9.71 Functional MRI of High-Level Vision
Fall 2007

Lecture 6: Visual Attention 9.71
October 11, 2007

Reminder: Term paper Outline due October 25 & Midterm Nov 1

Outline of Today's Visual Attention Lecture

A. Introduction to attention

limited capacity and selectivity

B. Three questions about attention

1. How "early" is attentional selection?
2. What are the units of attentional selection?
3. How exactly does attention affect neural responses?

C. Presentations

Tess, on Corbetta et al (2005)

Leah, on Muller & Kleinschmidt (2003)

Lisa, on McMains & Somers (2004)

Term Paper Topics/Outlines due Nov 1!
Must be an fMRI Study of High-level Vision

No idea? Here are some strategies to try for coming up with an experiment:

1. List 3 of your favorite topics from this class.
2. Remind yourself what the key questions are in this area (see lectures notes and syllabus).
3. Read the assigned articles on those topics, in order to help answer #2 and #4. Also type the relevant keywords into Pubmed and browse.
4. Come up with either a new way to answer one of these questions, or a related question that is not already answered.

Or:

Think of an experiment that used a particularly cool method. What other questions might you be able to answer by applying this method to another question?

Some Questions

• what method would you use to find out if a representation (say of chairs) is invariant to changes in position?

• what visual area lies in the calcarine sulcus?

• can fMRI tell you if a brain region is necessary for carrying out a task?

• what is a counterbalanced design?

• how could you determine if neurons in the FFA can discriminate between different coffee cups?

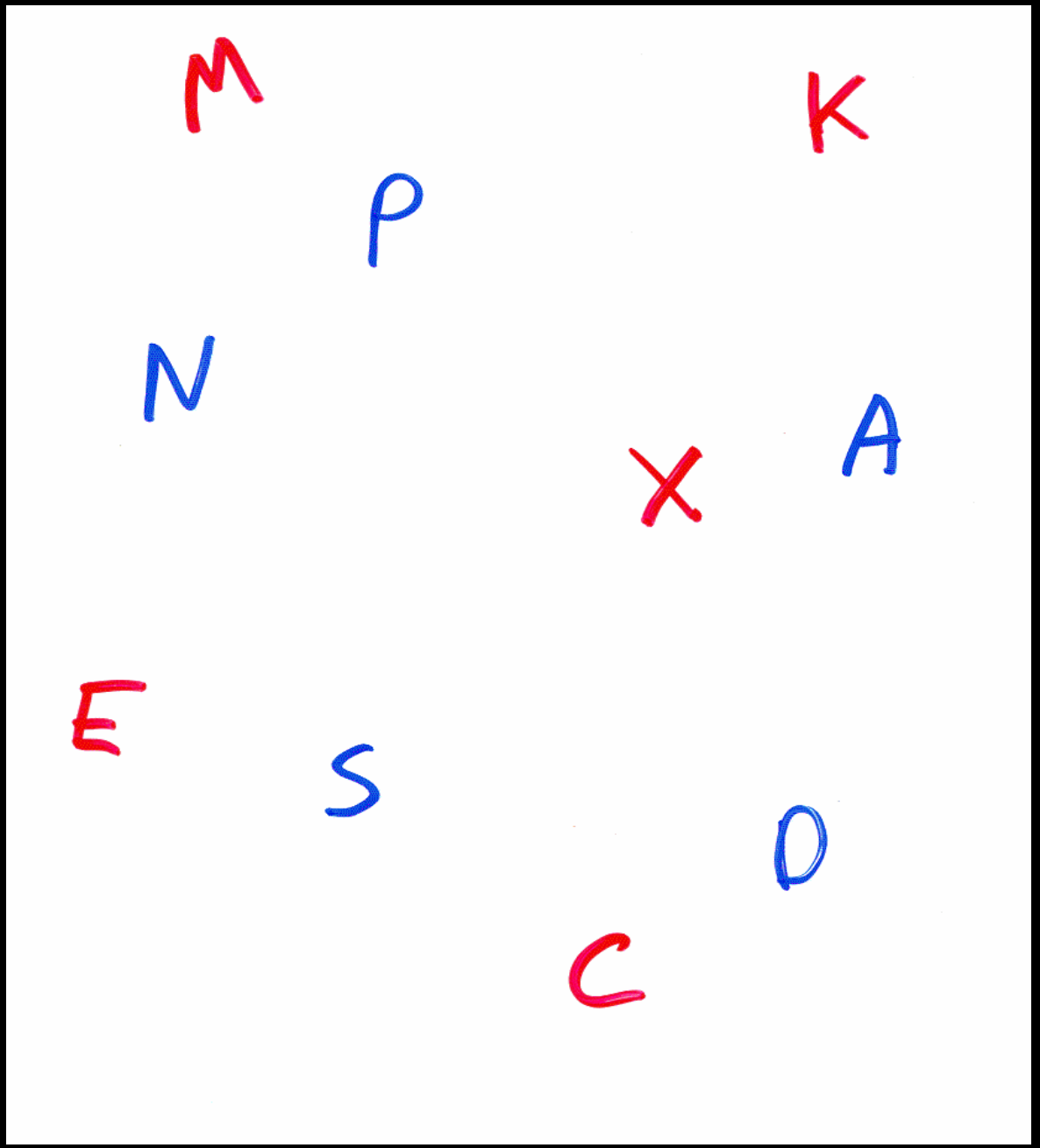
Question to Consider

How do you feel about people driving while talking on their cell phones. Is this a good idea?

Why/why not?

The notion of *capacity*, or *resources*.
The "toaster model": when you plug in the toaster the lights dim.
Which mental processes are "on the same circuit"?
Can you listen to music and read at the same time?
Recognize faces and scenes at the same time?

Identify (to yourself) the blue letters in the following display


M
K
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C

Identify (to yourself) the blue letters in the following display


M
K
P
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X
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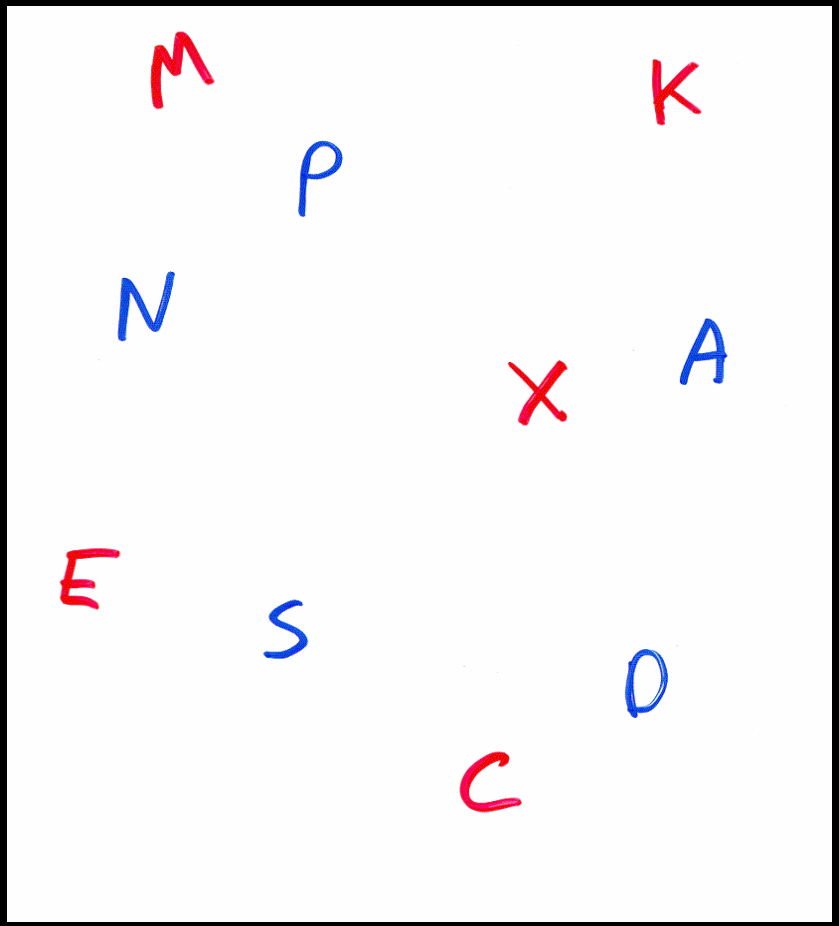
C

Probability of reporting “N” is higher for 2nd display than the 1st

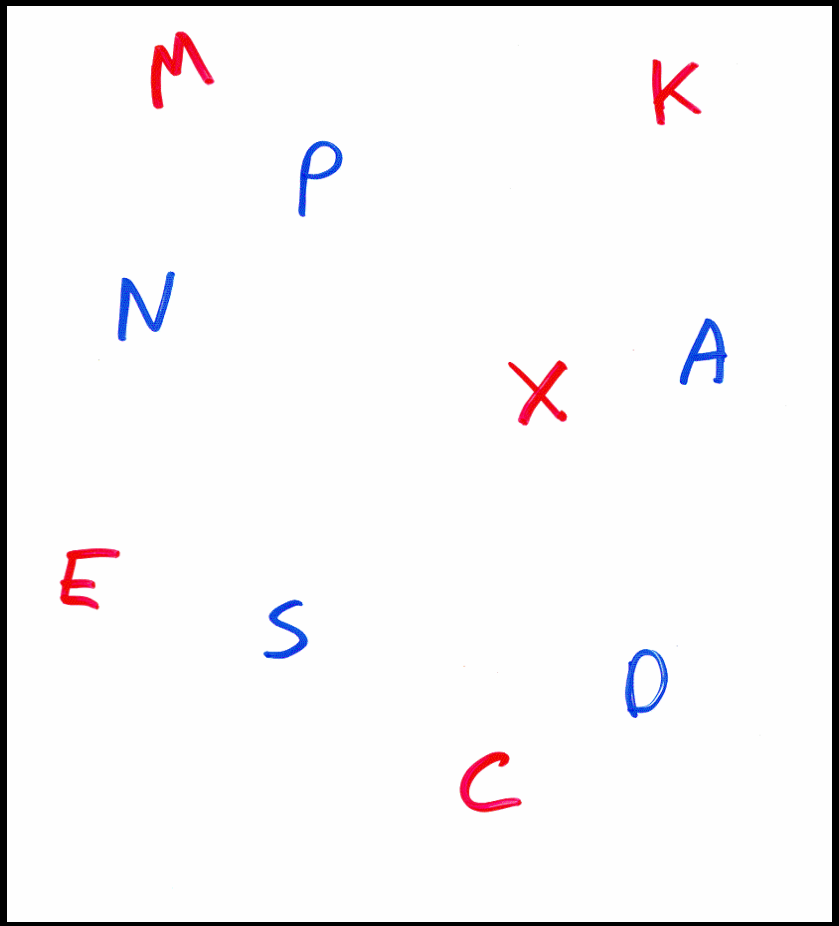


Display 1

Limited capacity – Only a small amount of information on the retina can be fully processed and used for behavior

Selectivity – We have the ability to filter out unwanted information (e.g., the red letters)

Probability of reporting “N” is independent of the number of red letters.



Display 1

Why is our capacity to process visual information limited?

1. Full analysis of everything in the visual field is impossible.
   BUT: Given the massively parallel structure of the human visual system, why cant we process everything at once?

