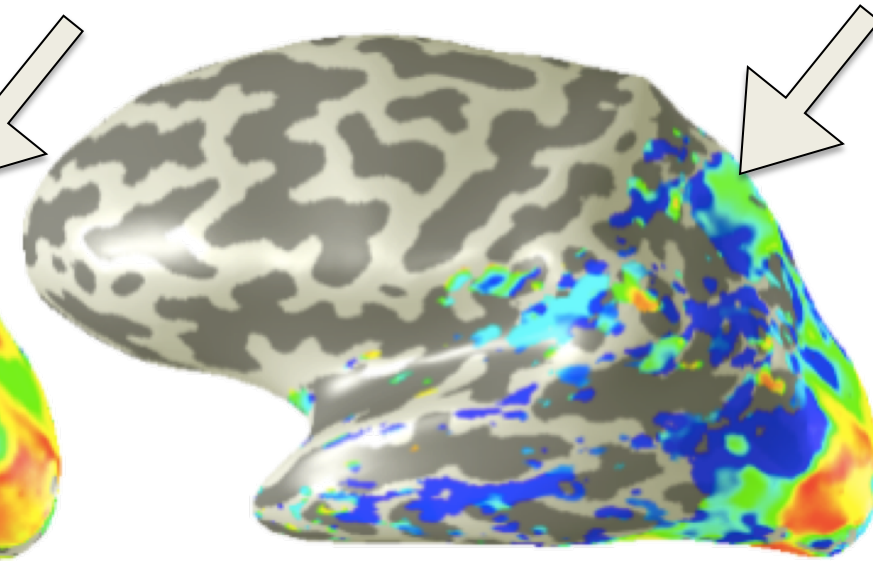
# IPS: pRF centers are stimulus dependent

- The pRF position shift is also substantial in the IPS region
- This region was identified by Cohen et al. (2007) as significant for modulating responses in VOTRC

