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9.71 Functional MRI of High-Level Vision
Fall 2007

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9.71 Class 5 October 4
Outline for Today

5A: Bare Basics of Visual Neuroanatomy
The Visual Pathway
Neuranatomical Landmarks

5B: Face Perception and the FFA

<break>

Student Presentations

Grace presents Avidan et al (2005)

Ravi presents Gauthier et al (2000)

Peter presents Rotshtein et al (2005)

Face Perception

Faces are particularly important stimuli because

- they convey many kinds of critical information:
identity, age, sex, mood, and direction of attention
- faces are among the stimuli we look at most frequently in daily life
- the ability to perceive faces was probably critical
to the survival of our primate ancestors

Evidence that special mechanisms may be used in face perception from:
lesions, neurophysiology, behavior, ERPs, MEG and fMRI

1. Prosopagnosia

- many reported cases (several dozen ?)
- lesion in inferior temporal cortex
- Impairs face discrimination & recognition, not face detection
- In rare cases where lesion is small, deficit can be very specific, leaving object recognition intact.

e.g. the patient of Wada & Yamamoto, 2001

Image removed due to copyright restrictions.

Figure 1 in Wada, Y. and T. Yamamoto. "Selective Impairment of Facial Recognition due to a Haematoma Restricted to the Right Fusiform and Lateral Occipital Region." *J Neurol Neurosurg Psychiatry* 71 (2001): 254-257.

a double dissociation of face and object recognition.

2. Face-Selective Neurons in Macaque IT

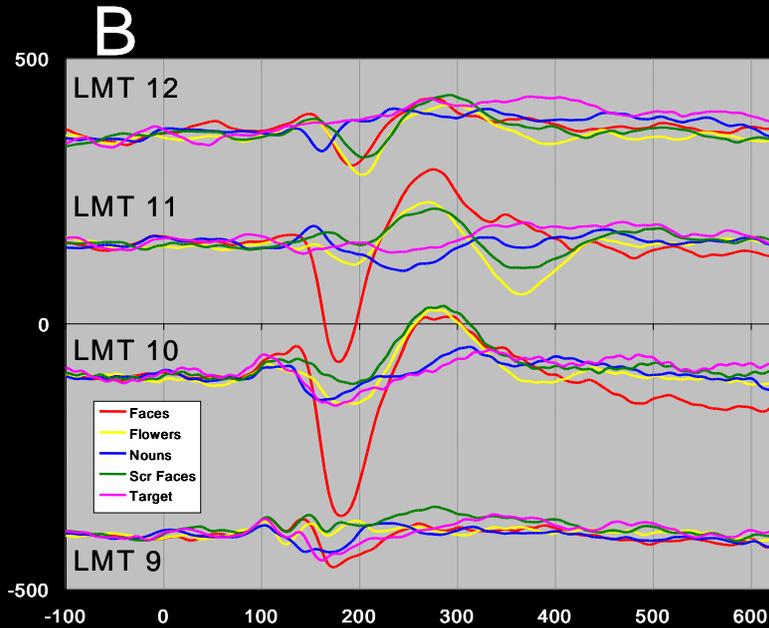
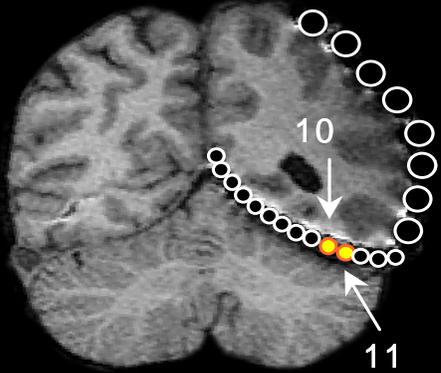
Image removed due to copyright restrictions. Diagram of responses to different faces.

Bruce, Perrett, Desimone, Gross, Tanaka, and many others

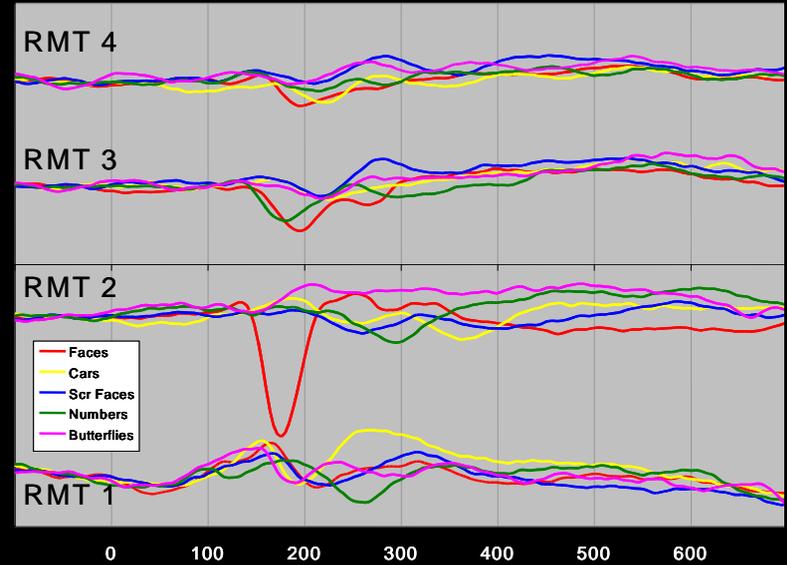
3. Face-Selective electromagnetic responses

a. Subdural ERPs

2 A



C



Courtesy of Gregory McCarthy. Used with permission.

Source: Greg McCarthy

3. Face-Selective electromagnetic responses

b. The MEG “M170”

Image removed due to copyright restrictions.

Modification of Fig. 1b in Liu, J., Harris, A. and Kanwisher, N.

"Stages of processing in face perception: an MEG study." in

Nature Neuroscience 5, no. 9 (2002): 910-916.

<http://web.mit.edu/bcs/nklab/media/pdfs/LiuHarrisKanwisherNN02.pdf>

4. Brain Regions Involved in Face Perception

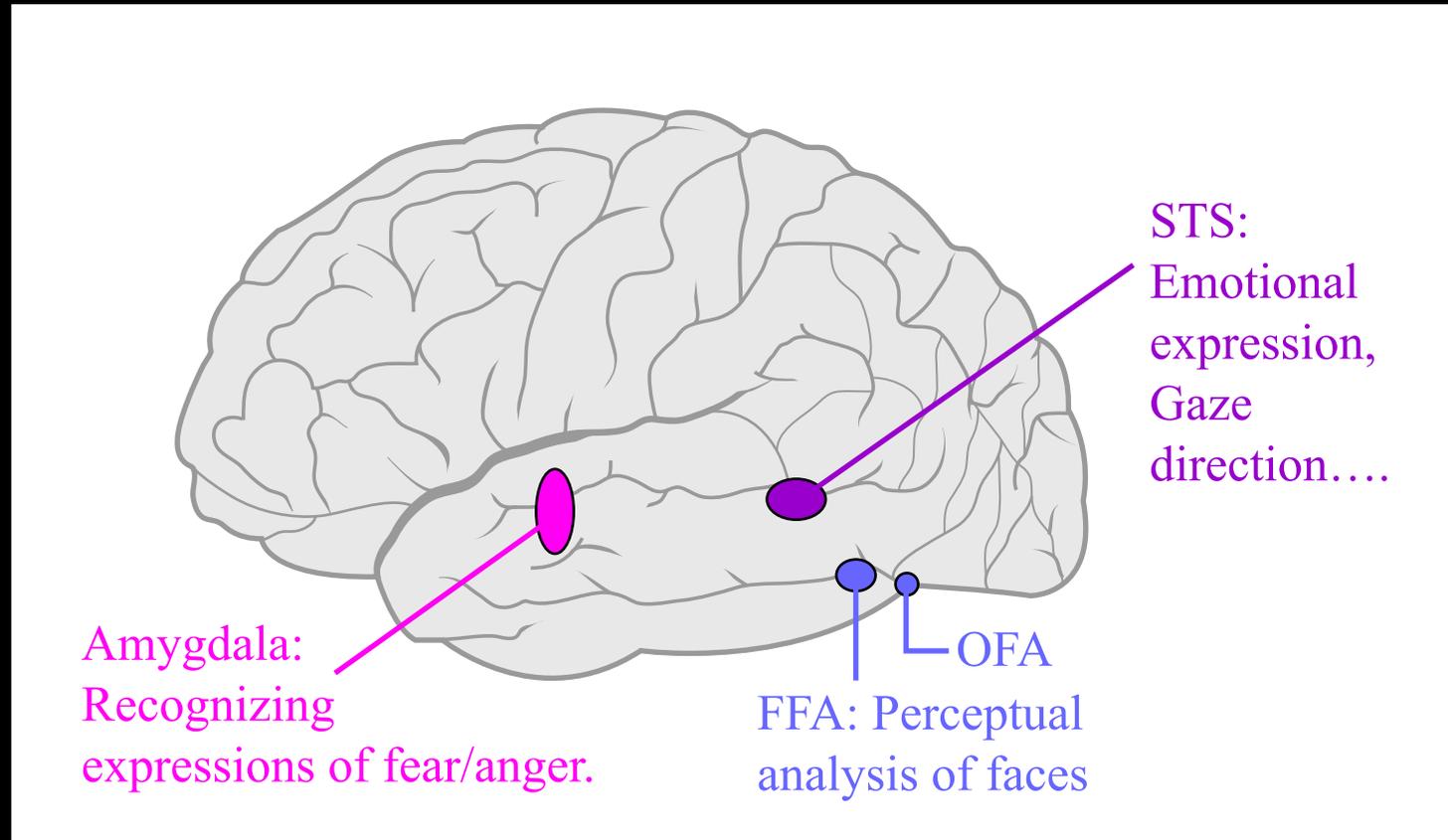


Figure by MIT OpenCourseWare.

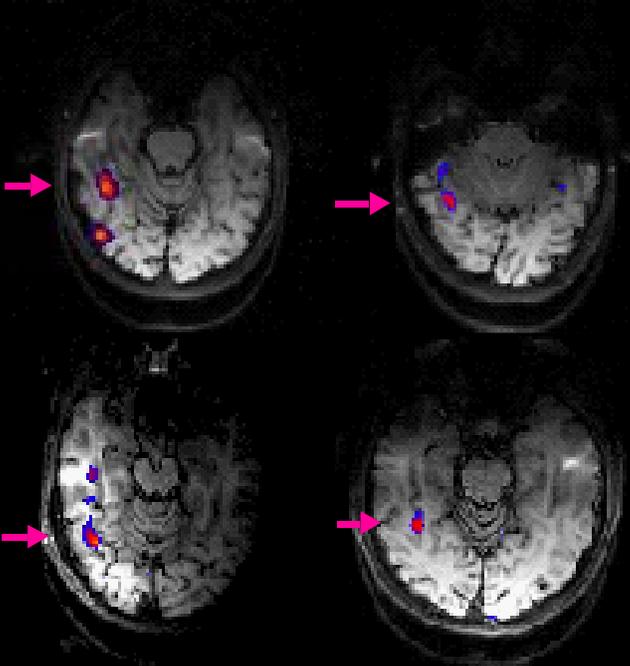
Collateral Sulcus (red) and Fusiform Gyrus (pink)

Image removed due to copyright restrictions. See Jody Culham's slides on Cortical Sulci
p. 6 in http://psychology.uwo.ca/fmri4newbies/Tutorials/9_Louvain_Cortical%20Sulci.ppt

4. Fusiform Face Area

Kanwisher, Tong, McDermott, Chun, Nakayama, Moscovitch, Weinrib, Stanley, Harris, Liu

Face photos modified by OCW for privacy considerations.



