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9.71 Functional MRI of High-Level Vision
Fall 2007

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Lecture 10:

Effect of experience on extrastriate cortex

9.71 Fall 2007

- I. Brief comment from midterm
- II. Cool stuff from SFN
- III. Main lecture on effects of experience on cortex

From midterm:

- The PPA is not in the dorsal pathway! (neither is hippocampus with its “place cells”).

PPA : perception of the shape of space

and/or recognition of that place

Hippocampal place cells: where you are in the world.

- Dorsal pathway: where objects are in the visual field, not where you the organism are in the world

Cool stuff from SFN

- Pitcher et al

- Loc info in ventral pathway

 - About 5 papers!

- Moeller, Friedrich, & Tsao (microstim of face patches)

- Freiwald & Tsao (characterization of face patches)

• Is all this structure fixed, or does it depend on experience?

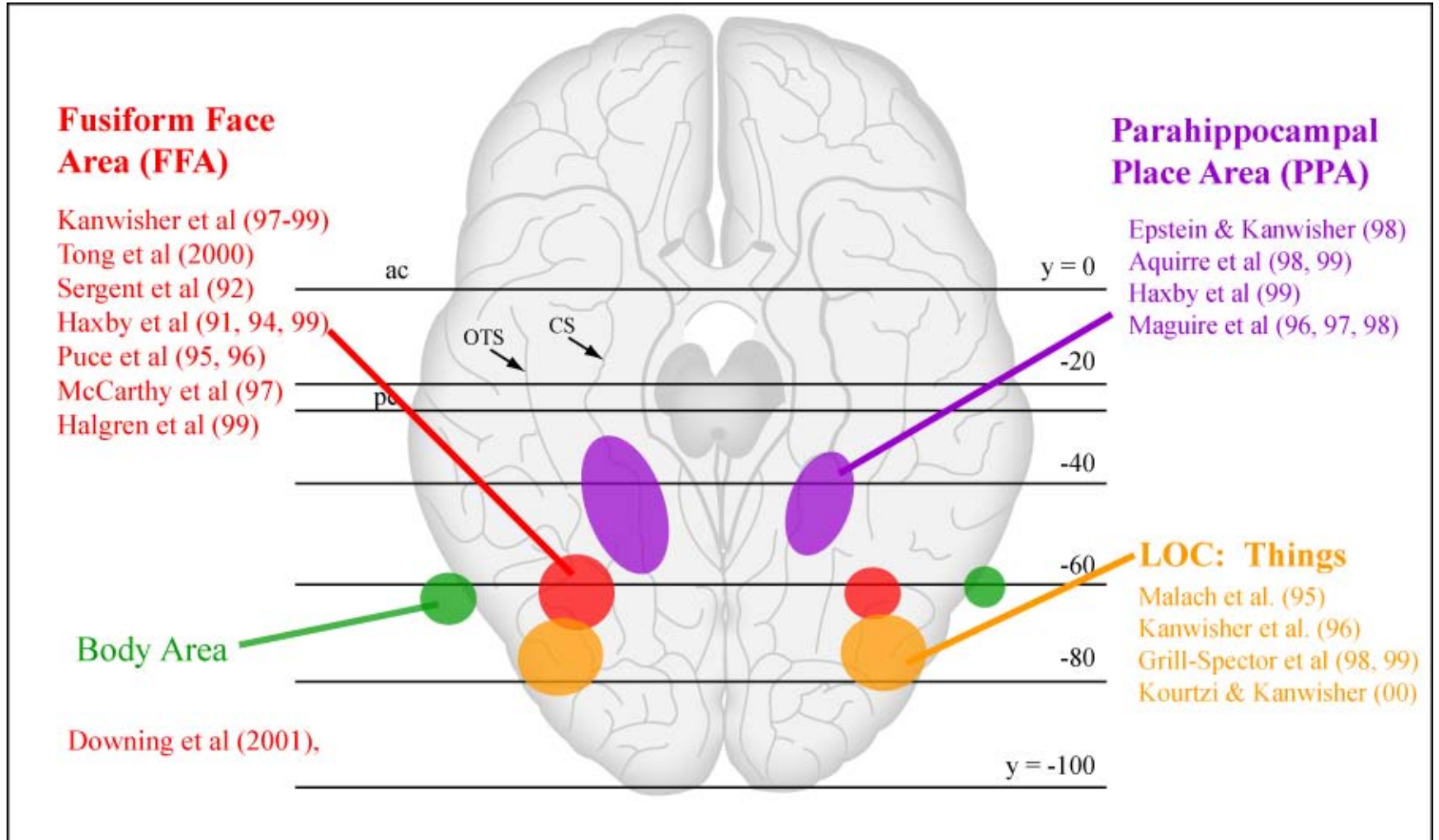


Figure by MIT OpenCourseWare. After Allison, 1994.

Why might/should experience change visual cortex?


Can't build in everything innately
(e.g., what toasters look like)

Need to be able to learn:
new objects,
statistical regularities in the world

Learning implies *some* kind of change in the brain.

Questions

1. *Does* experience affect fMRI responses to learned stimuli?

 under what conditions?
even in adulthood?
even in primary visual areas?

2. *How* does experience affect fMRI responses?

What kind of fMRI changes are predicted from different kinds of neural changes?

Does the fMRI response go up? Down? Some of each?

What is spatial distribution of experience effects?

clusters? new areas? distributed changes?

Two related but importantly different questions:

Origins: How does a functionally distinctive region of cortex arise during development?

What role does experience play in wiring up this region?
e.g., how does the FFA get there in the cortex? (and why THERE?).


Adult Plasticity: Once a region exists (in adulthood), to what extent can experience alter its response profile?

Fine tuning, or radically different response?

Are some areas more shaped by adult experience than others? (e.g. FFA? “higher” areas more than “primary”)?

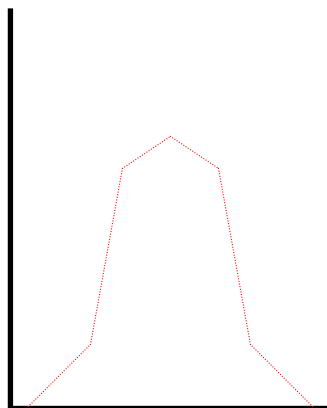
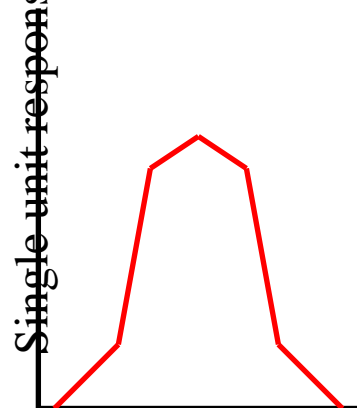
How much experience is necessary?

Questions

1. *Does* experience affect fMRI responses to learned stimuli?
under what conditions?
even in adulthood?
even in primary visual areas?
2. *How* does experience affect fMRI responses?
 What kind of fMRI changes are predicted from different kinds of neural changes?
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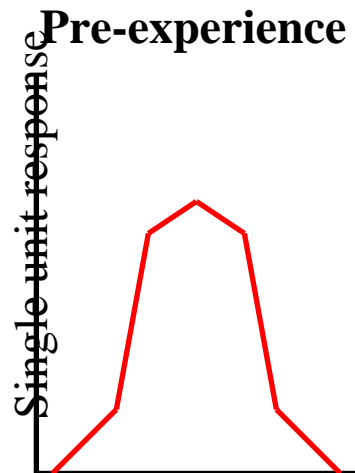
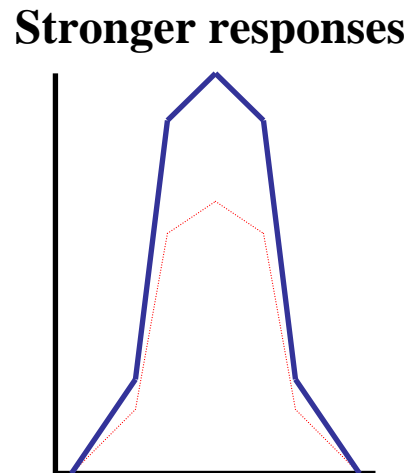
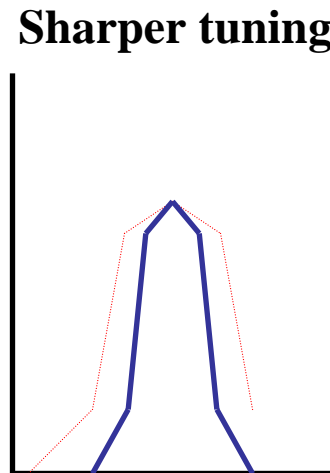
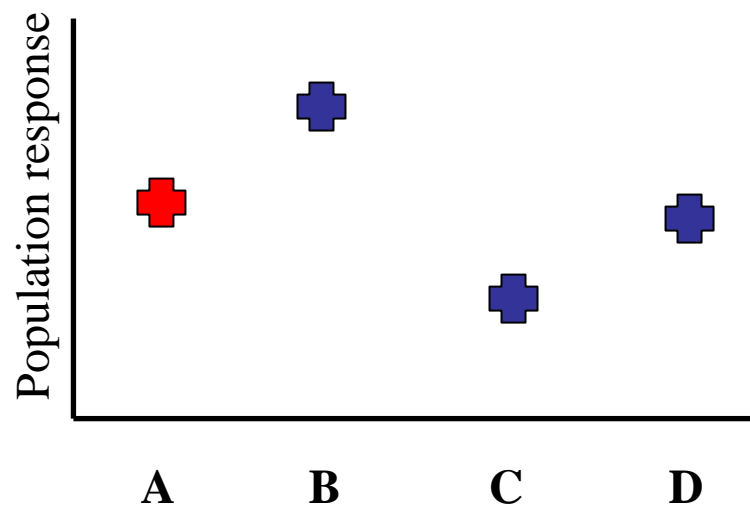
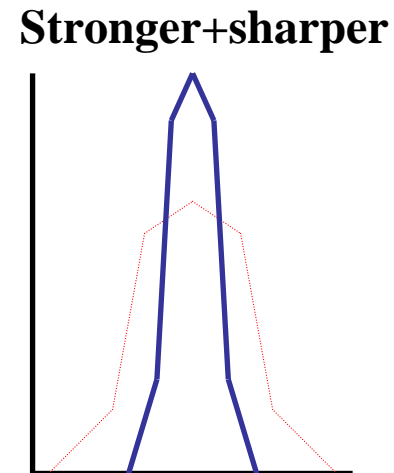
A**B****C****D****Pre-experience****Stronger responses****Sharper tuning****Stronger+sharper**

Single unit response



Population response

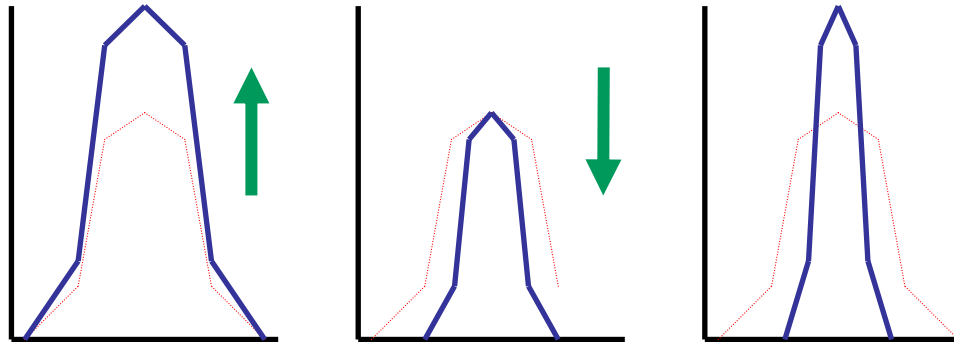
**A****B****C****D**

A**B****C****D**

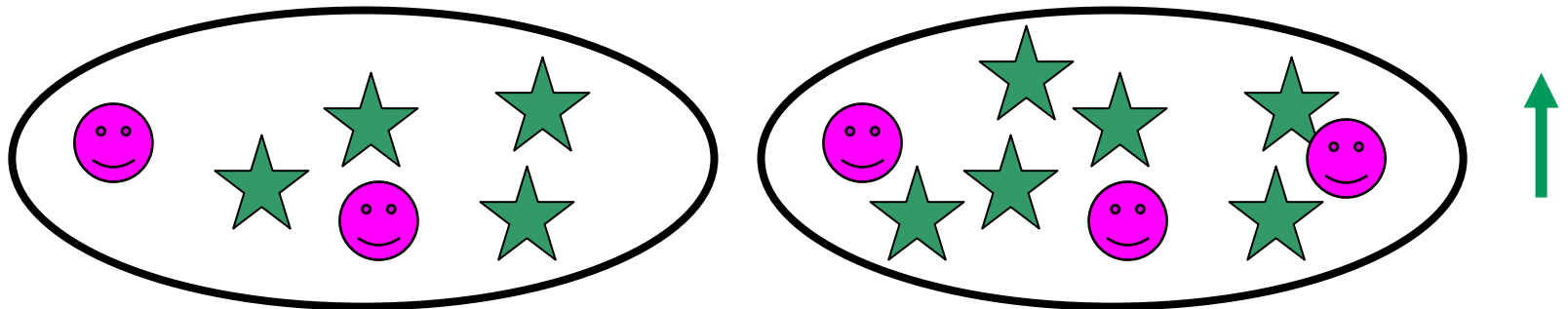
With experience, neural responses might change...

