# Multisensory Integration and Visual Perception in the Human Brain Studied with Electrocorticography, fMRI and TMS

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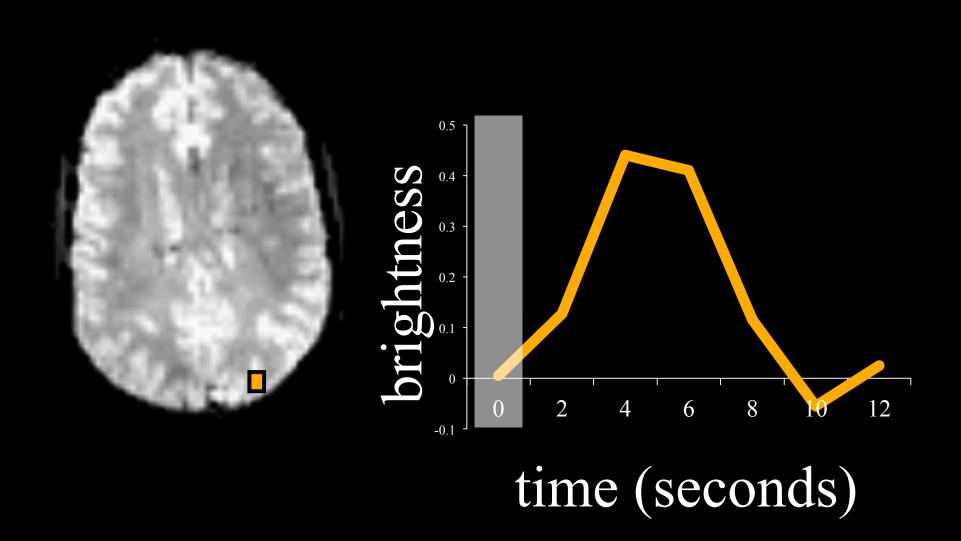




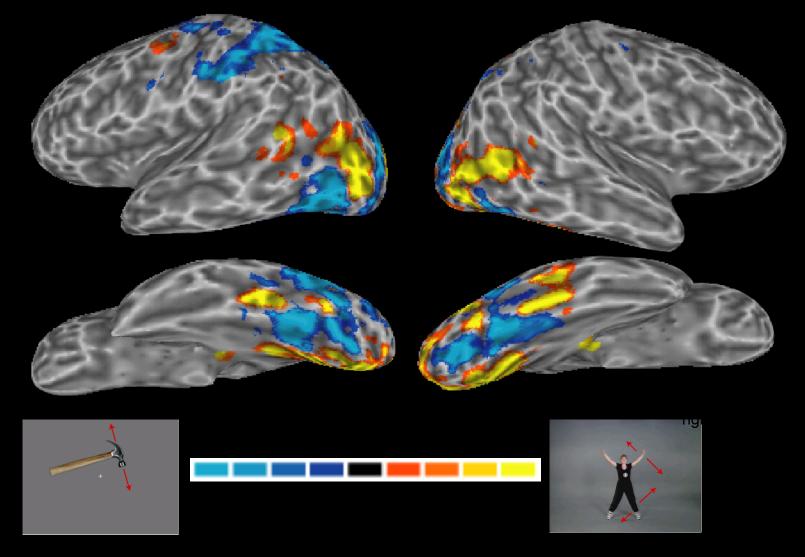
## Overview http://openwetware.org/wiki/Beauchamp

- 1) The STS, a hub for biological motion and multisensory integration Beauchamp, et al., Neuron (2002); Beauchamp, et al., Journal of Cognitive Neuroscience (2003); Beauchamp, et al., Neuron (2004); Beauchamp, et al., Nature Neuroscience (2004)
- 2) Temporary Disruption of the STS impairs multisensory integration Beauchamp, et al., Journal of Neuroscience (2010)
- 3) Interindividual Differences in the STS account for differences in multisensory integration
- Nath, Fava, and Beauchamp, Journal of Neuroscience (2011), Nath and Beauchamp, Neuroimage (2011)
- 4) Neural mechanisms for Bayesian multisensory integration: STS connectivity
- Nath and Beauchamp, Journal of Neuroscience (2011)
- 5) Conscious perception of visual stimuli in the temporo-parietal junction Beauchamp, et al., Nature Neuroscience (2012)

#### Typical fMRI experiment



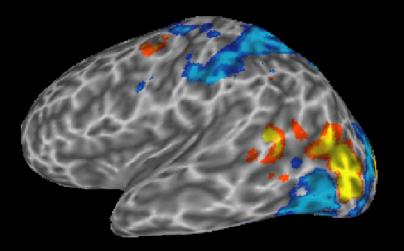
#### fMRI reveals large-scale brain networks

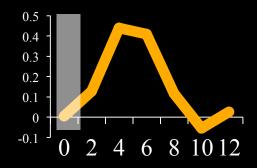


Beauchamp, et al., Neuron (2002); Journal of Cognitive Neuroscience (2003)

#### General problems with fMRI

- What do the blobs mean?
  - Is activity in the area linked to behavior or perception?
  - Is activity in an area truly required for a cognitive function?
- Poor match between analysis (simple) and data (complex)
  - O How do areas operate as a network?
- Slow temporal resolution
  - Neuronal responses are on a ~ms time scale, fMRI operates on a ~sec time scale





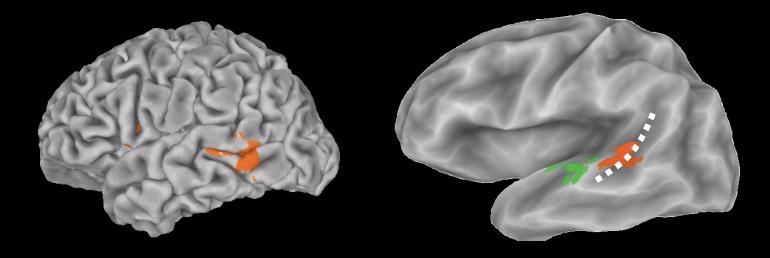
#### How we've tackled these problems

- What do the blobs mean?
  - Is activity in the area linked to behavior or perception?
  - Is activity in an area truly required for a cognitive function?
- Poor match between analysis (simple) and data (complex)
  - o How do areas operate as a network?
- Slow temporal resolution
  - Neuronal responses are on a ~ms time scale, fMRI operates on a ~sec time scale

- Multisensory integration, esp. speech perception
  - Temporary and permanent lesions of the STS
- Link between STS
   activity and perception of
   multisensory speech
- Connectivity of the STS during speech perception
- Electrocorticography with ms time resolution (TPJ)

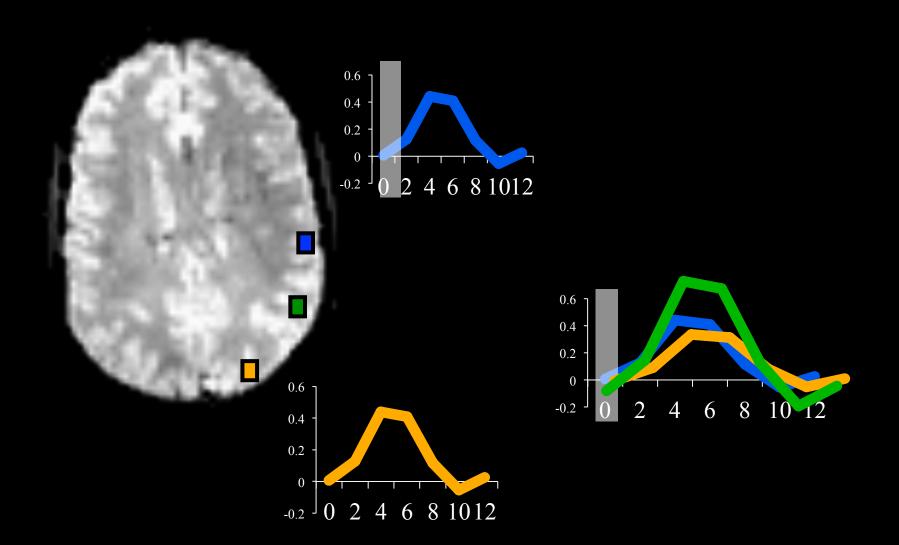
#### **Superior Temporal Sulcus**

A brain hub for multisensory integration and biological motion perception

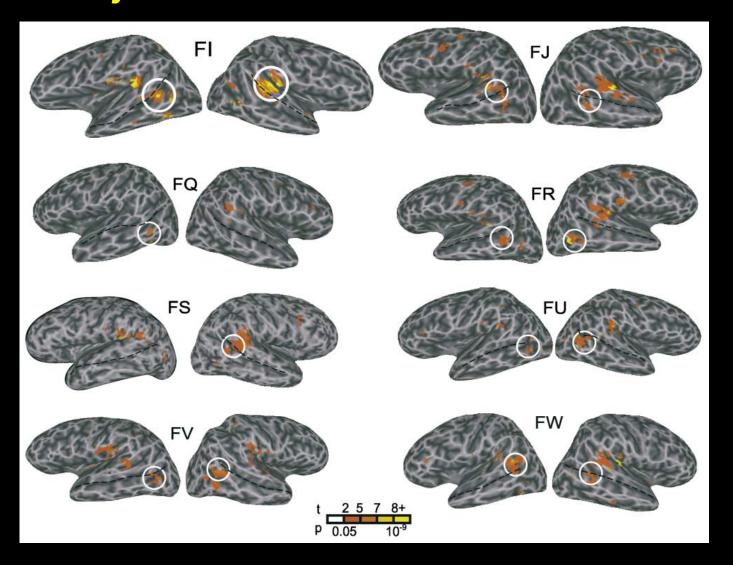


Beauchamp et al., Neuron, 2002; Journal of Cognitive Neuroscience, 2003, Neuron, 2004; Nature Neuroscience, 2004; Neuroimage, 2008; Journal of Neuroscience, 2010, Journal of Neuroscience, 2011a; Neuroimage, 2011, Journal of Neuroscience, 2011b

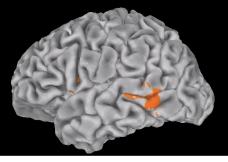
#### Multisensory fMRI experiment

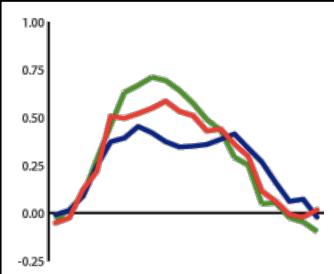


## Multisensory enhancement across subjects

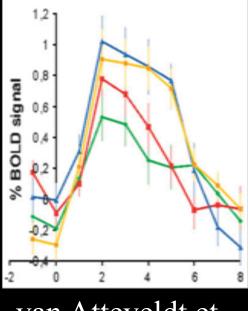


#### fMRI of multisensory integration in the STS

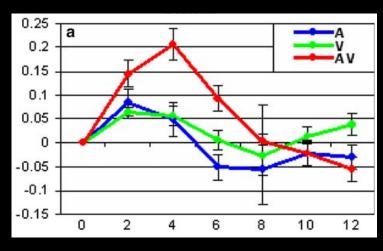




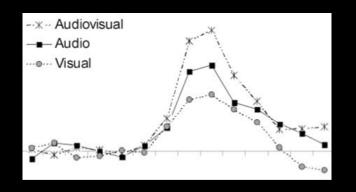
Beauchamp et al., *Neuron*, 2004



van Atteveldt et al., 2007

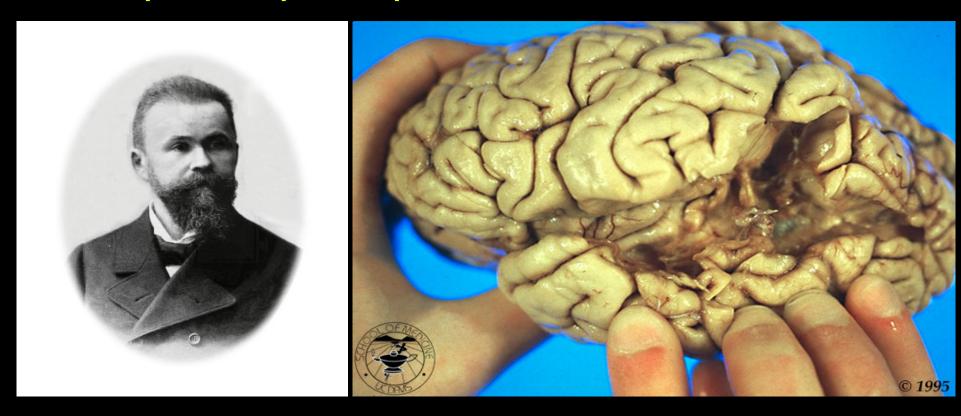


Stevenson et al., 2007



Wright et al., 2003

#### Speech perception



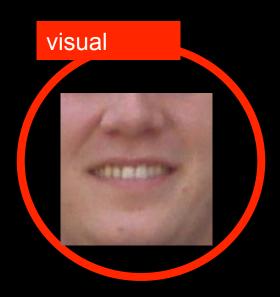
Wernicke's Area: Carl Wernicke, 1874

+ a network of areas (e.g. Scott & Johnsrude, 2003)

### General utility of multisensory integration

• Independent sources of information about the world







L. Rosenblum, University of California Riverside

### The McGurk-MacDonald effect, a multisensory speech illusion

Hearing lips and seeing voices

HARRY McGurk John MacDonald

Nature Vol. 264 December 23/30 1976

#### **Auditory-only McGurk**



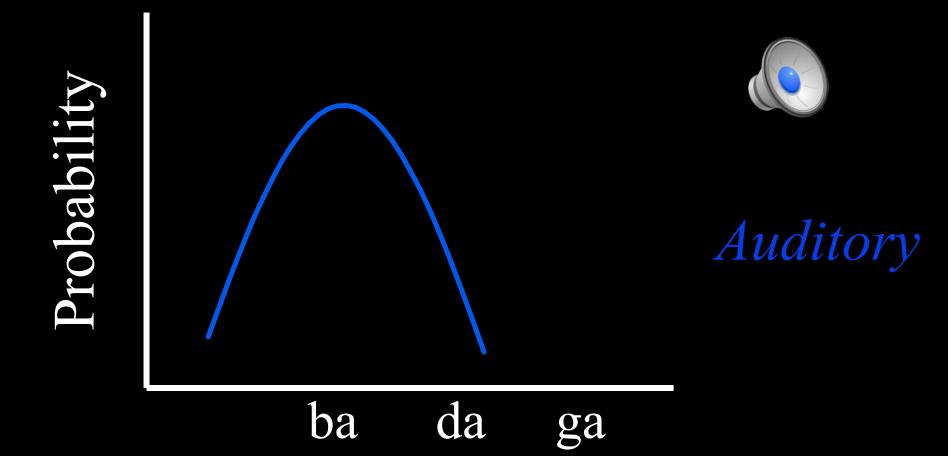




#### Summary

- Speech perception is multisensory: humans use both auditory and visual modalities
- Multisensory integration occurs in the superior temporal sulcus, which contains patches of neurons that respond to auditory stimuli, visual stimuli or both

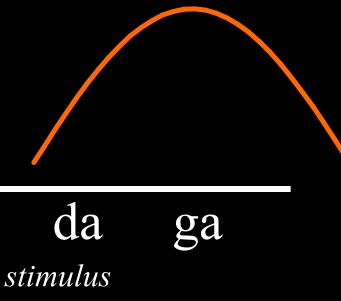
### Part 2: Is the STS necessary for multisensory speech perception?