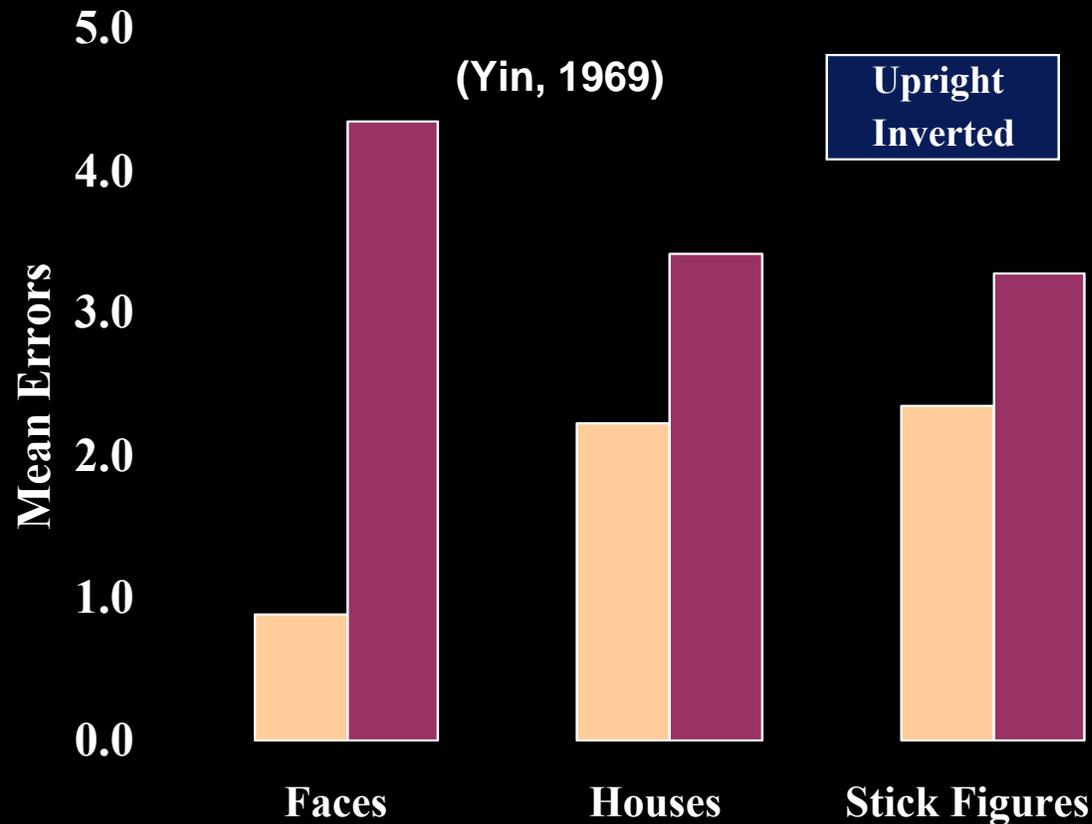
Courtesy of Society for Neuroscience. Used with permission.

Face photos modified by OCW for privacy considerations.

Generality	Front-View	Profile-View	"Mooney"	No Eyes	Cartoon
					Image removed due to copyright restrictions.
	19-2.3	1.8	2.0	1.7	1.7
	Inv. Grey	Cat Face	Human Head	Animal Head	Inv. Cartoon
					Image removed due to copyright restrictions.
	1.6	1.6	1.7	1.3	1.4
	Eyes Only	Inv. Mooney	Whole Animal	Human Body	Schematic
	1.3	1.3	0.9		0.9
	Hand	Buildings	Back of Head	Animal Body	Object
0.7	0.6	1.0	0.8	0.6-1.1	

5. Behavioral Signatures of Face Perception

- A. The “face inversion effect”: a greater decrease in performance for upside-down compared to upright stimuli for faces than other stimuli (Yin, 1969).



5. Behavioral Signatures of Face Perception

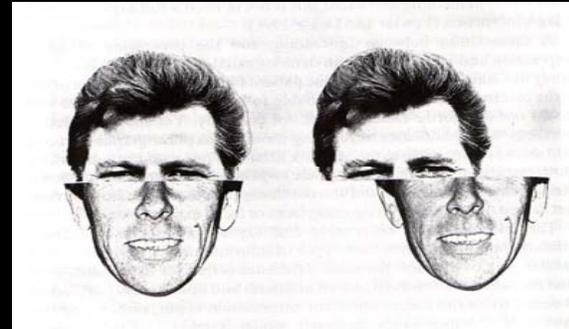
- B. Holistic Processing: Mandatory processing of the whole face, and interactive processing of face parts.

Whole-part effect
(Tanaka and Farah, 1993)

Image removed due to copyright restrictions.

Subjects are better able to discriminate parts in the context of the whole face than when presented alone.

Composite face effect
(Young et al., 1987)



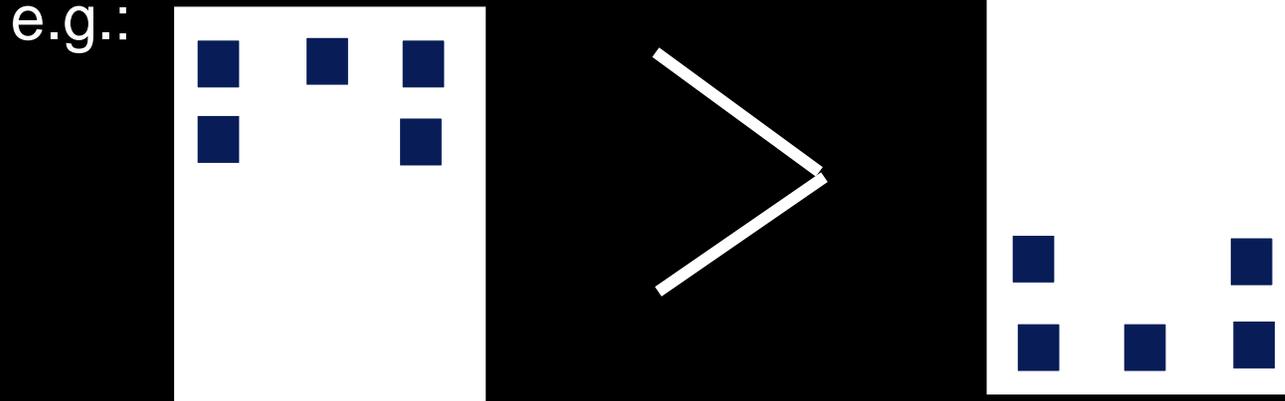
Subjects are slower to identify half the face when it is aligned than misaligned (cannot ignore whole). Courtesy of Andy Young. Used with permission.

Neither effect is found at all for inverted faces!

5. Behavioral Signatures of Face Perception

- C. Newborn Infants Preference for Faces Suggest Innateness.

- Johnson & Morton (1991): look longer at schematic faces than inverted schematic faces. >> may lead to greater experience with faces and hence cortical development of “special” face mechanisms.
- Simion et al (2002): They look more at *any* topheavy stimulus, e.g.:



Simion argues this is therefore not really a *face* mechanism, but in practice it may serve to pick out faces for infants.

So: lesions, neurophysiology, behavior, ERPs, MEG and fMRI
all suggest that special mechanisms may be used in face perception

Probably multiple face-processing mechanisms,
unclear which methods are measuring the same thing
e.g. does the M170 come from the FFA?

Focus for today: the FFA.

Questions about the FFA:

1. Does the FFA process faces only (the “Face Specificity Hypothesis”)?
Or is it also engaged in processing nonface objects:
 - via overlapping “distributed codes” (Haxby)
 - individuation of exemplars within any category
 - individuating exemplars of objects of expertise
 - “configural” processing
 - “holistic” processing

Who Cares?

Localization of Function in the Brain

The brain is not a homogeneous and undifferentiated mush in which all the bits are “equipotential”. Rather, at least some mental functions are physically segregated (to at least some degree) in the brain.

LoF is uncontroversial for primary sensory & motor cortex, but a debate has long raged concerning the degree to which it is also true of high-level cognition....

Domain Specificity of Cognition

Is the mind composed of special mechanisms for specific domains of cognition - e.g. faces, language, number, etc.?

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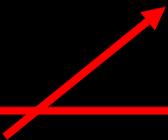
Controversies and Questions about Category-selective Regions of Cortex

Alternative view I: The brain is not organized around content *domains* (e.g., faces or places), but instead around *processes* (e.g. fine-grained discrimination) that can be conducted on any stimulus type.

Alternate view II: faces, places, and objects are represented not by focal regions of cortex, but by distributed patterns of activation spanning centimeters of cortex.

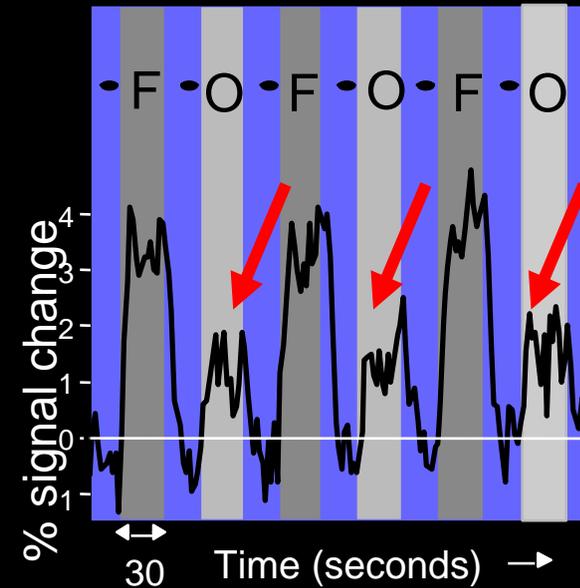
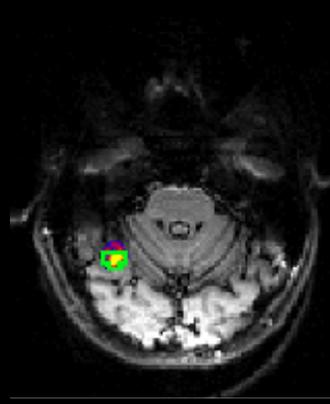
Is face information spread far beyond the FFA?

Does the FFA contain information about nonfaces?



Nonpreferred Responses in the FFA

Faces > Objects



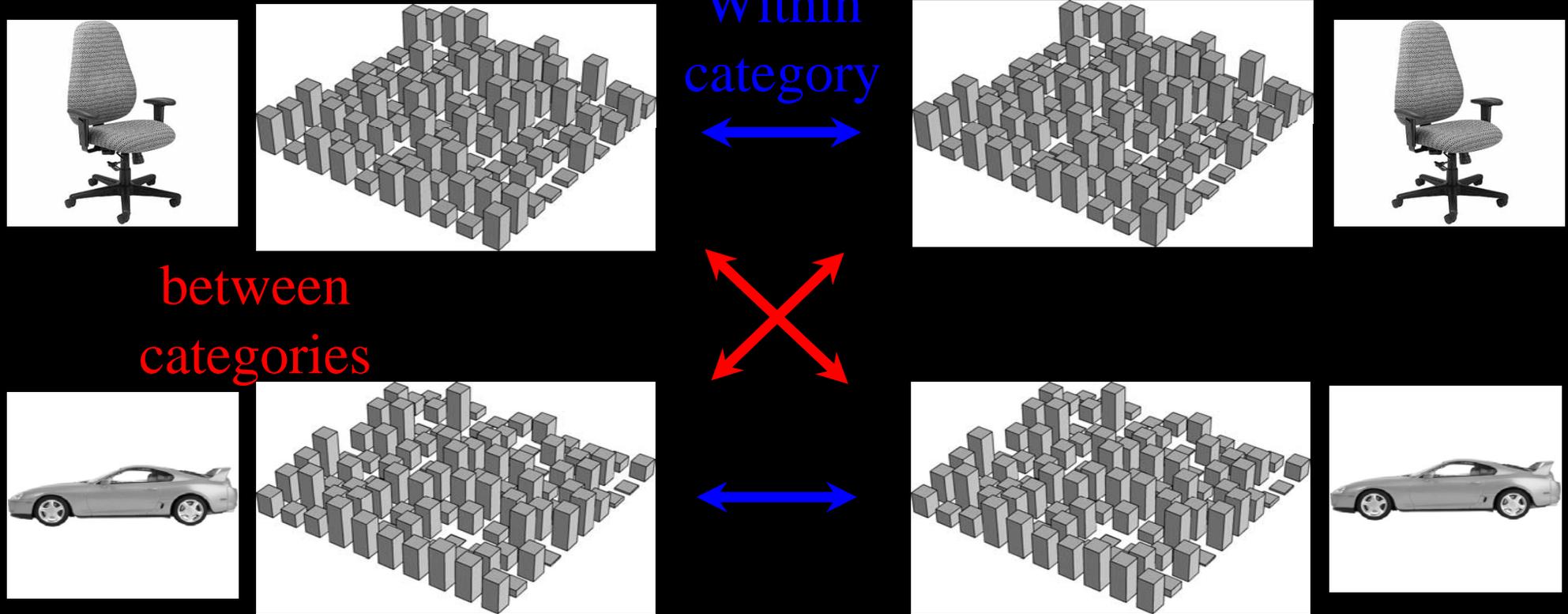
Courtesy of Society for Neuroscience. Used with permission.