i) selectivities of individual neurons

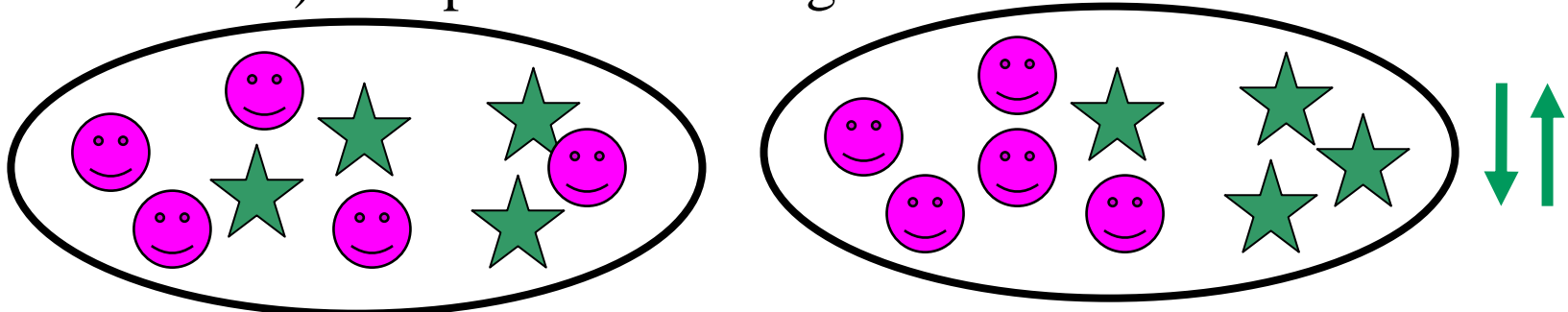
What changes will fMRI "see" after experience with



ii) the total # of neurons w/ a certain selectivity



iii) the spatial clustering of selective neurons



Questions

1. *Does* experience affect fMRI responses to learned stimuli?
under what conditions?
even in adulthood?
even in primary visual areas?
2. *How* does experience affect fMRI responses?
What kind of fMRI changes are predicted from different kinds of neural changes?
Does the fMRI response go up? Down? Some of each?
What is spatial distribution of experience effects?
clusters? new areas? distributed changes?

Next: 5 case studies that address these questions.

Case 1: The Other-Race Effect

Image removed due to copyright restrictions.

A pair of portrait photos: African-American and European-American males

Golby, Gabrieli et al. (2001). *Nature Neuroscience*, 4, 845-850.

Behavioral Data

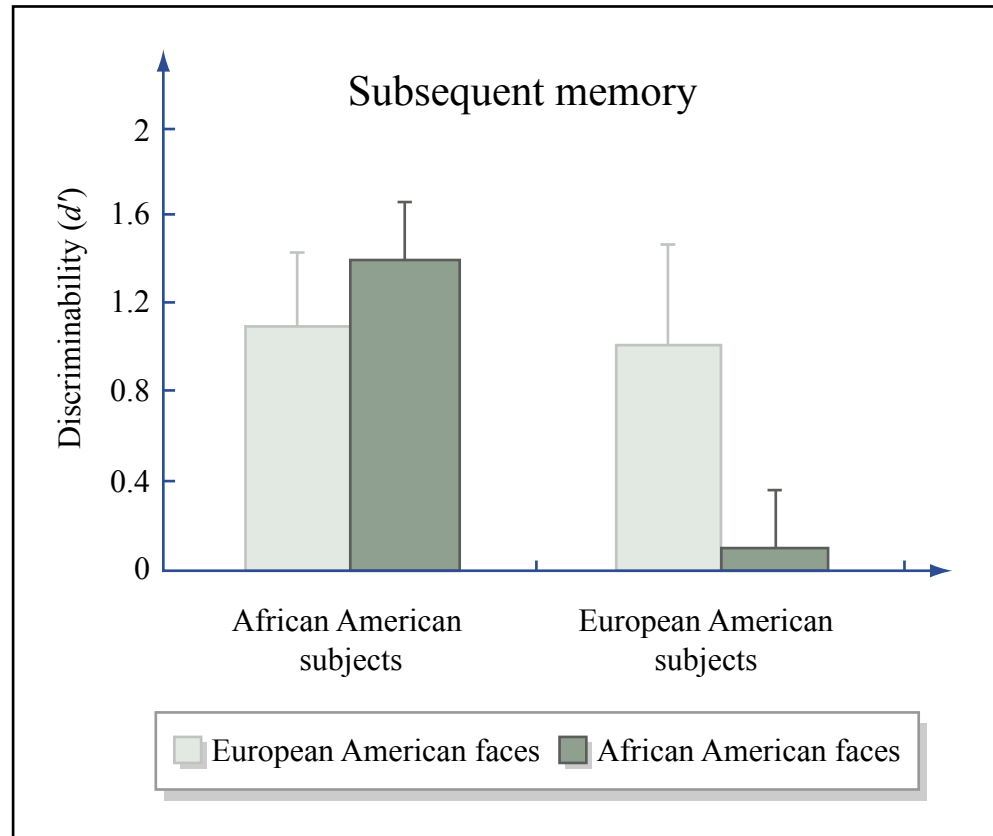


Figure by MIT OpenCourseWare. After Golby et al., *Nat Neurosci* 2001.

Postscan memory for own-race faces is better than for other-race faces. Presumably this is not genetic, but learned. Does this learning affect FFA responses to faces?

fMRI Data

Localizer: Faces versus radios

Image removed due to copyright restrictions.
MRI activation maps, Figure 2 in Golby et al.,
Nat Neurosci 4, 845-850. doi:10.1038/90565.

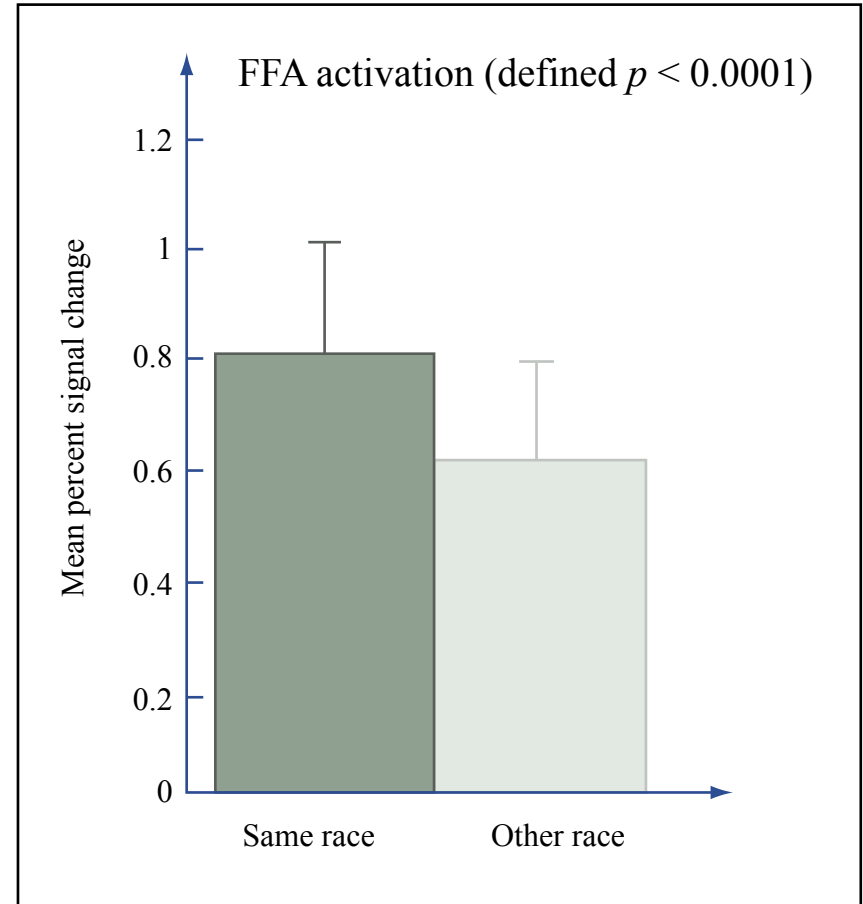


Figure by MIT OpenCourseWare. After Golby et al., *Nat Neurosci* 2001.

So: FFA response to a face depends on experience with similar faces.
i.e., FFA is tuned by experience
other accounts?
Do these data indicate that the FFA is not innate?

Two related but importantly different questions:

Origins: How does a functionally distinctive region of cortex arise during development?

What role does experience play in wiring up this region?
e.g., how does the FFA get there in the cortex? (and why THERE?).

Adult Plasticity: Once a region exists (in adulthood), to what extent can experience alter its response profile?

Fine tuning, or radically different response?

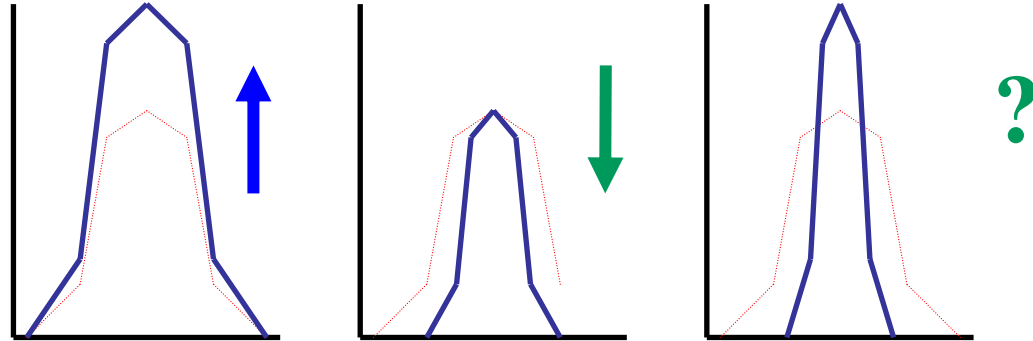
Are some areas more shaped by adult experience than others? (e.g. FFA? “higher” areas more than “primary”)?

How much experience is necessary?