Words



Checkers



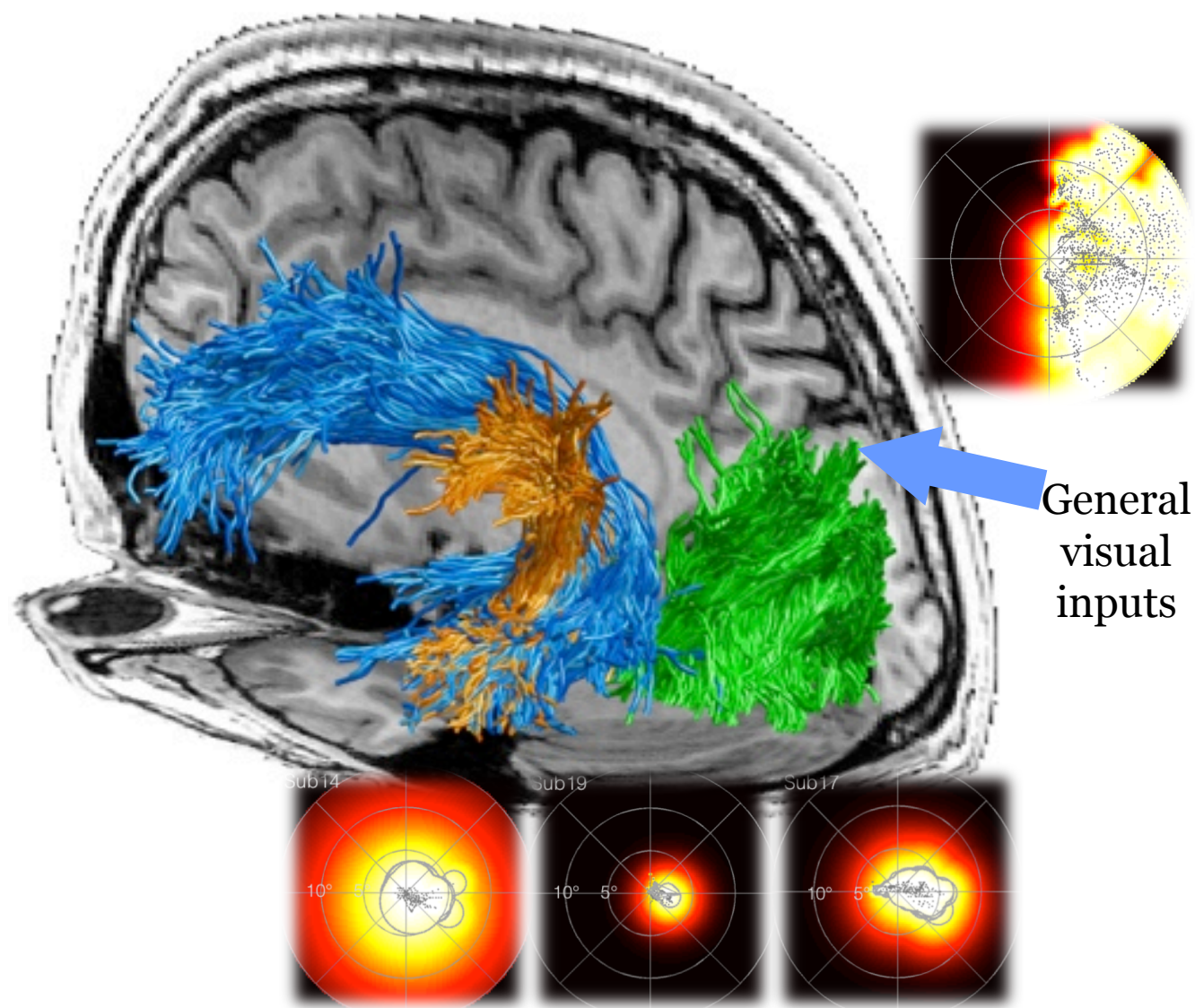
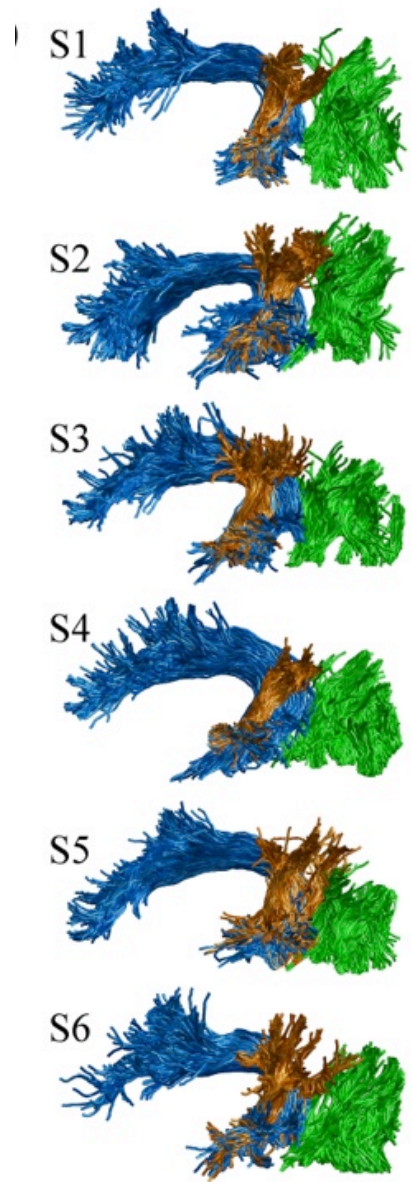
“word degradation led to an amplification of activation in the posterior visual word form area, at a level thought to encode single letters.