- Do “nonpreferred” responses carry information about nonpreferred stimuli?
- A potential challenge to the domain specificity of the FFA.

Using Haxby’s method to ask whether the FFA contains info about nonfaces....

Correlation-based Classification Analysis (Haxby et al., 2001)

1. Scan each subject while they view multiple stimulus categories.
2. Split the data in 1/2; generate activation maps for each category.
3. Compute correlation across activation maps.



between
categories

Within
category

If $r(\text{Within}) > r(\text{Between})$

the region contains category information

*What do we find for
nonfaces in the FFA?*

Does the Pattern of Response Across the FFA contain information that discriminates between nonfaces?

Haxby et al (2001): yes

*“Regions such as the ‘FFA’ are **not dedicated to representing only** human faces,.. but, rather, are part of a more extended representation for all objects.”*

Spiridon & Kanwisher (2002): no

Tsao et al (2003), in face patches in monkey brains: no

O’Toole, Haxby et al. (2005): no (sort of):

*“preferred regions for faces and houses **are not well suited to object classifications** that do not involve faces and houses, respectively.”*

Reddy & Kanwisher (submitted): yes (sort of).

BUT: maybe these tests are unfair, in two ways:

- i) Spatial resolution limits of fMRI necessarily entail some influence of neural populations outside the region in question.
- ii) The presence of discriminative information does not mean it plays an important role in perception!

The Ultimate High Resolution: Single-Unit Neurophysiology

Tsao et al (2003, *NN*) fMRI in monkeys:

Image removed due to copyright restrictions.

Diagram of macaque brain surface, highlighting middle face patch and body response regions.

In Kanwisher, N. "What's in a Face?" *Science* 311 no. 5761 (2006): 617-618.

<http://web.mit.edu/bcs/nklab/media/pdfs/Kanwisher.science2006.perspec.pdf>

Response of all 320 visually-responsive neurons in the faces patches of two monkeys to 96 different stimuli

Image removed due to copyright restrictions.

Fig.2B in Tsao, Doris. “A Cortical Region Consisting Entirely of Face-Selective Cells.”
Science 311 no. 5761 (2006): 670-674.
doi:10.1126/science.1119983.

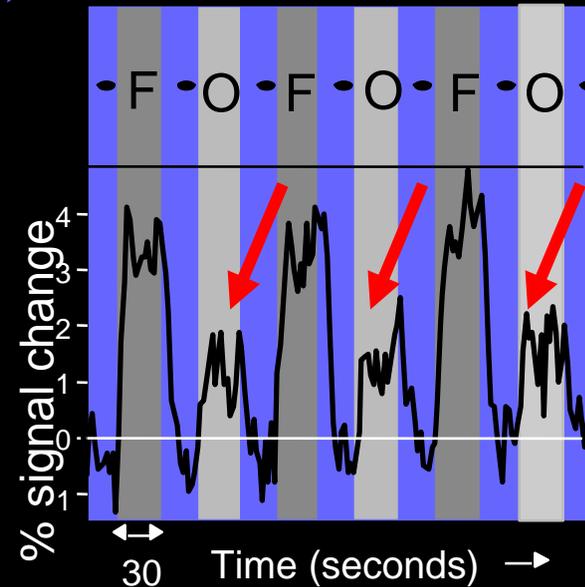
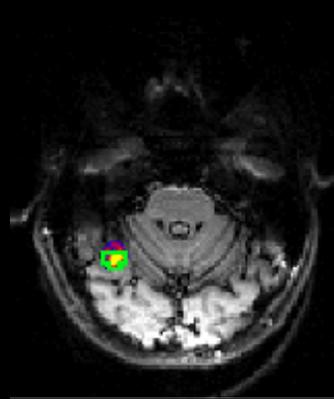
The cells in this patch respond selectively, indeed virtually exclusively to faces.

Tsao et al (2006), *Science*

A Basic fMRI Experiment

Kanwisher et al (1997)

Faces > Objects



Courtesy of Society for Neuroscience. Used with permission.

- Selectivity looks *pretty* strong, but....
- Recall that we typically have hundreds of thousands of neurons per voxel.
- **How strong is selectivity at the level of single units?**

VERY! (at least in macaques)

Not much room for “overlapping codes”

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Correlating fMRI signals with behavioral outcomes

Grill-Spector, Knouf, & Kanwisher (2004)

Overall Strategy:

Have Ss perform perceptual task in scanner;

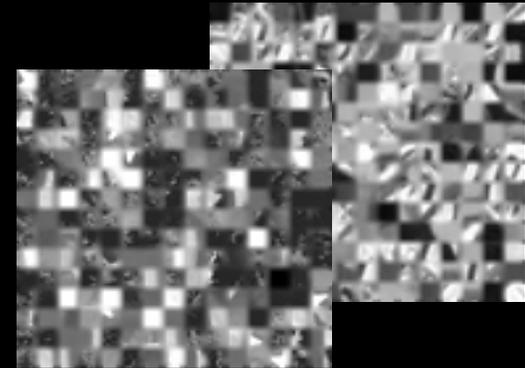
Make task difficult so subjects make some mistakes;

bin fMRI data by behavioral response;

Look for correlations btwn behavioral responses and fMRI signal.

Task: is this

- i) Harrison Ford**
- ii) some other guy**
- iii) nothing**



4000ms



2000 ms



0

image exposure
33ms or 50ms:
Near threshold

Face photos modified by OCW
for privacy considerations.

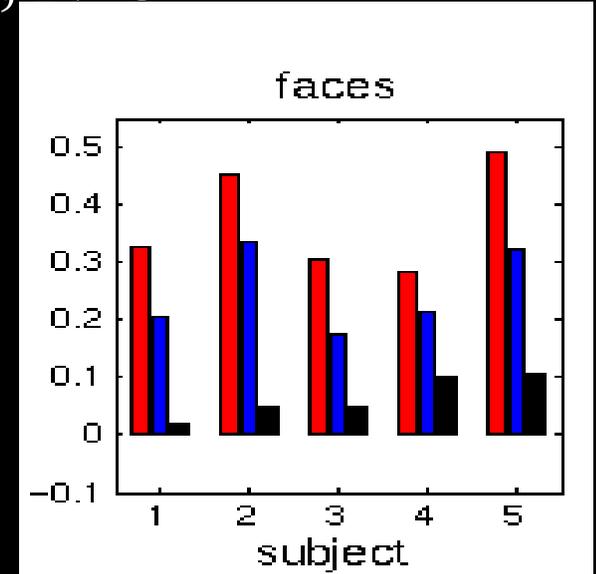
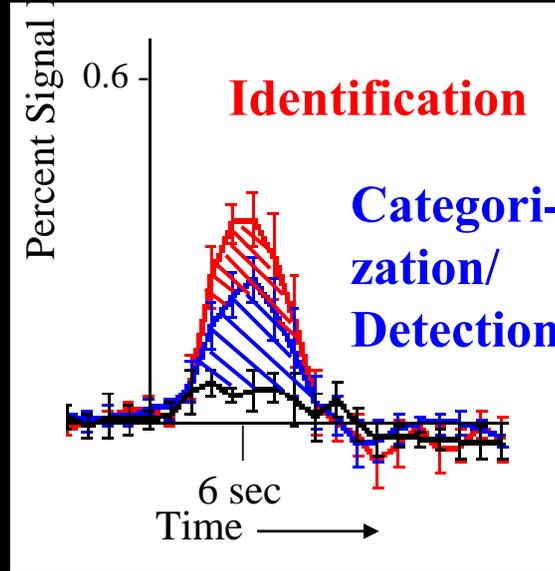
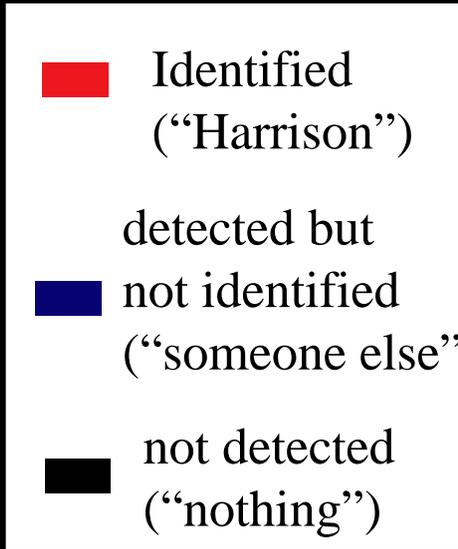
Stimulus images not repeated

Grill-Spector, Knouf, & Kanwisher (2004)

Courtesy of K. Grill-Spector. Used with permission.

Figures from: Grill Spector K, N. Knouf, and N. Kanwisher. "The Fusiform Face Area Subserves Face Perception, not Generic Within-Category Identification." *Nat Neurosci* 7, no. 5 (May 2004): 555-62.

Right FFA Response to Target Faces (e.g., Harrison) As a Function of Performance, N=5



**FFA Involved in:
Detect & Ident of faces**

**What about other
kinds of objects?**

Courtesy of K. Grill-Spector. Used with permission.

Figures from: Grill Spector K, N. Knouf, and N. Kanwisher. "The Fusiform Face Area Subserves Face Perception, not Generic Within-Category Identification." *Nat Neurosci* 7, no. 5 (May 2004): 555-62.

Task: is this

- i) electric guitar**
- ii) other guitar**
- iii) nothing**

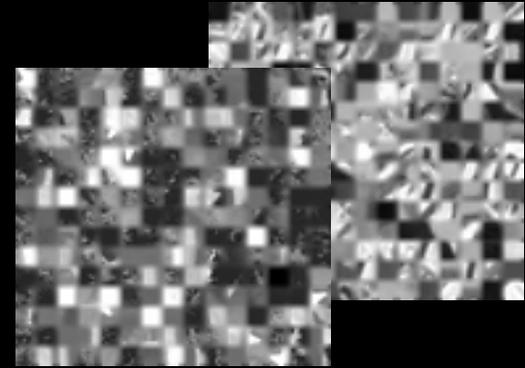


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33ms or 50ms



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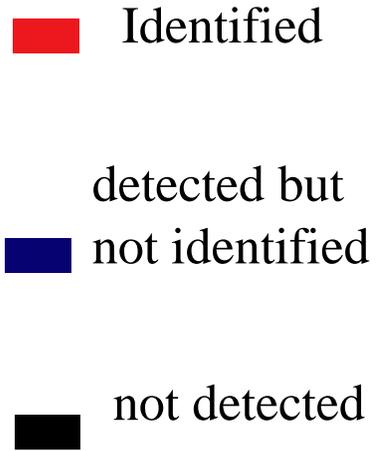
Courtesy of K. Grill-Spector. Used with permission.