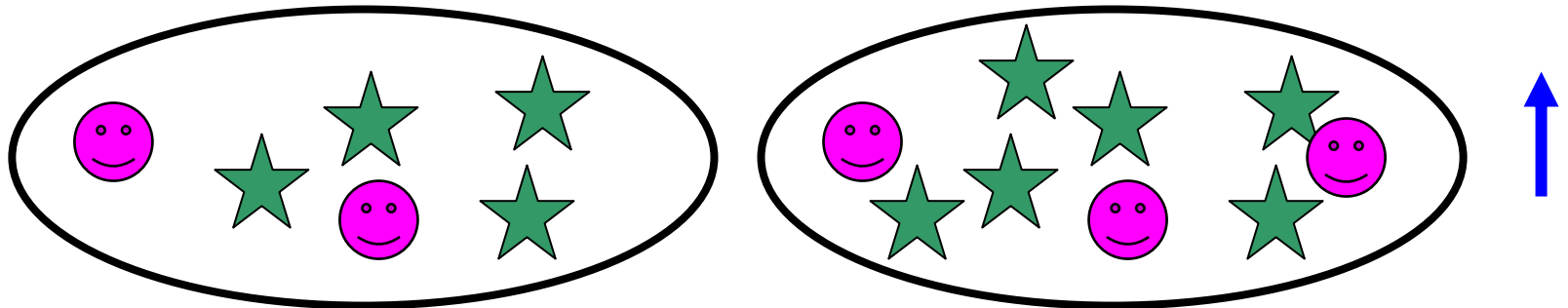
This increase in response with familiarity could reflect an increase in

i) selectivities of individual neurons

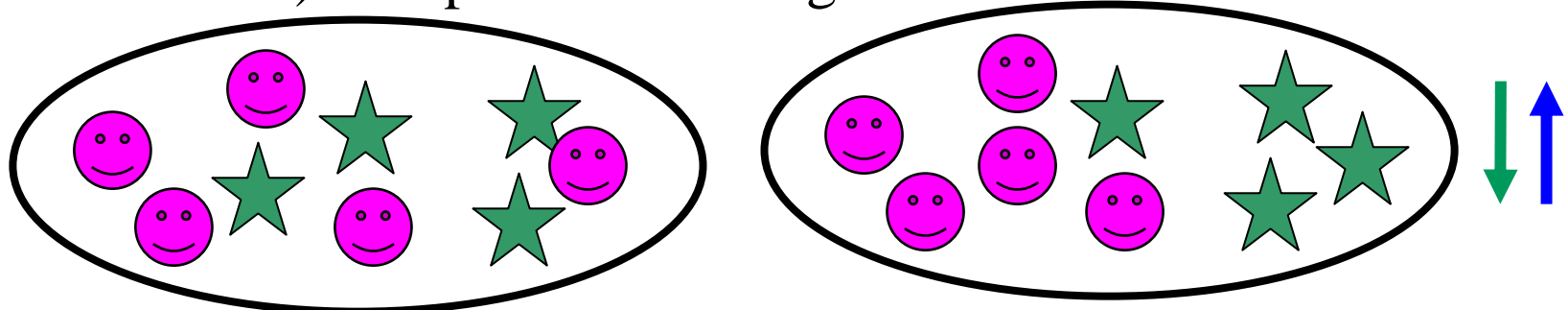
Changes fMRI
will “see” after
experience with:



ii) the total # of neurons w/ a certain selectivity



iii) the spatial clustering of selective neurons



Questions

1. *Does* experience affect fMRI responses to learned stimuli?
under what conditions? **Not clear when this experience happened.**
even in adulthood? **Could find out.**
even in primary visual areas? **How?**
2. *How* does experience affect fMRI responses?
What kind of fMRI changes are predicted from different kinds of neural changes?
Does the fMRI response go up? Down? Some of each? **up**
What is spatial distribution of experience effects?
clusters? new areas? distributed changes?

Next: three lab training studies in adults....

Case 2: Training Object Recognition

Effect of training in backward masking

(Grill-Spector et al., 2000, Nature Neuroscience)

Image removed due to copyright restrictions.

Figure 1 (Sample object photos used in experiment: object epochs vs. scrambled epochs.)

Grill-Spector, K., et al. "The dynamics of object-selective activation correlate with recognition performance in humans." *Nature Neuroscience* 3 no. 8 (2000): 837-43.

doi:10.1038/77754.

Task: covert naming.

Image removed due to copyright restrictions.

Figure 3 graph: sensitivity of recognition and fMRI activation to object duration.
Grill-Spector, K., et al. “The dynamics of object-selective activation correlate with recognition performance in humans.” *Nature Neuroscience* 3 no. 8 (2000): 837-43.
doi:10.1038/77754.

**Use “percent of max” to put both behavior and fMRI on the same scale.
Response in LO and related regions correlated w/ recognition performance!**

Image removed due to copyright restrictions.

Figure 4 graph: Training effect – psychophysics.

Grill-Spector, K., et al. “The dynamics of object-selective activation correlate with recognition performance in humans.” *Nature Neuroscience* 3 no. 8 (2000): 837-43.
doi:10.1038/77754.

**5-7 days of training on naming these 60 images presented for 40 ms.
Performance improved for all subjects.**

a. Increased response to 40 ms stimulus after vs before training in 2 Ss:

Image removed due to copyright restrictions.

Figure 5 set of graphs: Training effect – brain activation.

Grill-Spector, K., et al. "The dynamics of object-selective activation correlate with recognition performance in humans." *Nature Neuroscience* 3 no. 8 (2000): 837-43.
doi: 10.1038/77754.

b. Training effect across all Ss and ROIs:

c. Training effect is (partly) specific to the trained stimulus: greater for trained than novel stimuli.

Case 3: How does the response to novel objects (“Greebles”) change w/ training?

(Gauthier et al., 1999, Nature Neuroscience)

Image removed due to copyright restrictions.

Greebles and sample trials from the sequential-matching task.
Figure 1 in Gauthier, I., et al. (1999). "Activation of the middle fusiform "face area" increases with expertise in recognizing novel objects." *Nature Neuroscience* 2(6): 568-573. doi:10.1038/9224.

Sequential
matching
task used in
scanner

Expertise hypothesis: changes should be largely in the rFFA.

Method:

1. Define rFFA as an 8x8 voxel square that responds more to faces > objects.
2. Collect the sum of the t-values for each voxel in this ROI from a comparison of upright - inverted faces, and for upright minus inverted greebles, longitudinally over the course of training.
3. Show that this number increases in the “rFFA” ROI over training w/ greebles.

White = Faces
Grey = Greebles

Image removed due to copyright restrictions.

Figure 2d (graph) in Gauthier, I., et al. (1999). "Activation of the middle fusiform "face area" increases with expertise in recognizing novel objects." *Nature Neuroscience* 2(6): 568-573. doi:10.1038/9224.

“rFFA”

What is wrong with this picture?

Faces>objects Greebles>objects

Faces>objects Greebles>objects

“images are thresholded at the arbitrary threshold of 0.75”.

Image removed due to copyright restrictions.

Set of fMRI activation maps.

Figure 4 in Gauthier, I., et al. (1999). "Activation of the middle fusiform "face area" increases with expertise in recognizing novel objects." *Nature Neuroscience* 2(6): 568-573. doi:10.1038/9224.

3 novices

3 experts

Why didn't they show us the same subjects?

How does the response to novel objects (“Greebles”) change w/ training?

(Gauthier et al., 1999, Nature Neuroscience)

Image removed due to copyright restrictions.

Greebles and sample trials from the sequential-matching task.
Figure 1 in Gauthier, I., et al. (1999). "Activation of the middle fusiform "face area" increases with expertise in recognizing novel objects." Nature Neuroscience 2(6): 568-573. doi:10.1038/9224.

Expertise hypothesis: changes should be largely in the rFFA.

Have they shown this? How could you do better?

Case 4: Effects of Object Discrim. Training in Ventral Pathway

Op de Beeck, Baker, DiCarlo & Kanwisher, 2006

Are object representations fixed, or are they shaped continually by experience?

Does training produce:

increases in response?

decreases in response?

increases in selectivity?

Are training effects (if any) found:

in LOC?

in rFFA?

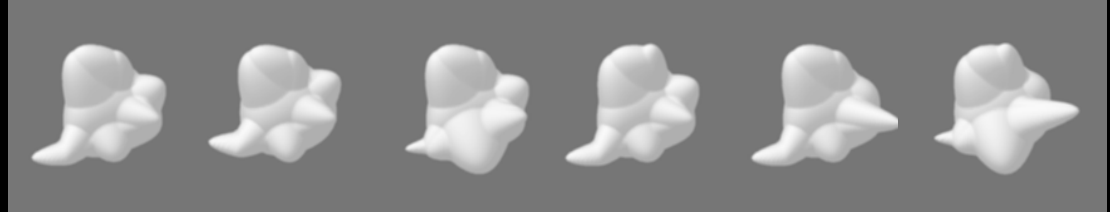
in new discrete region?

scattered & discontinuous?

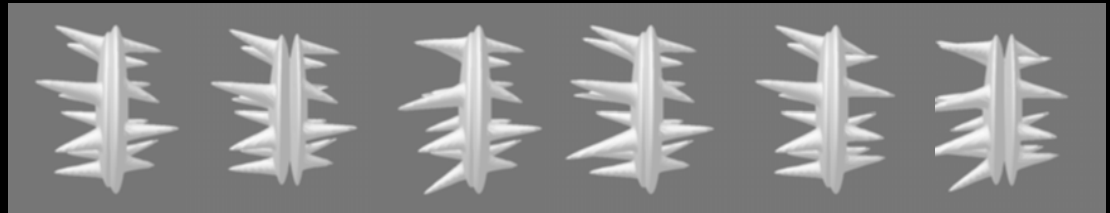
Effects of Object Discrim. Training in Ventral Pathway

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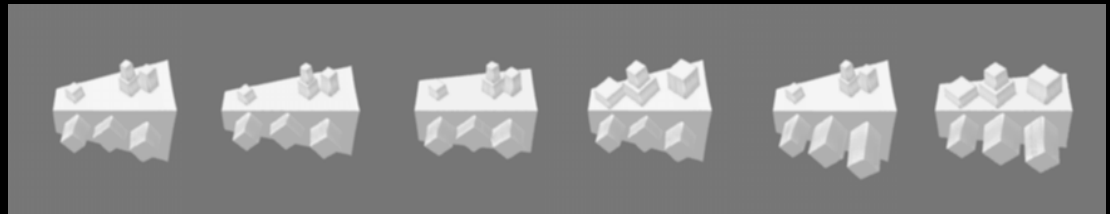
Smoothies



Spikies

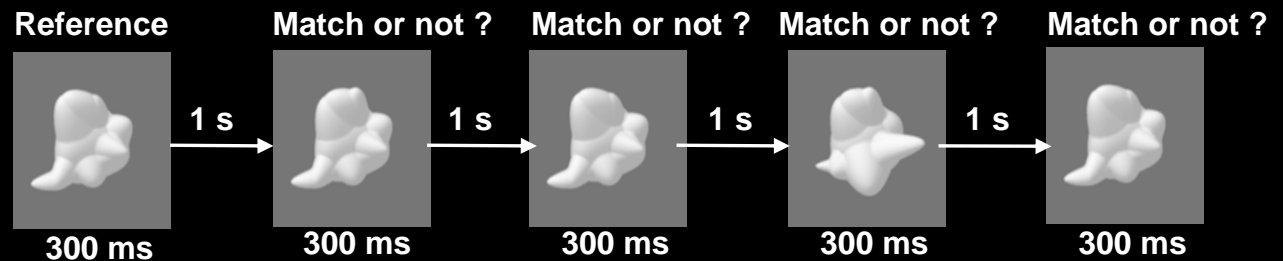


Cubies



Design:
Scan Ss
before & after
10 hours
of training on
discrimination
of one of three
object classes.

Shape
discrimination
task:

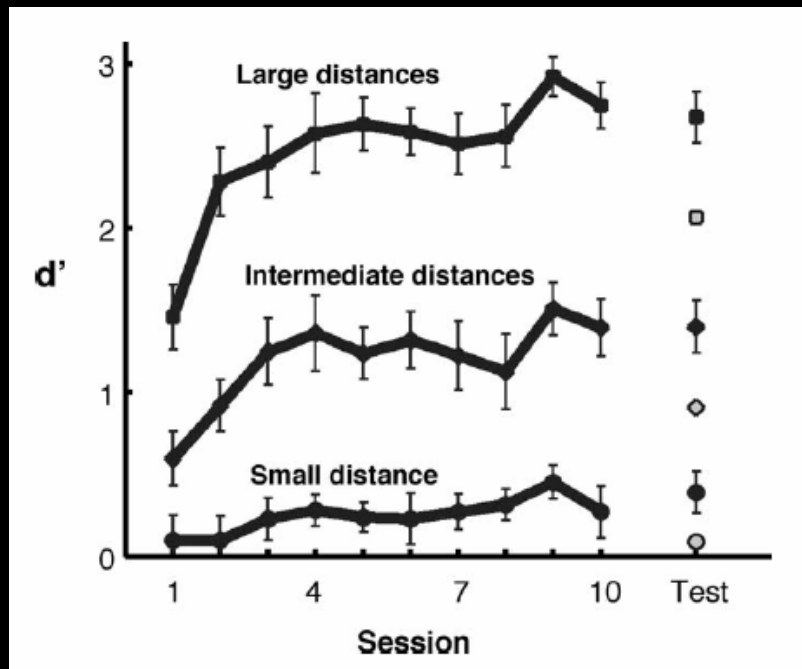


Courtesy of the Society for Neuroscience. Used with permission.