2. We can only direct action to one object or portion of the visual field at a time.
   A pikefish put in a tank with 10 sticklebacks will take much longer to catch the first stickleback than a pikefish put in a tank with 1 stickleback. But why, exactly?

Attention

Attention as a filter that lets attended/selected information in but filters out unattended information.

Two key properties of attention that go hand in hand:

- capacity limits - we cant efficiently process everything at once.
- selectivity - so we select a subset of the available information for detailed analysis

An important distinction realized long ago by Helmholtz…..

Helmholtz: Attention is Different from Fixation

" ...our attention is quite independent of the position and accommodation of the eyes, and of any known alteration in these organs, and free to direct itself by a conscious and voluntary effort upon any selected portion of a dark and undifferentiated field of view. This is one of the most important observations for a future theory of attention."

Physiological Optics, circa 1860, quoted in James Principles, pg. 414

Overt versus Covert Visual Attention

• “overt attention” - eye movements - change in retinal *input*
a very powerful selection mechanism because of the fovea

• “covert attention” - no eye movements, only changes in the way the same retinal image is *processed*

Distinctions re Visual Attention

- overt versus covert attention

- automatic/stimulus-driven attention
  e.g. web pop-ups
  versus controlled/voluntary attention
  e.g. sneaking a peak on your neighbors computer screen

  partly distinct mechanisms

- the *source* of attentional control, versus its *site* and *effect*
  e.g. “who” is turning the knobs versus what brain regions are affected and how exactly are they affected?
  for today, we’ll focus on the latter.

Outline: Three Classic Questions about Attention

1. How “early” is attentional selection?

2. What are the units of attentional selection?

3. How exactly does attention affect neural responses?

Outline: Three Classic Questions about Attention

1. How “early” is attentional selection?
   - Anatomically
   - Temporally

2. What are the units of attentional selection?

3. How exactly does attention affect neural responses?

How "early" does attention select? Anatomy:

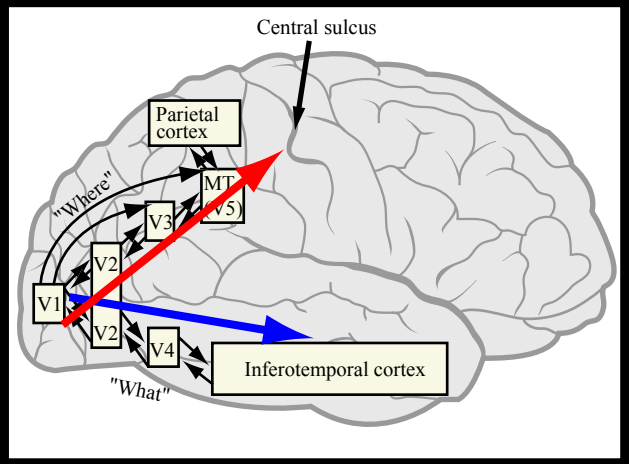
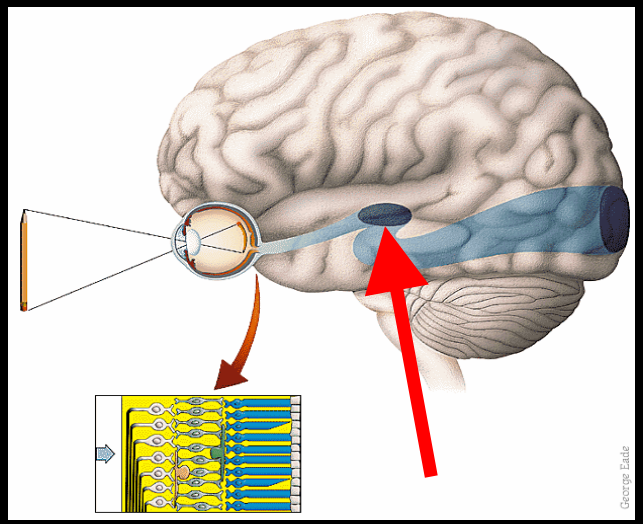


Figure by MIT OpenCourseWare.

Prerequisite for attentional control: Bidirection information flow.



Courtesy of George Eade. Used with permission.

First structure in visual pathway that Receives feedback from higher centers: The LGN.

Where along this pathway can we first see attentional effects?

Attentional effects in V1 w/ Physiology

Early physiological studies found little evidence for attentional effects in V1 but large effects at later stages.

But three studies that did report some effects in V1:

Motter et al (1993)

Vidyasagar (1998)

Roelfsema et al (1998)

None of this really convinced the field.

Then people started testing this question with fMRI….

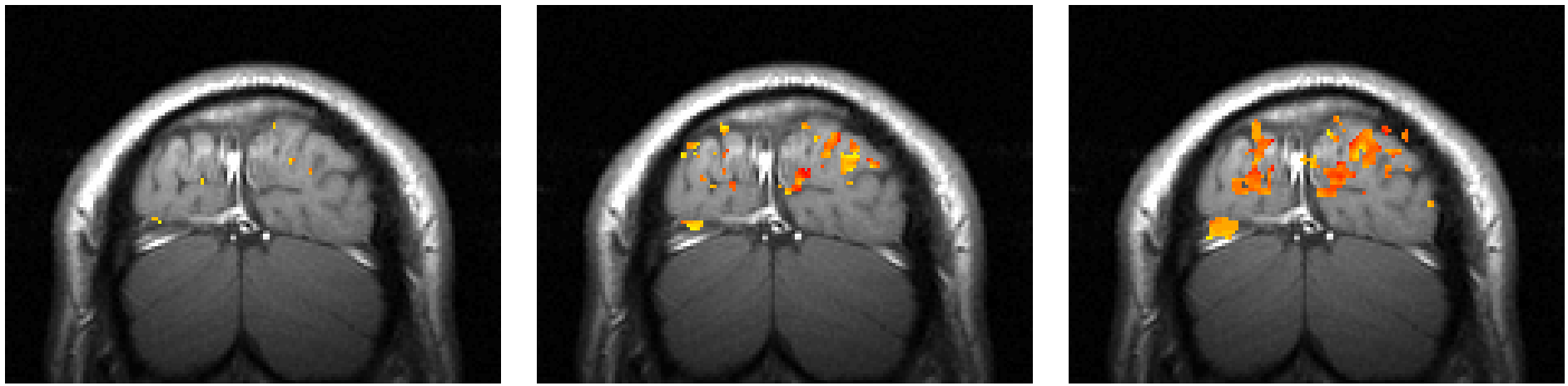
Attentional Effects in V1 w/ fMRI

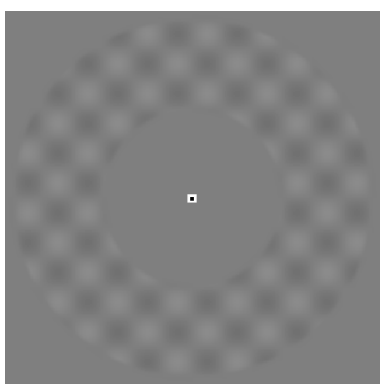
In 1998-9, six papers were published showing often large effects of attention on V1:

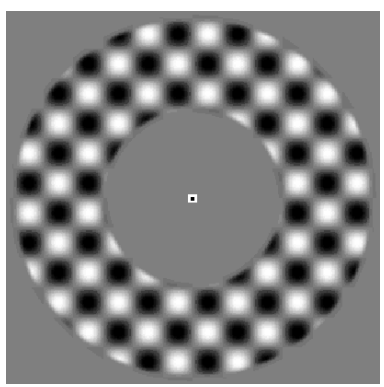
- Watanabe et al, 98
- Somers et al, 99
- Brefczynski & DeYoe, 99
- Kastner et al, 99
- Martinez et al, 99
- Ghandhi et al, 99

I'll describe one of the most elegant studies in detail:
Ress, Backus, & Heeger, *Nat Neurosci* **3:**940-, 2000

Responses increase with stimulus contrast in V1





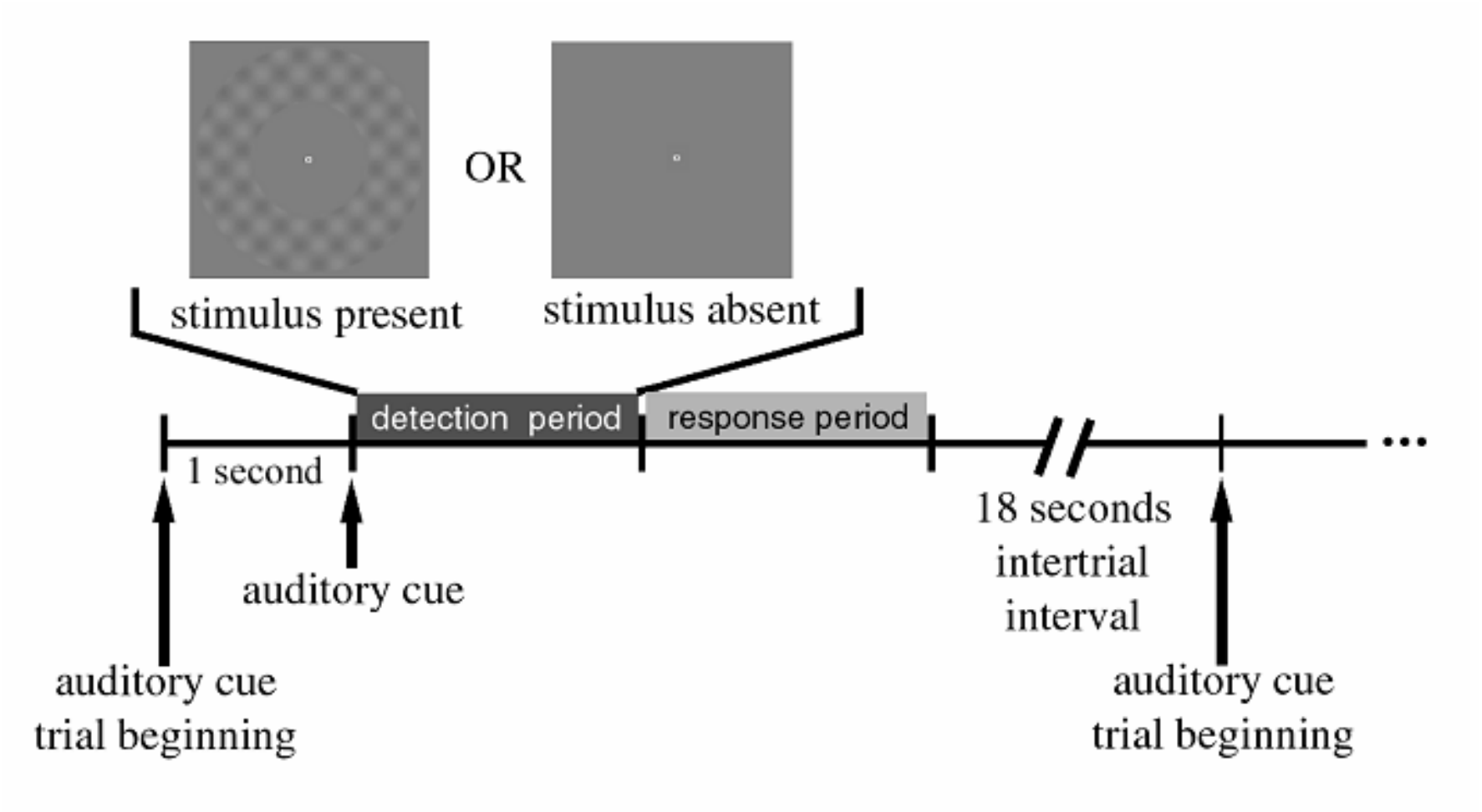


stimulus contrast

low → high

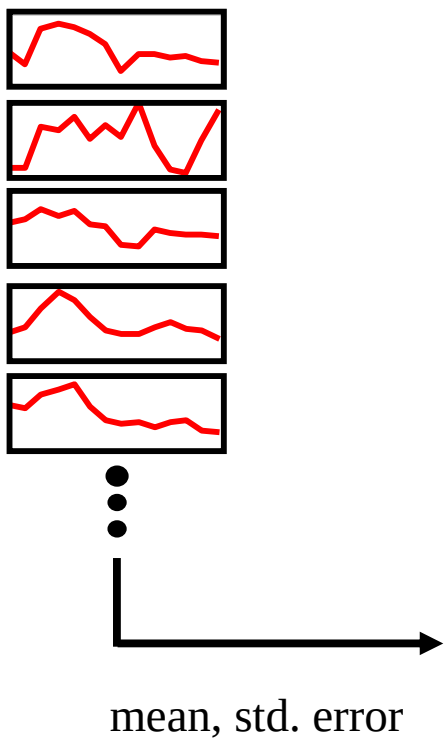
Ress, Backus, & Heeger, *Nat Neurosci* **3:**940-, 2000