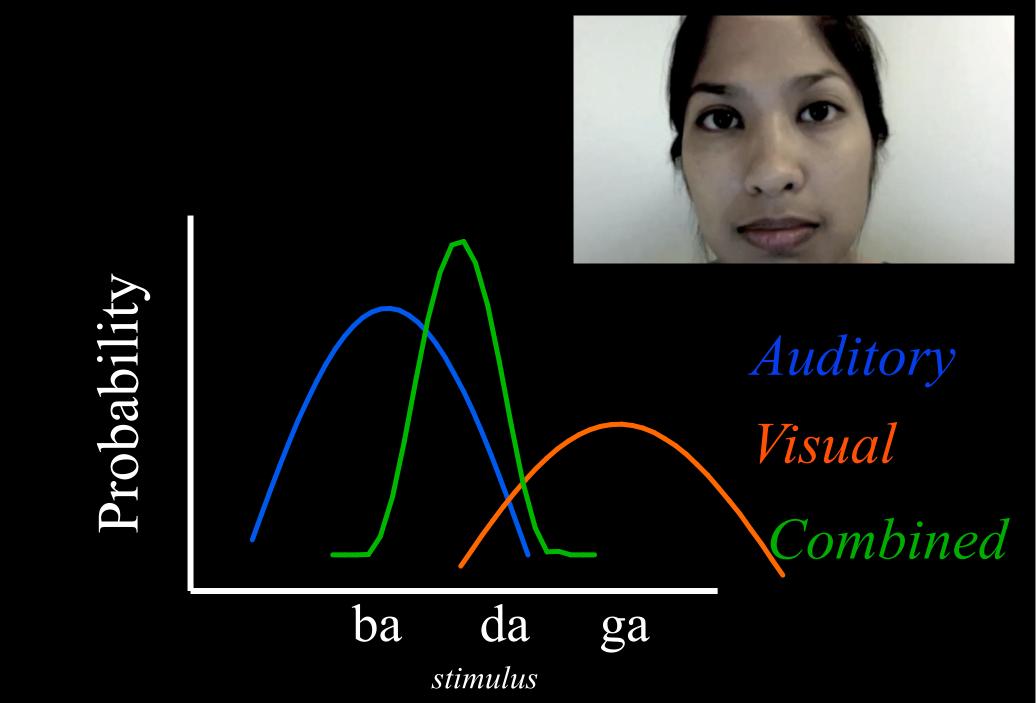
stimulus



Visual

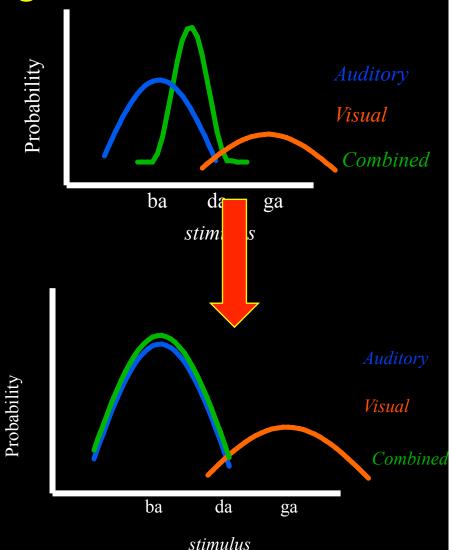


ba

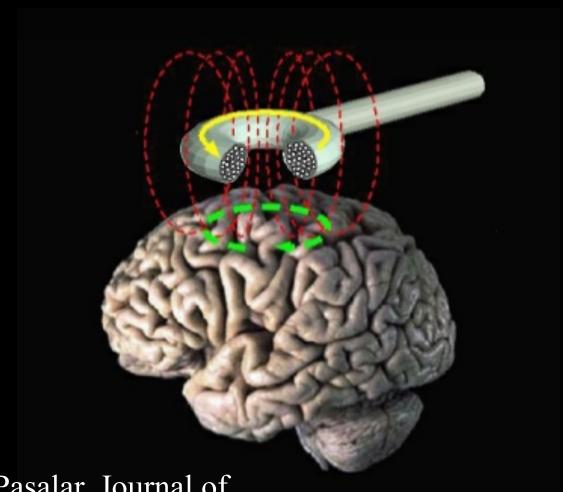


### How can we prove that the STS is really critical for multisensory integration?

Hypothesis: disrupting STS should reduce multisensory integration

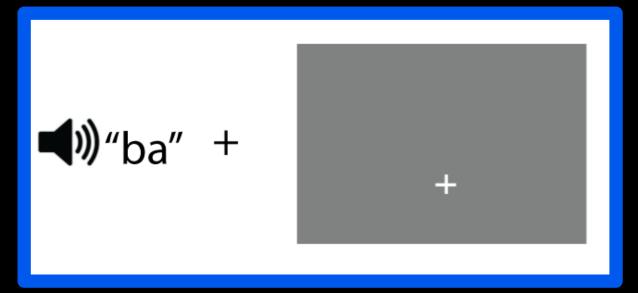


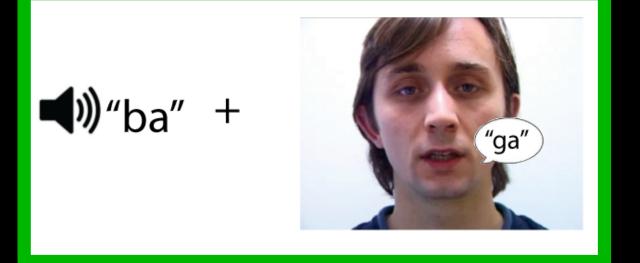
#### Transcranial Magnetic Stimulation (TMS)

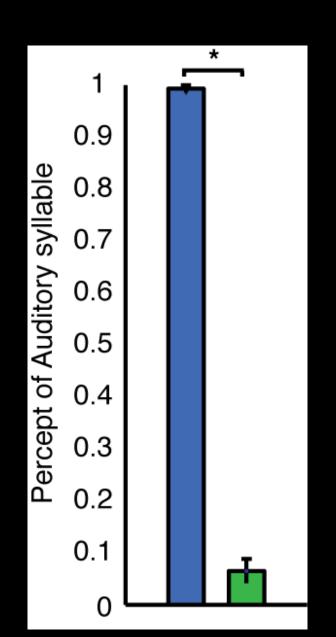


Beauchamp, Nath, Pasalar, Journal of Neuroscience, 2010

#### Behavioral Paradigm

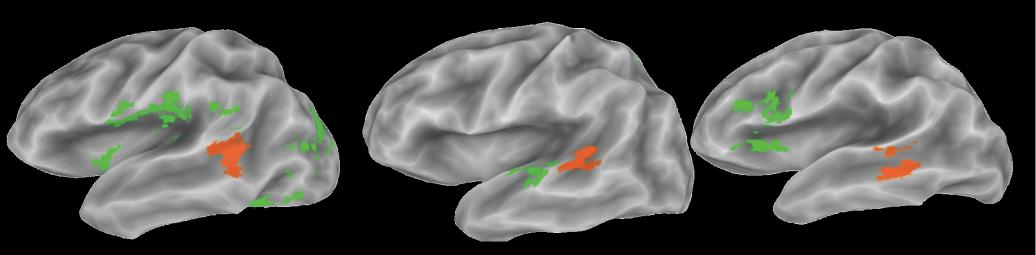






#### Method: combine fMRI with TMS

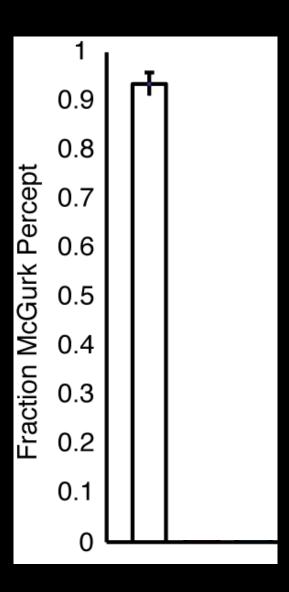
- First, scan subjects with fMRI to identify active brain areas
- Second, target these brain areas with TMS and examine behavior





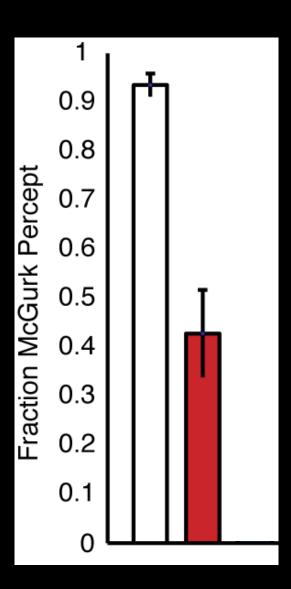
### Experimental Paradigm

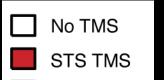
#### Experiment 1 (/ba/ + /ga/ ~= da)



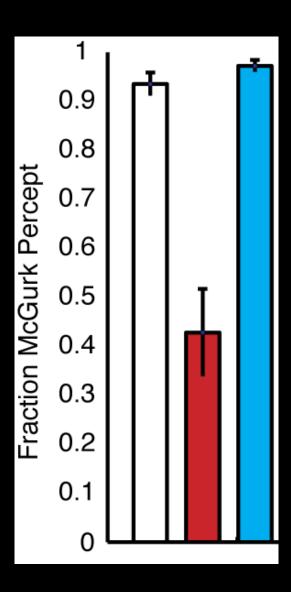
☐ No TMS

#### TMS Experiment 1



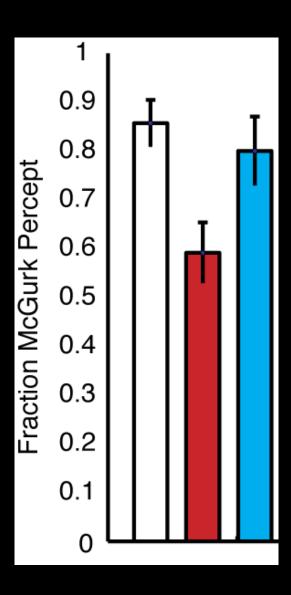


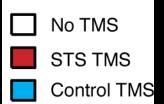
#### TMS Experiment 1



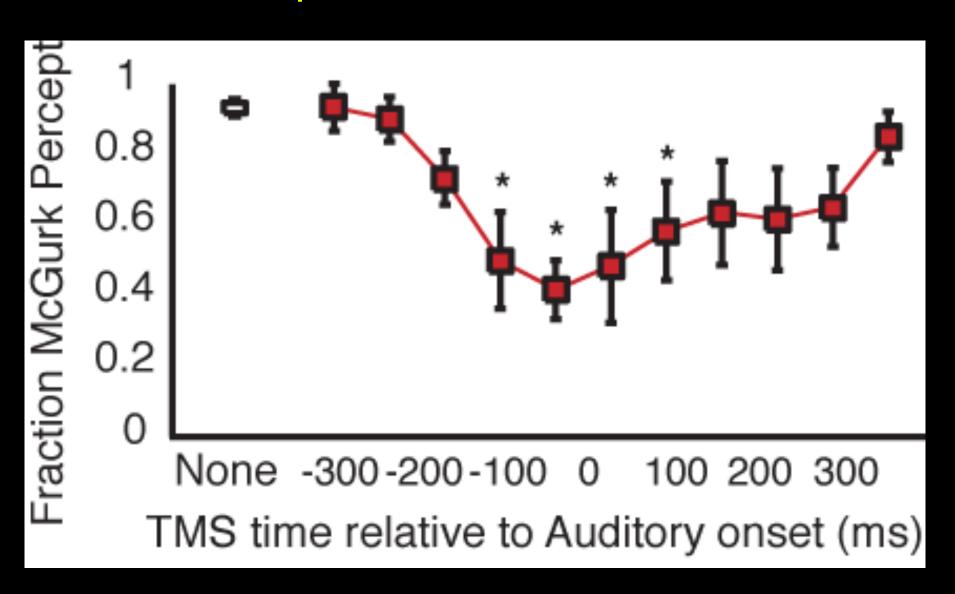


#### TMS Experiment 2 ( $/pa/ + /na/ \sim = ta$ )





#### TMS Experiment 3



#### Part 2: Summary

• interfering with activity in the left STS interferes with the McGurk effect, showing a causal role for STS in auditory-visual integration in speech perception

### Part 3: Interindividual differences in speech perception

#### Hearing lips and seeing voices

HARRY MCGURK
JOHN MACDONALD

Stimuli					Responses
Auditory	Visual	Subjects	Auditory	Visual	Fused
ba-ba	ga-ga	18-40 yr $(n=54)$	2	0	98