Effects of Object Discrim. Training in Ventral Pathway

Op de Beeck, Baker, DiCarlo & Kanwisher, 1996

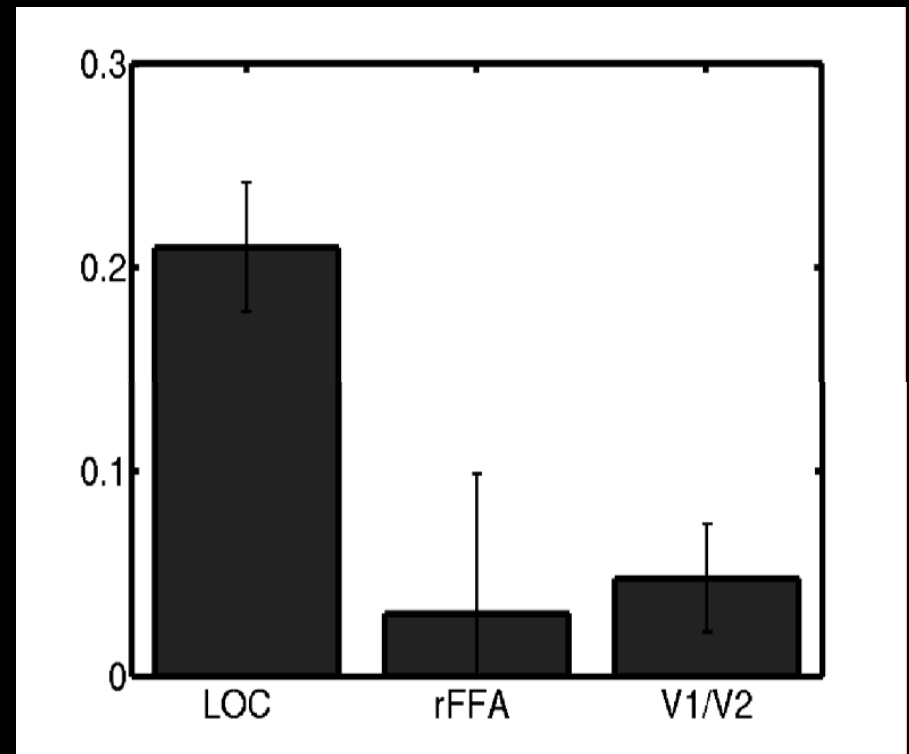
***D'* as a function of training session**



Courtesy of the Society for Neuroscience. Used with permission.

fMRI Training Effect:

PSC: $(Tr - Untr)_{after} - (Tr - Untr)_{before}$



So: responses to trained objects increase in LOC, not FFA.

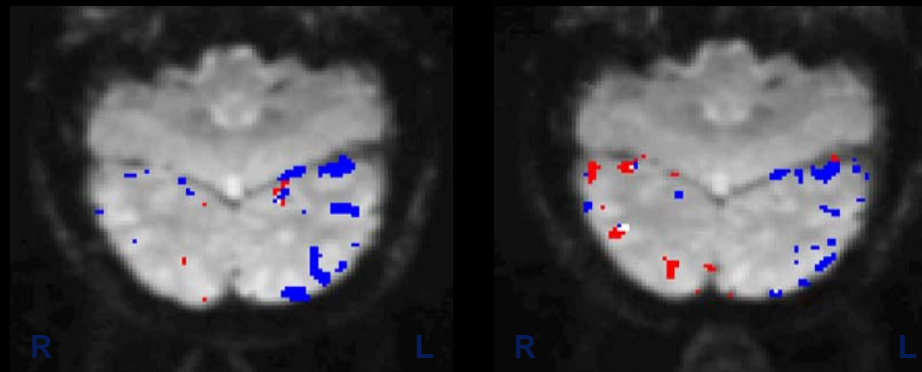
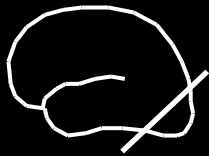
Effects of Object Discrim. Training in Ventral Pathway

Op de Beeck, Baker, DiCarlo & Kanwisher, 1996

Sig trained > untrained effect in 366 voxels after training, vs 82 before ($p < .02$).

But only some of those effects are in LOC - for example:

Spikies



Objects > scrambled



Overlap



Trained > untrained



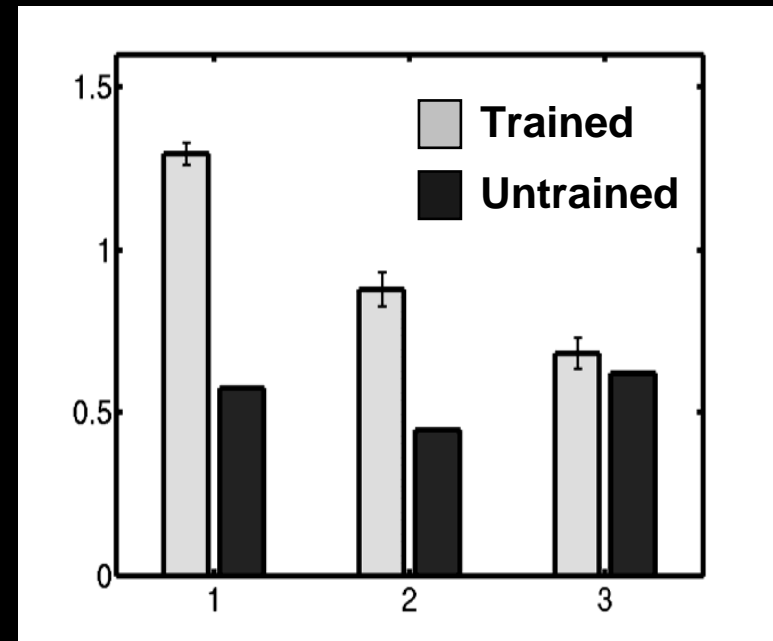
How do we find replicable and quantifiable training effects when they are scattered?

Effects of Object Discrim. Training in Ventral Pathway

Op de Beeck, Baker, DiCarlo & Kanwisher, 1996

How do we find replicable and quantifiable training effects when they are scattered?

- 1. find “training effect voxels” in half of the data from the post-training session**
- 2. look in same voxels at other half of the data from the post-training session**
- 3. look at same voxels in the pre-training session**



>>Replicable two-fold selectivity for trained objects after training (not before).

Effects of Object Discrim. Training in Ventral Pathway

Op de Beeck, Baker, DiCarlo & Kanwisher, 1996

Are object representations fixed, or are they shaped continually by experience?

Does training produce:

increases in response?

decreases in response?

increases in selectivity?

Are training effects (if any) found:

in LOC?

in rFFA?

in new discrete region?

scattered & discontinuous

Effects of Object Discrim. Training in Ventral Pathway

Op de Beeck, Baker, DiCarlo & Kanwisher, 1996

Are object representations fixed, or are they **shaped continually by experience?**

Does training produce:

- ✓ increases in response?
- ✗ decreases in response?
- ✓ increases in selectivity?

Are training effects (if any) found:

- ✓ in LOC?
- ✗ in rFFA?
- ✗ in new discrete region?
- ✓ scattered & discontinuous: a change in profile of response across cortex?

Effects of Object Discrim. Training in Ventral Pathway

Op de Beeck, Baker, DiCarlo & Kanwisher, 1996

Are object representations fixed, or are they **shaped continually by experience?**

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- ✗ decreases in response?
- ✓ increases in selectivity?

Are training effects (if any) found:

- ✗ in LOC?
- ✗ in rFFA?
- ✓ in new discrete region?

scattered & discontinuous: a **change in profile of response across cortex?**

Questions

1. *Does* experience affect fMRI responses to learned stimuli? **Yes!**
under what conditions? **A few hours of lab training**
even in adulthood? **Yes!**
even in primary visual areas?

2. *How* does experience affect fMRI responses?

What kind of fMRI changes are predicted from different kinds of neural changes?

Does the fMRI response go up? Down? Some of each? **Up only.**

What is spatial distribution of experience effects?

clusters?

No major “new blobs”.

 new areas?

But maybe a few hours is not enough.

distributed changes?

Case 4: Words

Can a special-purpose bit of brain hardware be constructed from experience, without any specific genetic blueprint?

Chris Baker, Jia Liu et al (2007), PNAS

Perfect test case: visually presented WORDS! (Polk & Farah)

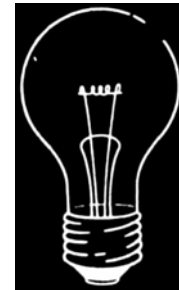
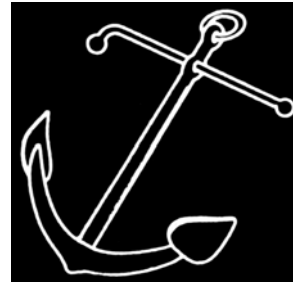
- **Experience is on a par with experience with faces.**
- **People have only been reading for a few thousand years, not enough for natural selection to create a specialized visual word recognition system.**
- **Finding a region selective for visual words would be an existence proof that extensive experience can be sufficient.**
- **Ongoing debate about “visual word form area”; specificity and role of experience is unclear.**

Initial criterion

words

line drawings

coat



calf

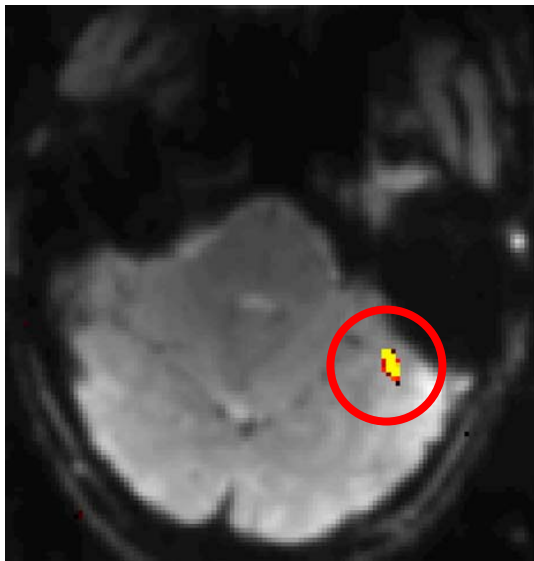
>

duck



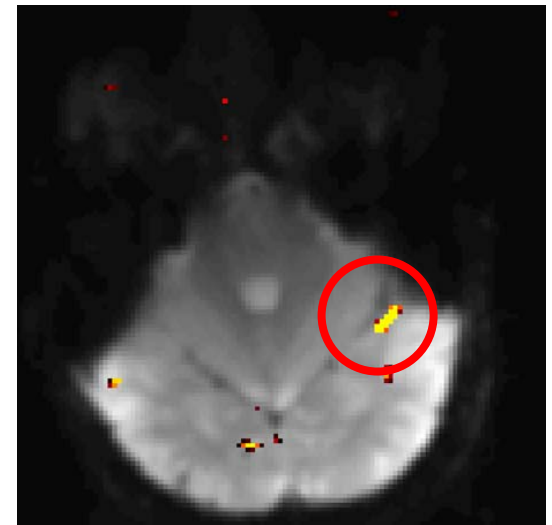
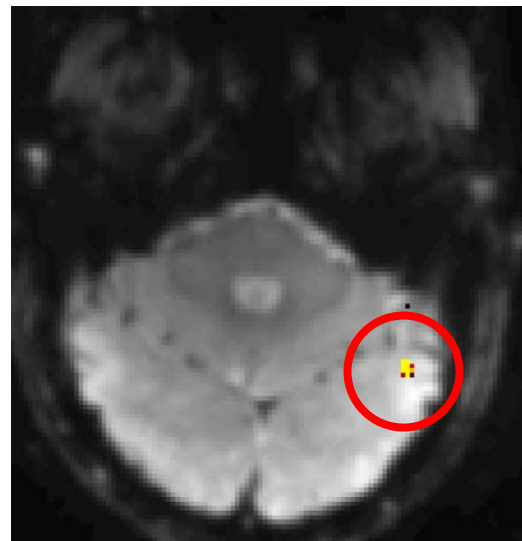
Didn't see much (groups, individuals, passive, 1-back...)
What about higher resolution?