Pattern detection protocol



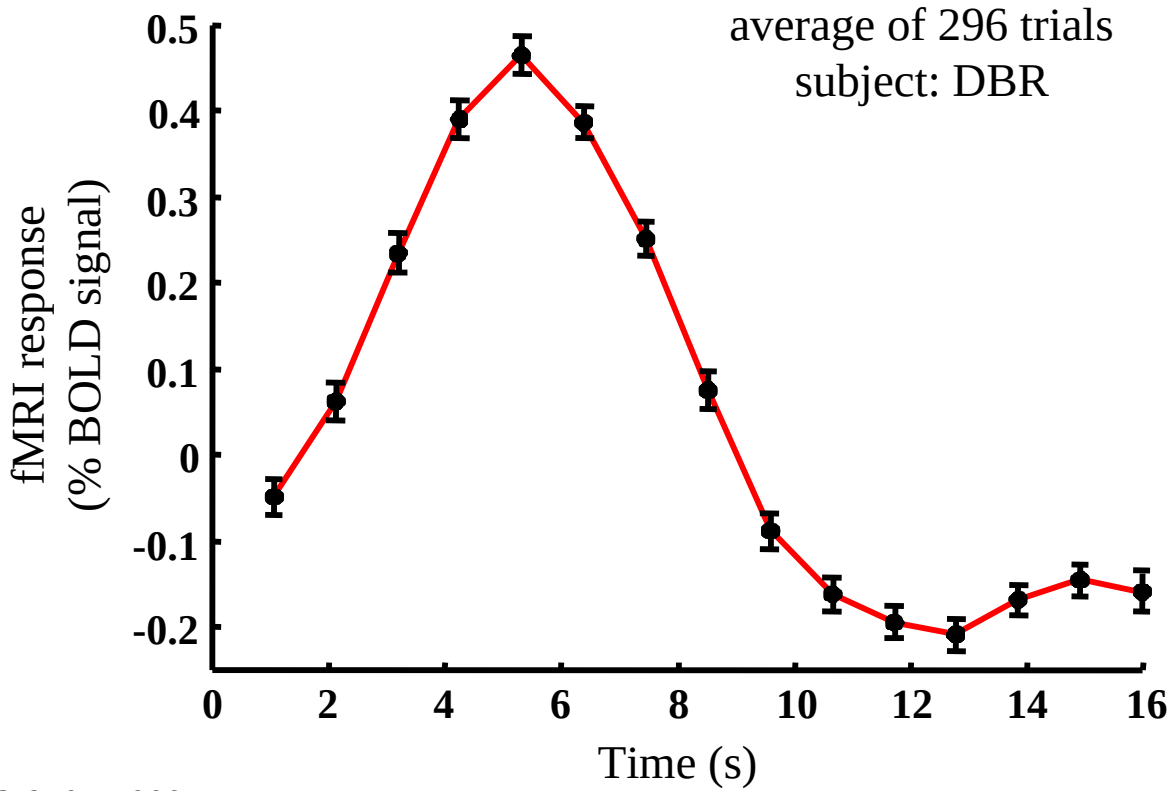
Strong response when stimulus present

Individual trial time series



mean, std. error

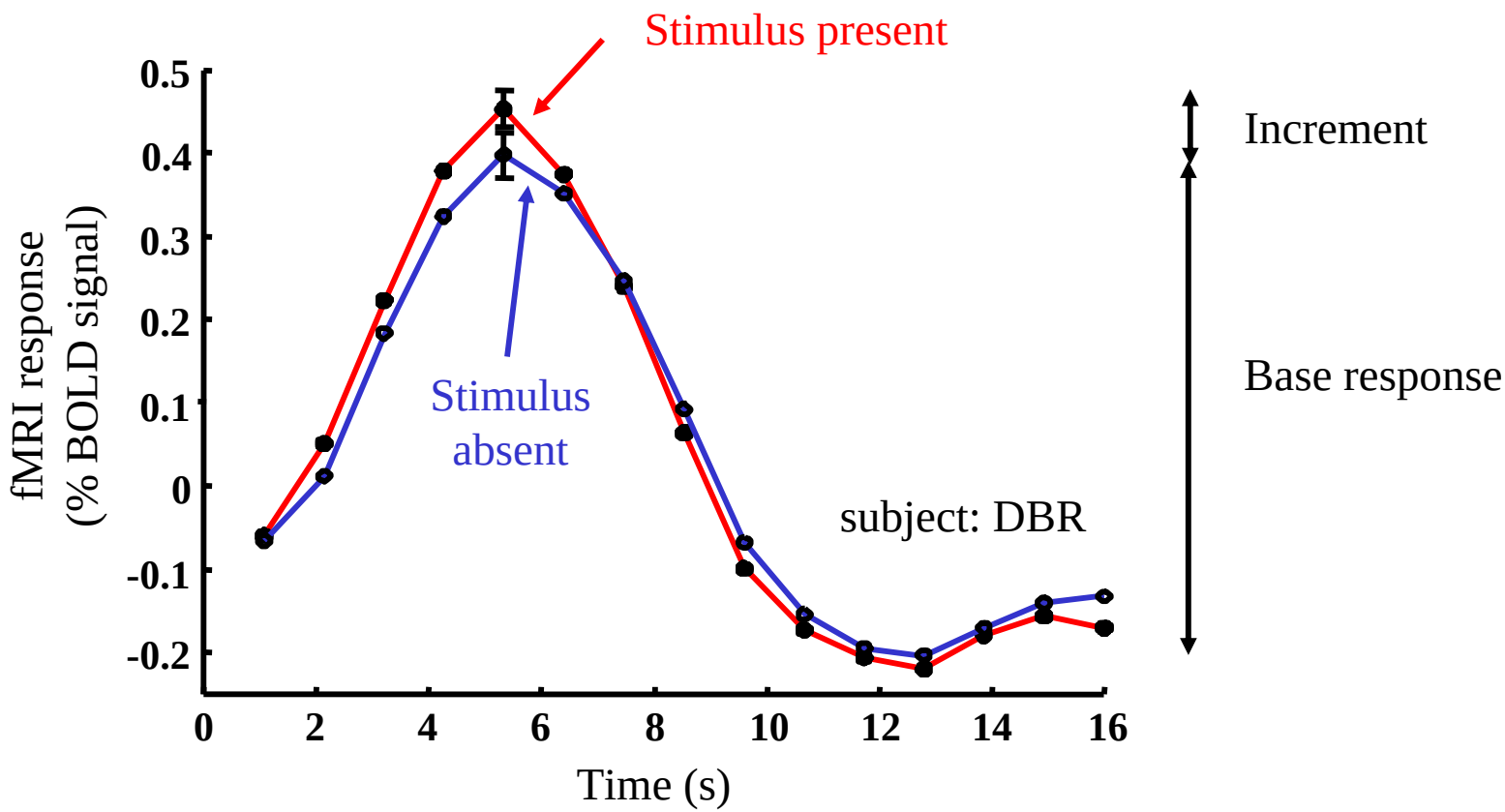
What do you expect to see when the stimulus is *absent*?



Ress, Backus, & Heeger, *Nat Neurosci* **3:**940-, 2000

Large response even when stimulus absent!

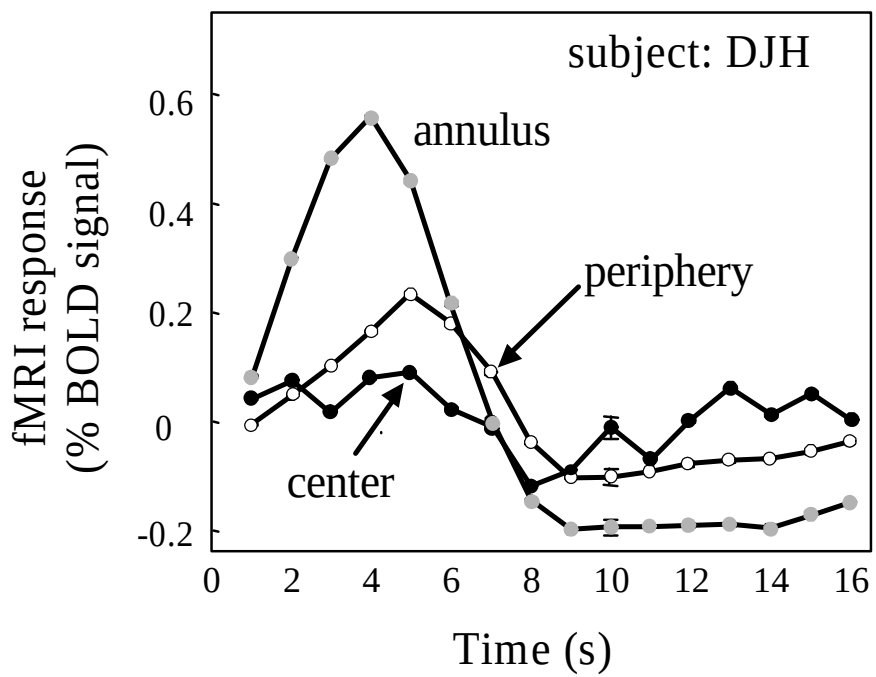
- Base response when stimulus absent — attention?
- Small increment when stimulus present — sensory signal?