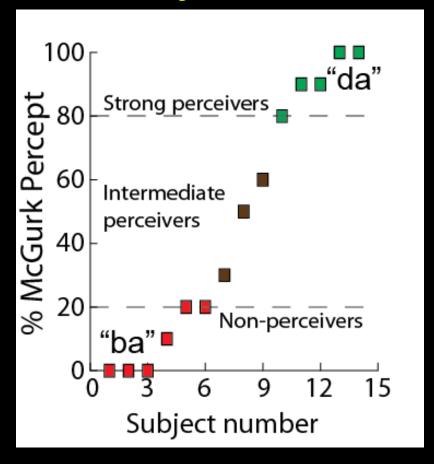
Table 2

Nature Vol. 264 December 23/30 1976

#### What about in this audience?

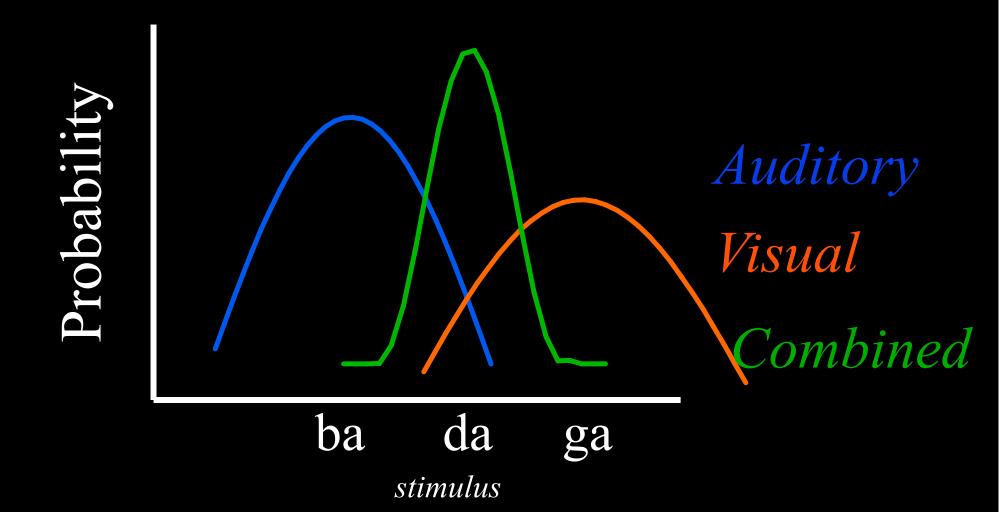


#### Intersubject Variability

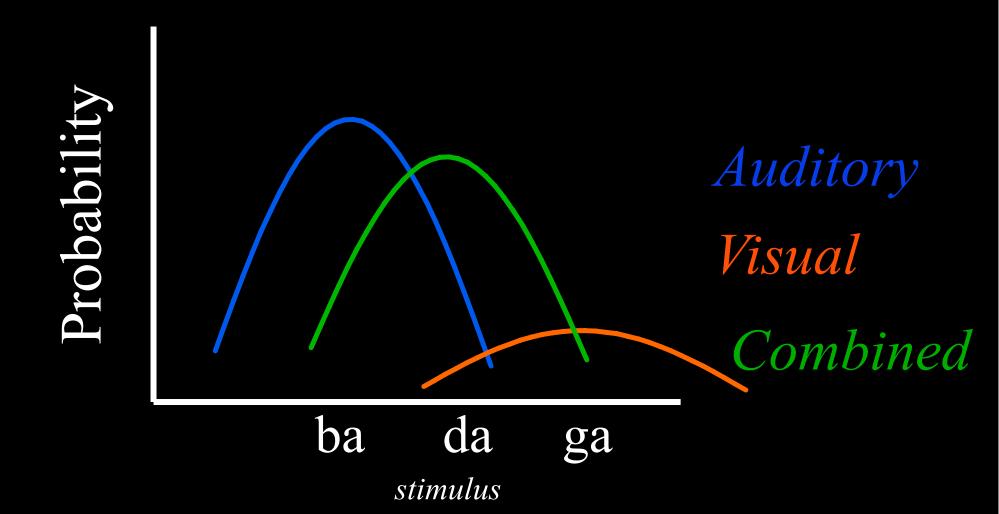


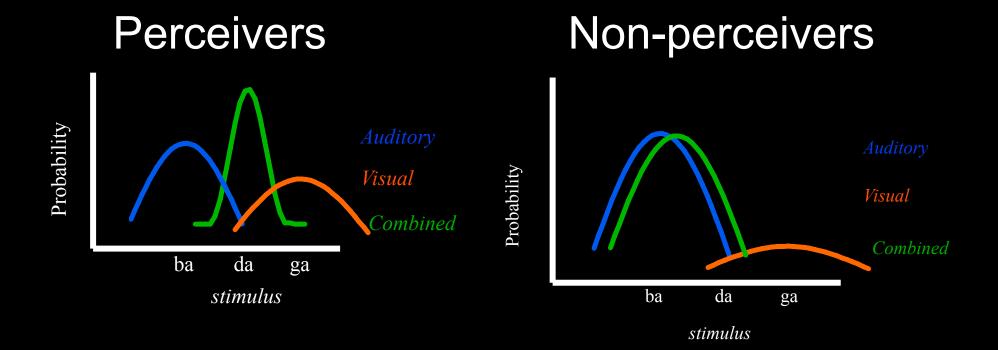
Nath, Fava, Beauchamp, Journal of Neuroscience, 2011 Nath and Beauchamp, Neuroimage, 2012

#### **Strong Perceivers**



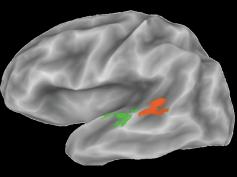
#### Non-perceivers

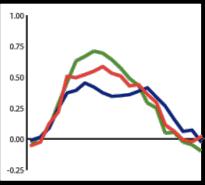




Hypothesis: perceivers integrate incongruent audiovisual speech, non-perceivers do not.

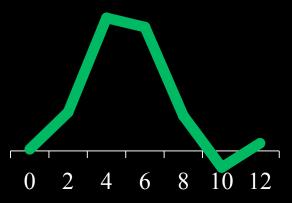
#### Test hypothesis with fMRI of the STS



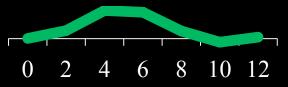


Beauchamp et al., Neuron, 2004

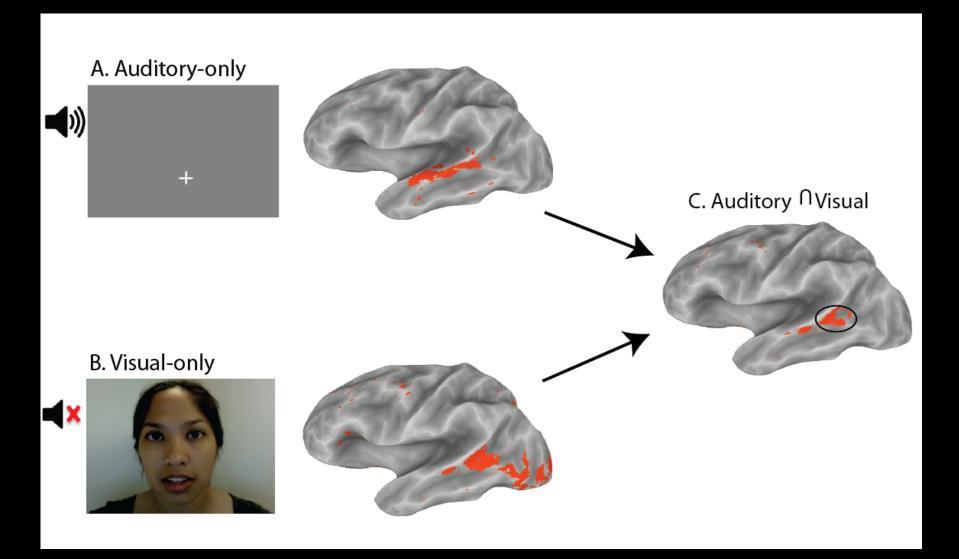
#### Perceivers



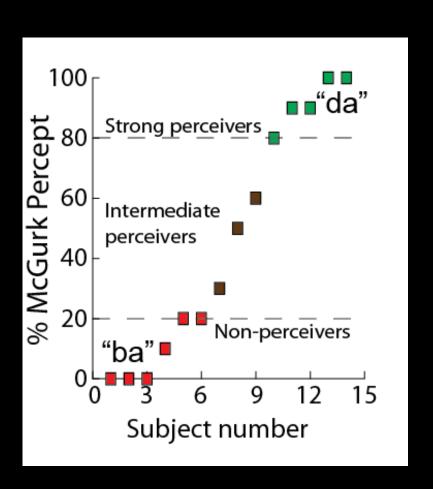
#### Non-perceivers

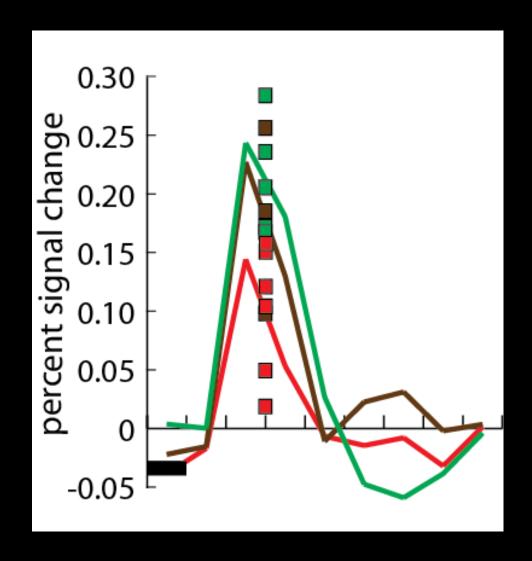


# Independent Functional Localizers to avoid "voodoo correlations"

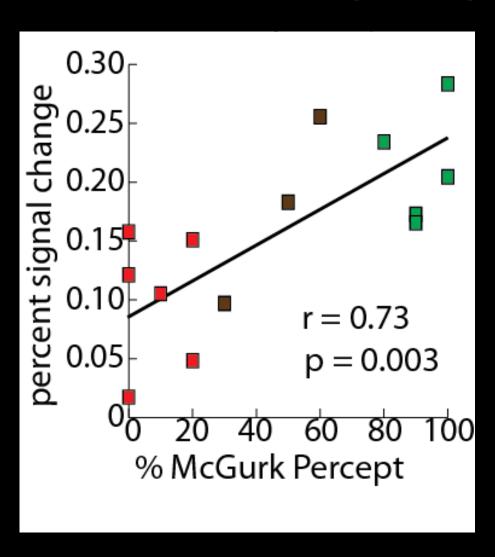


# Measure fMRI Response to Incongruent Speech

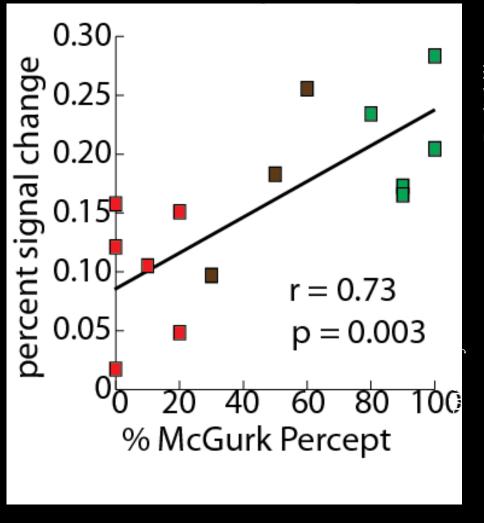


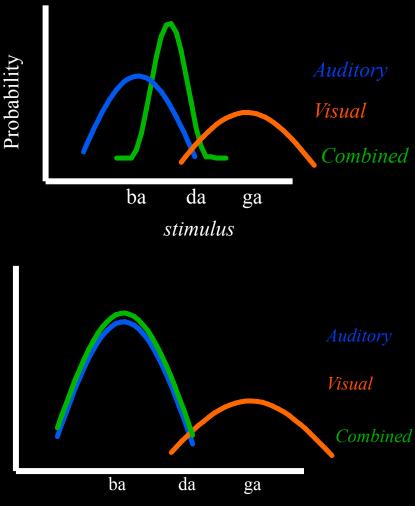


#### Correlation with perception



#### Correlation with perception





stimulus

#### Part 3: Summary

 Activity in the STS predicts perception of auditoryvisual incongruent speech

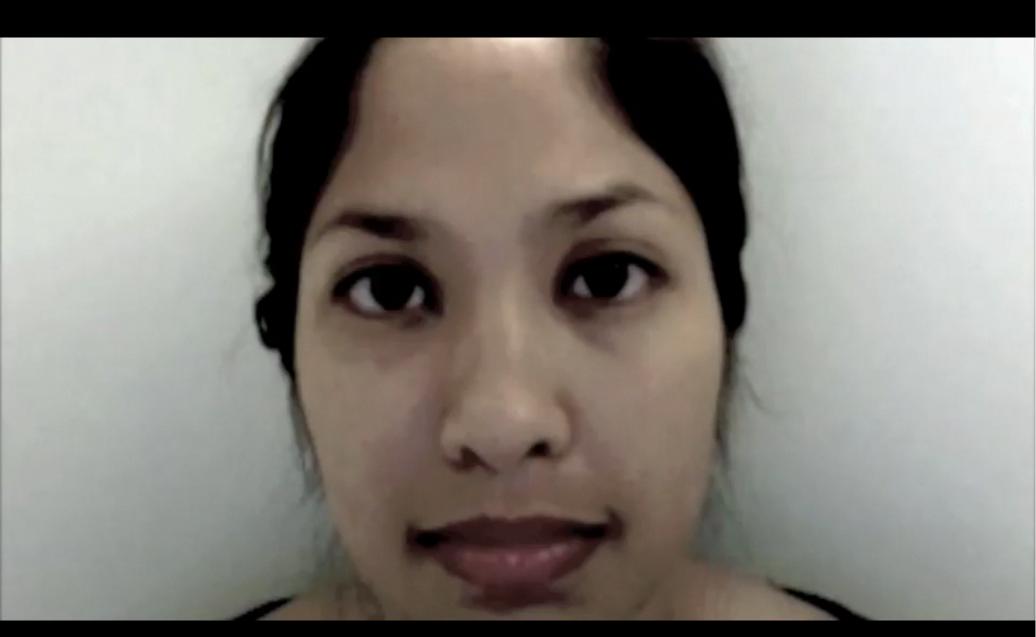
# Part 4: Neural mechanisms for Bayesian multisensory integration: STS connectivity