**(Cohen et al., 2007, Neuroimage, abstract)”**

**pRF eccentricity (°)**



# Connectionism: Mismatch hypothesis



General visual inputs

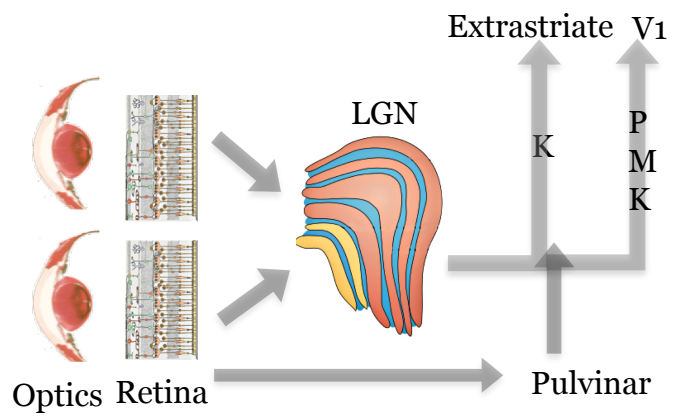
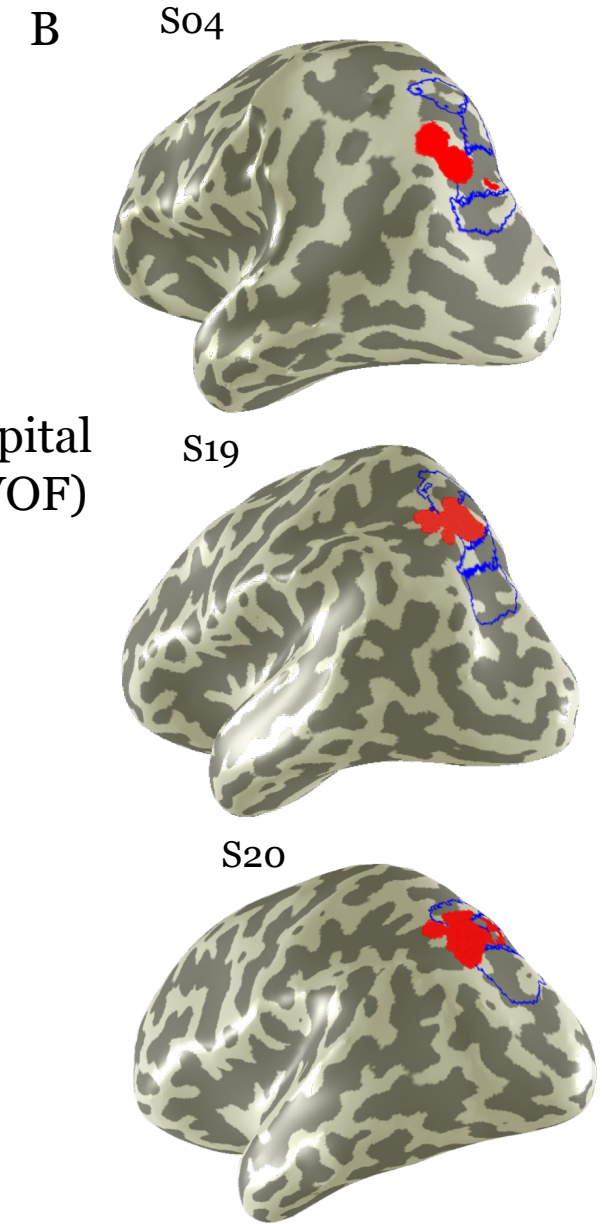
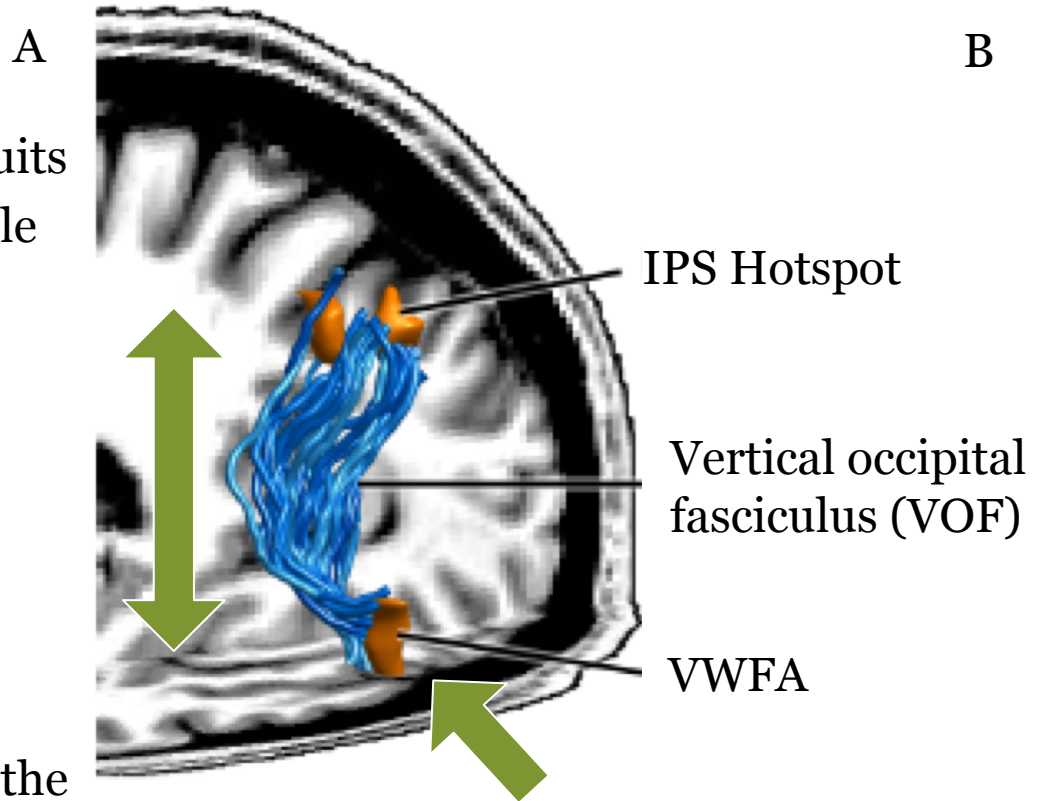
Ensemble Tractography  
Takemura, Caiafa; Wandell;  
Pestilli. **PLoS Computational  
Biology** (2016).