Ress, Backus, & Heeger, *Nat Neurosci* **3:**940-, 2000

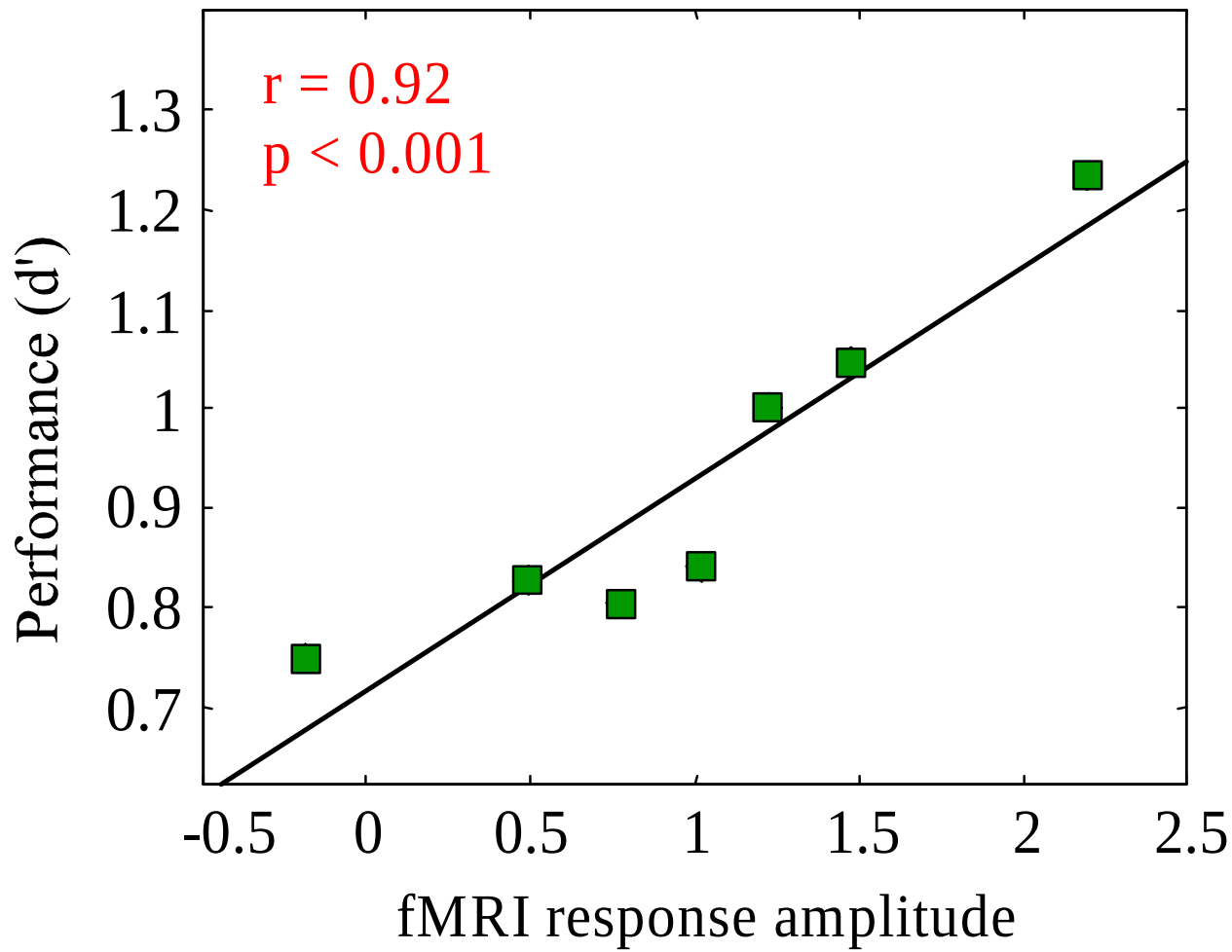
Base response is spatially selective

Analyzed data in each of 3 subregions of V1:



Ress, Backus, & Heeger, *Nat Neurosci* **3:**940-, 2000

Base response predicts performance



Ress, Backus, & Heeger, *Nat Neurosci* **3:**940-, 2000

How "early" does attention select?
Anatomy:

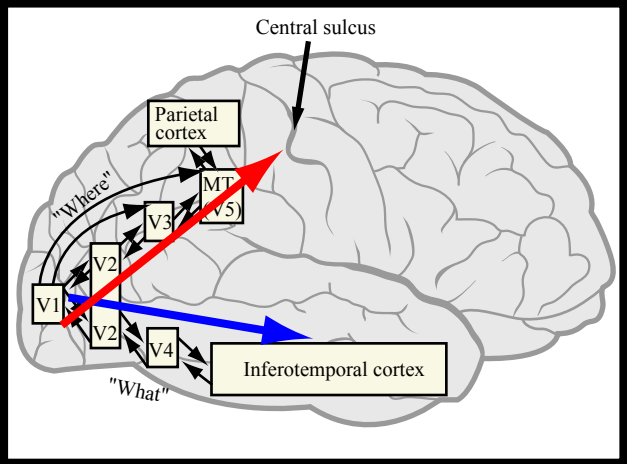
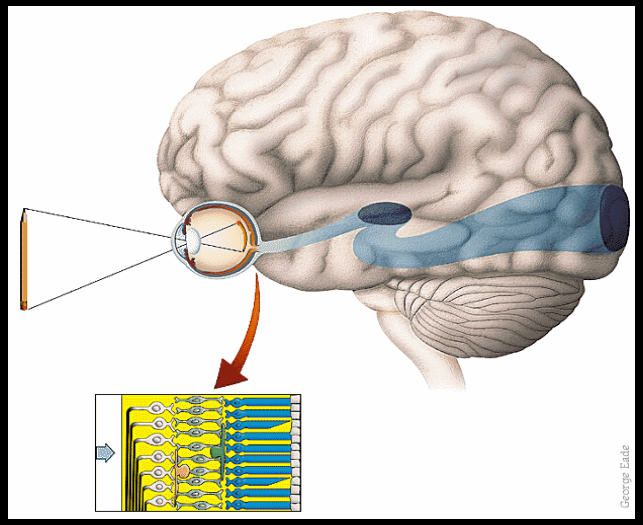


Figure by MIT OpenCourseWare.



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So: clear attentional effects in V1

What about the LGN?

Massive direct cnxns from V1 to LGN
& via the thalamic reticular complex (TRN).

Crick (1984) and Koch & Ullman (1985)
Hypothesized a major role for these structures in attention.

But few studies. and little evidence for this until:
Vanduffel et al (2000) deoxyglucose
O'Connor et al (2002)….

Attentional response modulation in the human LGN

O’Connor, Fukui, Pinsk, & Kastner

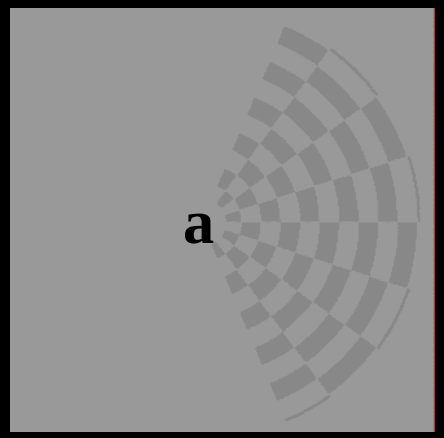
(Nature Neuroscience, November 2002)

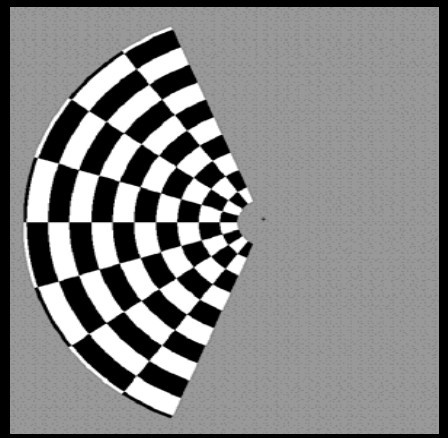
Activating the human LGN: Checkerboards

Images removed due to copyright restrictions.
See Fig. 1 in O'Connor, D., M. M. Fukui, M. A. Pinsk, and S. Kastner.
"Attention modulates responses in the human lateral geniculate nucleus."
Nature Neuroscience 5 (2002): 1203-1209.

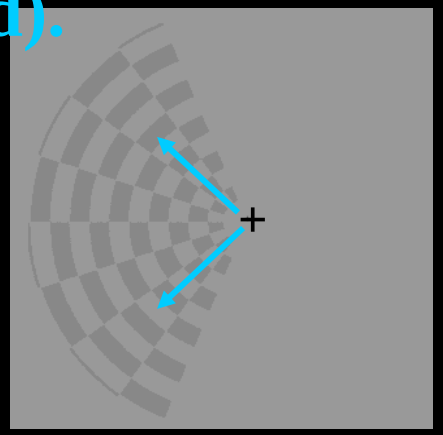
Experimental Design

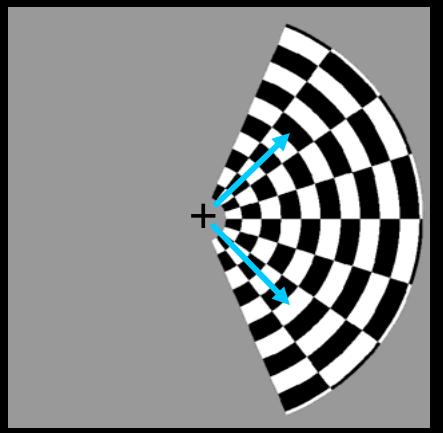
Unattended (task: count letters among digits in RSVP)





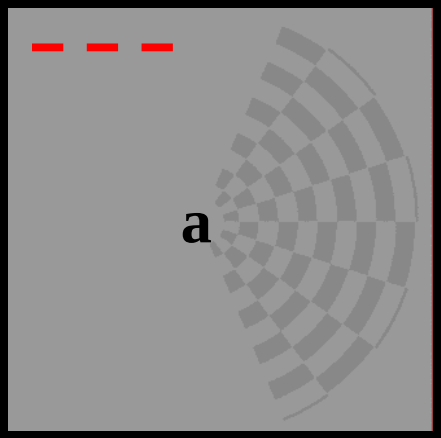
Attended (task: report luminance changes in checkerboard).