A small region in the left hemisphere shows higher activation for words than line drawings in > 80% of subjects



R

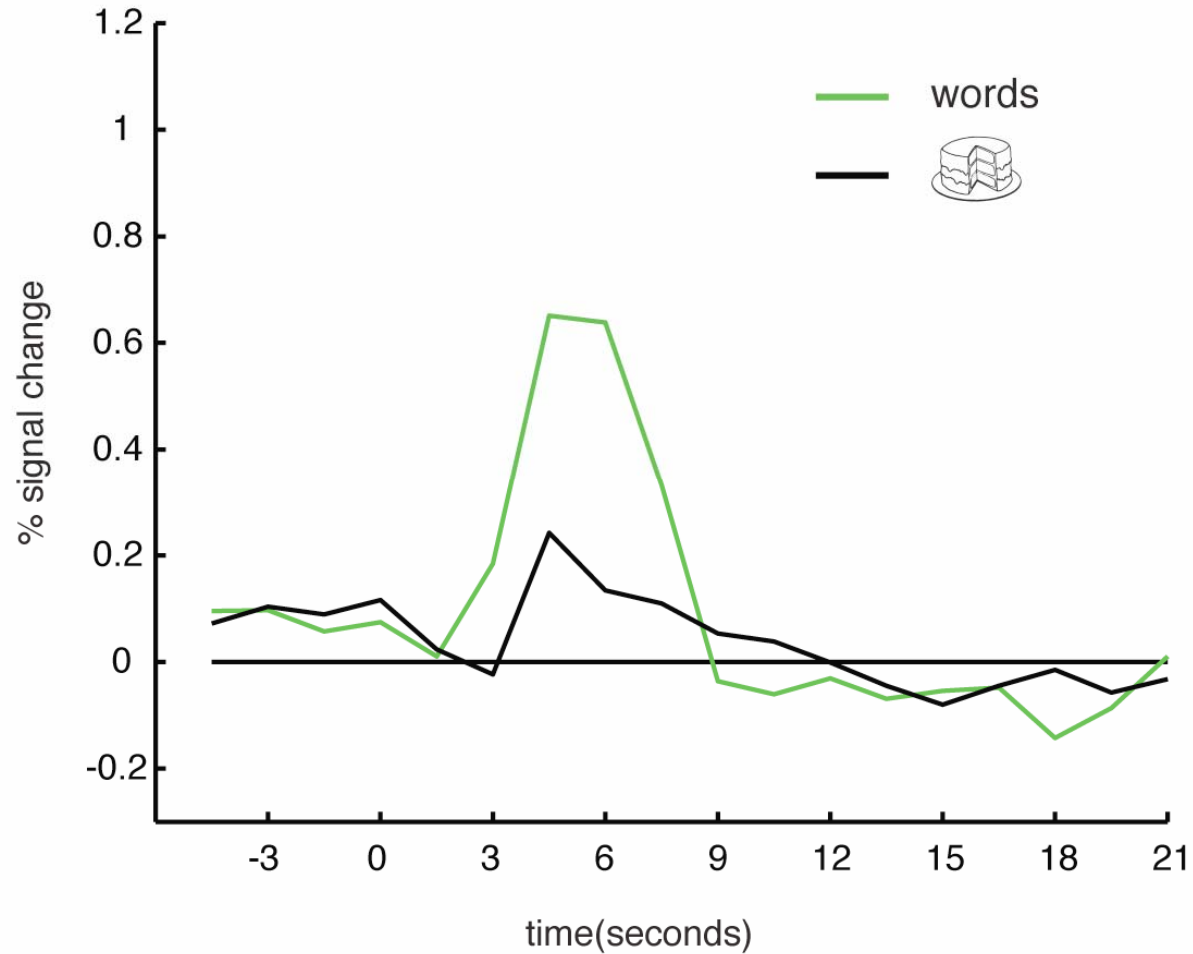
L



$p < 10^{-4}$

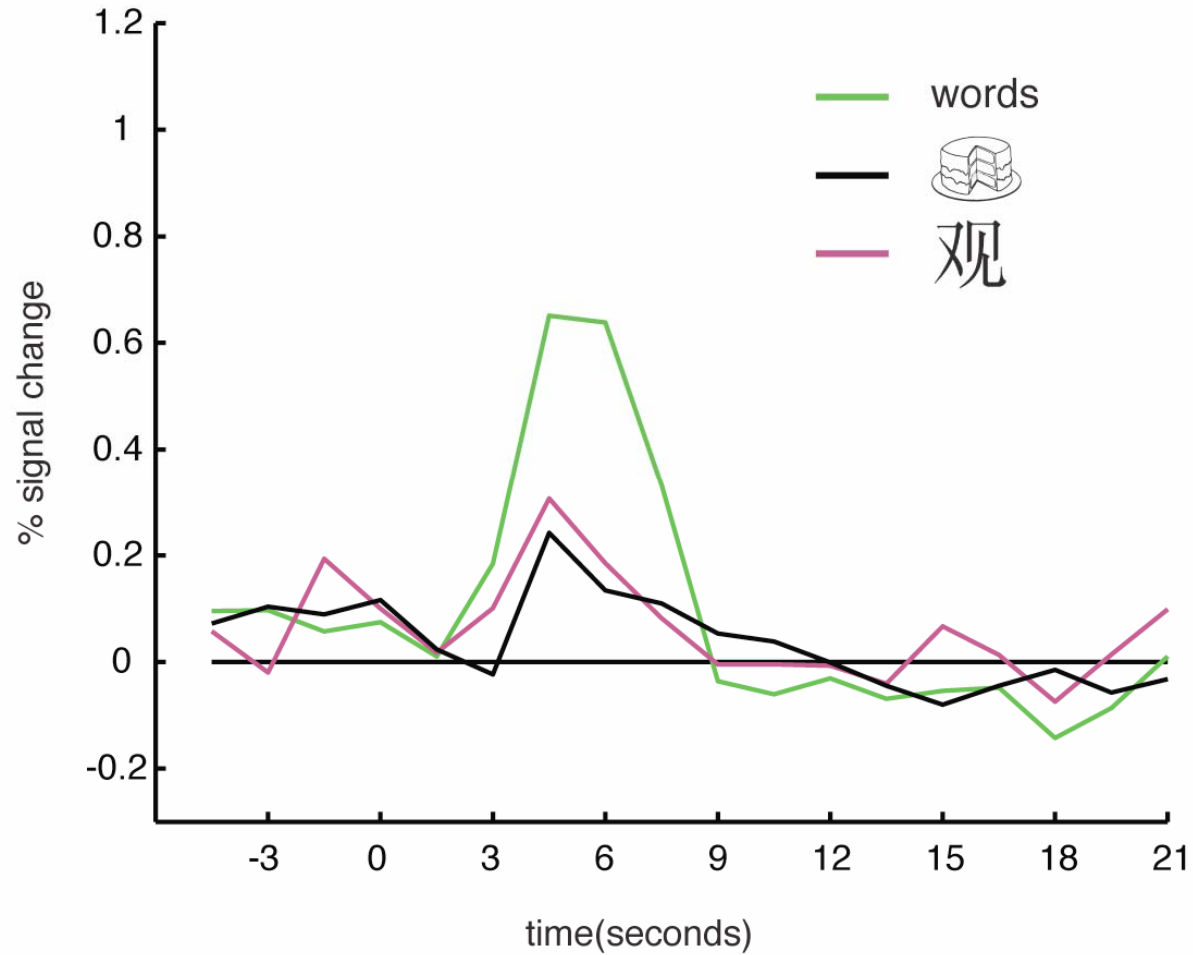
How selective is this region?

N=9



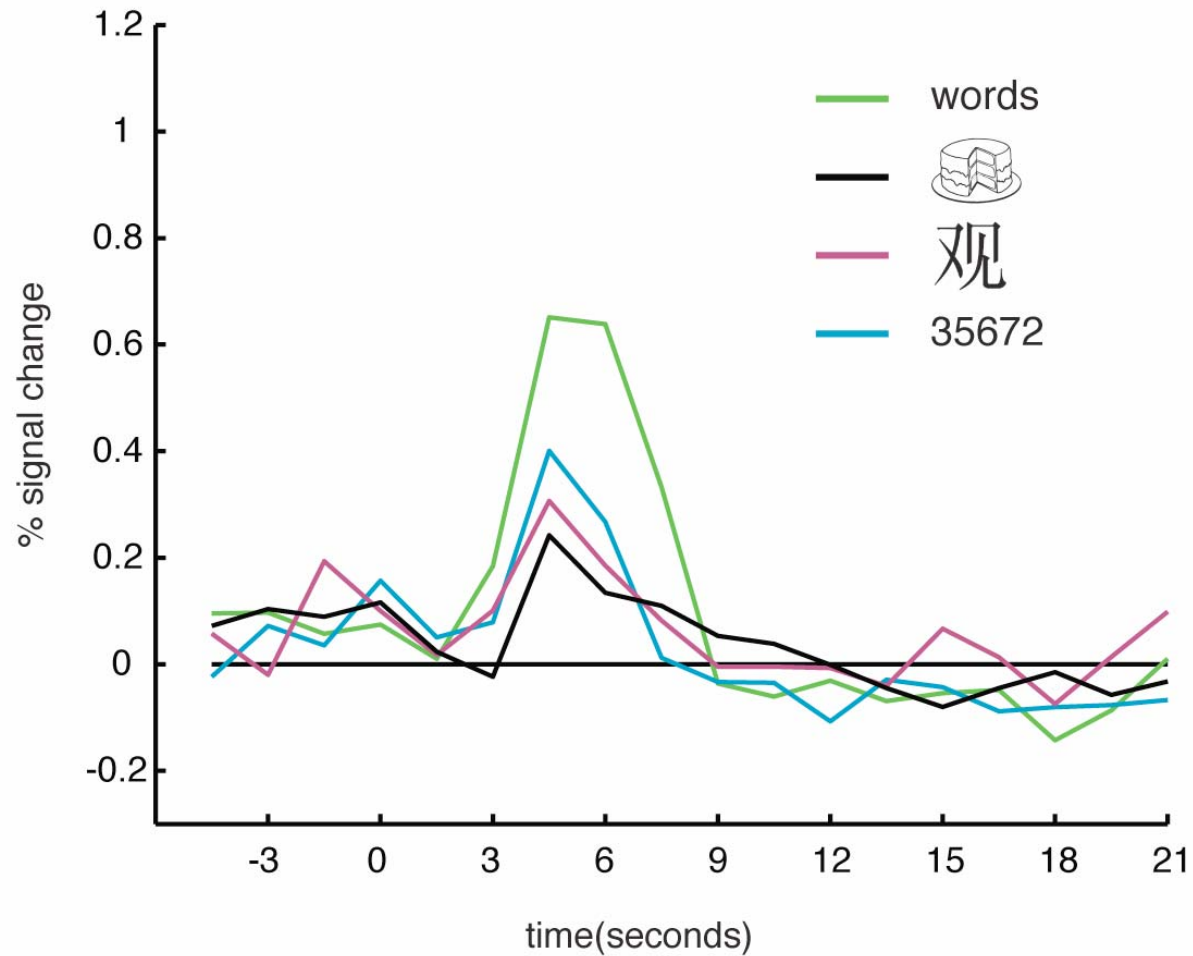
How selective is this region?

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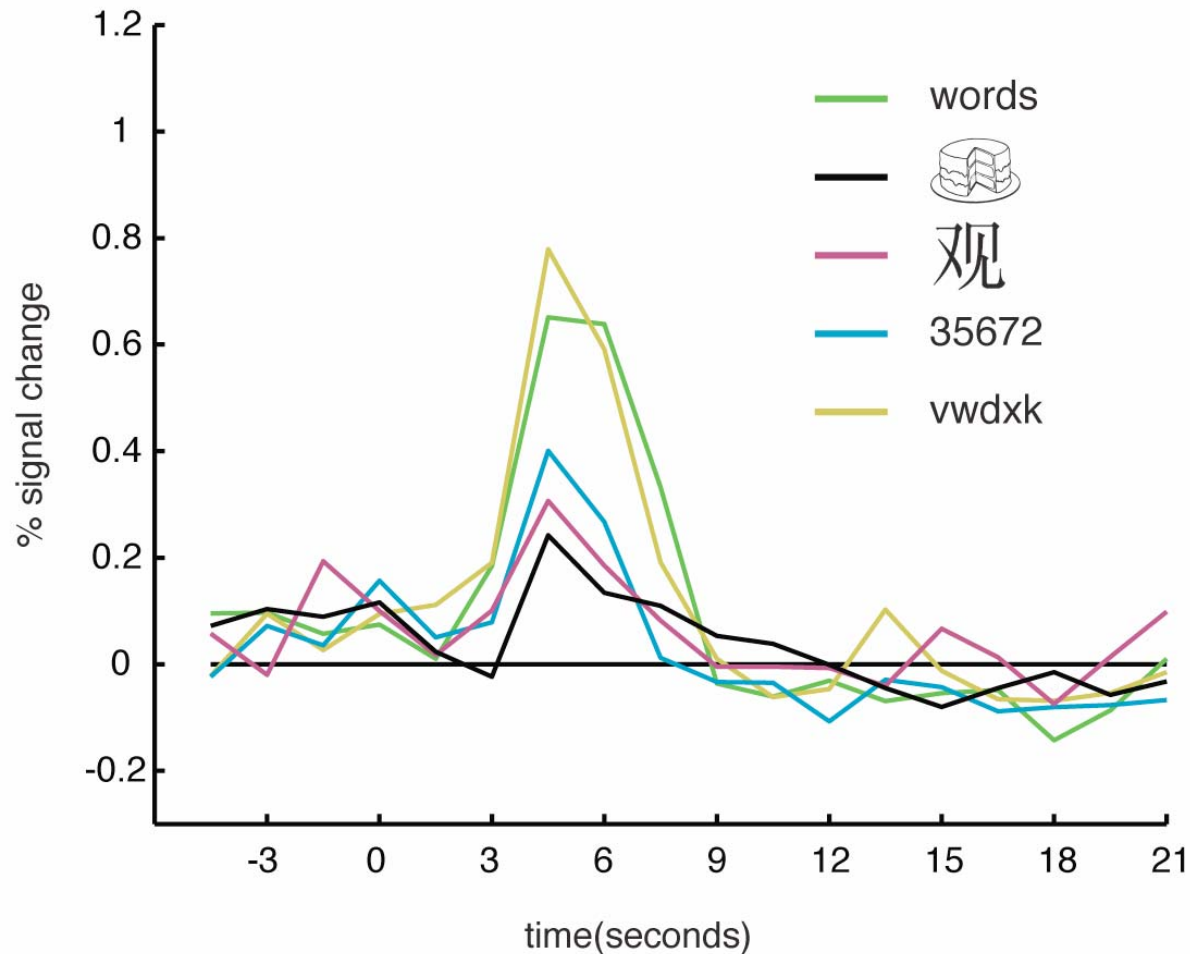
How selective is this region? Quite!