# Speech Multisensory Integration: Auditory Only



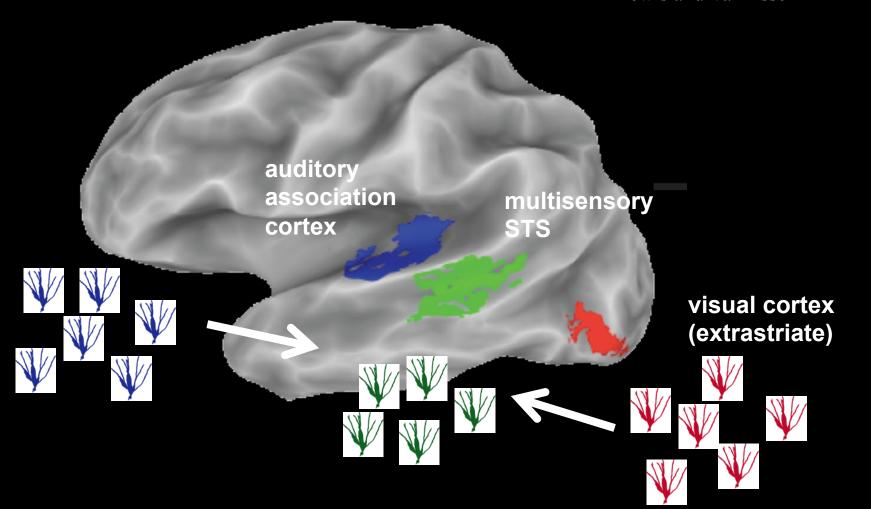
*e.g.* Sumby and Pollack (1954)

## Auditory + Visual



# Anatomical and Functional Connections of the STS

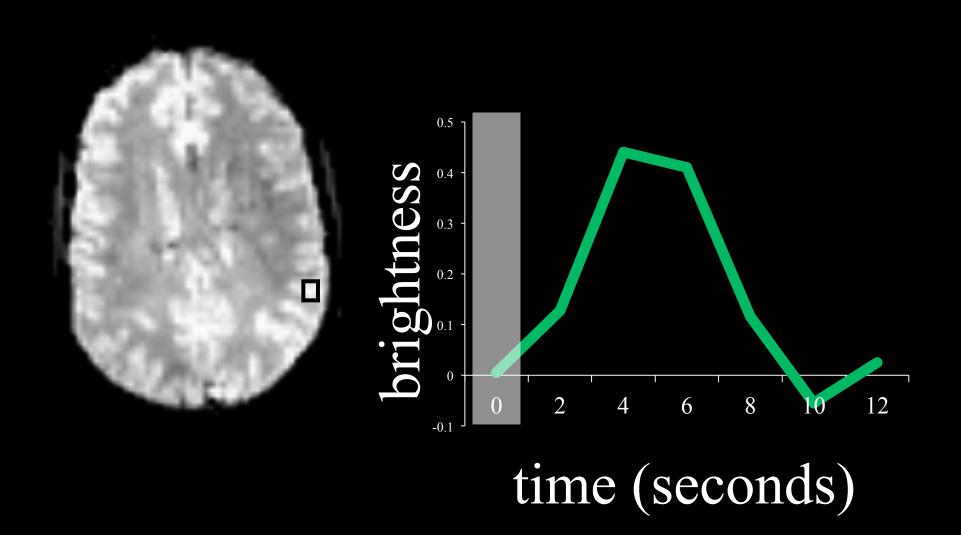
e.g. Cusick et al., Seltzer at al., Lewis and Van Essen



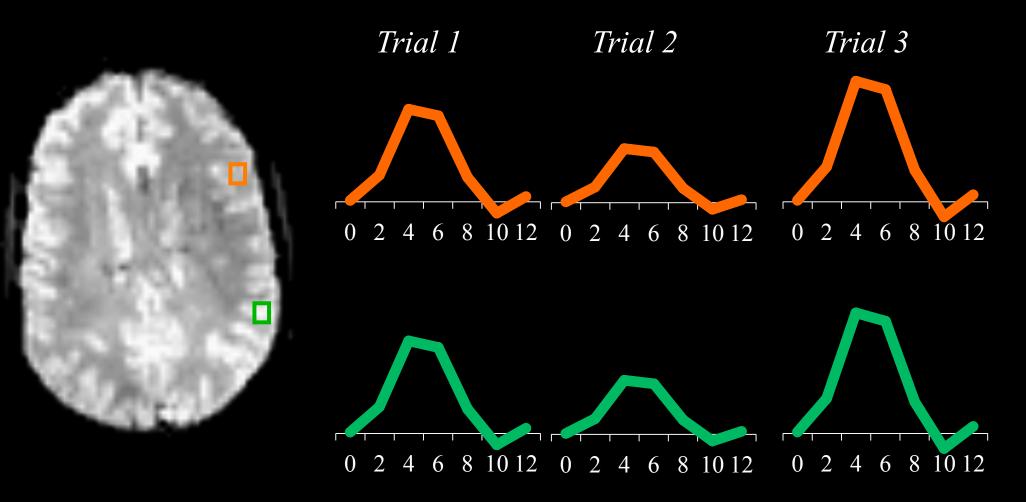
# How do we measure functional connections?

- Functional imaging to measure functional connectivity in the human brain
- McIntosh et al (1994); Horwitz et al., (1995); Friston etal., (1995)

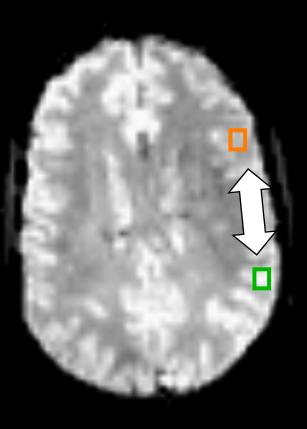
#### Basic fMRI experiment



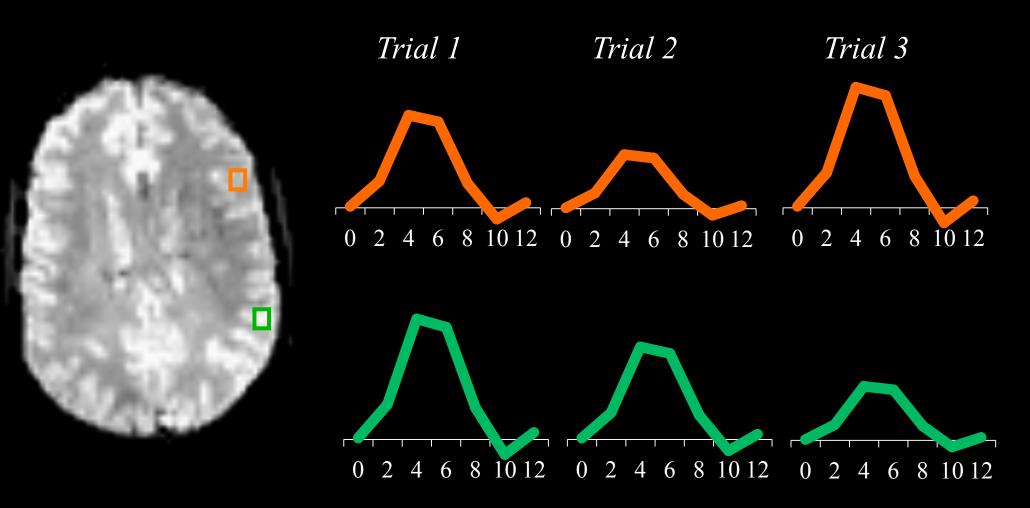
## Connectivity fMRI ("fcMRI") experiment



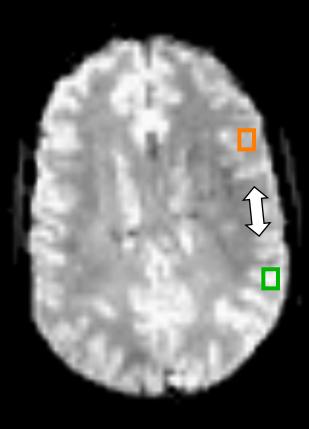
# Connectivity fMRI experiment: connected regions



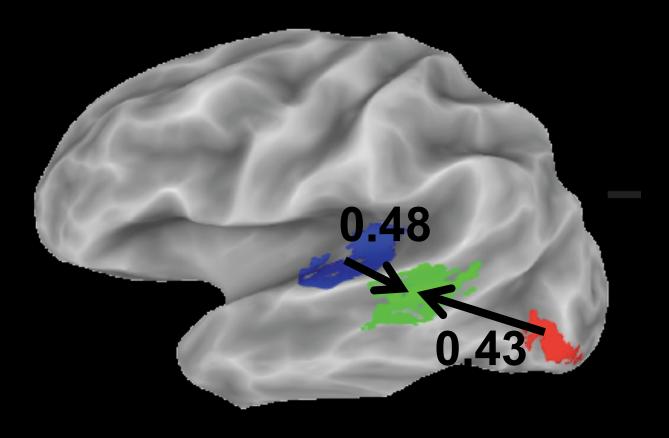
## Connectivity fMRI ("fcMRI") experiment



## Connectivity fMRI experiment

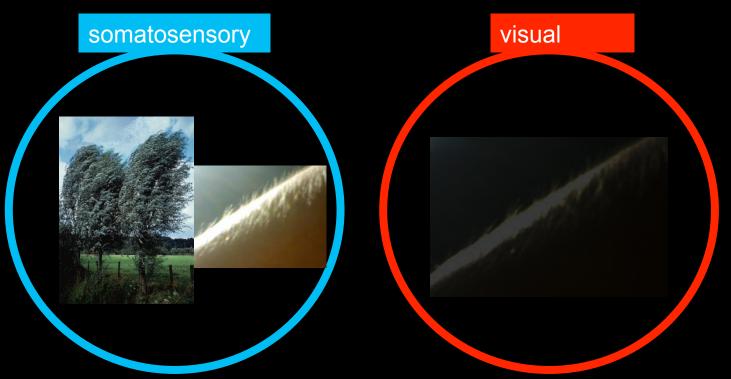


Result I: Strong functional connectivity between extrastriate visual cortex, auditory association cortex, and STS



# Reliability-weighted multisensory integration

■ Independent sources → independently varying noise levels

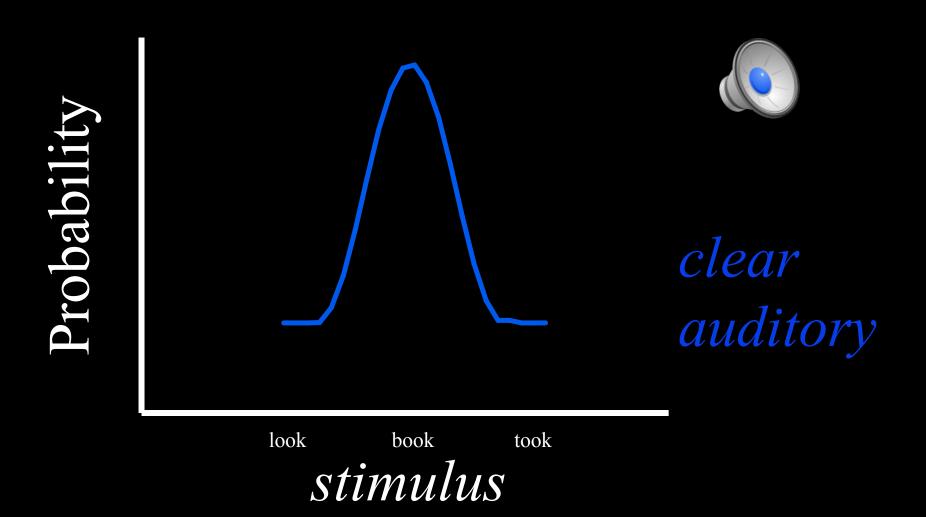


Ernst and Banks (2002); Alais and Burr (2004); Battaglia at el (2003); Pouget et al (2004); Ma et al (2006) Saunders, Knill, Jacobs (1999); Young et al. (1993); Landy & Kojima (2001)

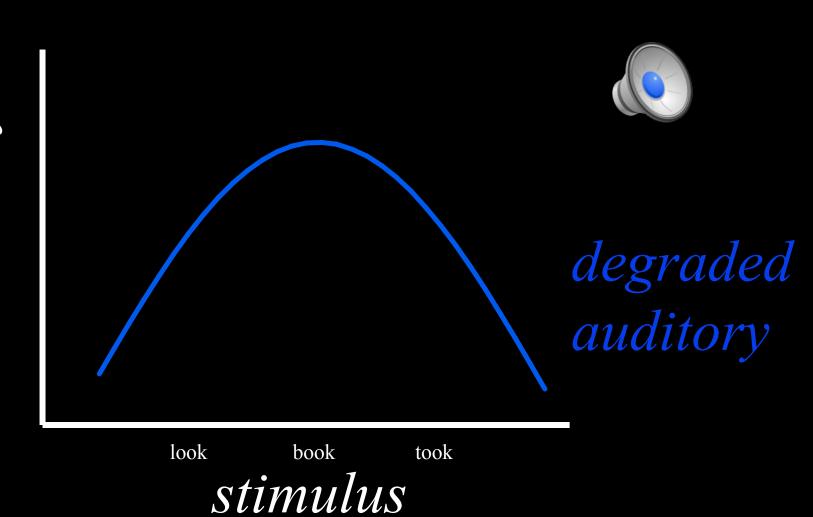
#### Bayesian approach

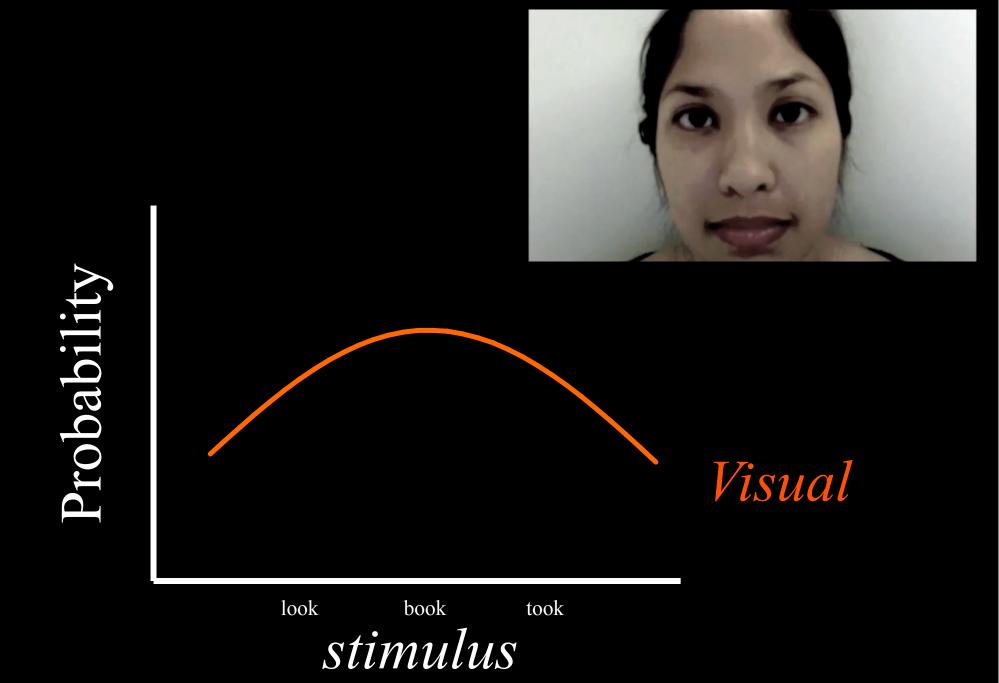
- Bayesian Approach: Statistical Inference for Optimal Perception
- calculate probability of a real-world event given an observation,
   combined with information about prior probability of the event
- Ernst and Banks (2002); Alais and Burr (2004); Battaglia at el
   (2003); Pouget et al (2004); Ma et al (2006)
- also known as cue integration; maximum-likelihood estimation
- Saunders, Knill, Jacobs (1999); Young et al. (1993); Landy &
   Kojima (2001)