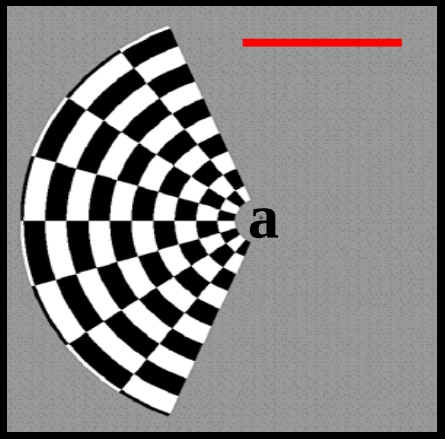


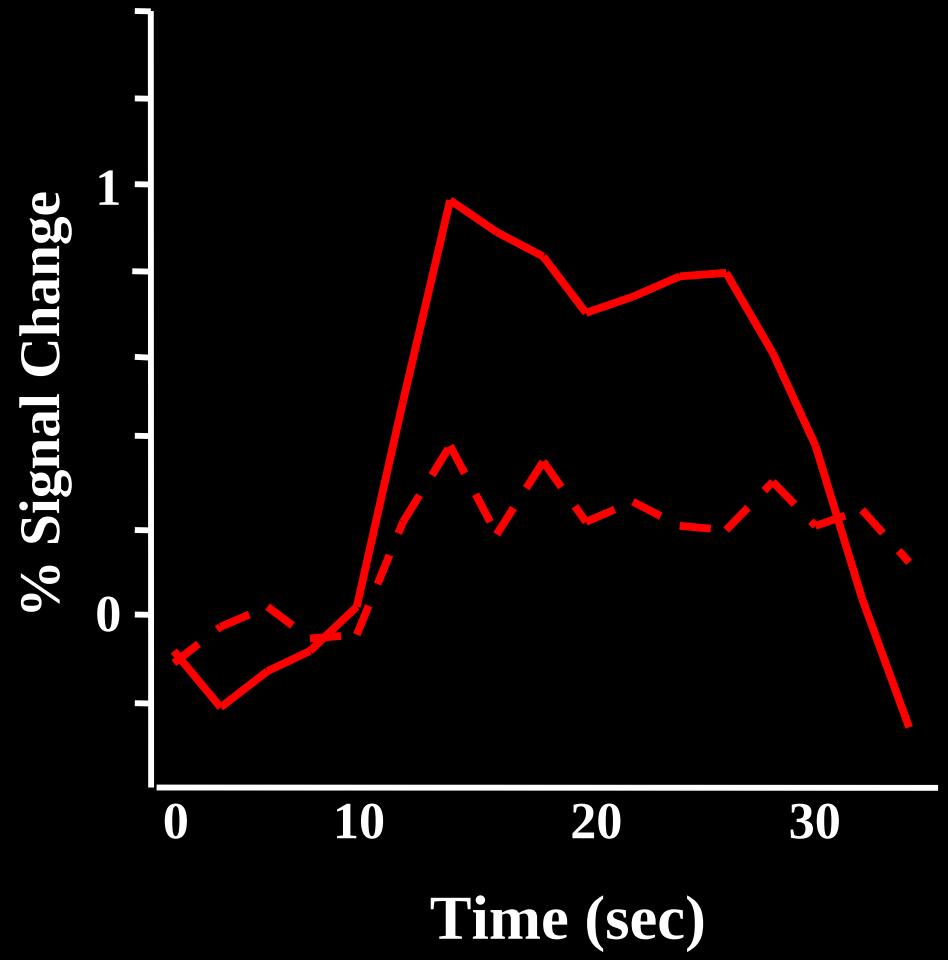


LGN: Contrast Effects

Unattended





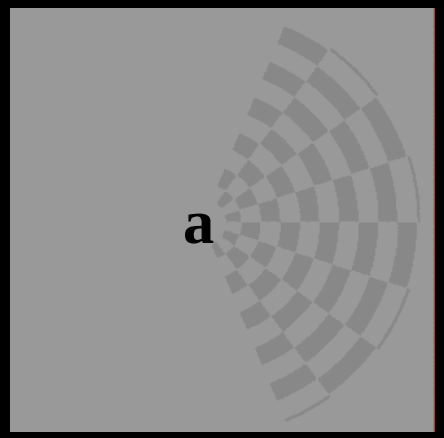


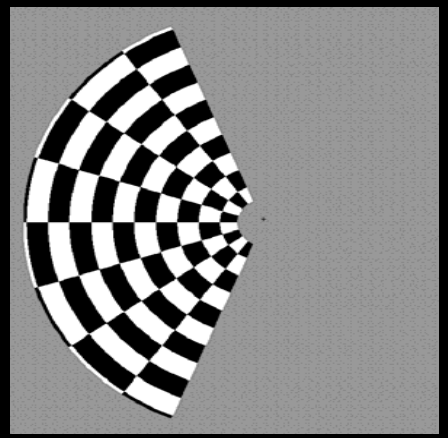
N=4

Courtesy of Sabine Kastner. Used with permission.

Experimental Design

Unattended (task: count letters among digits in RSVP)





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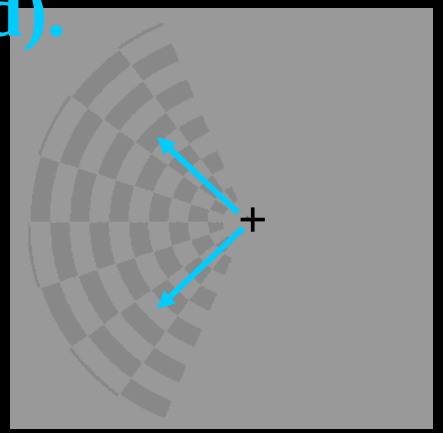
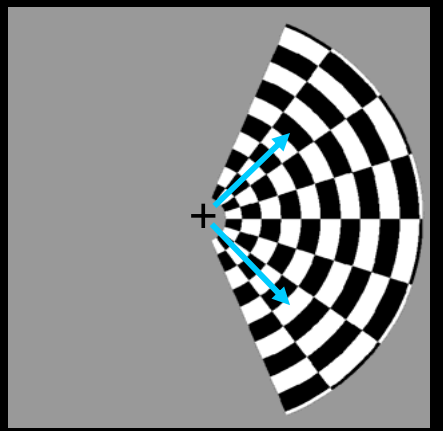
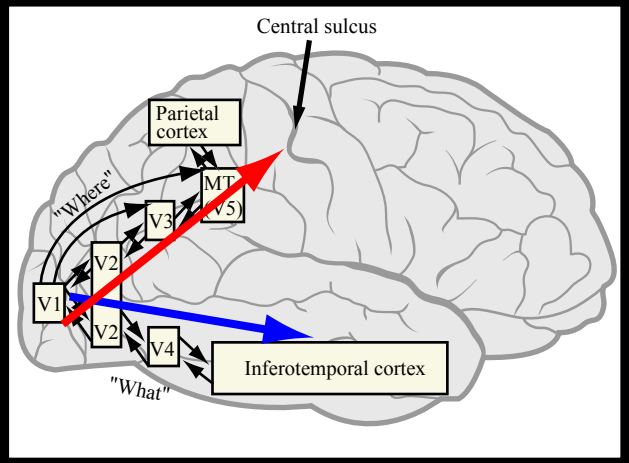




How *anatomically* "early" does attention select?



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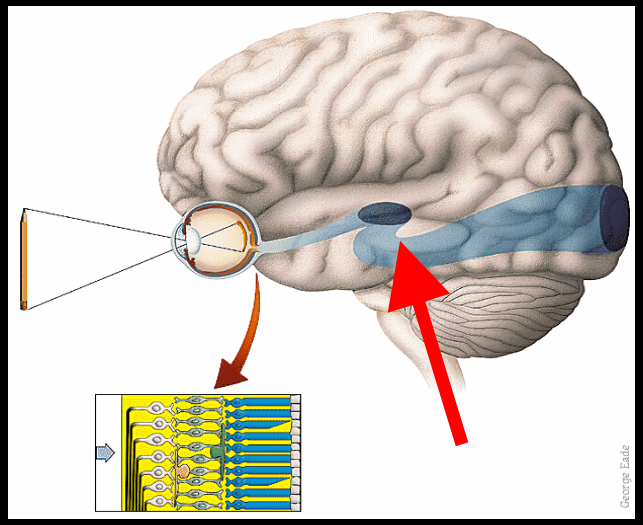

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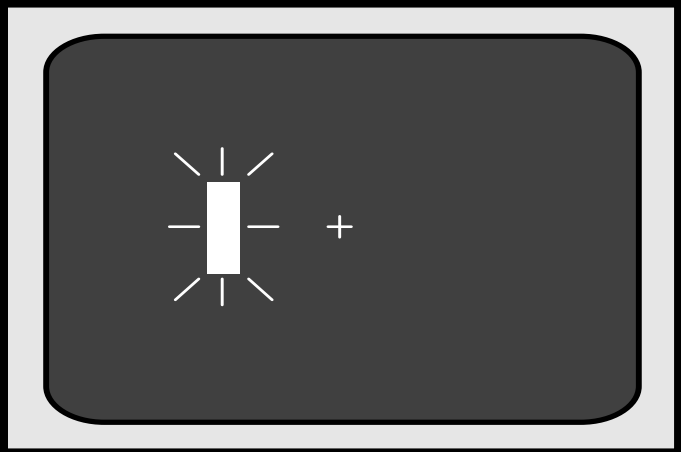
Can already find attentional modulation in the LGN, the first structure in the visual pathway that receives feedback from higher centers. That's an anatomically early stage.

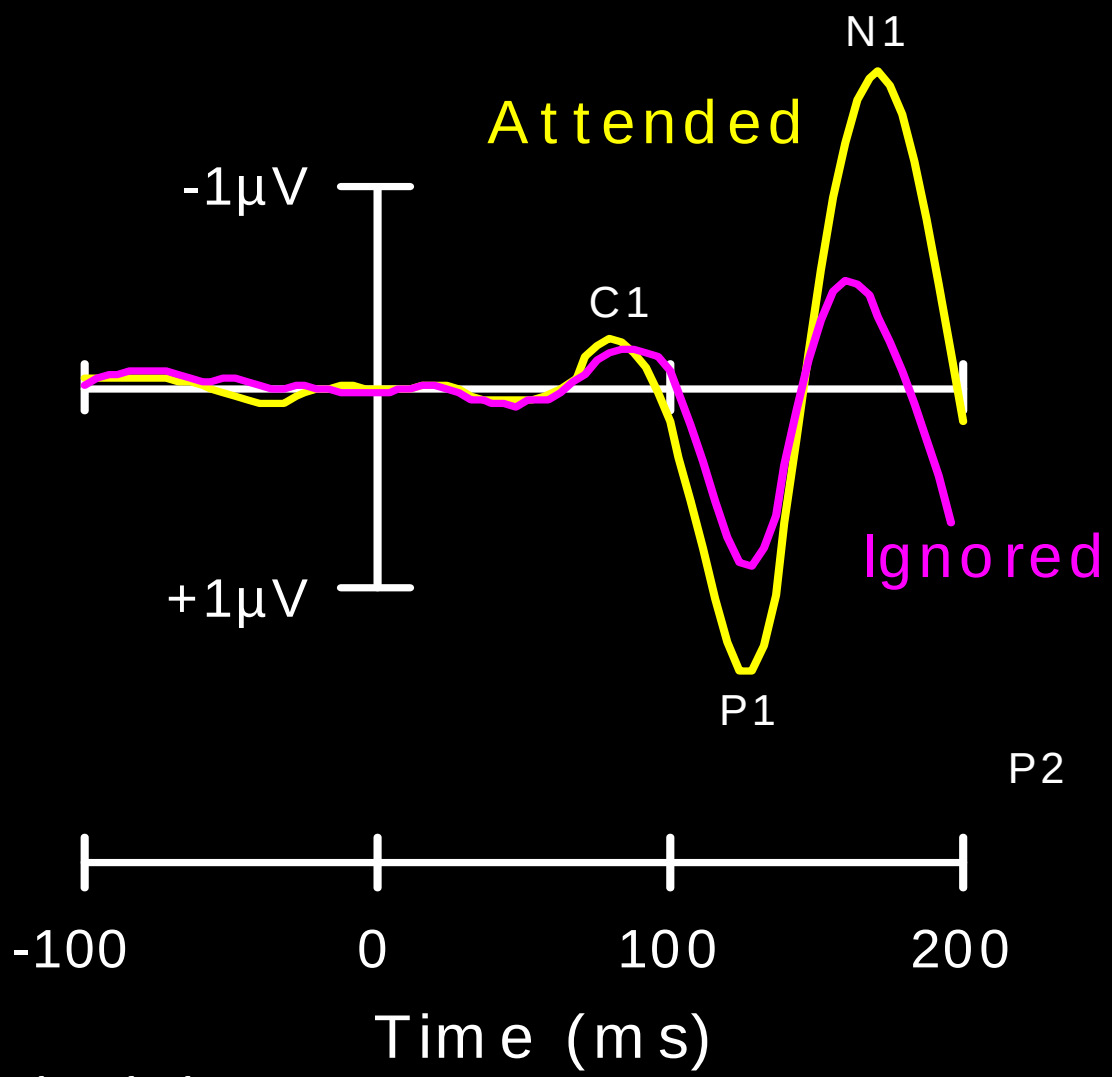
BUT: are these modulations of the first pass of visual information up the visual system, or do they occur only at later latencies?