N=9



How selective is this region?

N=9



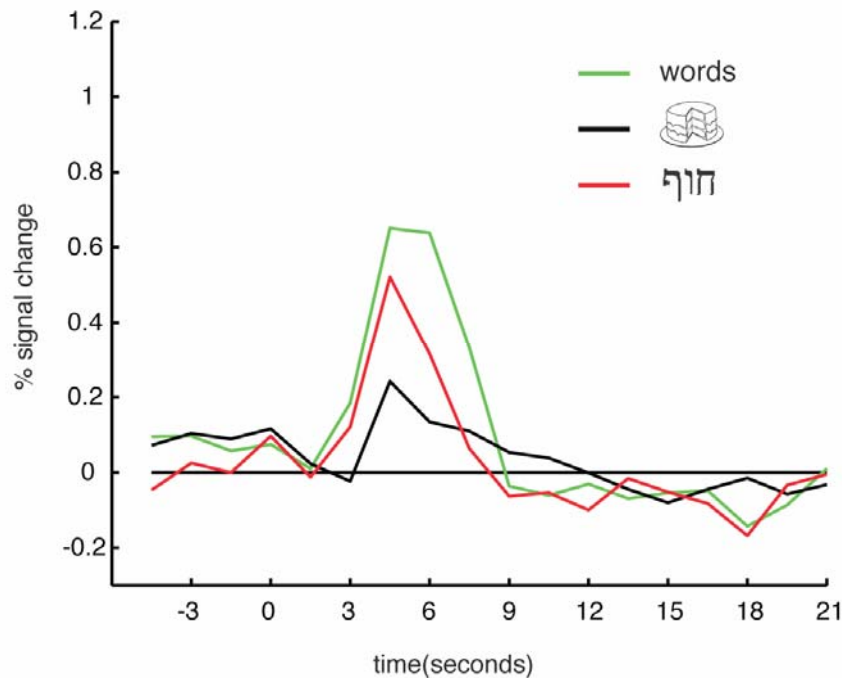
But it's not exactly a VWFA

Is it shaped by experience?

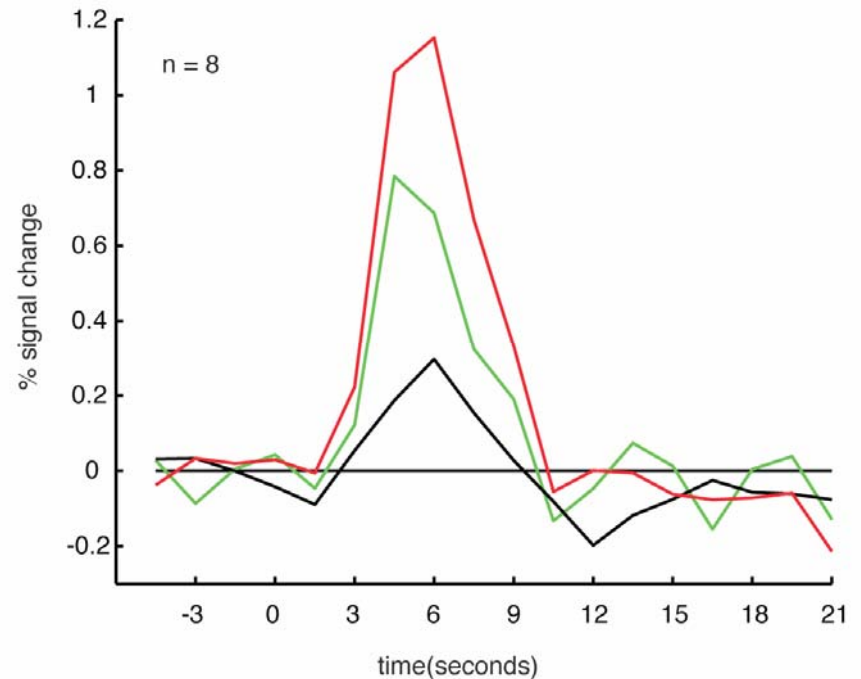
Need to vary experience to know.

Experience modulates responsiveness of this region

Non-Hebrew readers



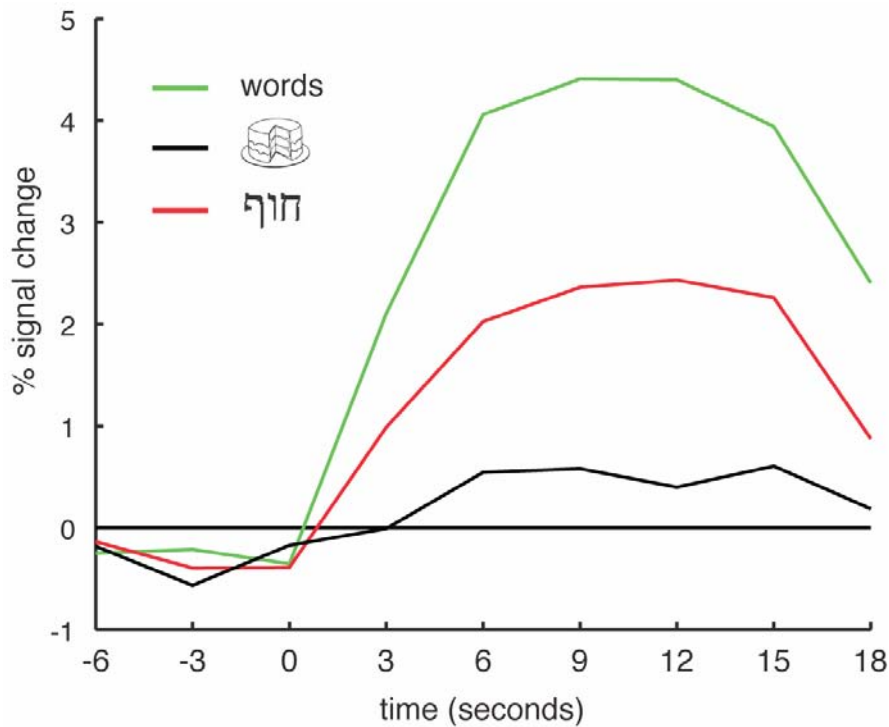
Hebrew readers



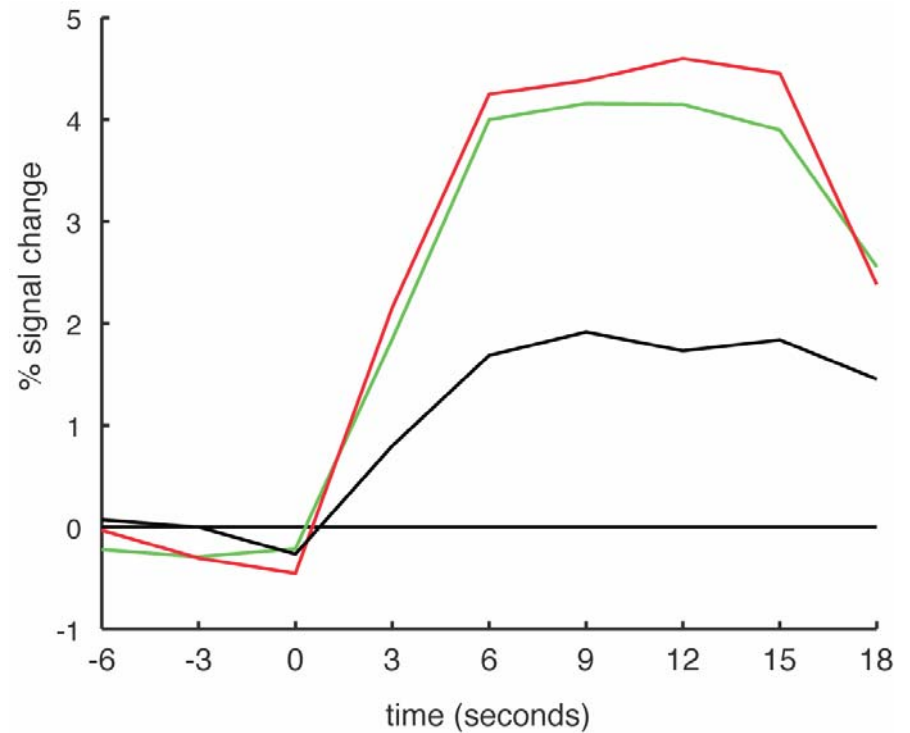
Is this “just attention”?

1-back task, blocked

Non-Hebrew readers



Hebrew readers



Not “just attention”; experience shapes selectivity.

Case 4: Words

Can a special-purpose bit of brain hardware be constructed from experience, without any specific genetic blueprint?

Chris Baker

Yes!

Jia Lia

Unclear if this is the origin of FFA, PPA, EBA

Perfect test case: visually presented WORDS! (Polk & Farah)

- **Experience is on a par with experience with faces.**
- **People have only been reading for a few thousand years, not enough for natural selection to create a specialized visual word recognition system.**
- **Finding a region selective for visual words would be an existence proof that extensive experience can be sufficient.**
- **Ongoing debate about “visual word form area”; specificity and role of experience is unclear.**

Questions

1. *Does* experience affect fMRI responses to learned stimuli? **Yes!**
under what conditions? **A few hours of lab training**
even in adulthood? **Yes!**
even in primary visual areas?

2. *How* does experience affect fMRI responses?

What kind of fMRI changes are predicted from different kinds of neural changes?

Does the fMRI response go up? Down? Some of each? **Up only.**

What is spatial distribution of experience effects?

clusters?

Yes, can get a “new blob, if

new areas?

experience is strong enough.

distributed changes?

Test Case: Macular Degeneration

*with Chris Baker
and Eli Peli*

- Affects 10s of millions of people worldwide
- Retinal disease: destroys the fovea
- Causes total loss of central vision
- Central 2 degrees of vision maps to about twenty cm² of cortex

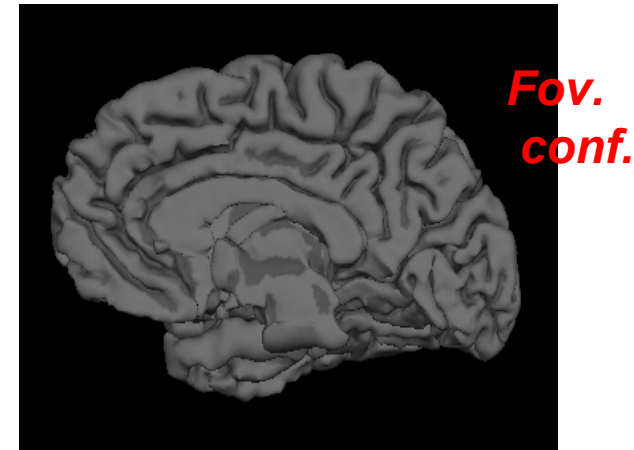
Image removed due to copyright restrictions.
See Fig 7 in: Dougherty, R. F., et al.
Journal of Vision 3, no. 10
(2003): 586-598.
(<http://www.journalofvision.org/3/10/1/article.aspx>).

What happens to this cortical region in MD when it is deprived of input?

Test case: Macular Degeneration - Loss of foveal retina in adulthood

“Foveal confluence” in normal subject: 20 cm²

Q: What happens to this region in Subjects with MD and no foveal vision?