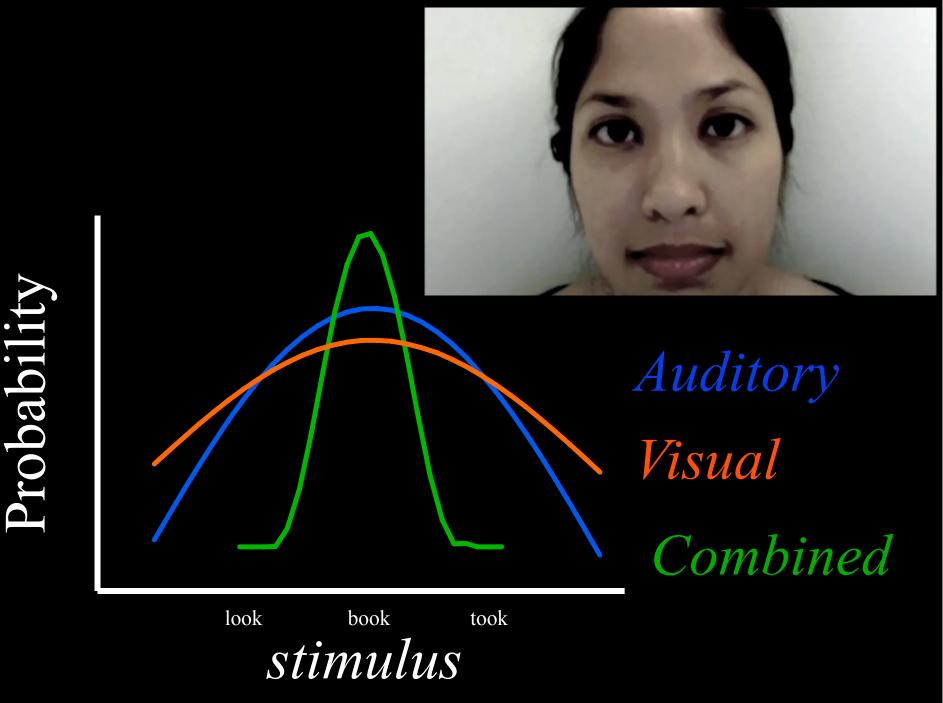
## Bayesian Approach



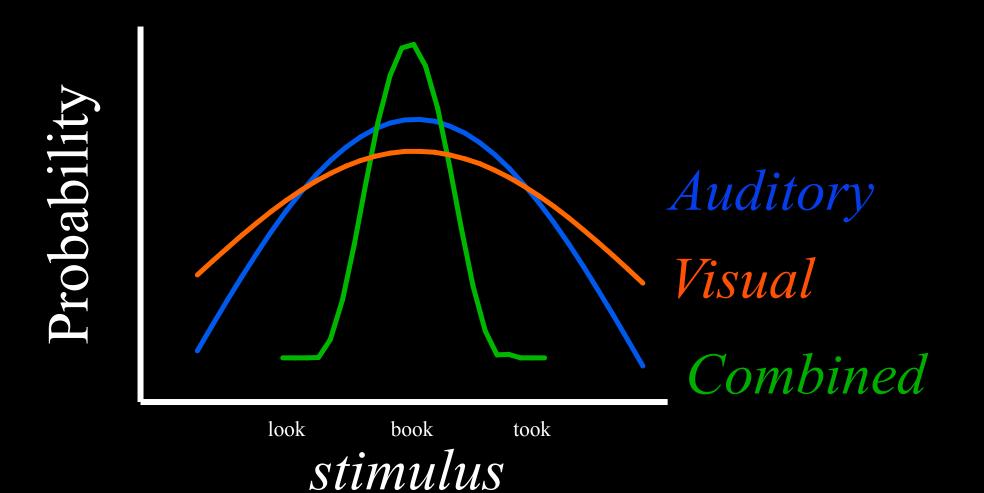
# Probability







$$\sigma_{AB}^2 = \frac{\sigma_A^2 \sigma_B^2}{\sigma_A^2 + \sigma_B^2}$$



## Reliability-Weighted Integration

## **Auditory-only**





## Visual-only



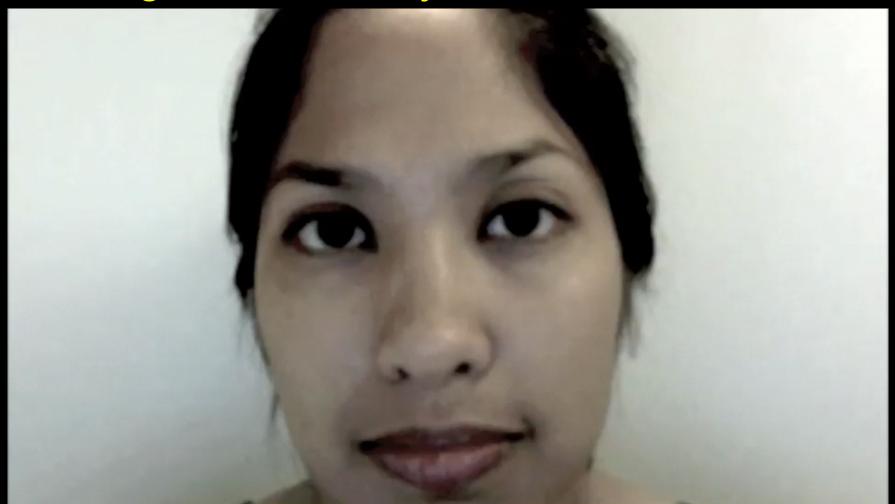


## **Degraded Auditory**

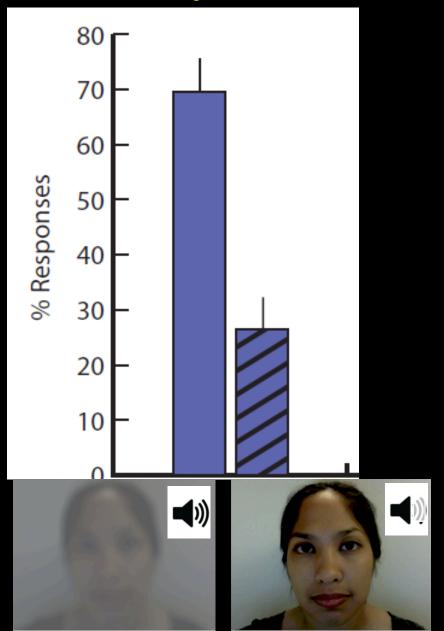


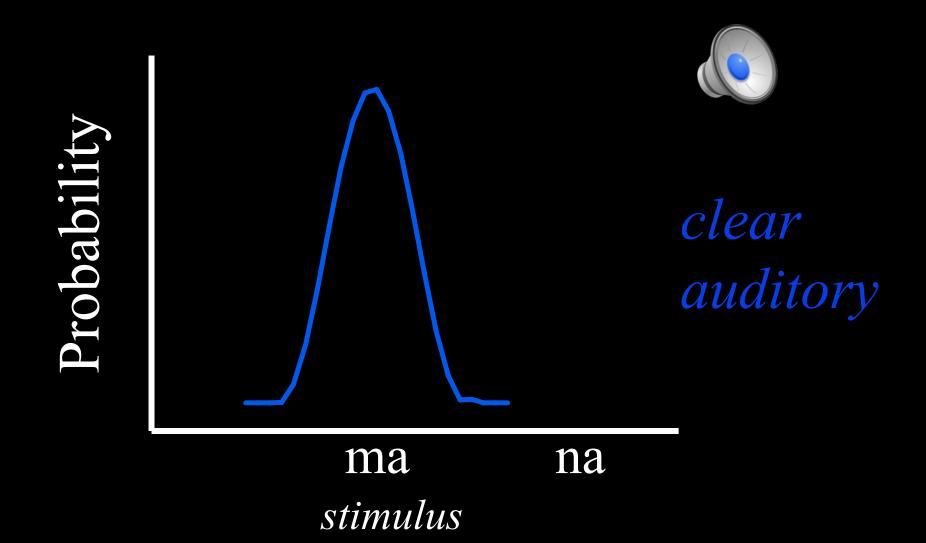


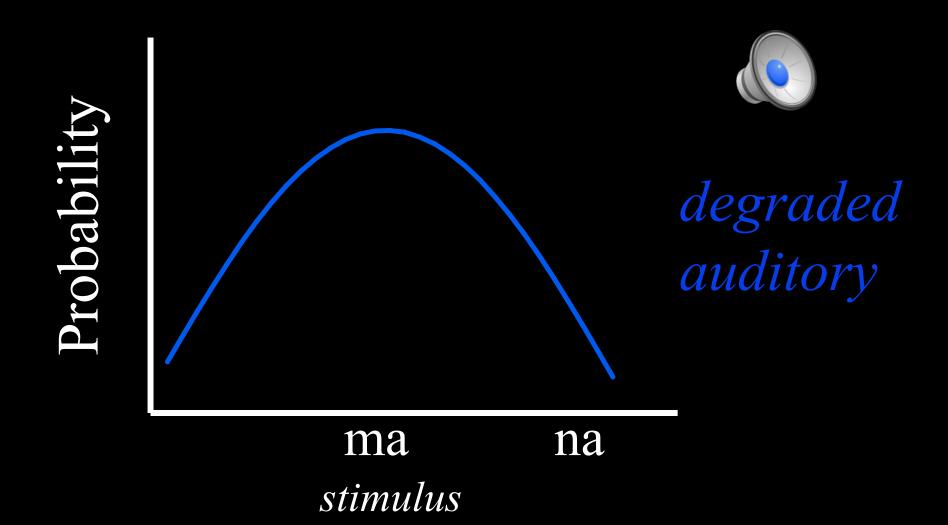
## Incongruent auditory-visual stimuli

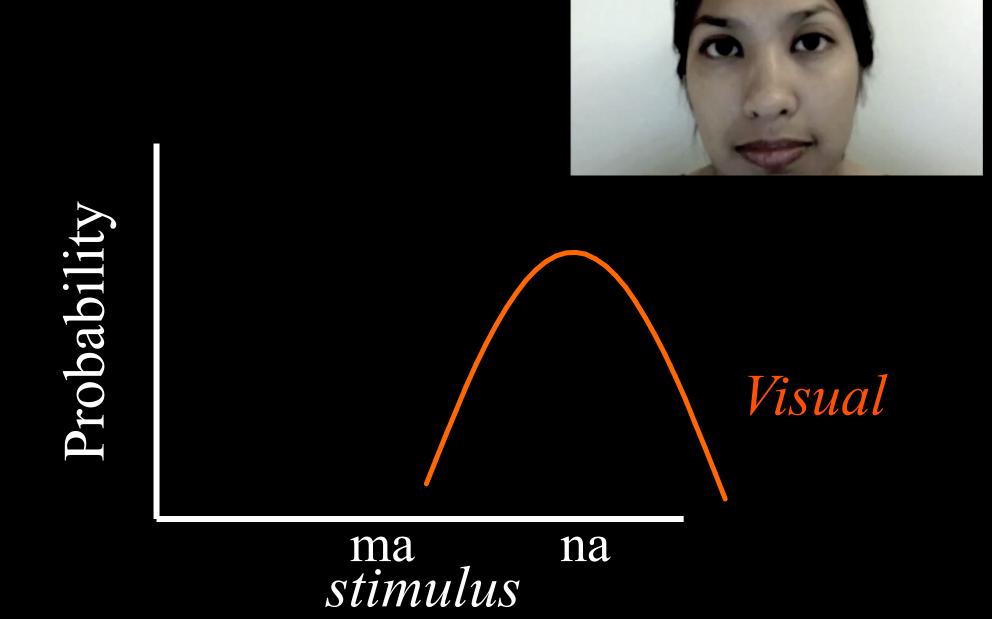


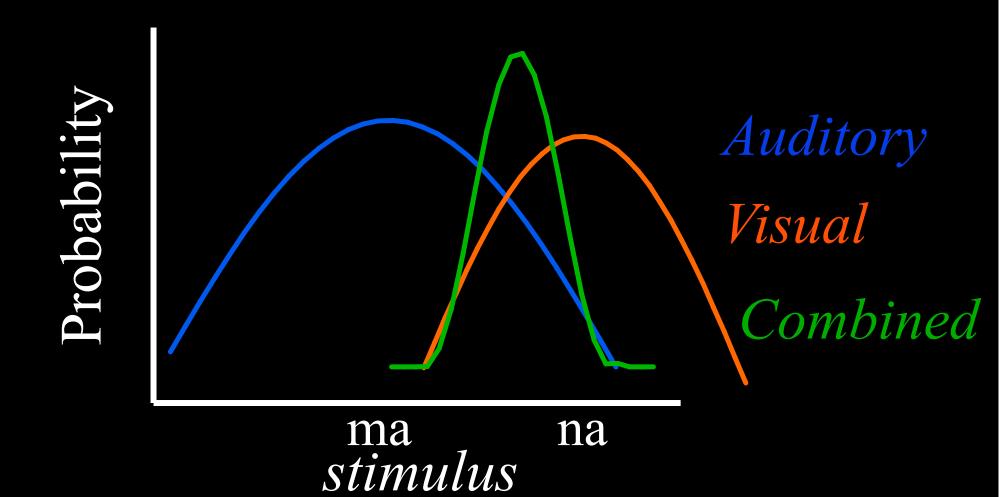
## Incongruent auditory-visual stimuli



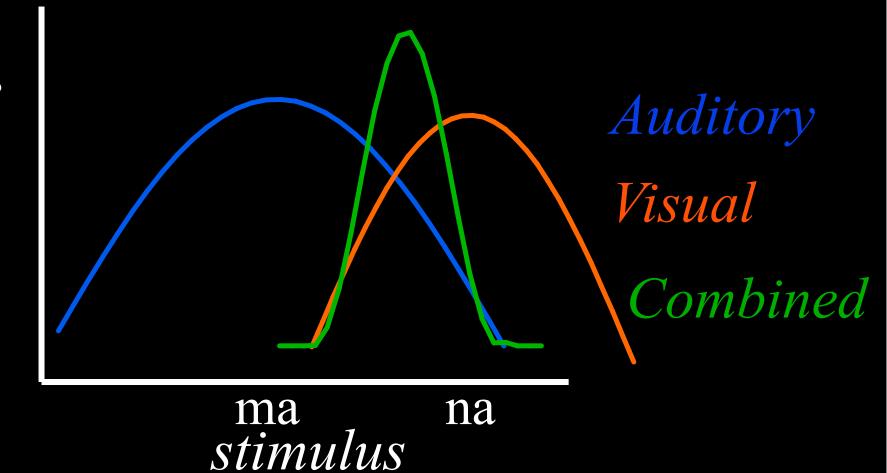






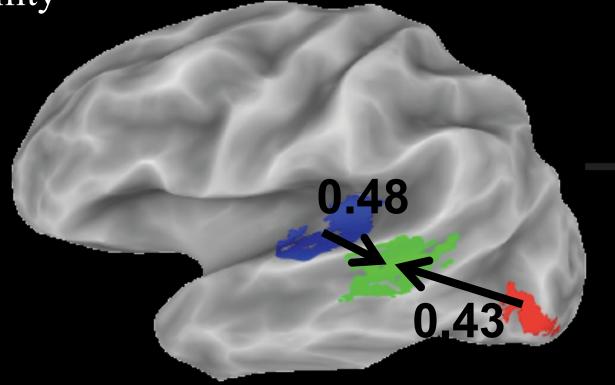


$$\hat{S} = \sum_{i} w_{i} \, \hat{S}_{i} \quad w_{i} = \frac{1/\sigma_{i}^{2}}{\sum_{j} 1/\sigma_{j}^{2}}$$

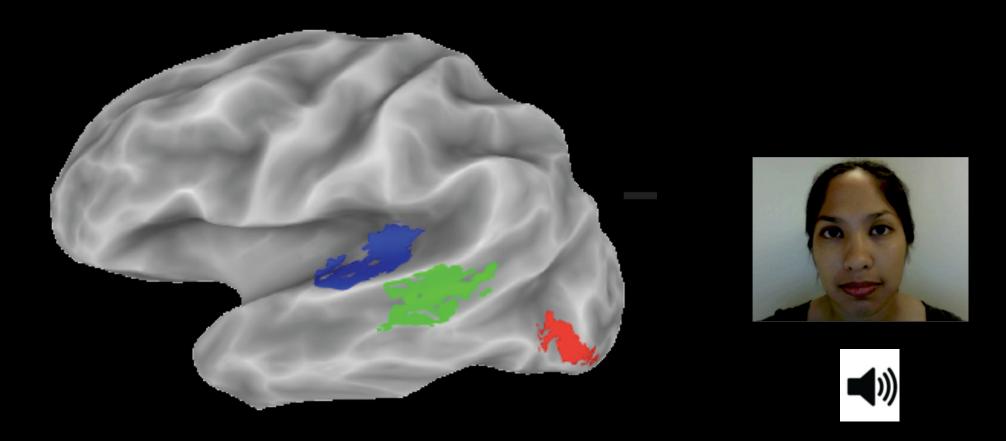


### Hypothesis

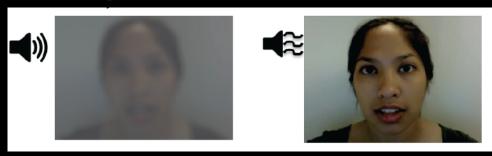
Functional connectivity reflects stimulus reliability



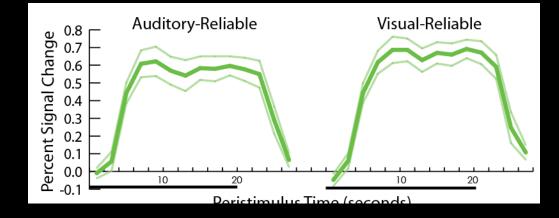
### Methods I: Functional Localizers



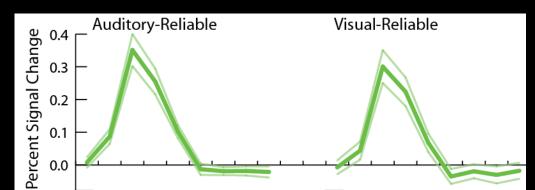
## STS responses



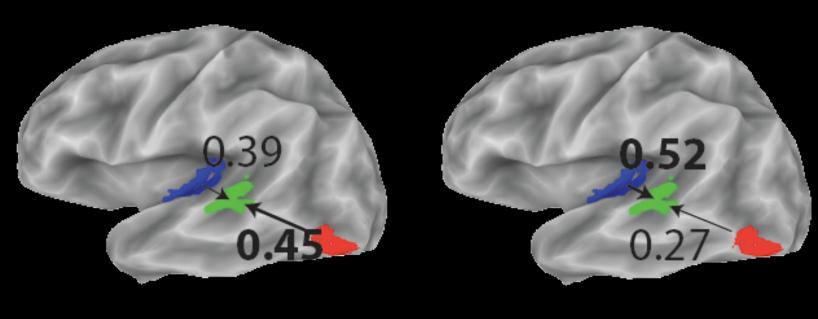
## Expt 1



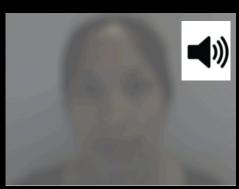
Expt 2



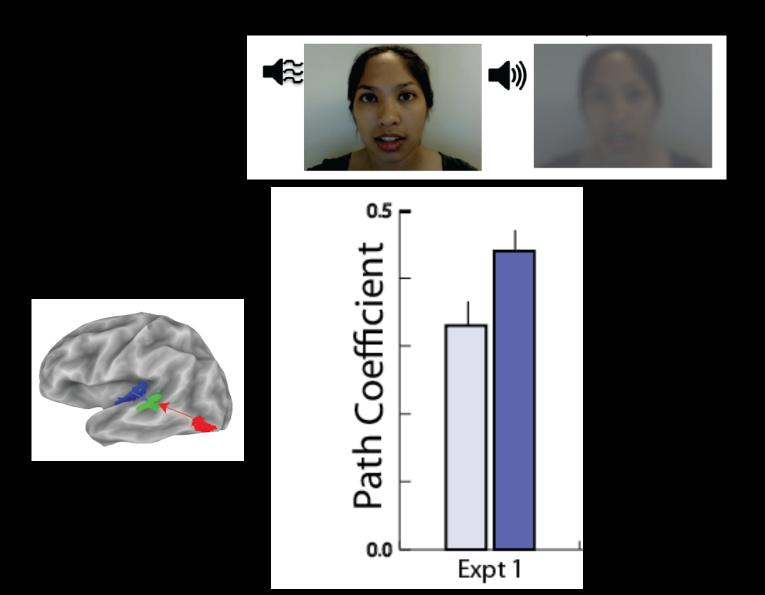
### Results: Experiment 1, one subject



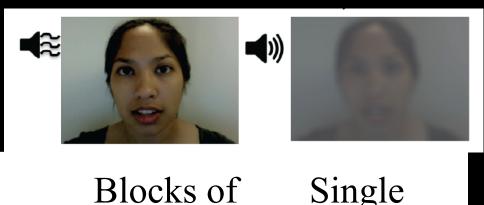


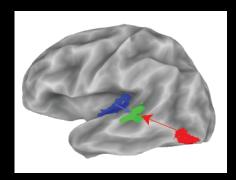


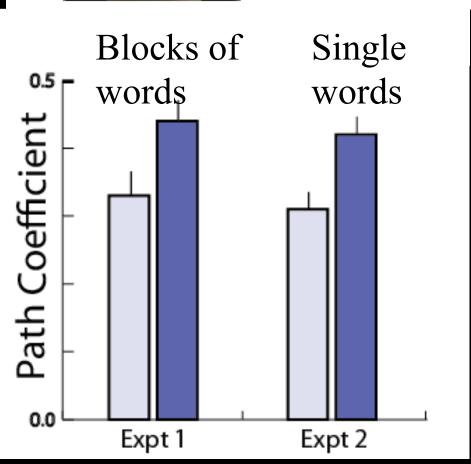
## **Auditory Cortex to STS**



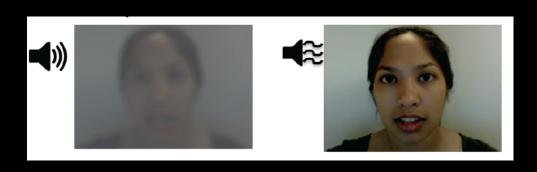
### **Auditory Cortex to STS**

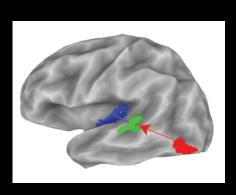