With fMRI we cannot tell.

But ERPs can be very informative…

Spatial Attention: 40-200 ms





“C1” wave comes from V1; Does not show attentional modulation.

Outline

1. How “early” is attentional selection?
   - Anatomically: very early (LGN)
   - Temporally: after the first feedforward pass thru V1.

2. What are the units of attentional selection?

3. How exactly does attention affect neural representations?

Outline

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Test: when you try to select a particular feature at a particular location,

Does attention select: what else “comes along for the ride”?

locations? >>>other features at the same location

objects? >>>other features in the same object

features? >>> other stimuli sharing the same features

Neural responses a good way to answer this kind of question.

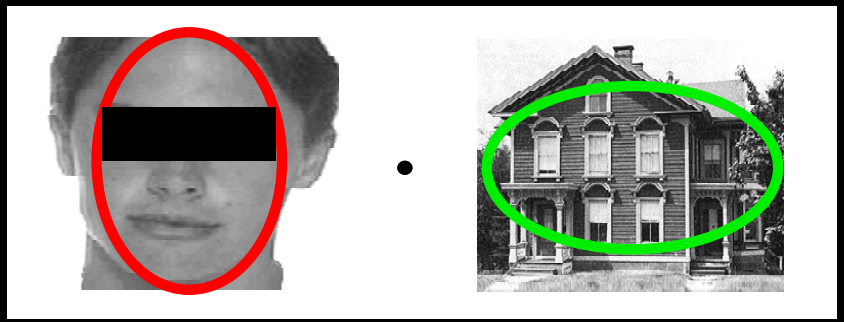
Note: these are not mutually exclusive.

1. Does attention select locations?

Downing & Kanwisher

PREDICTION OF LOCATION-BASED ATTENTION:
All the visual information at the attended location will be enhanced, *whether task-relevant or not*.

For example, in this stimulus:

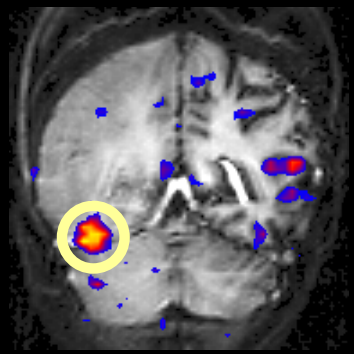


attention to red oval >> enhancement of representation of face
attention to green oval >> enhancement of representation of house

Face photo modified by OCW for privacy considerations.

Overall Logic

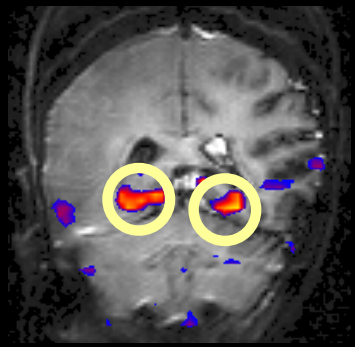
Fusiform face area
(FFA)



Faces > Houses

fMRI signal from FFA:
a measure of the strength of the neural response to a face stimulus

Parahippocampal place area
(PPA)



Houses > Faces

fMRI signal from PPA:
a measure of the strength of the neural response to a house stimulus

Note: this use of fMRI signals as markers of particular processes is very useful in attention research, since we can measure the response to a stimulus without asking subjects about it & hence making it attended.

Does attention select locations?

Downing & Kanwisher

•stimuli like this appear for 160 ms, once every 2 sec in a random order

•Ss fixate the center dot; attend to the red oval or green oval (cued by block)

• Ss report orientation of attended oval

• faces and houses are never task relevant

• all stimulus conditions randomly interleaved

Face photo modified by OCW for privacy considerations.

Does Attention Select Locations?

Downing & Kanwisher

Predictions of Location-Based Selection

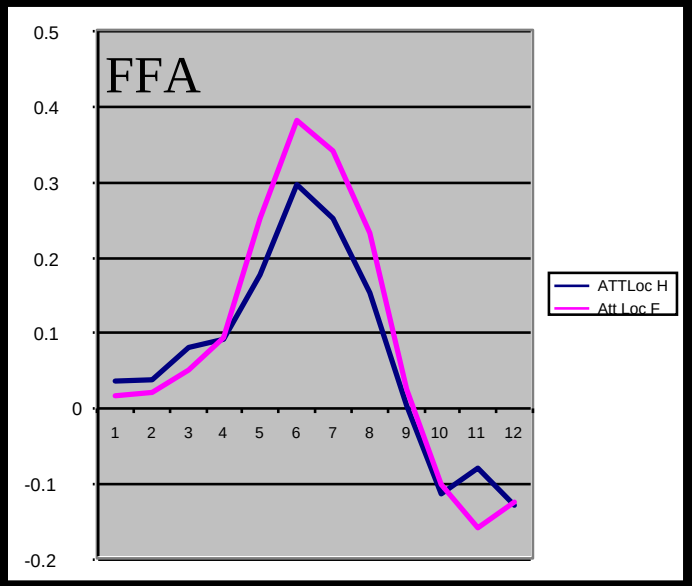
FFA: MR signal higher when the face is at attended location than when the house is

PPA: MR signal higher when the house is at attended location than when the face is

Does Attention Select Locations?

Downing & Kanwisher

YES!



Predictions of Location-Based Selection

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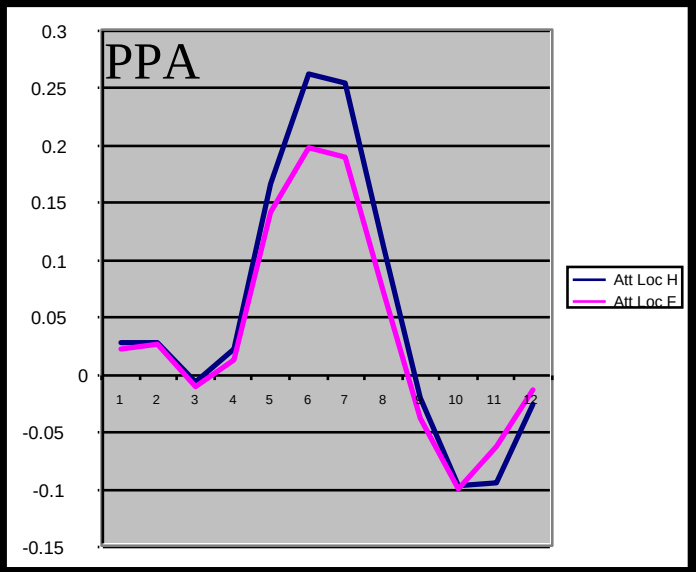
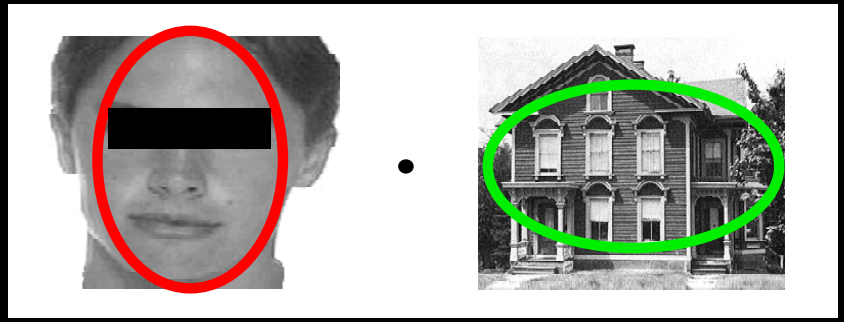


What does attention select?

locations?

enhancement of irrelevant information at the same location



Similar single-unit results by Connor et al 96

"objects"?

enhancement of irrelevant attributes of the attended object

features?

enhancement of irrelevant objects sharing features w/ the target object.

Does attention select “objects”?

O’Craven, Downing & Kanwisher (1999)

PREDICTION OF OBJECT-BASED ATTENTION:
All the visual attributes *of the attended object* will be enhanced, *whether task-relevant or not*.

For example, in this stimulus:

faces moves back and forth
house remains stationary
and is slightly off center

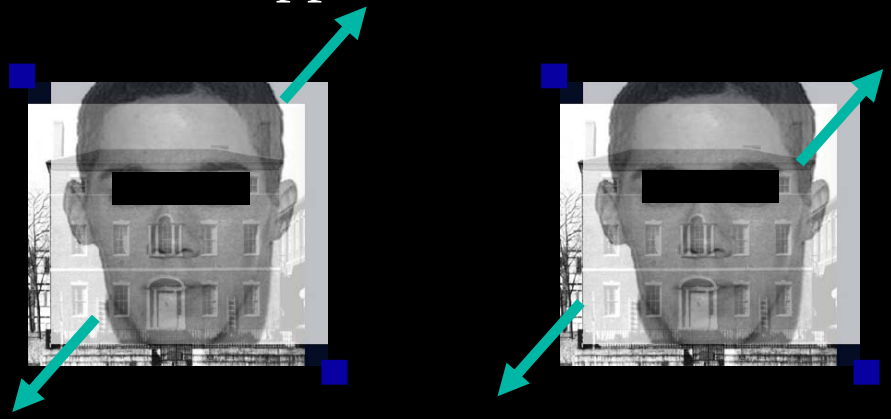
attention to motion >> enhancement of representation of face
attention to position >> enhancement of representation of house

Face photo modified by OCW for privacy considerations.

Does Attention Select Objects?

O'Craven, Downing & Kanwisher (1999)

•stimuli like this appear for 200 ms, once every 2 sec



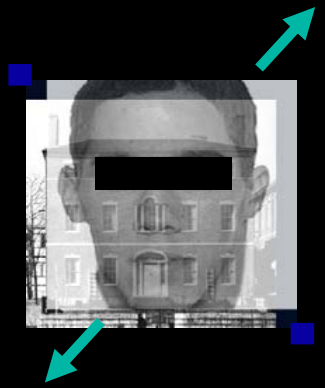
•either face moves,or house moves in a random order

•Ss fixate the center dot; attend to motion or position (cued by block)

• faces and houses never task relevant

• all visual features are superimposed in the same location

Face photos modified by OCW for privacy considerations.



Does Attention Select Objects?