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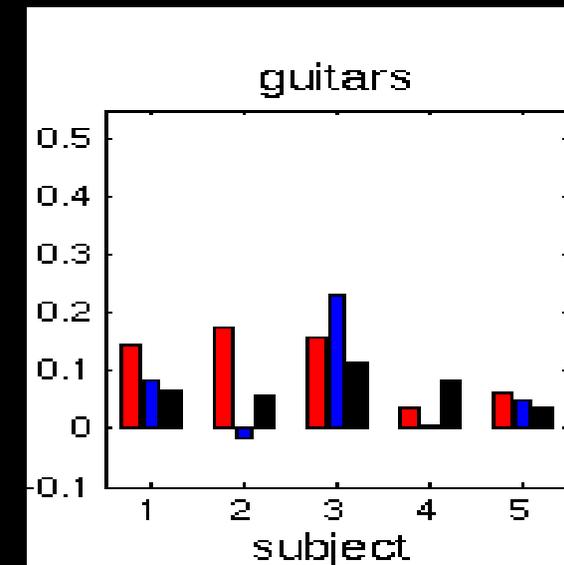
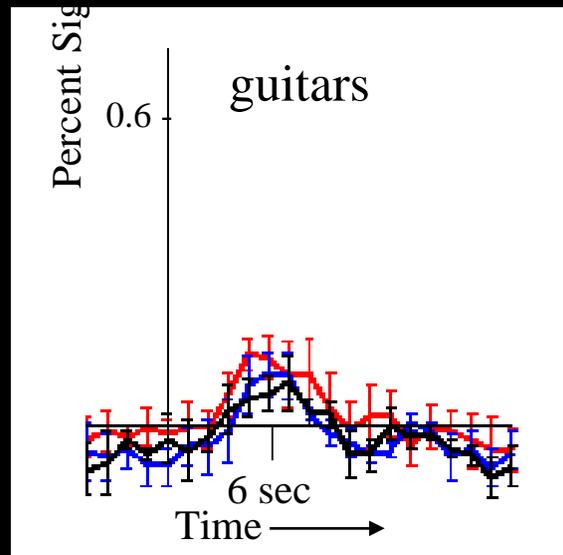
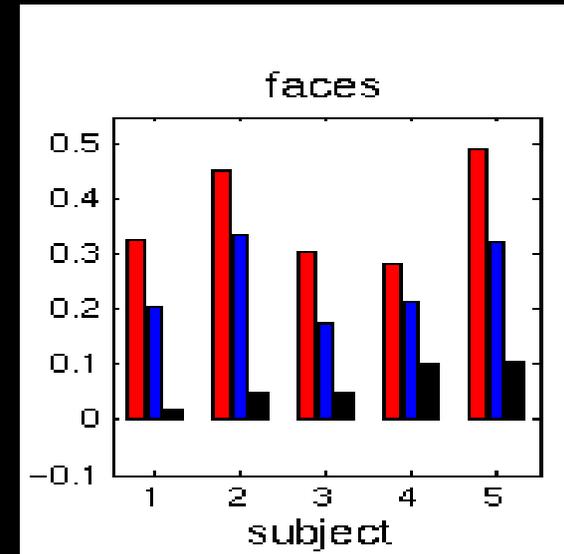
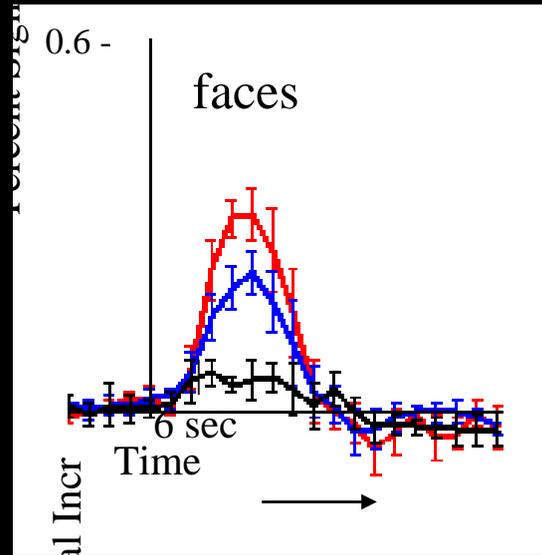
Stimulus images not repeated

Grill-Spector, Knouf, & Kanwisher (2004)

Right FFA Response to Target Faces or Guitars As a Function of Performance, N=5



FFA involved in:
Detec & Ident of faces
Neither detect nor ident
Of guitars



Courtesy of K. Grill-Spector. Used with permission.

Figures from: Grill-Spector K, N. Knouf, and N. Kanwisher.
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Expertise Hypothesis

(Gauthier & Tarr; Carey & Diamond)

Face-selective neural mechanisms are not specialized for processing faces per se, but rather for processing any class of visual stimuli

- i) for which the subject has gained substantial visual expertise and*
- ii) upon which the subject is making fine-grained “subordinate-level” discriminations between exemplars that share the same basic configuration.*

Lots of evidence **against** this idea - e.g.:

Double dissociation betwn face recognition and expertise on nonfaces.

Strongest evidence **for** it: Gauthier et al, (2000) & Xu (2005)

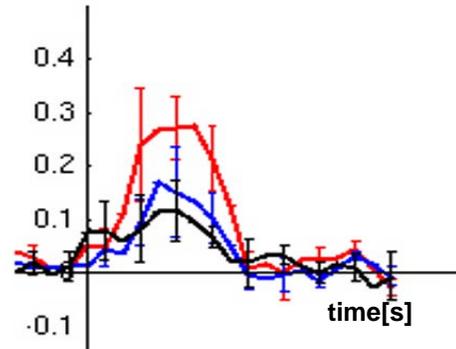
Ravi will present Gauthier et al (2000)

BUT....

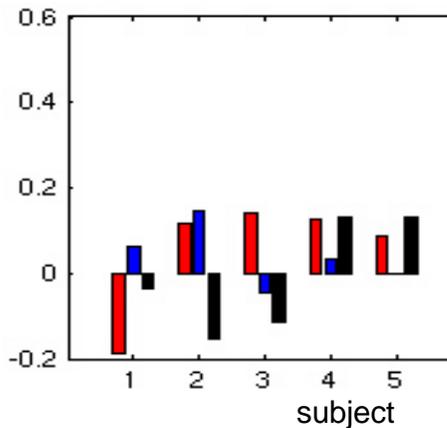
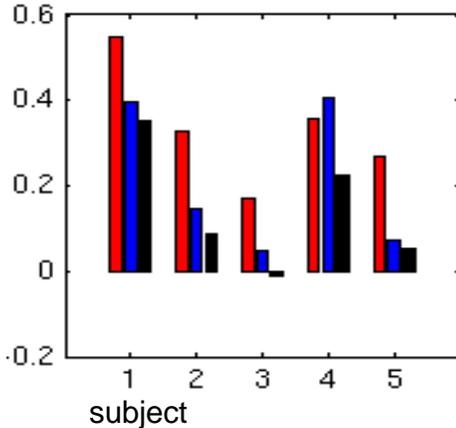
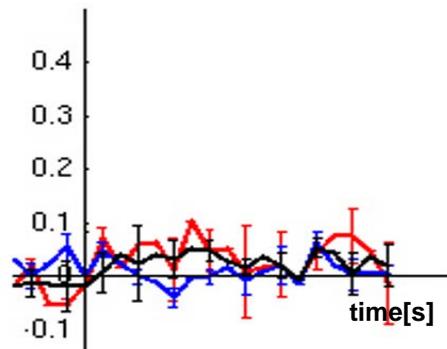
FFA Response in 5 Car Experts

% signal

(a) Faces



(b) Cars



■ identification hit
■ detection hit

■ detection miss

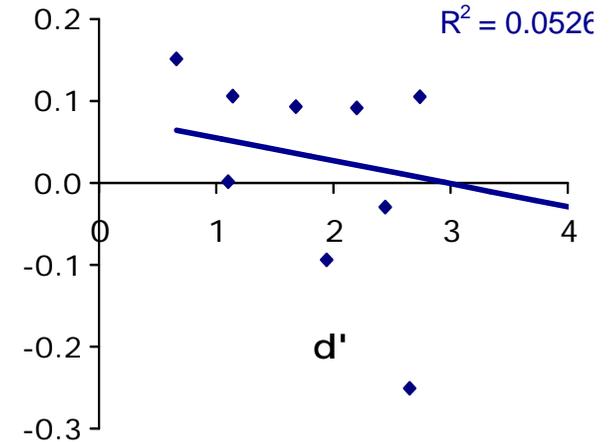
No evidence that FFA response is correlated trial-by-trial with successful identification of objects of expertise.

Courtesy of K. Grill-Spector. Used with permission.

Figures from Grill-Spector K, N. Knouf, and N. Kanwisher. "The Fusiform Face Area Subserves Face Perception, not Generic Within-Category Identification."

Nat Neurosci 7, no. 5 (May 2004): 555-62.

(c) FFA response for cars as a function of expertise



No evidence that FFA response during car identification is correlated across subjects with car expertise.

So: FFA apparently involved in detection and identification of faces but not detection or identification of other objects, including objects of expertise.

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Yovel & Kanwisher (2004)

1. Does the FFA primarily process information about face configurations (rather than face parts)?

2. Is the FFA truly face-specific, or can it be engaged on nonface stimuli if we force subjects to process those stimuli like faces?

Suppose we get subjects to process a nonface stimulus *in the same way they process a face*, then will the FFA become engaged?

Part versus Configuration Discrimination Tasks



Face part

Face Configuration

On Faces

Courtesy Elsevier, Inc., <http://www.sciencedirect.com>. Used with permission.



House part

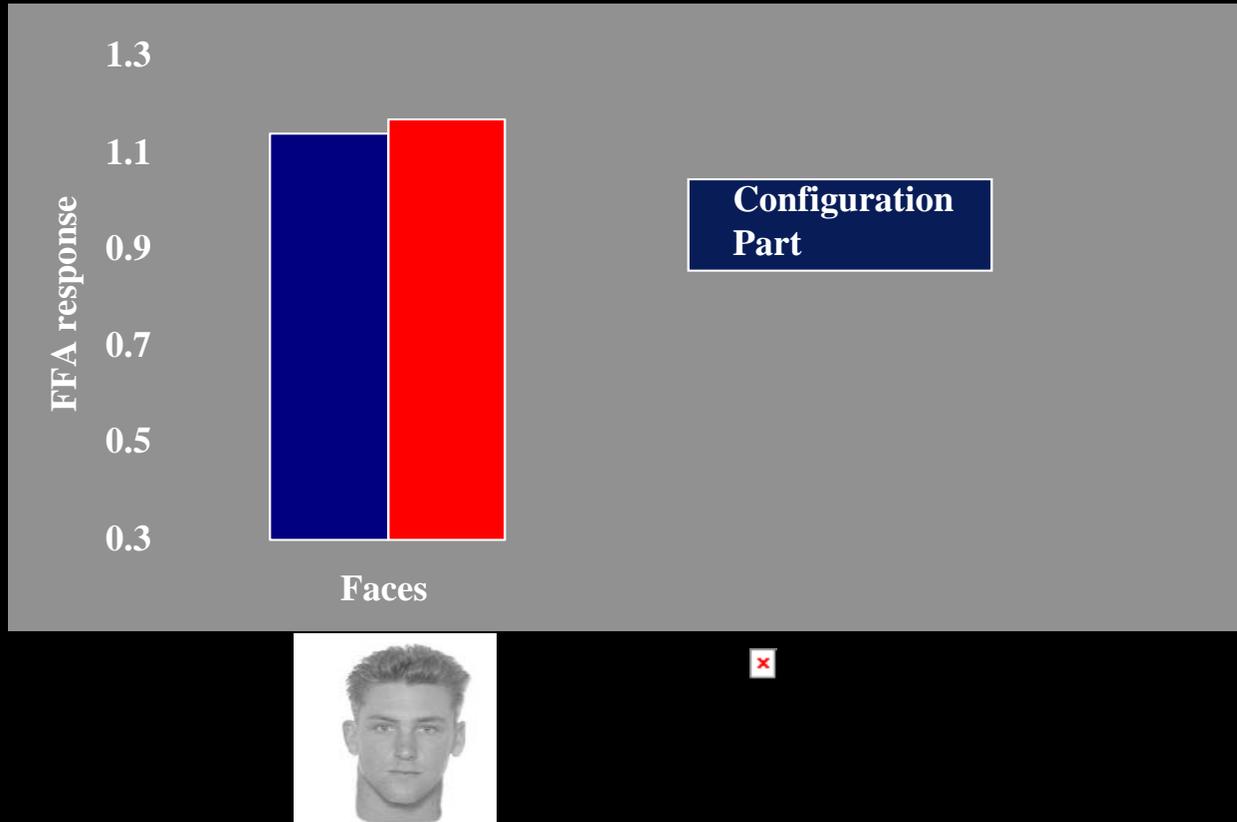
House Configuration

On Houses



rFFA Response

Yovel & Kanwisher (2004), *Neuron*



Courtesy Elsevier, Inc., <http://www.sciencedirect.com>. Used with permission.

- FFA is equally engaged in part and config. discriminations on faces.