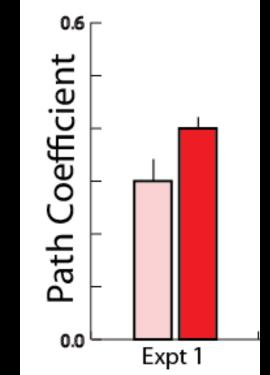




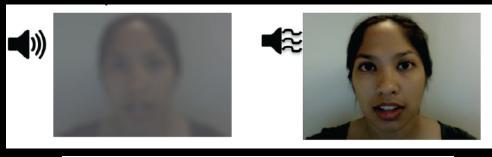
### Visual Cortex to STS

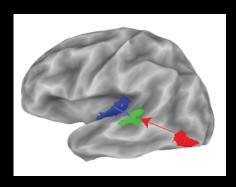


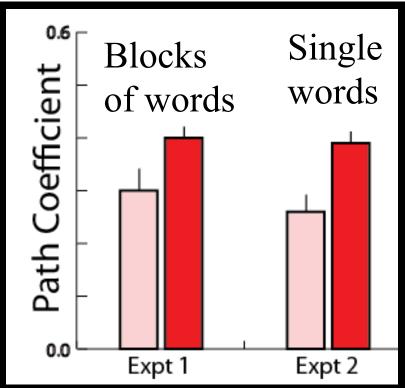




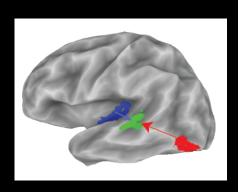
### Visual Cortex to STS

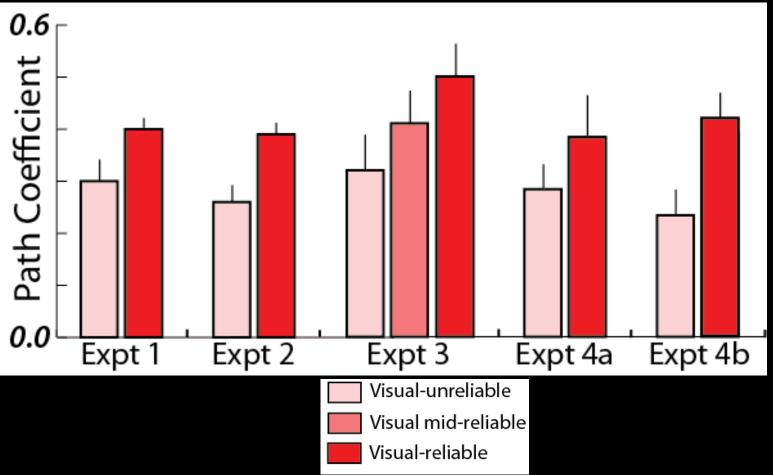






#### Visual Cortex to STS





#### Part 4: Summary

- Behaviorally, multisensory integration is optimal: humans perform similarly to ideal observers, weighting each sensory modality by its reliability
- Optimal mutisensory perception is an emergent property of cortical networks: functional connections between sensory areas and multisensory areas are weighted by the reliability of each modality
- Changes in functional connectivity within the network are a strong candidate mechanism for behavioral reliability-weighting

### How we've tackled these problems

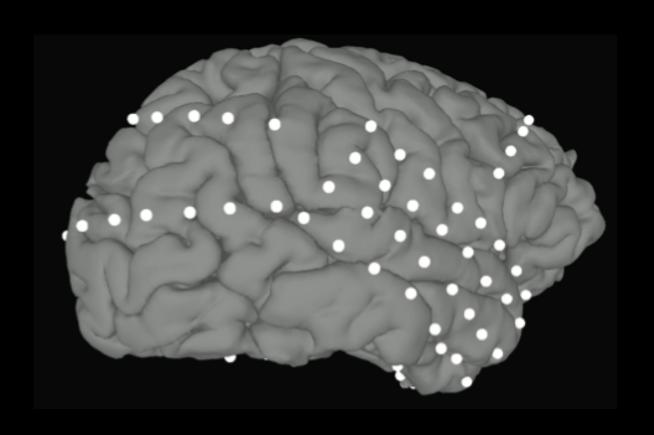
- What do the blobs mean?
  - Is activity in the area linked to behavior or perception?
  - Is activity in an area truly required for a cognitive function?
- Poor match between analysis (simple) and data (complex)
  - o How do areas operate as a network?
- Slow temporal resolution
  - Neuronal responses are on a ~ms time scale, fMRI operates on a ~sec time scale

- Multisensory integration, esp. speech perception
  - Temporary and permanent lesions of the STS
- Link between STS
   activity and perception of
   multisensory speech
- Connectivity of the STS during speech perception
- Electrocorticography with ms time resolution (TPJ)