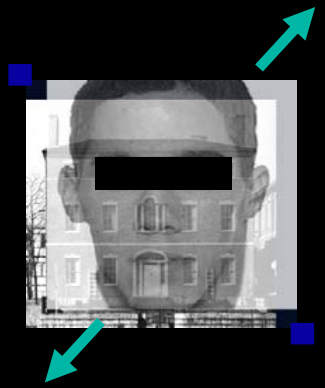
O'Craven, Downing & Kanwisher (1999)

Predictions of Object-based Selection

FFA: MR signal higher when the face is the irrelevant property of attended object than when the house is

PPA: MR signal higher when the house is the irrelevant property of attended object than when the face is

Face photo modified by OCW for privacy considerations.



1b. Does Attention Select Objects? YES!

O'Craven, Downing & Kanwisher (1999)

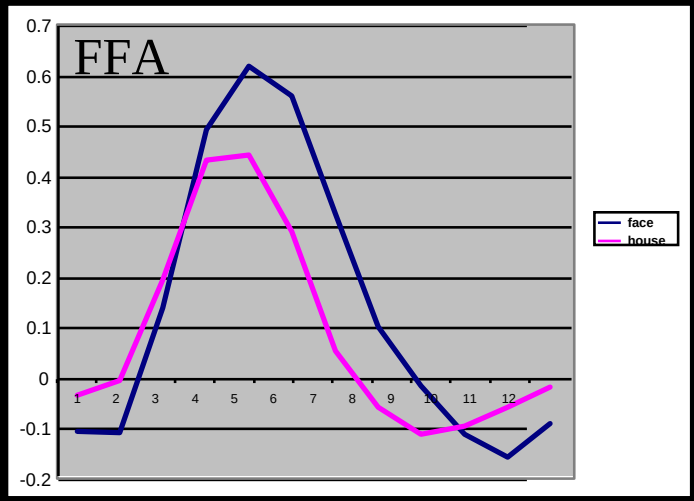
Predictions of Object-based Selection

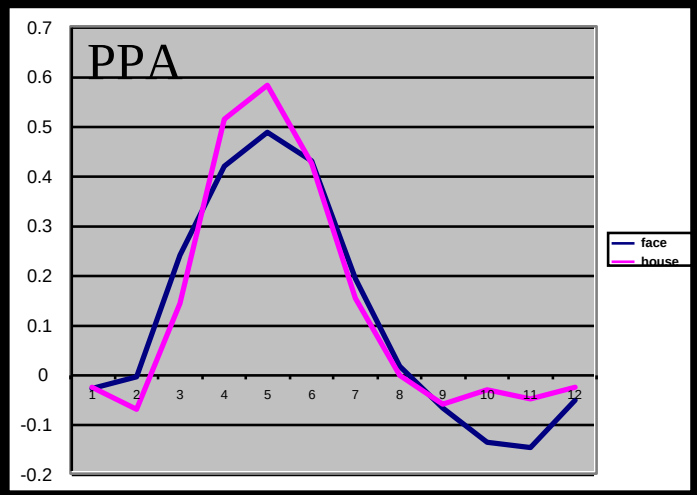
FFA: MR signal higher when the face is the irrelevant property of attended object than when the house is

PPA: MR signal higher when the house is the irrelevant property of attended object than when the face is

- loc-based selection cannot easily explain

Results



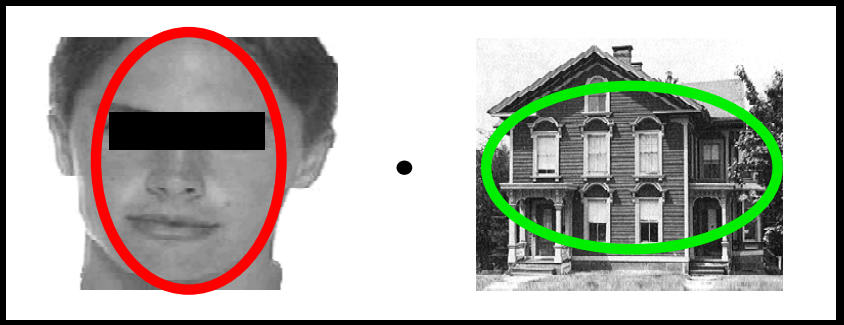


Face photo modified by OCW for privacy considerations.

What does attention select?

locations?

enhancement of irrelevant information at the same location



"objects"?

enhancement of irrelevant attributes of the attended object

features?

enhancement of irrelevant objects sharing features w/ the target object.

Logic:

If attention selects visual features, then when a subject tries to attend to a given feature in a given location, other instances of that same feature elsewhere in the visual field will get enhanced along with the attended item.

Saenz et al (2002) tested this hypothesis for color and for motion, following the logic of a similar paper by Treue & Trujillo (1999).

Experiment 1: Influence of unattended motion features on visual cortex

target **ignored**

Attend one direction of motion in the target area (cued to shift attention from up to down every 20s)

Two stimuli per trial.

Task: which stimulus has faster motion?

Image removed due to copyright restrictions. See Fig. 1a in Saenz, M., G. Buracas and G. Boynton. “Global effects of feature-based attention in human visual cortex.” Nature Neuroscience 5, no. 7 (2002): 631-632.

-Recorded BOLD signal in V1, V2, V3, V3A, MT+ in hemisphere contralateral to ignored stimulus

-baseline: just fixation point

BOLD response over time for ignored stimulus for MT+

(same v. different direction as attended direction)

Image removed due to copyright restrictions. See Fig. 1b in Saenz, M., G. Buracas and G. Boynton. “Global effects of feature-based attention in human visual cortex.” Nature Neuroscience 5, no. 7 (2002): 631-632.

All visual areas responded more strongly to ignored stimulus when it moved in the same direction as the attended motion.

Response amplitudes to ignored motion stimulus (same vs diff direc of motion as target direction)

Image removed due to copyright restrictions. See Fig. 1c in Saenz, M., G. Buracas and G. Boynton. “Global effects of feature-based attention in human visual cortex.” *Nature Neuroscience* 5, no. 7 (2002): 631-632.

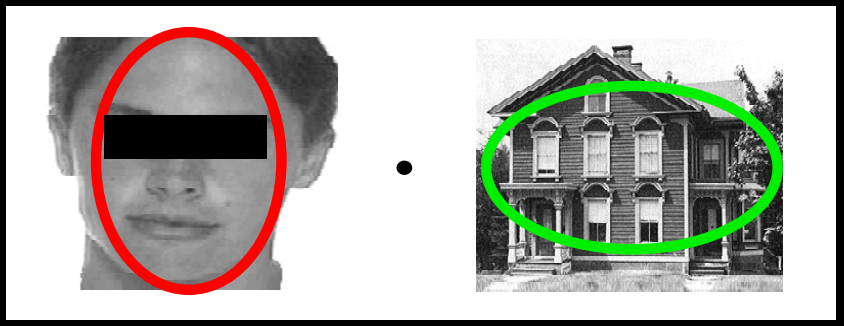
Exp 2: Find same thing with color.

Saenz et al (2002)

What does attention select?

locations?

enhancement of irrelevant info at the same location



"objects"?

enhancement of irrelevant attributes of target object

features?

enhancement of irrelevant objects sharing features w/ the target object.

Image removed due to copyright restrictions. See Fig. 1a in Saenz, M., G. Buracas and G. Boynton. “Global effects of feature based attention in human visual cortex.” Nature Neuroscience 5, no. 7 (2002): 631 632.

Duncan & Desimone’s “biased competition” model: features with common object, location, or feature “stick together” in the competition.

Face photos modified by OCW for privacy considerations.

Biased Competition Model of Attention (Desimone & Duncan, 95)

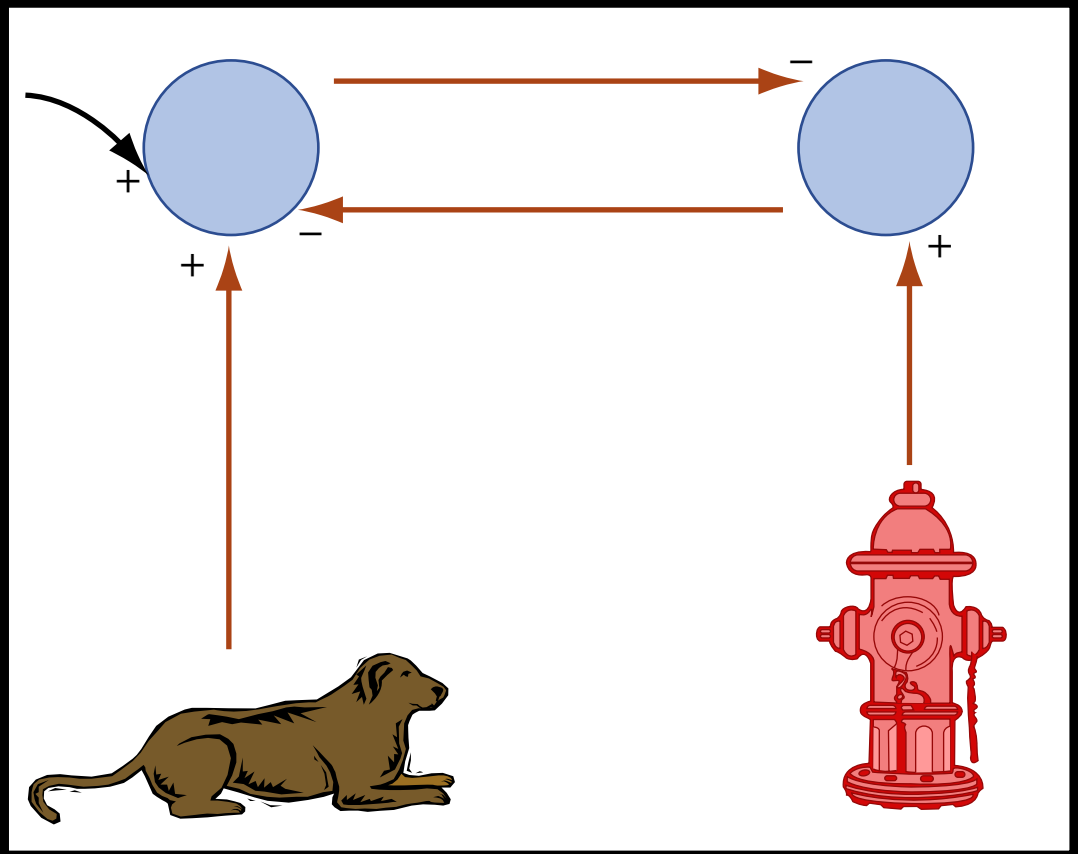


Figure by MIT OpenCourseWare.

1. Objects or locations compete for representation at upper levels of the visual system

2. Attention results when a certain object or location wins the competition.

3. The competition can be biased toward certain items by bottom-up or top-down signals that add more excitation to to-be-attended items

Mystery: *How* does the visual system bias competition, e.g. in this case, how does it "know" whether it is the face or the house that is moving when the two are superimposed?

- Duncan & Desimone's Biased Competition model *presumes* that the binding problem has already been solved, but does not say how.
- It is unlikely that the necessary information is available in MT, FFA, & PPA; earlier stages of the visual system are probably involved.