The vertical occipital fasciculus:  
... Yeatman, Weiner, Pestilli,  
Rokem, Mezer, and Wandell.  
**PNAS** (USA) (2014).

# Reading circuit modeling – IPS and VOTRC

- pRF responses reflect the activity of circuits distributed across cortex (of course, single units do too)
- We confirm the positions from our own dorsal responses and from those in the literature (MNI resolution, Cohen)
- For me the most important point is the notion of the circuit model; this extends the compartment model concept quite a bit.
- Not sure we are ready

Bottom-up and top-down computations in word- and face-selective cortex. Kay & Yeatman (2017), *eLife*



# References



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## Learning to See Words

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## Diagnosing the Neural Circuitry of Reading

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## The neurobiological basis of seeing words

Brian A. Wandell

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## The field of view available to the ventral occipito-temporal reading circuitry

Rosemary Le; Nathan Witthoft; Michal Ben-Shachar; Brian Wandell



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[www.elsevier.com/locate/ynimg](http://www.elsevier.com/locate/ynimg)  
NeuroImage 40 (2008) 353–366

## Reading normal and degraded words: Contribution of the dorsal and ventral visual pathways

Laurent Cohen,<sup>a,b,d,\*</sup> Stanislas Dehaene,<sup>b,c</sup> Fabien Vinckier,<sup>b,d</sup> Antoinette Jobert,<sup>b,c</sup> and Alexandra Montavont<sup>b</sup>

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## Bottom-up and top-down computations in word- and face-selective cortex

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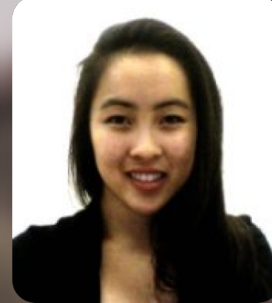
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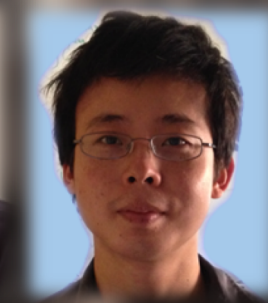
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## Computational neuroimaging and the cortical pathways for seeing words

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There has been extraordinary progress in measuring and modeling the tissue properties and activity in the living human brain using magnetic resonance imaging. Reliable functional measurements can be made at the millimeter scale in individual subjects, significantly enhancing the value of these techniques for both scientific and clinical applications. One goal of visual and cognitive neuroscience is to build computable models that predict these functional responses. Such computational neuroimaging comprises a small fraction of functional neuroimaging, which mainly focuses on statistical comparisons of different groups or statistical comparisons of a single group measured with different stimuli or tasks. I will describe why computational neuroimaging applied to individual subjects is a useful method for both scientific applications and developing diagnostic measures of visual and cognitive disorders. I will illustrate these ideas with examples from work designed to clarify the brain circuitry that is essential for seeing words. I am hopeful that combining quantitative measurements and computational models, supported by reproducible research tools, can provide a strong foundation for a human neuroscience that benefits society.

### References

Computational imaging of human visual cortex. Brian A. Wandell, *Annu. Rev. Neurosci.* 1999. 22:145–73.

Computational neuroimaging and population receptive fields Brian A. Wandell<sup>1</sup> and Jonathan Winawer. *Trends in Cognitive Sciences*, June 2015, Vol. 19, No. 6

Diagnosing the Neural Circuitry of Reading. Brian A. Wandell and Rosemary K. Le, *Neuron* 96, October 11, 2017