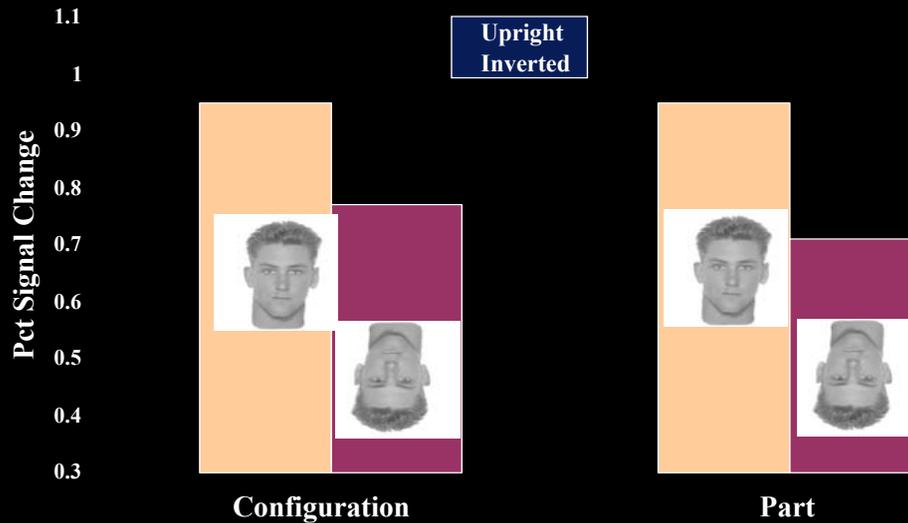
- FFA is NOT strongly engaged when subjects do very similar discriminations on nonface stimuli.

- FFA is stimulus-specific, not process-specific.

Is this a case of shallow *neural* domain specificity without a corresponding *functional* domain specificity? Test with...

Face inversion effects

rFFA
response

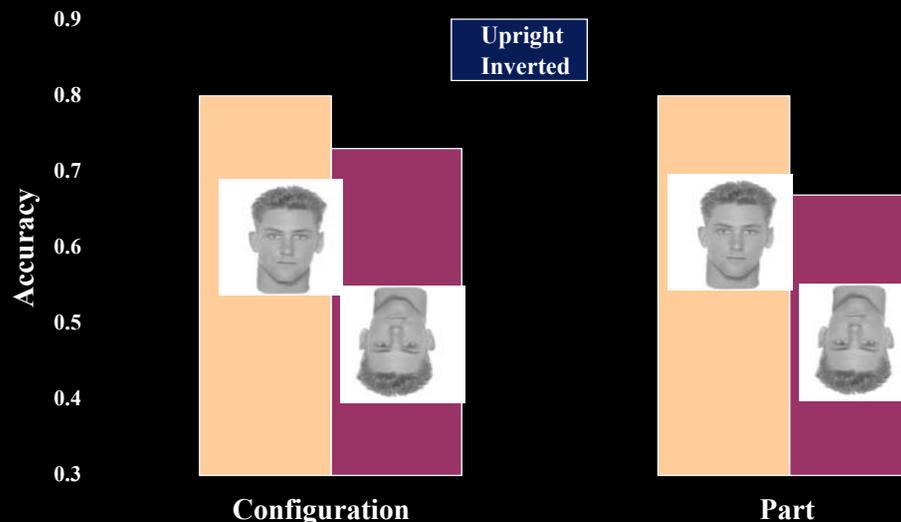


- fMRI inversion effects for faces (both tasks), mirroring behavioral data.

Are these inversion effects linked?

Courtesy Elsevier, Inc., <http://www.sciencedirect.com>. Used with permission.

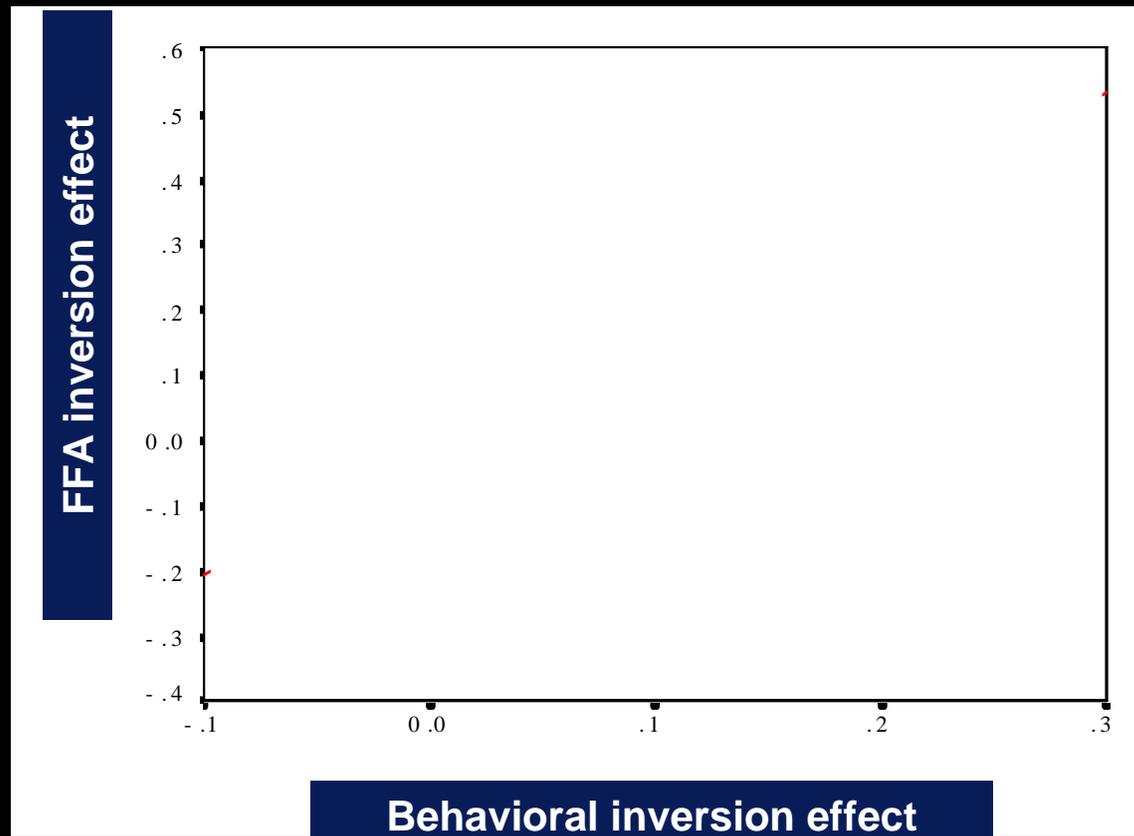
Behavioral
performance
in the scanner



- Behavioral inversion effects found for faces (both tasks), not for houses.

Yovel & Kanwisher (2004), *Neuron*

If behavioral inversion effects originate in the FFA, we should find a correlation across subjects between fMRI inversion effects and behavioral inversion effects.



Courtesy Elsevier, Inc., <http://www.sciencedirect.com>. Used with permission.

This correlation implicates FFA in the face inversion effect.

Yovel & Kanwisher (2004), *Neuron*

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- X • individuation of exemplars within any category
- X • individuating exemplars of objects of expertise
- X • “configural” processing
 - “holistic” processing

2. What does the FFA do with faces?

- ✓ • face detection?
- ✓ • Identification?
- ✓ • processing face parts?
- ✓ • face configurations?
- does it reflect psychological (versus physical) similarity btwn faces?
- Gaze discrimination? Expression?

Peter will present a paper on this....

Questions about the FFA:

1. Is the FFA “domain-specific” for faces (“Face Specificity Hypothesis”)?

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Identity, Expression, & Gaze in the FFA and STS

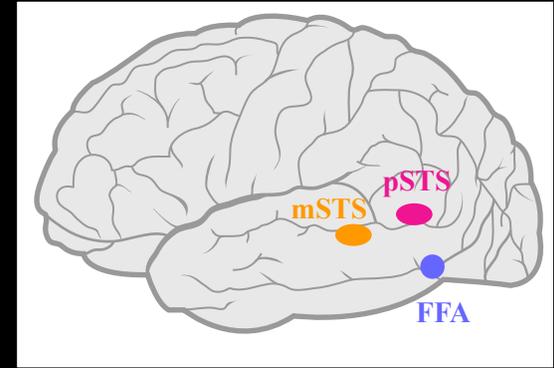


Figure by MIT OpenCourseWare.

Hoffman & Haxby (2000):

manipulated selective attention to gaze vs identity on same stimuli

- FFA: identity > gaze
- STS (prob pSTS): gaze > identity (weakly)

Winston et al (2004): used event-related fMRI adaptation

- FFA: identity, not expression
- pSTS: identity and expression
- mSTS: expression, not identity

		Expression of second face			
		Same		Different	
Identity of second face	Same	 1	$S_1 S_c$ 2	 1	$S_1 D_c$ 2
	Different	 1	$D_1 S_c$ 2	 1	$D_1 D_c$ 2

Courtesy of the American Physiological Association. Used with permission.
Source: Winston, J. S. et al. *J Neurophysiol* 92 (2004): 1830-1839. doi:10.1152/jn.00155.2004.

Developing consensus:

- “STS” codes changeable properties of face (expression & gaze)
- FFA codes face identity.

Questions about the FFA:

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Or is it engaged in “domain-general” processing :

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- X (?) • Gaze discrimination? Expression?

Important Open Questions

- What is the nature of the representations in the FFA?
invariances to viewpoint, expression, etc?
(how) do they differ from representations of objects?
- How are these representations extracted?
- Does FFA hold any information about nonfaces? Is this information *used*?
- Division of labor between FFA and other areas?
Connections and interactions between these areas?
- Where and how are face percepts matched to memories (recognition)?
- How do FFAs arise in development?
Why in same place?
Why cant this area “move over” in prosopagnosia?
Why do we have FFA and not FCA (fusiform chair area)?

Question 2: Is the FFA *necessary* for face recognition??

Maybe!

*Barton, Press,
Keenan, & O'Connor*

**Tested four patients with
lesions in the region of the
Fusiform face area.**

**All were severely
impaired in discriminating
Faces that differed in terms
of changes in the spatial
positions of features.**