First: Activation from peripheral Stimuli in normal subject

Activation from peripheral stimuli in MD subject

Major functional reorganization of retinotopic cortex in adulthood!

Questions

1. *Does* experience affect fMRI responses to learned stimuli? **Yes!**
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even in primary visual areas? **Yes!**

2. *How* does experience affect fMRI responses?

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What is spatial distribution of experience effects?

clusters?

Yes, *can* get a “new blob, if

new areas?

experience is strong enough.

distributed changes?

• Is all this structure fixed, or does it depend on experience?

• Dynamic system: new areas arise & functional props can change.

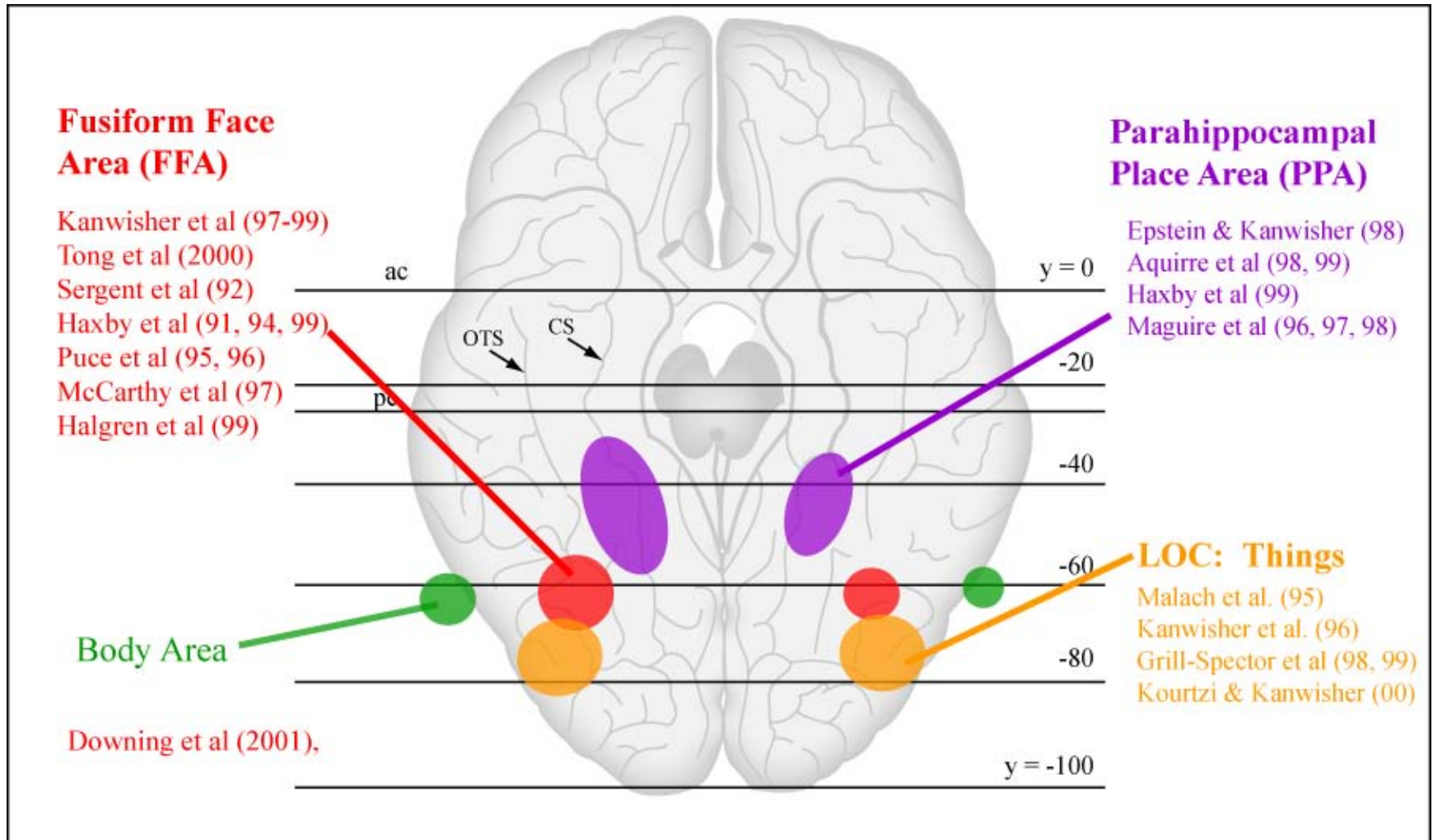


Figure by MIT OpenCourseWare. After Allison, 1994.

Many different time scales of experiential effects:

Some very fast:

Dolan RJ, Fink GR, Rolls E, Booth M, Holmes A, Frackowiak RS, Friston KJ. (1997). How the brain learns to see objects and faces in an impoverished context. *Nature*. 1997 Oct 9;389(6651):596-9.

Demo....

Sequence of three slides deleted due to copyright restrictions.

Faces: pre-learning, learning, and post-learning

Fig. 1 in Dolan RJ et al. (1997). "How the brain learns to see objects and faces in an impoverished context." *Nature* 389 no. 6651(1997): 596-9.

doi:10.1038/39309.

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Found: higher responses in ventral temporal regions associated with face processing after disambiguation than before.

Can you think of another very rapid experiential effect in fMRI?

1. Does experience affect fMRI responses to learned stimuli?

Yes it can; there are many cases of this.

2. Does the response go up? Down? Some of each?

Often responses go up with training.

But in adaptation they go down.

3. What is spatial distribution of experience effects?

clusters? new areas? distributed changes

Lab training (hours) neither uniformly distributed nor clustered.

Words: some clustering. (other kinds of expertise?)

4. Time scale of changes?

Can be short or fast. Probably different mechanisms.

Two related but importantly different questions:

Origins: How does a functionally distinctive region of cortex arise during development? **No one knows!**

What role does experience play in wiring up this region? e.g., how does the FFA get there in the cortex? (and why THERE?). **No one knows! But specialization for words suggests that a specific genetic predisposition for a particular stimulus class may not be necessary.**

Adult Plasticity: Once a region exists (in adulthood), to what extent can experience alter its response profile?

Fine tuning, or radically different response? **Some of each.**

Are some areas more shaped by adult experience than others? (e.g. FFA? “higher” areas more than “primary”)? **Not only higher areas.**

How much experience is necessary?

Even a small amount is enough to change responses...

Training studies:

Increases in population response as a result of experience.

Examples: - Greeble training (Gauthier et al., 1999)

- Backward masking (Grill-Spector et al., 2000)

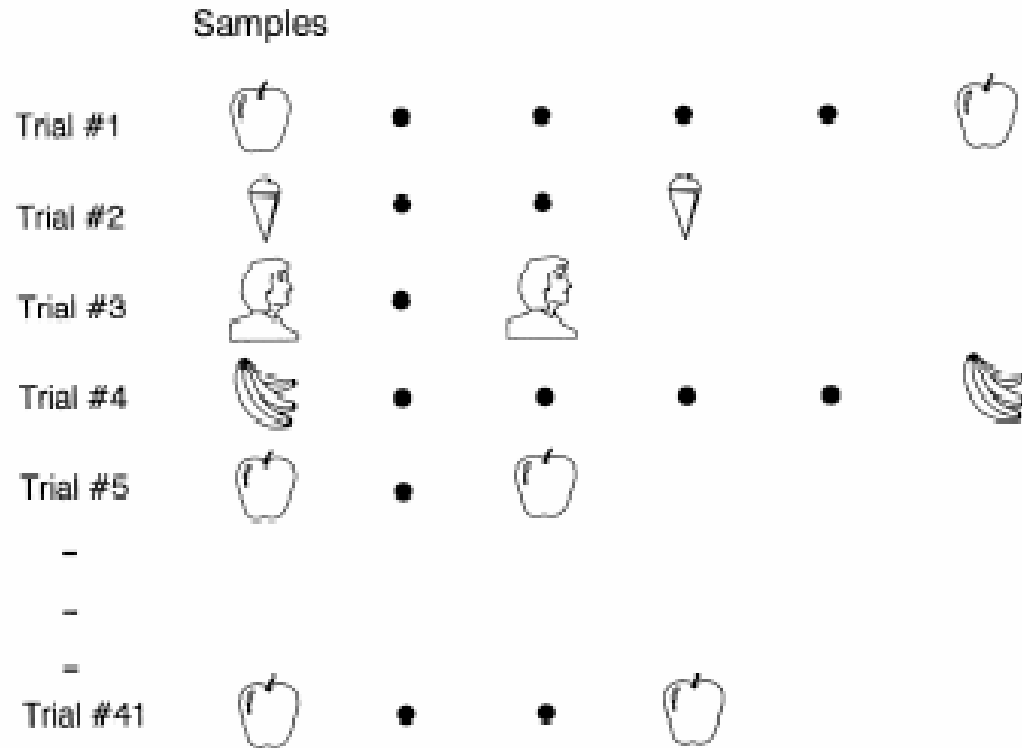
Priming

Repetition leads to:

- 1) Faster RTs
- 2) Increased accuracy

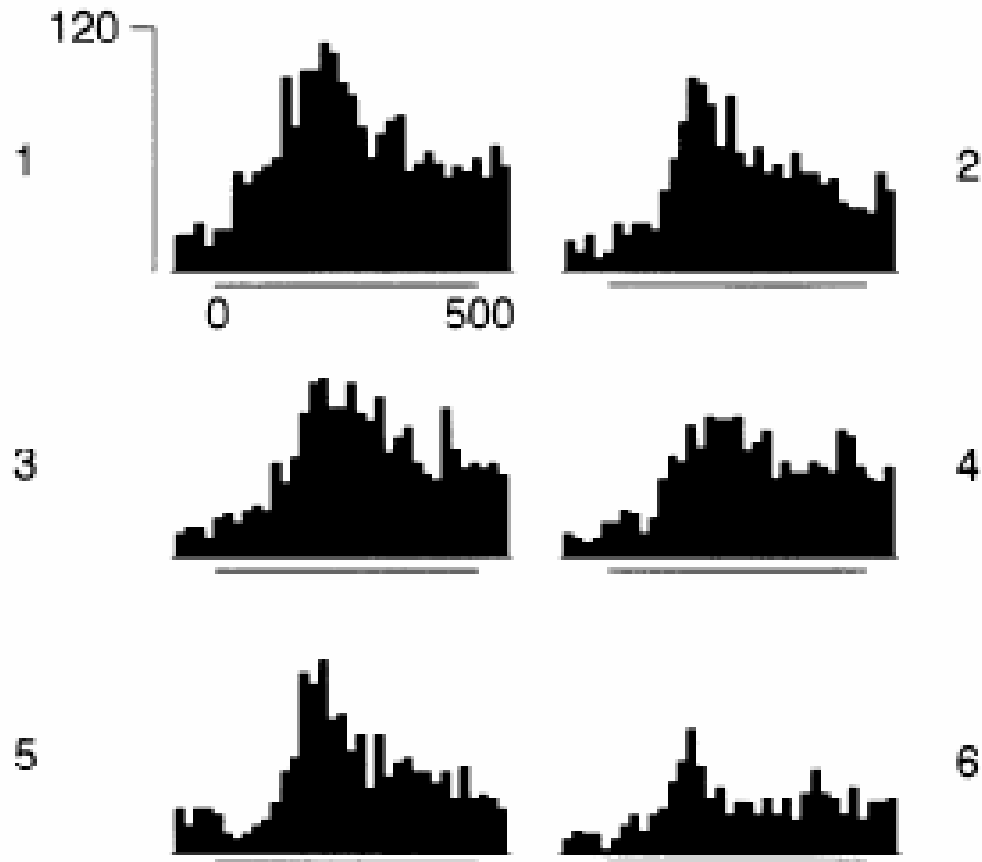
e.g. symmetry judgment, size judgment

Repetition Suppression in Neurons



Courtesy of the American Physiological Association. Used with permission.

Li, Miller and Desimone (1993). *Journal of Neurophysiology*, 69, 1918-1930.



Courtesy of the American Physiological Association. Used with permission.
Li, Miller and Desimone (1993). *Journal of Neurophysiology*,
69, 1918-1930.