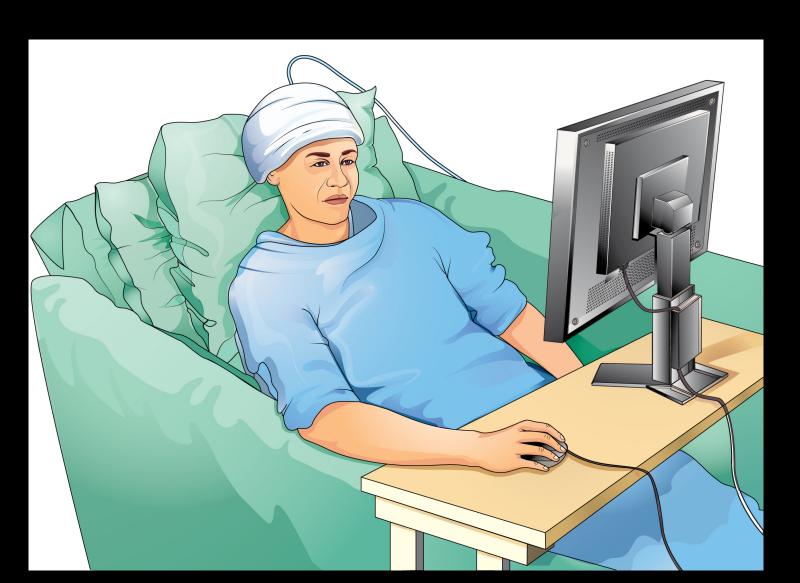
# Part 5: Conscious Perception of Visual Stimuli

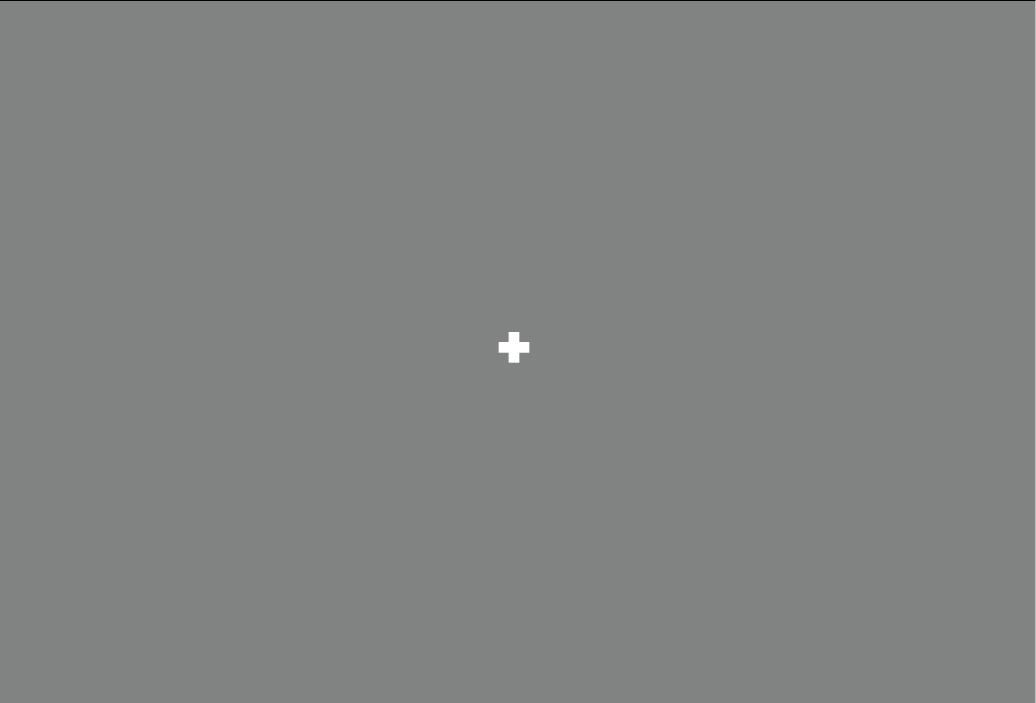


## eCoG and eStim

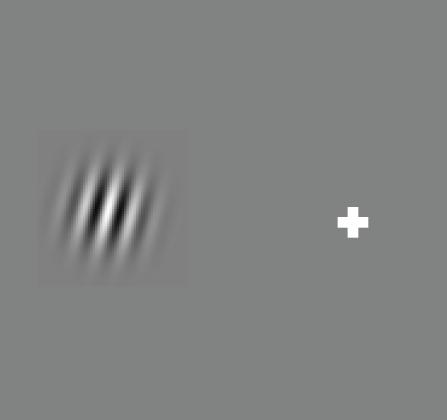


## Methods







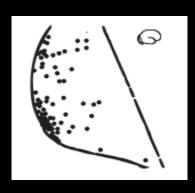




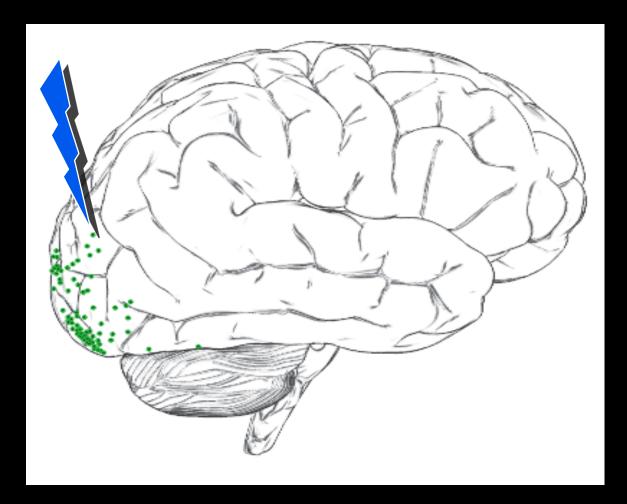




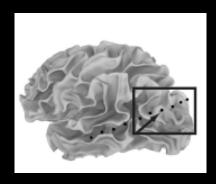
# eStim: stimulating the occipital lobe produces phosphenes.

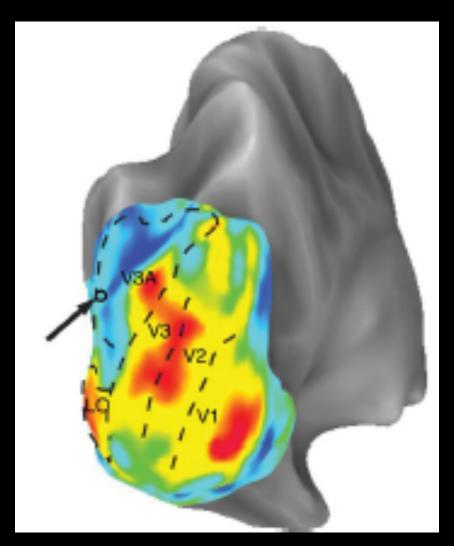


Penfield



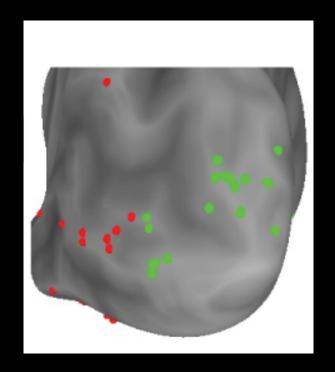
# Retinotopic maps with BOLD fMRI combined with electrical stimulation

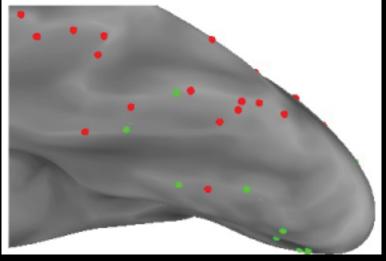


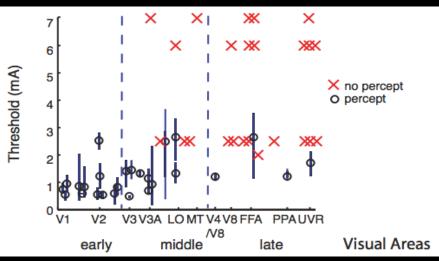


Murphey, Maunsell, Beauchamp, Yoshor, PNAS (2009)

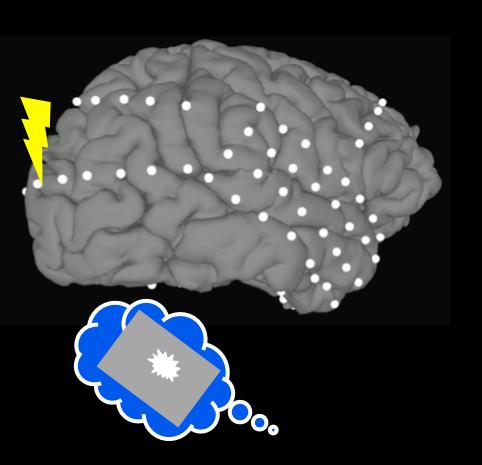
# Electrical stimulation of some identified areas produces phosphenes.

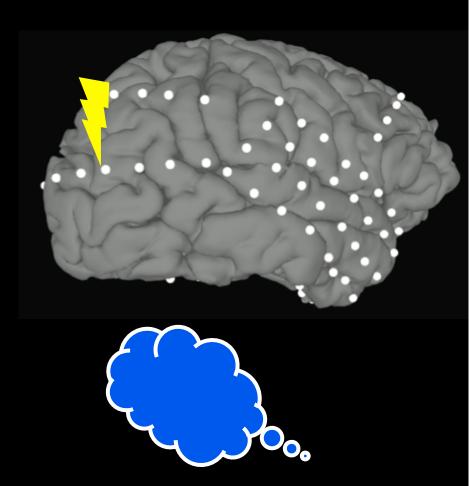




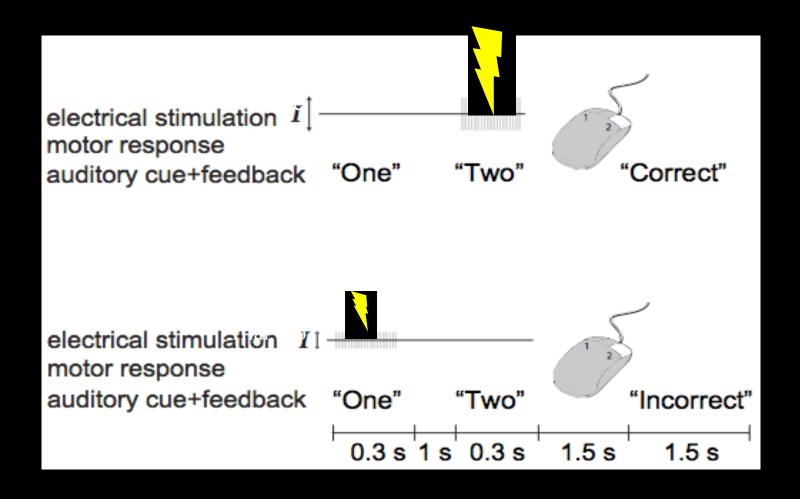


# Electrical stimulation of only some brain areas produces phosphenes.



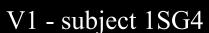


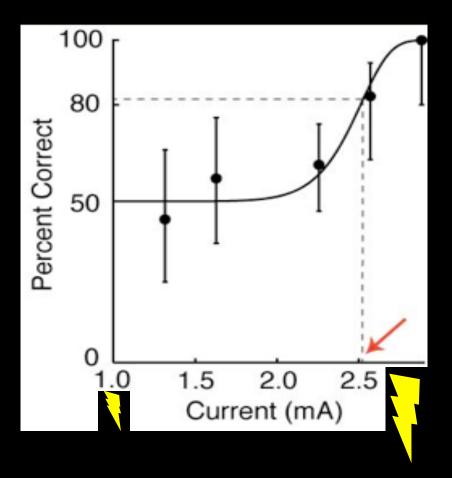
# Quantifying detectability of electrical stimulation trial by trial



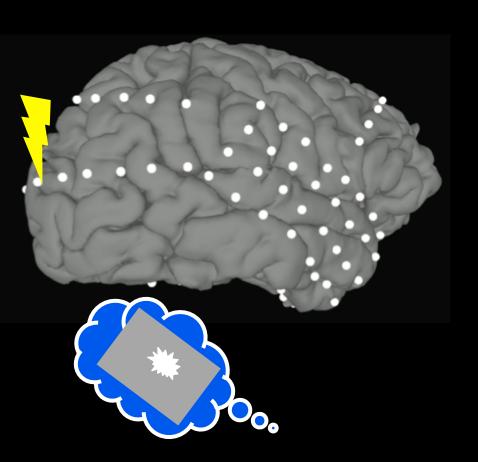
Murphey, Maunsell, Beauchamp, Yoshor, PNAS (2009)

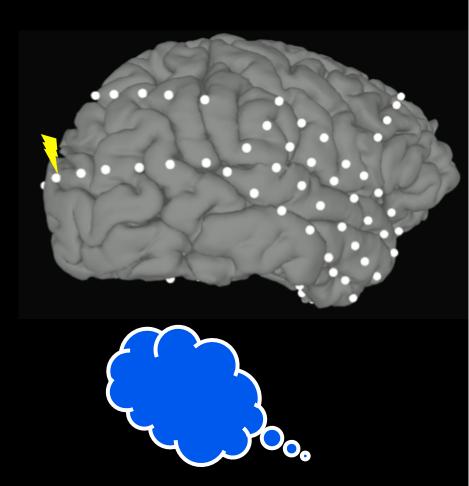
# Performance at different currents for one electrode



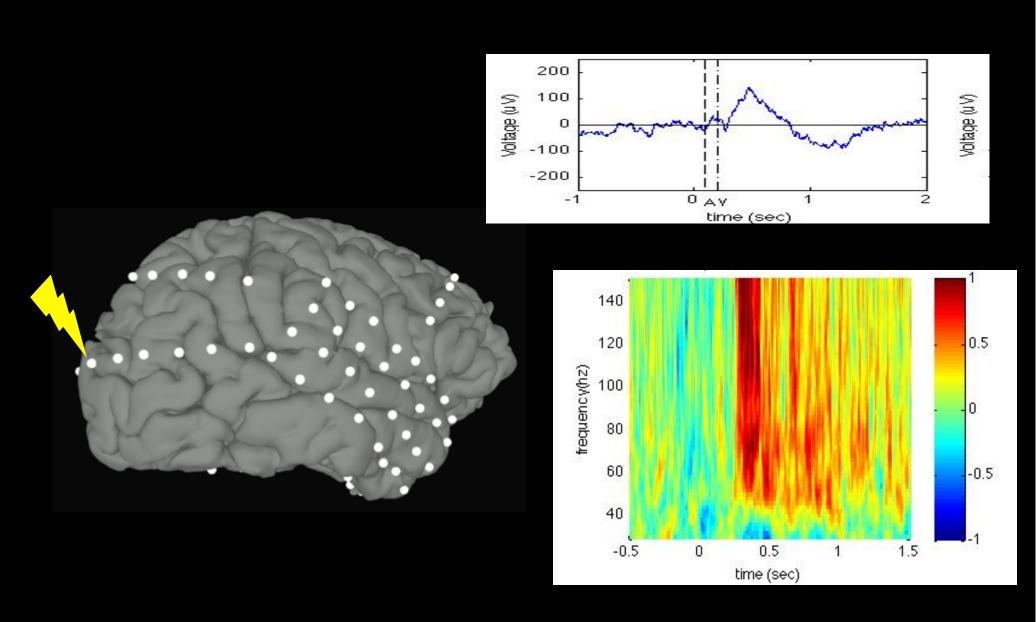


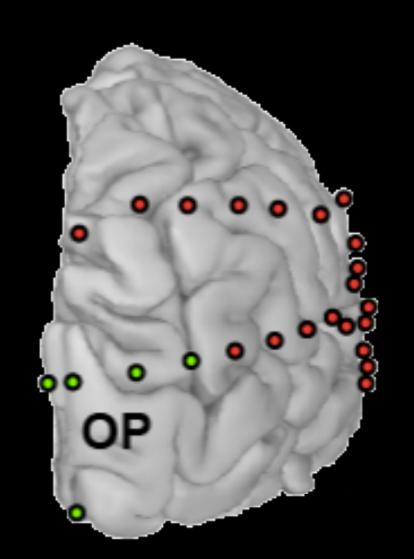
# There is a current threshold for phosphene production