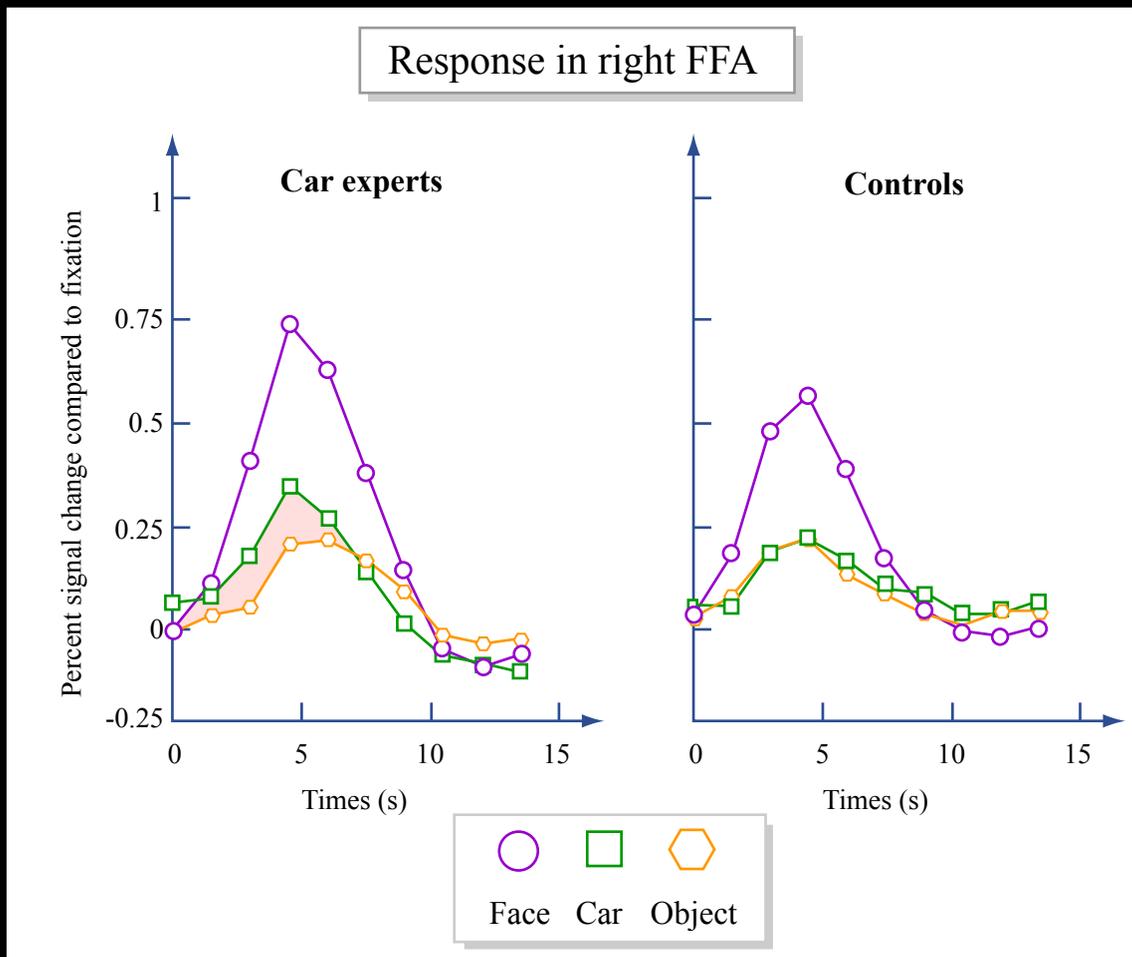


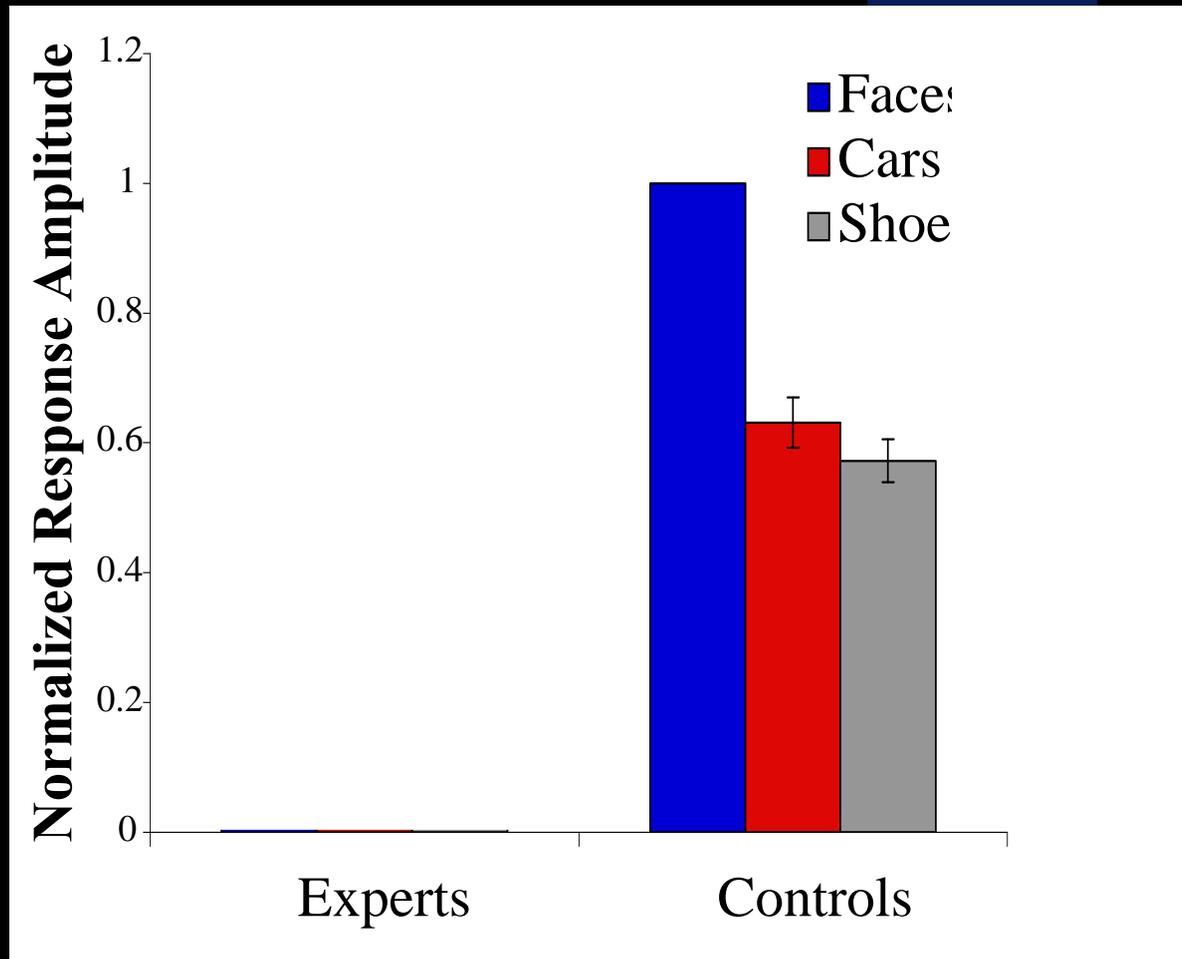
Figure by MIT OpenCourseWare.

- Why this small response to cars in car experts, if it isn't correlated with car identification?
- Attentional modulation, rather than perceptual identification of cars?

If this region is truly engaged in perceptual identification of cars (rather than simply getting modulated by attention), we should see expertise effects at early latencies when perceptual identification occurs, i.e. the M170.

Test: Is M170 response higher to cars than control objects in car experts?

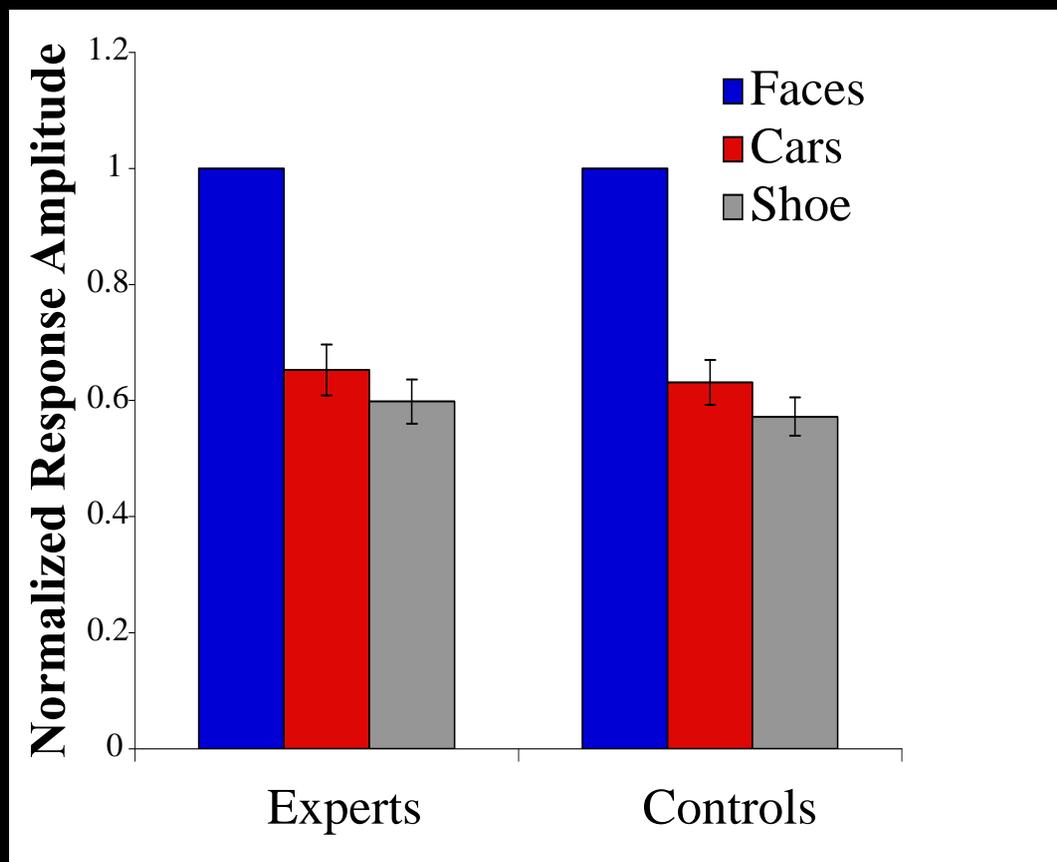
Sensor of Interest Approach: Find face-selective sensors in each subject, then measure the magnitude of response in these sensors while subjects view cars, faces, and objects.



Courtesy Elsevier, Inc.,
<http://www.sciencedirect.com>.

Used with permission.

Source: Xu Y., Liu, J., and Kanwisher, N. (2005) "The M170 is selective for faces, not for expertise." *Neuropsychologia* 43: 588-97



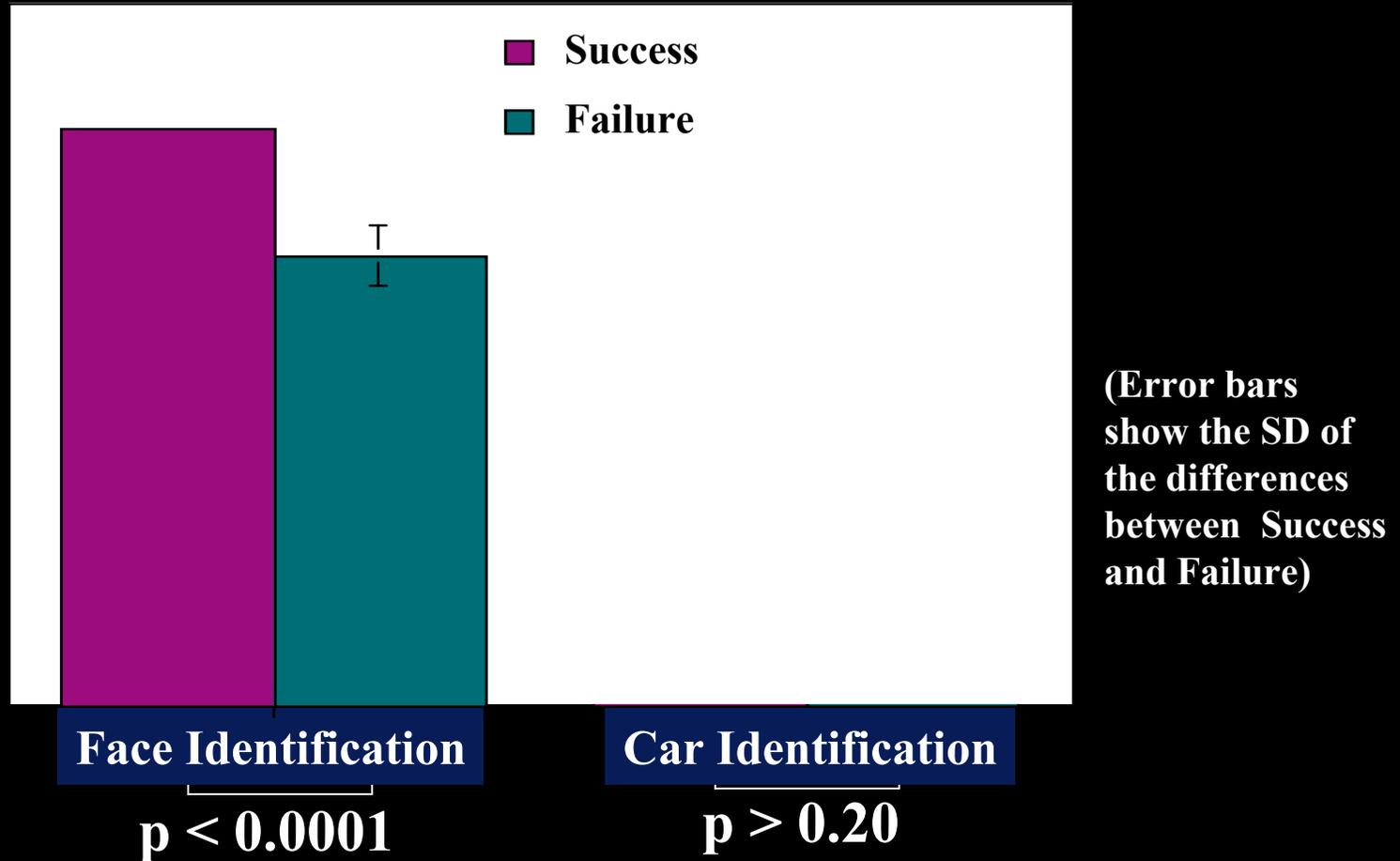
Courtesy Elsevier, Inc.,
<http://www.sciencedirect.com>.
Used with permission.
Source: Xu Y., Liu, J., and Kanwisher, N.
(2005) "The M170 is selective for faces, not
for expertise." *Neuropsychologia* 43: 588-97

No expertise effect on the M170. (And no interaction).