Priming and fMRI

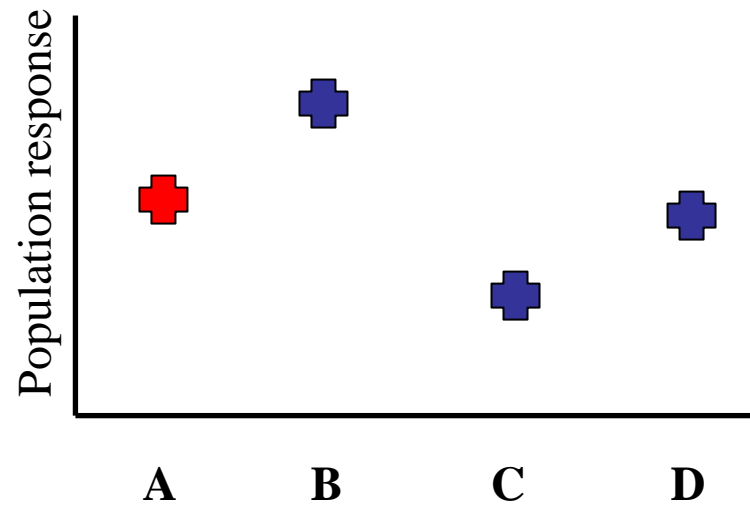
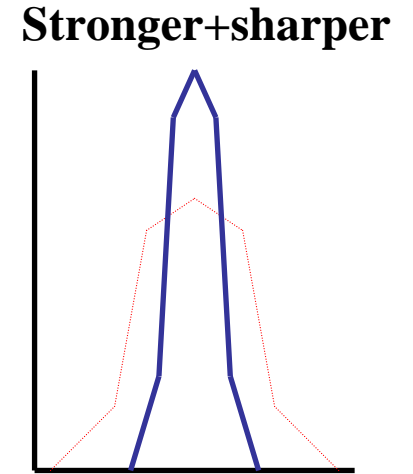
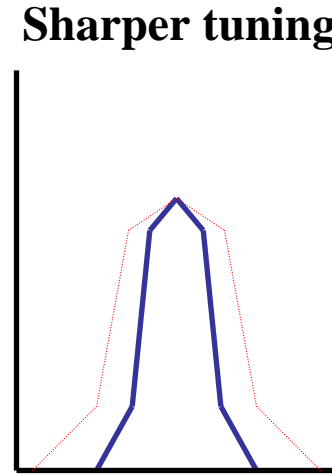
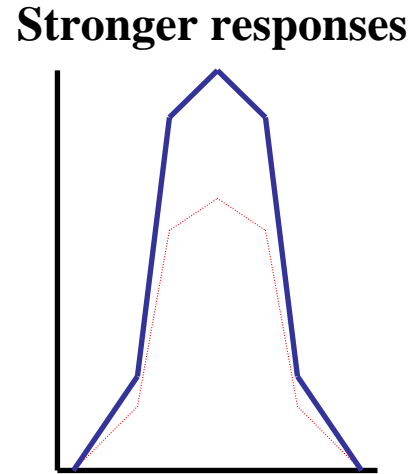
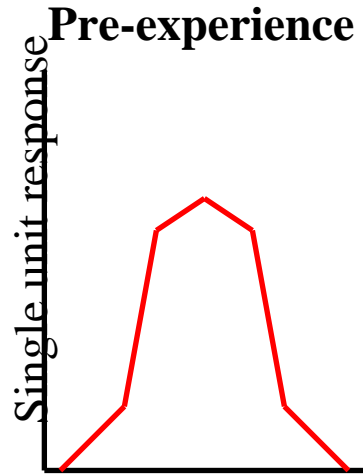
Three images removed due to copyright restrictions.

Figures 1, 2, and 3 from Henson, R., et al. (2000). « Neuroimaging Evidence for Dissociable Forms of Repetition Priming.” *Science*, 287, 1269-1272.
doi: 10.1126/science.287.5456.1269

Henson et al. (2000). *Science*, 287, 1269-1272

Conclusions

- Many different time-scales over which experience modifies both behavior and neural processing
- Likely to be multiple mechanisms

A**B****C****D**

Many different time scales:

- Experience throughout development

example: face recognition ?

Maybe not a good example !

(evolutionary arguments)

Many different time scales:

- Expertise acquired in adulthood

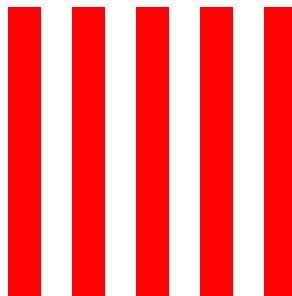
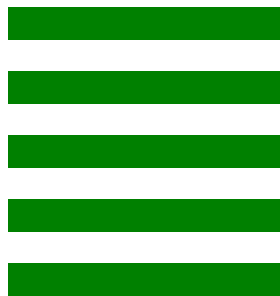
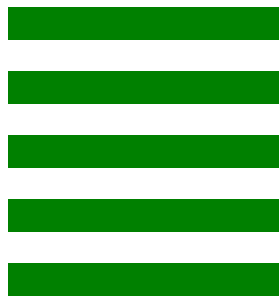
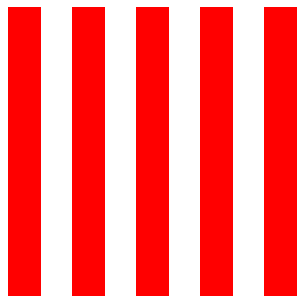
Examples: car and bird experts

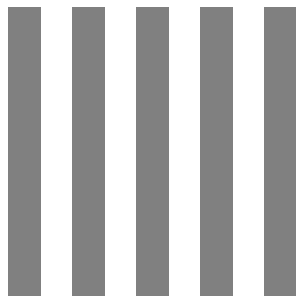
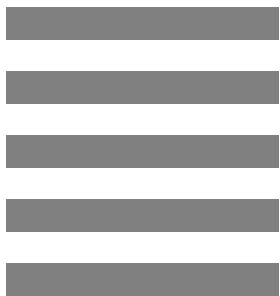
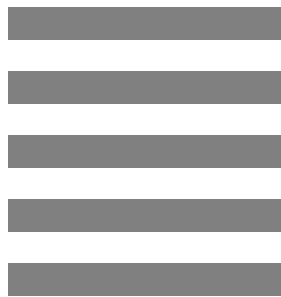
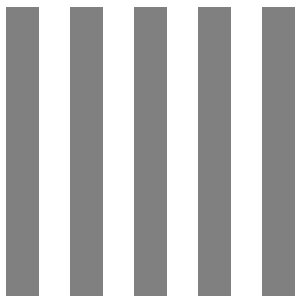
Many different time scales:

- Adaptation

Very short timescale

Example: McCullough effect

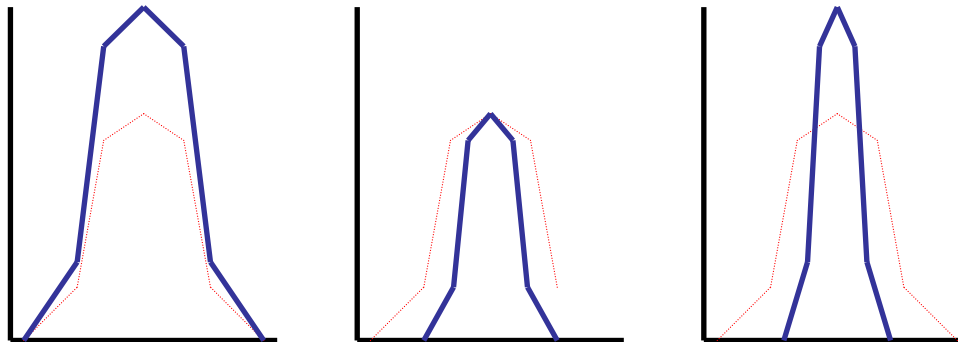




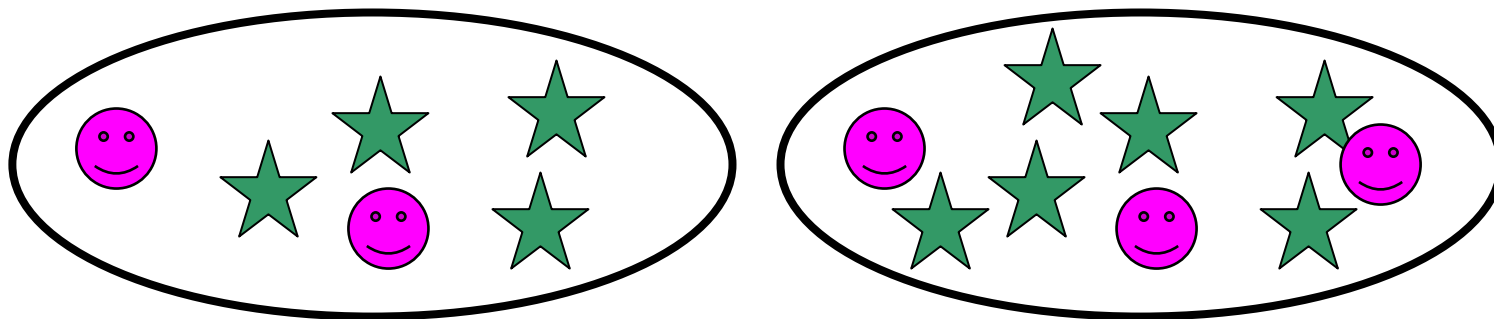
With experience, neural responses might change...

i) selectivities of individual neurons

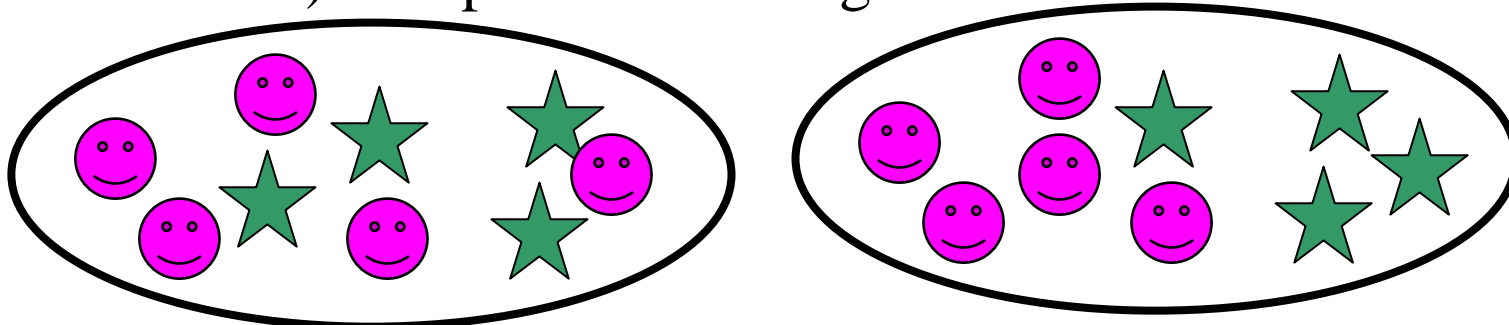
What changes will fMRI "see" after experience with



ii) the total # of neurons w/ a certain selectivity



iii) the spatial clustering of selective neurons



“Visual Word Form Area”

Image removed due to copyright restrictions.

Figure 1 in Cohen, L. et al. "Language-specific tuning of visual cortex? Functional properties of the Visual Word Form Area." *Brain* 125, no. 5 (2002): 1054-1069.
<http://brain.oxfordjournals.org/cgi/content/abstract/125/5/1054>

Cohen et al. (2002). *Brain*, 125, 1054-1069.

Also: Cohen and Dehaene (2004). *NeuroImage*, 22, 466-476

Many different time scales:

- Perceptual learning throughout multiple training sessions

Many studies in low- and high-level vision

Example: greeble training

Two greeble mages removed due to copyright restrictions.

Experience may affect responses over many different time scales:

- Experience throughout development (faces, letters)
- Expertise acquired in adulthood (e.g., car experts)
- Perceptual learning throughout multiple training sessions
- Priming
- Adaptation

Unresolved question:

To what extent distinct mechanisms at different time scales ?

“Visual Word Form Area”

Image removed due to copyright restrictions.

Figure 2 in Cohen, L. et al. "Language-specific tuning of visual cortex? Functional properties of the Visual Word Form Area." *Brain* 125, no. 5 (2002): 1054-1069.
<http://brain.oxfordjournals.org/cgi/content/abstract/125/5/1054>

Cohen et al. (2002). *Brain*, 125, 1054-1069.

Also: Cohen and Dehaene (2004). *NeuroImage*, 22, 466-476

Image removed due to copyright restrictions.

Figure 4 in Cohen, L. et al. "Language-specific tuning of visual cortex? Functional properties of the Visual Word Form Area." *Brain* 125, no. 5 (2002): 1054-1069.
<http://brain.oxfordjournals.org/cgi/content/abstract/125/5/1054>

Attention?