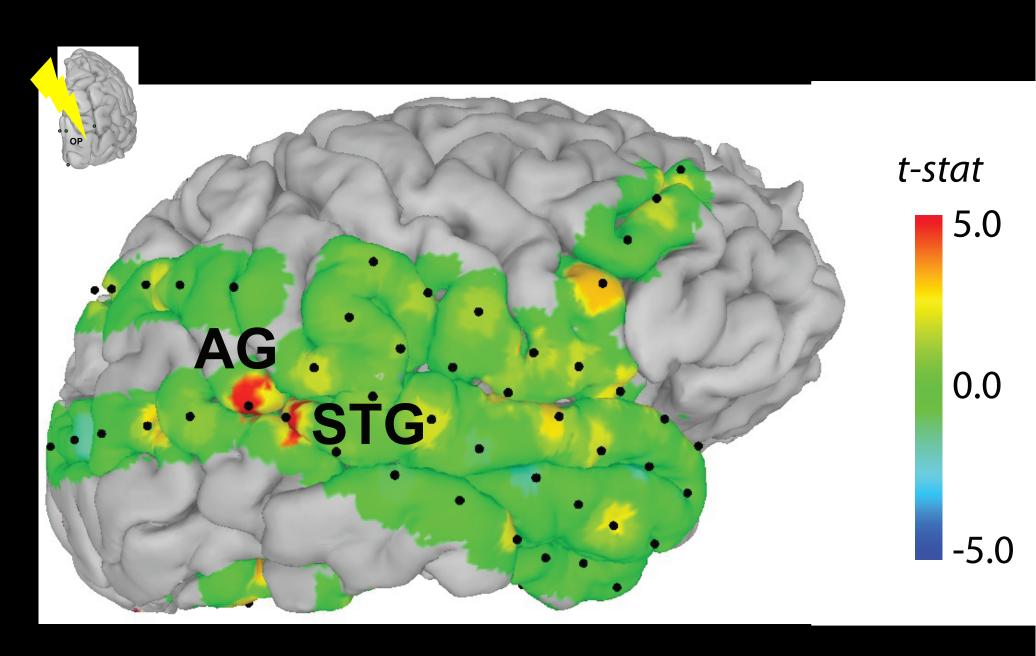


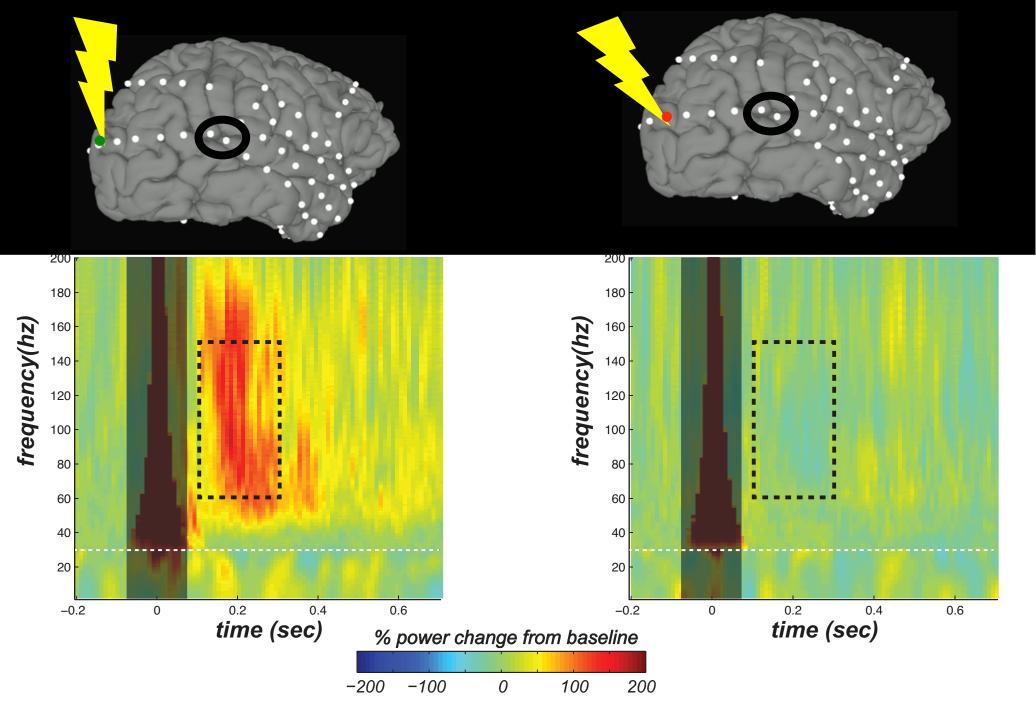


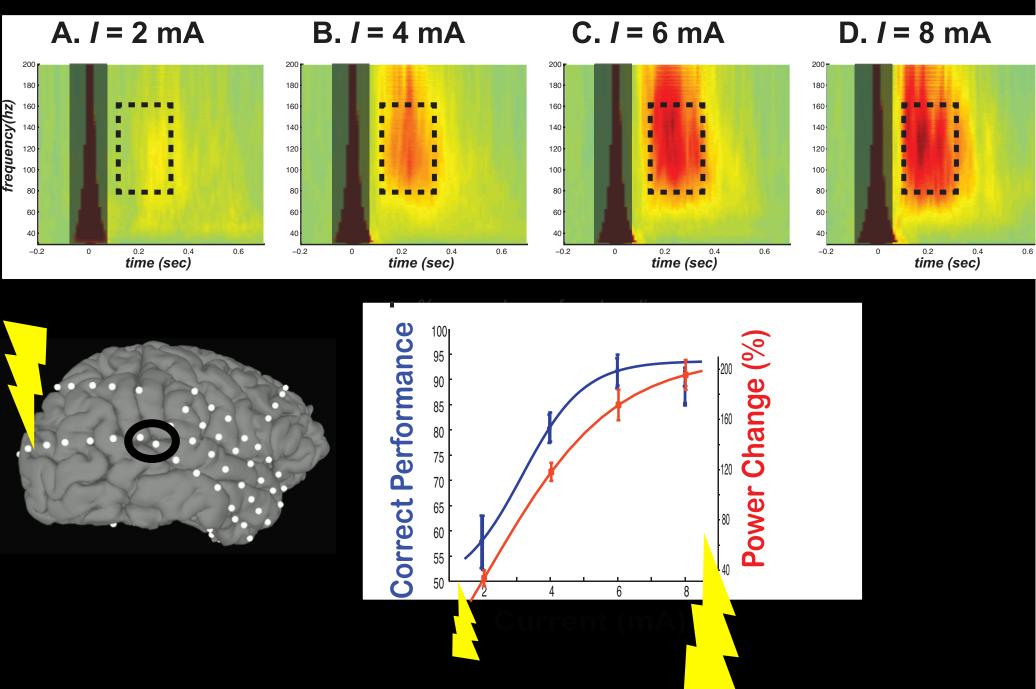
# Stimulate AND Record



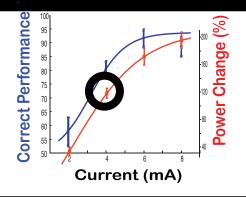




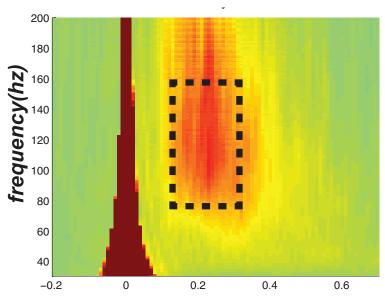


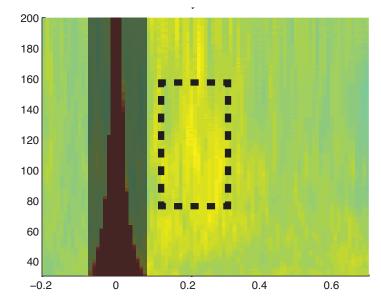


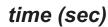


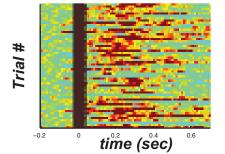


# Wrong

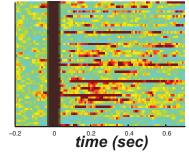


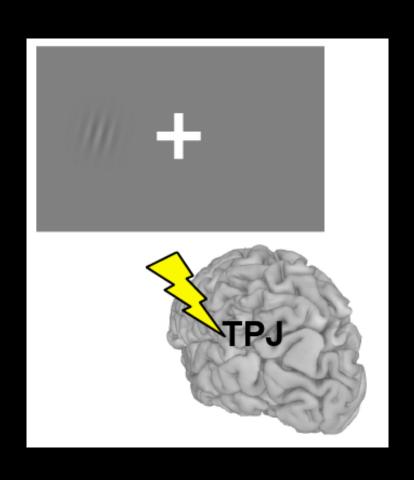


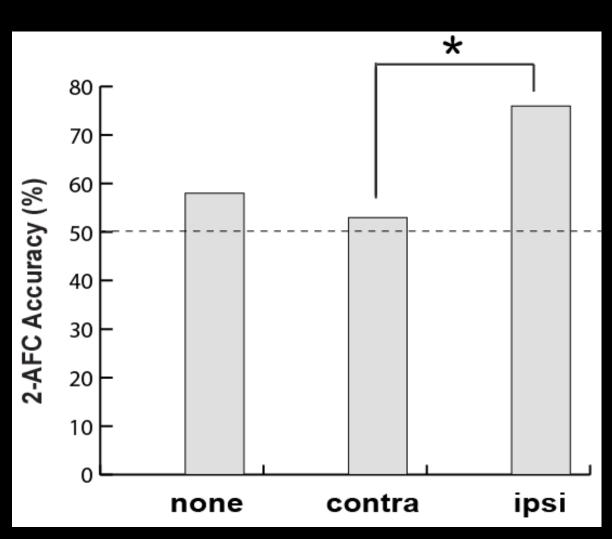




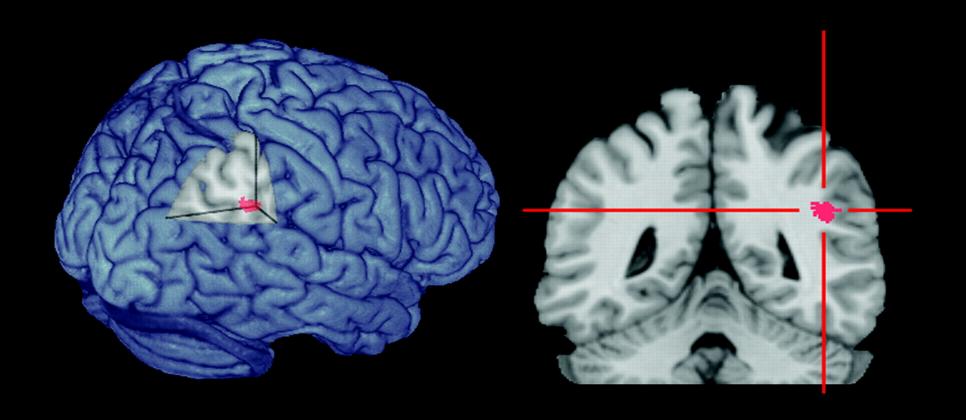
time (sec)







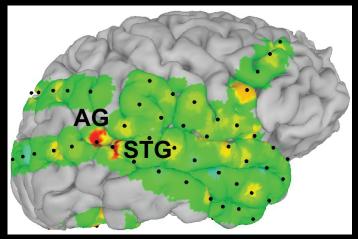
### Visual neglect



Mort D J et al. Brain 2003;126:1986-1997

# Part 5 Summary: Conscious awareness and the TPJ

- Conscious perception of eStim requires gamma activity in the temporo-parietal junction (TPJ)
- 1) Stimulation of percept-generating sites cause an increase in gamma power in TPJ
- 2) Neurometric-psychometric comparison: similar threshold and slope
- 3) Choice probability: at threshold stimulation, significantly more TPJ gamma in correct trials in 2IFC task



- Neglect, Exogenous orienting: Corbetta & Shulman,2002; Karnath, 2001
- Body perception: Blanke *et al.*, 2002

#### General principles

- Multisensory integration at the geographic intersection of different modalities
- Patchy organization
- MSI at every tier of the system—last time I gave this talk, someone asked about the superior colliculus....

### **Overall Summary**

- the STS is important for auditory-visual integration in speech perception
- The weight of unisensory inputs to multisensory areas depends on stimulus reliability (fMRI connectivity)
- Gamma band activity in parietal lobe underlie conscious awareness of weak stimuli (eCog, electrocorticography)

### **Funding and Collaborators**

#### **Speech Perception**

Audrey Nath
Sarah Baum
Debshila Basu

#### Autism

Alex Martin Rich Frye

#### **TMS**

Tony Ro Siavash Pasalar

#### Intracranial

Dan Yoshor
Dona Murphey
Ping Sun

#### **Development/NIRS**

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#### DTI & Methods

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DEPARTMENT OF VETERANS AFFAIRS



National Institute on Deafness and Other Communication Disorders

Improving the lives of people who have communication disorders





Sarah Baum

Tony Ro

Eswen Fava Audrey Nath











Siavash Pasalar