This mechanism is selective for identification of faces, not any expert category.

Is M170 correlated trial-by-trial with car identification in car experts?

Face Selective M 170 Amplitude in Car Experts



Significant interaction of faces versus cars and identification success ($p < 0.02$).

M170 does not show expertise effect. Suggests the small FFA expertise effect in some studies may reflect attentional modulation and/or postidentification processing.

General Questions Addressed Today

What does the FFA do with faces?

- ✓ ✓ • process individual face parts (eyes, nose, mouth)?
- ✓ ✓ • extract the configuration of the face (relative position of parts)?
- ✓ • face *detection*?
- ✓ • face *identification*?

Specificity: Does the FFA process faces only? Or is it also engaged in:

- X • configural processing of any stimulus type
- X X • individuation of any stimulus for which the subject is expert
- “holistic” processing of any stimulus type

Strongest car expert shows no correlation with success at car identification in rFFA

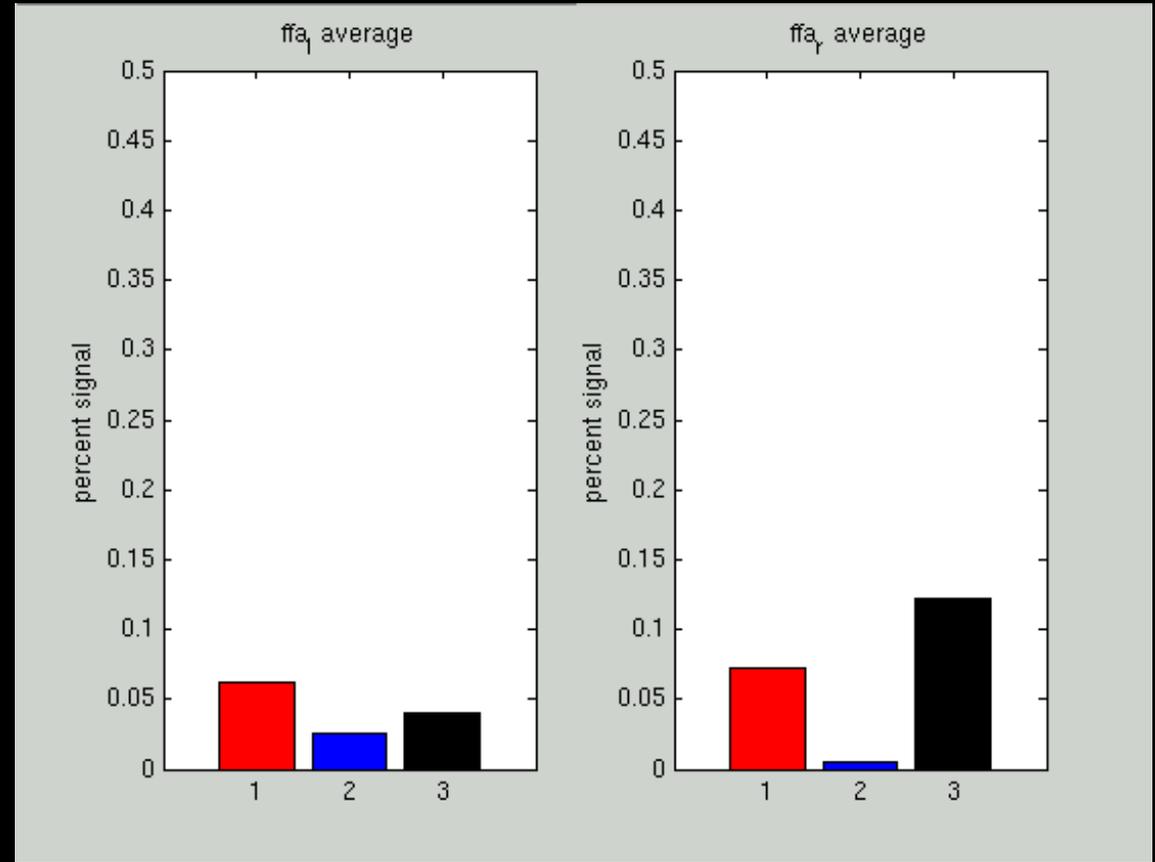
red= correct identification

blue= detection w/out identification

black = not detected

Left = lFFA

Right = rFFA



Is the FFA really Specialized for Face Perception?

Some Hypotheses concerning FFA function:

- perception of bodies (e.g., Peelen & Downing, 2005)?
- within-cat. discrim. of objects of expertise (Gauthier, Tarr)
- within-cat. discrim. of other categories (e.g., chairs)
- face recognition (discriminating one individual from another)

Partial voluming of two adjacent selectivities?

Let's try scanning at higher resolution

8 channel coil

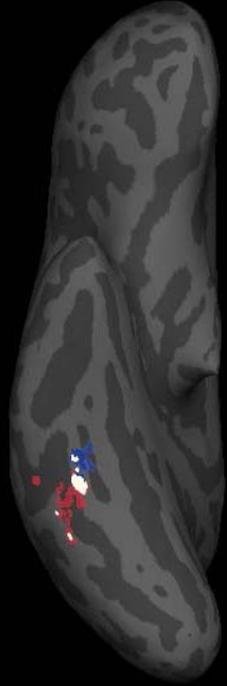
1.4x1.4x2mm voxels

Graph removed due to copyright restrictions.
See Fig. 4 (left) in Spiridon, M., B. Fischl,
and N. Kanwisher. "Location and Spatial
Profile of Category-Specific Regions in Human
Extrastriate Cortex." *Human Brain Mapping* 27
(2006): 77-89.

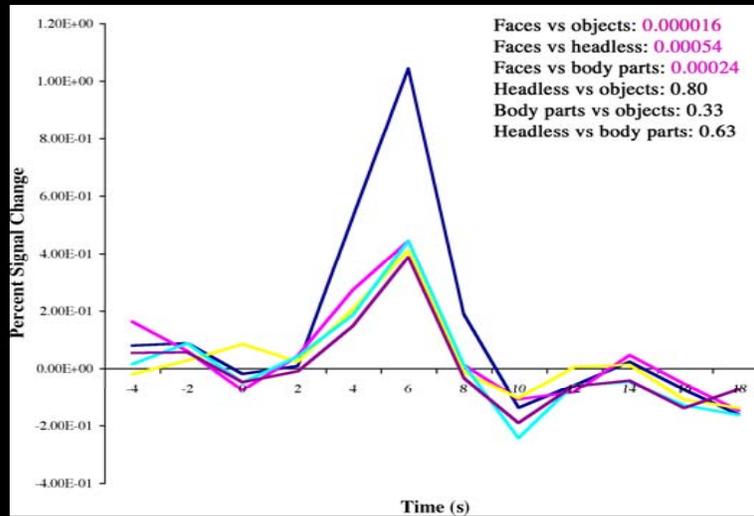
Spiridon, Fischl, & Kanwisher (in press), HBM.

Fusiform Responses to Faces & Bodies

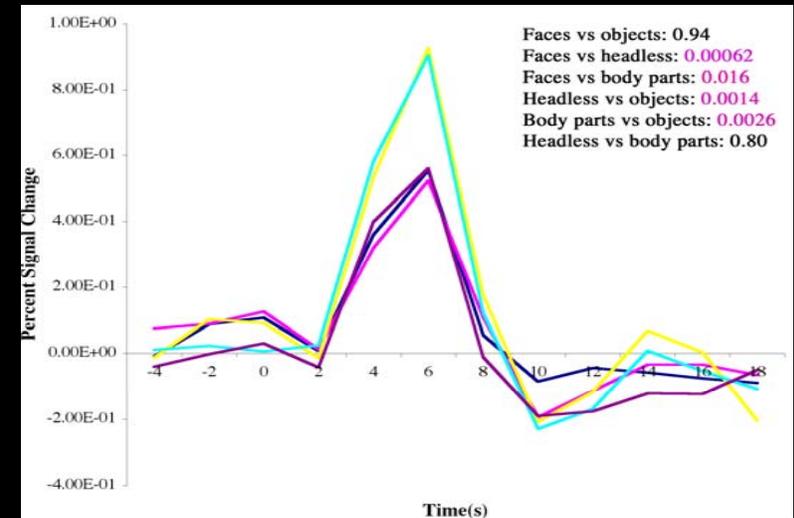
See Schwarzlose, Moore and Kanwisher
J Neurosci 25 no. 47 (2005): 11055–11059.



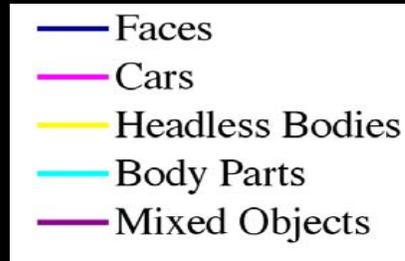
Face-Only Region N=9



Body-Only Region N=9



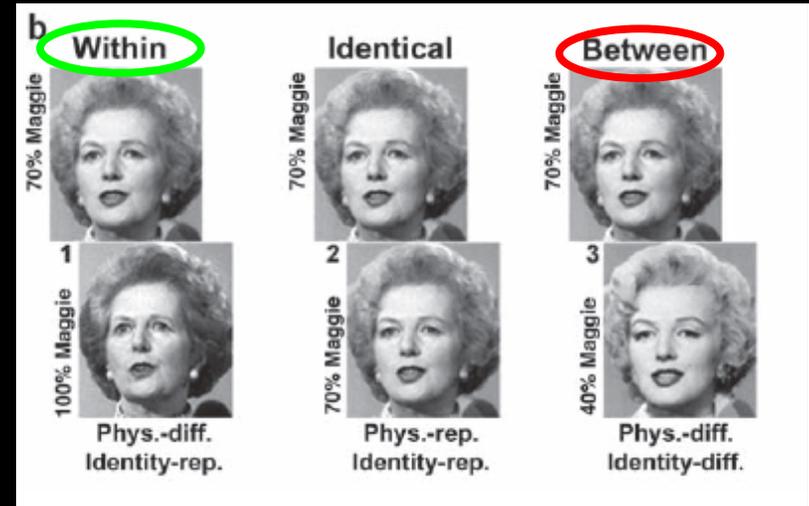
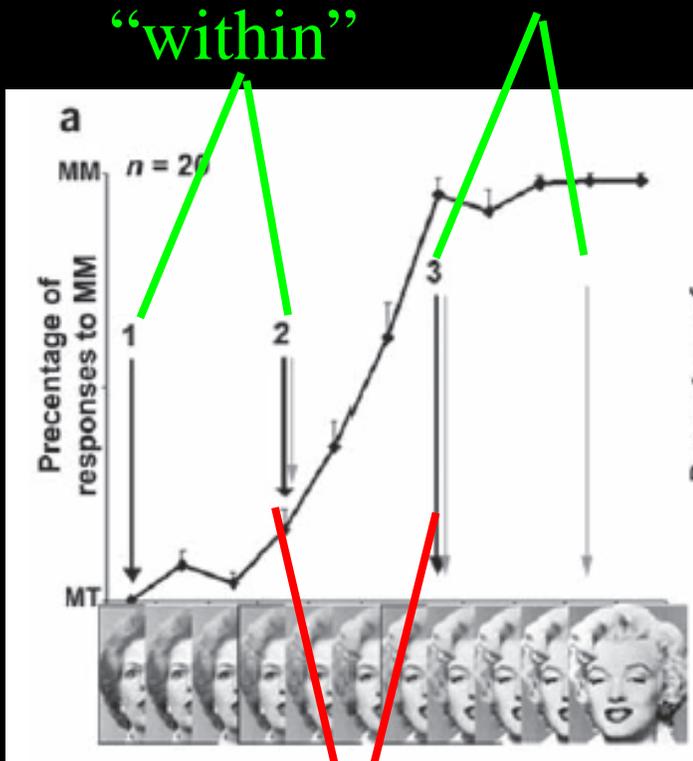
faces > objects
bodies > objects
overlap



At high resolution, face selectivity
can be dissociated from body
selectivity in the fusiform.

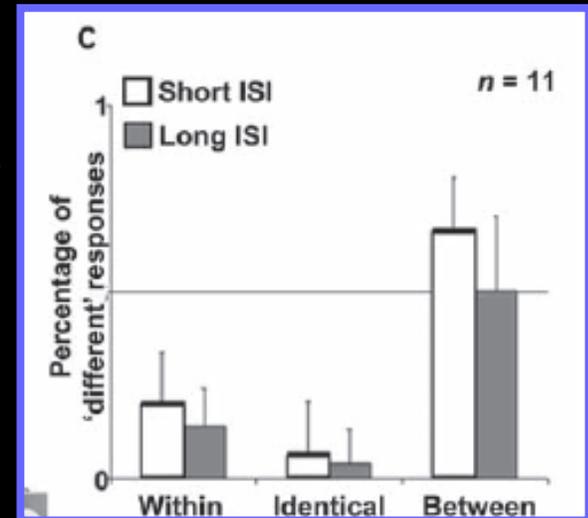
Categorical Perception of Faces

Rotshtein et al (2004)



Courtesy of Pia Rotshtein. Used with permission.

CP: Do subjects detect differences better when they straddle a category boundary than when they do not?



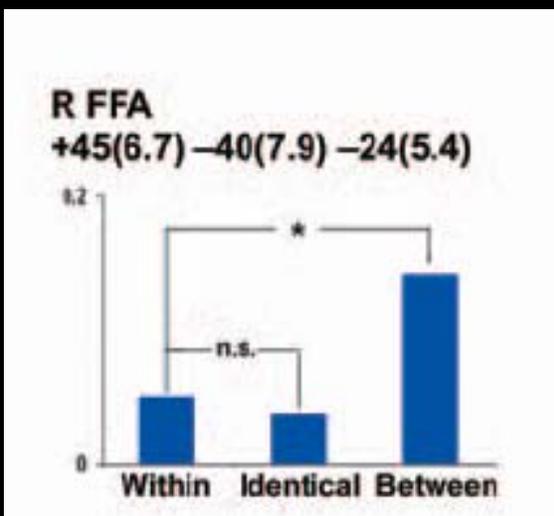
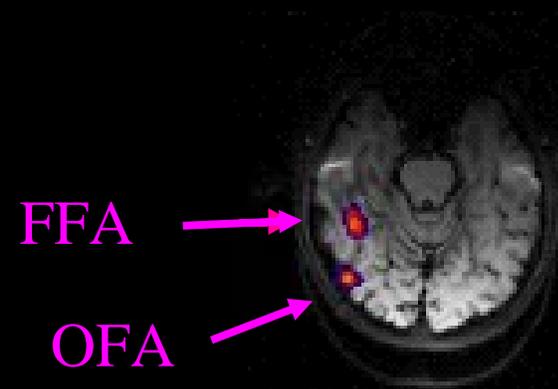
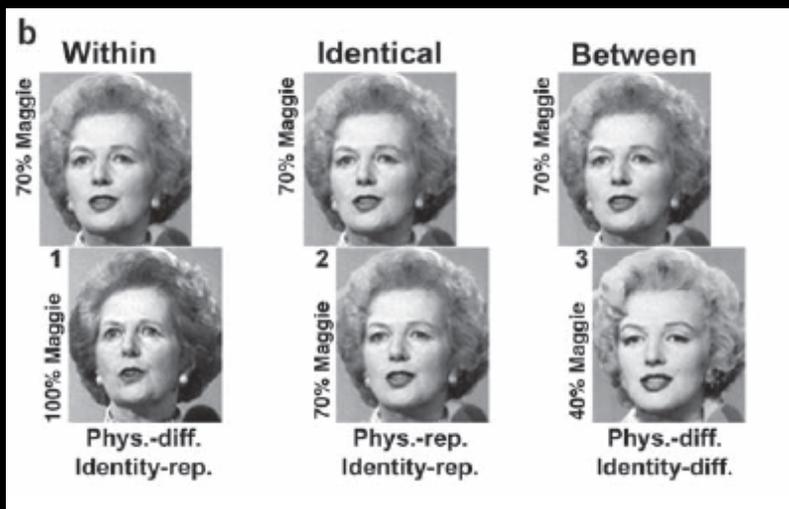
Does FFA represent physical or psychological distance?

Yes!

Categorical Perception of Faces

Rotshtein et al (2004)

fMRI:
Event-related
adaptation
experiment.



FFA represents perceived
(categorical) differences
between faces.

OFA represents physical
differences btwn faces.

Using fMRI-adaptation to ask
what stimulus differences the FFA is sensitive to.
Yovel & Kanwisher, submitted

DIFFERENT



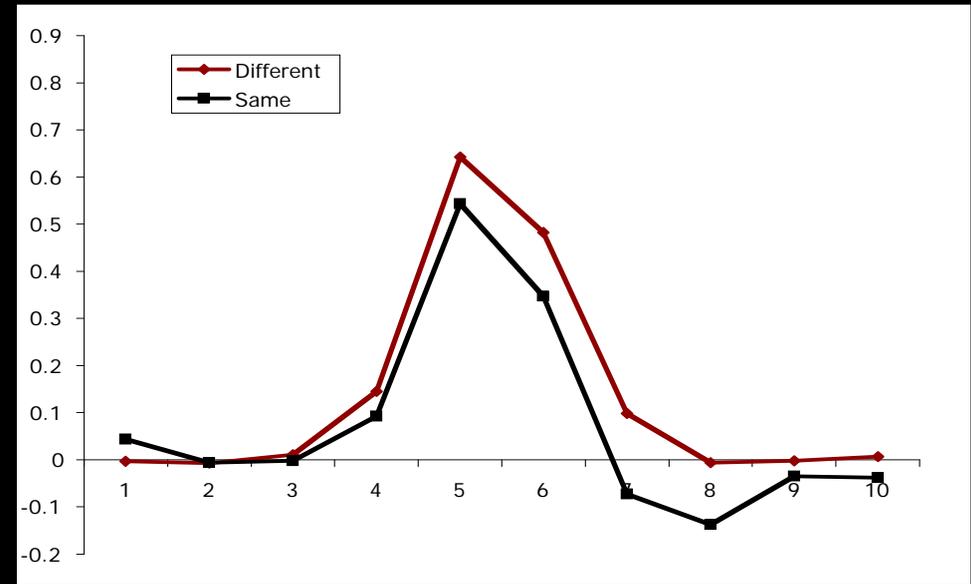
250ms 500ms 250ms

SAME



Counterbalanced across stimuli;
Displaced slightly; matching task.

FFA Response



So: FFA can discriminate btwn faces.

Is this specific to faces?? What about...

DIFFERENT



200ms

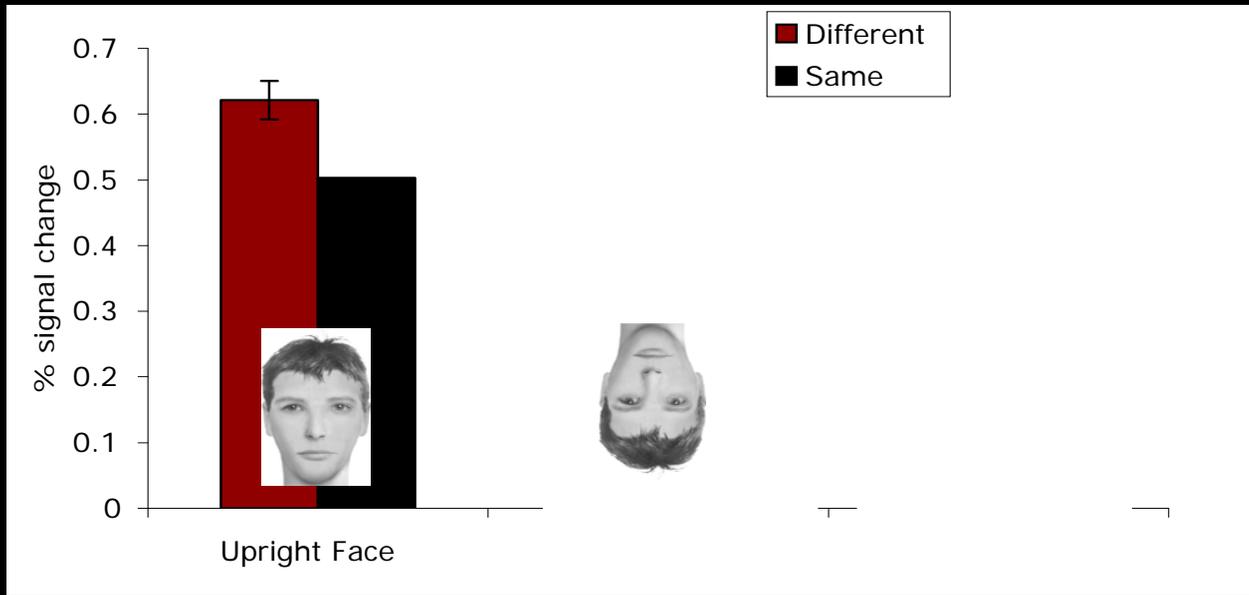
500ms

200ms

SAME



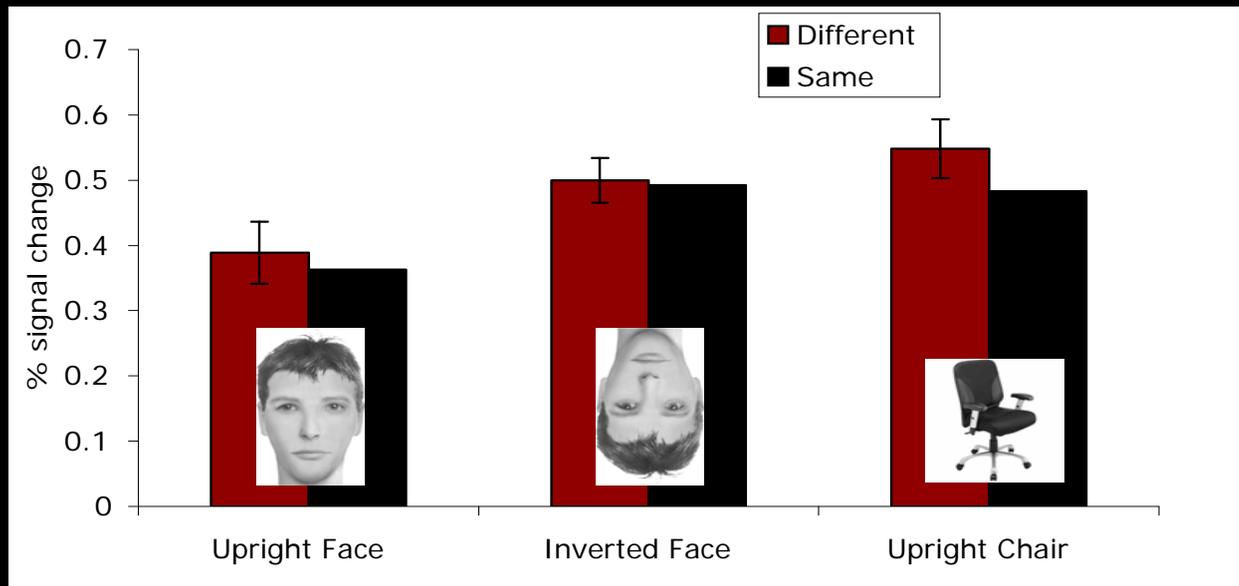
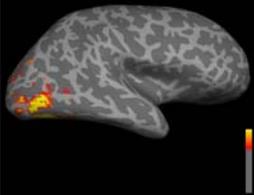
FFA



FFA is sensitive to diffs betwn upright faces, not chairs.

Apples & oranges!

LOC



Does salience account for face specificity?

No.

Area(FFA/LOC) x Stimulus (Face/InvFace/Chair) x Adaptation (Diff/Same) is $p < .02$