Outline

1. How “early” is attentional selection?
   - Anatomically
   - Temporally

2. What are the units of attentional selection?

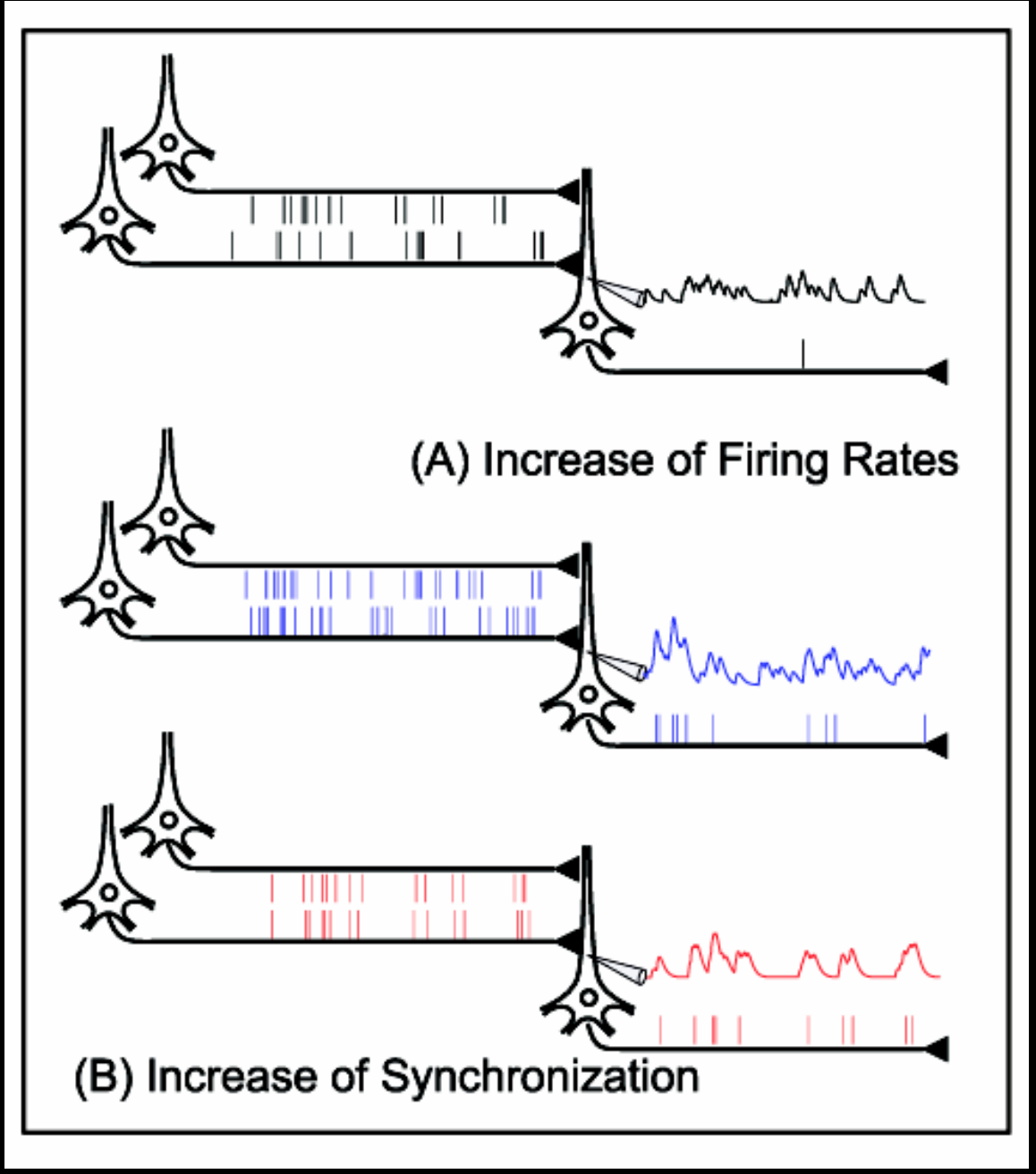
3. How exactly does attention affect neural representations?

Two ways attention might increase postsynaptic impact:

A.) Increase firing rate

B.) Increase synchronization (invisible to fMRI).

Fries et al (2001): attention in RF not only increases firing rate, but also increases synchronization of spikes with LFP, specifically in 35-50 Hz range.



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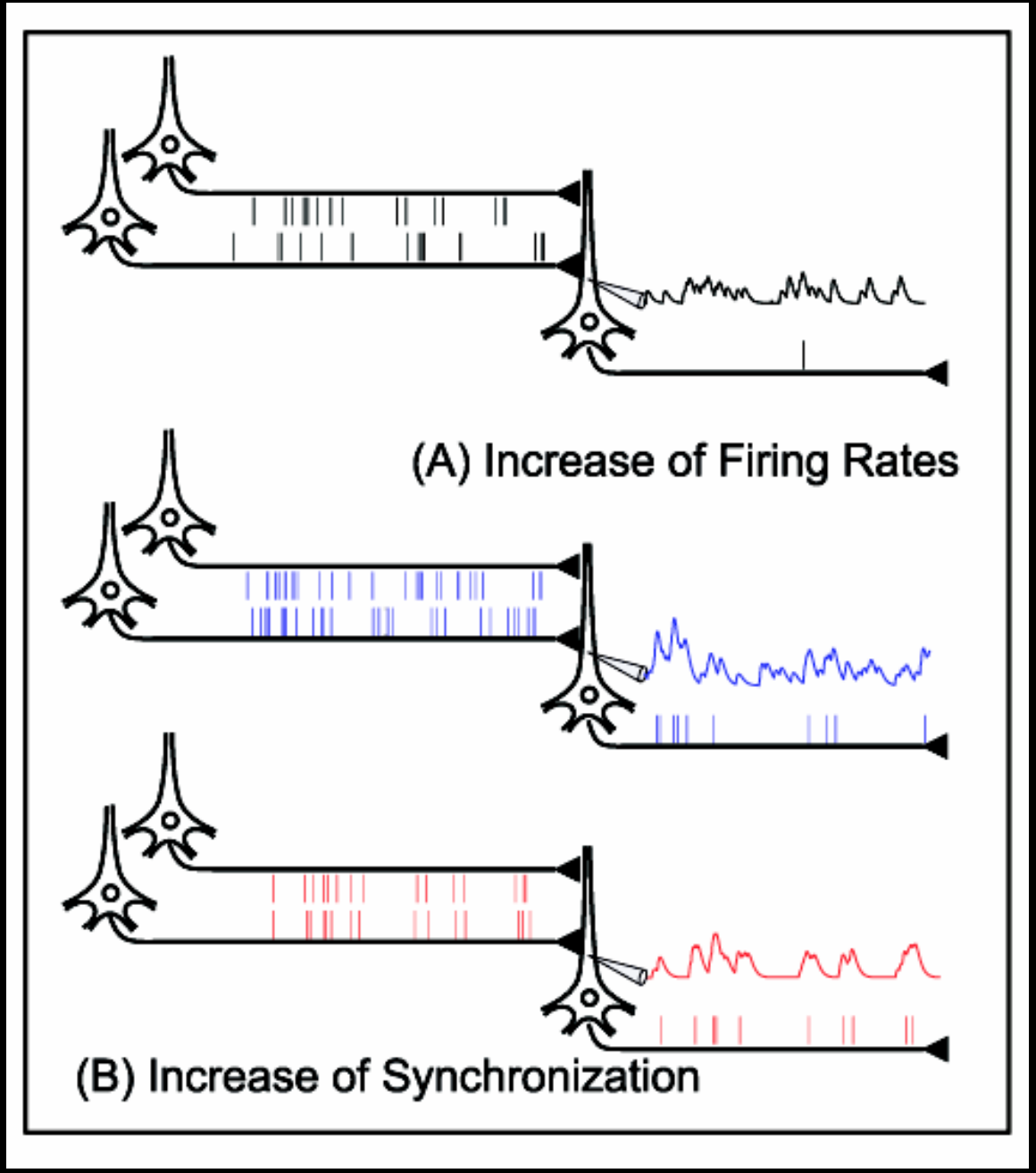
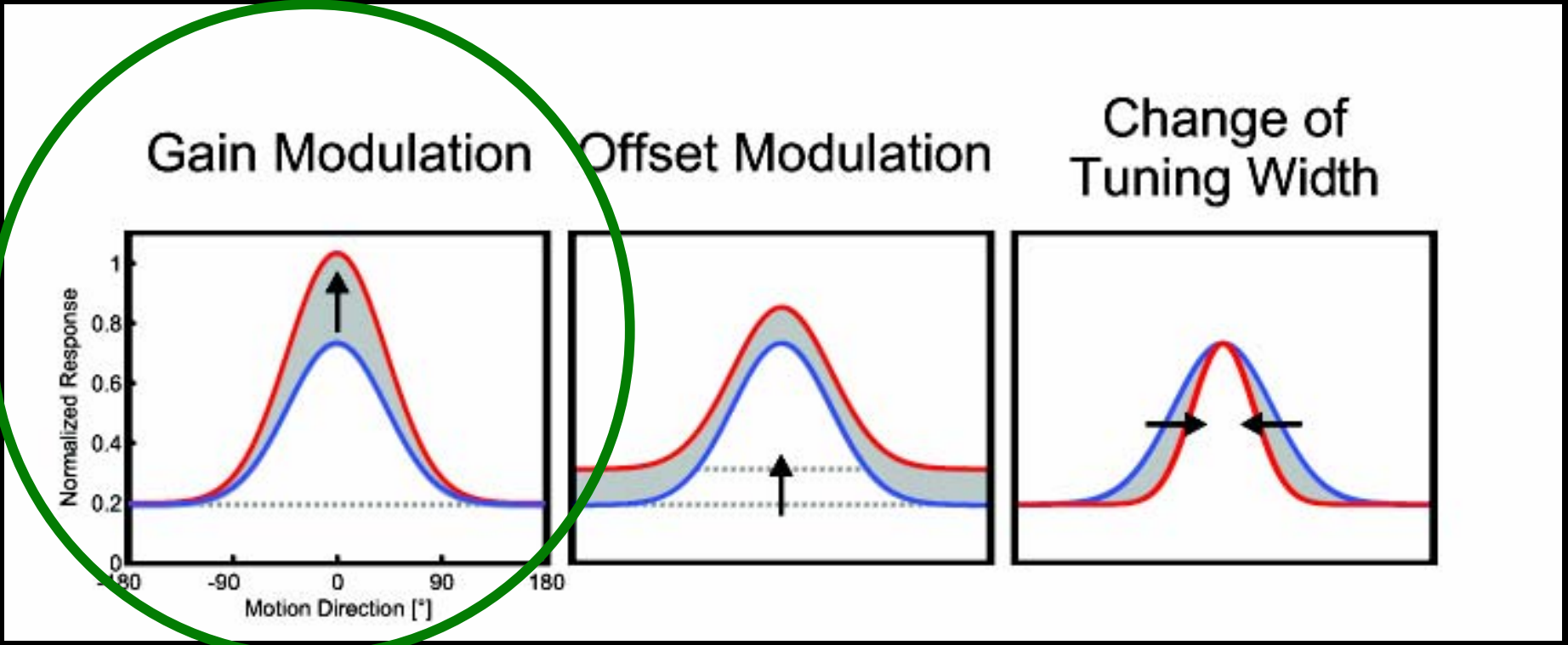


Firing Rate Effects

1. Possible effects of Attention on Neural Response:

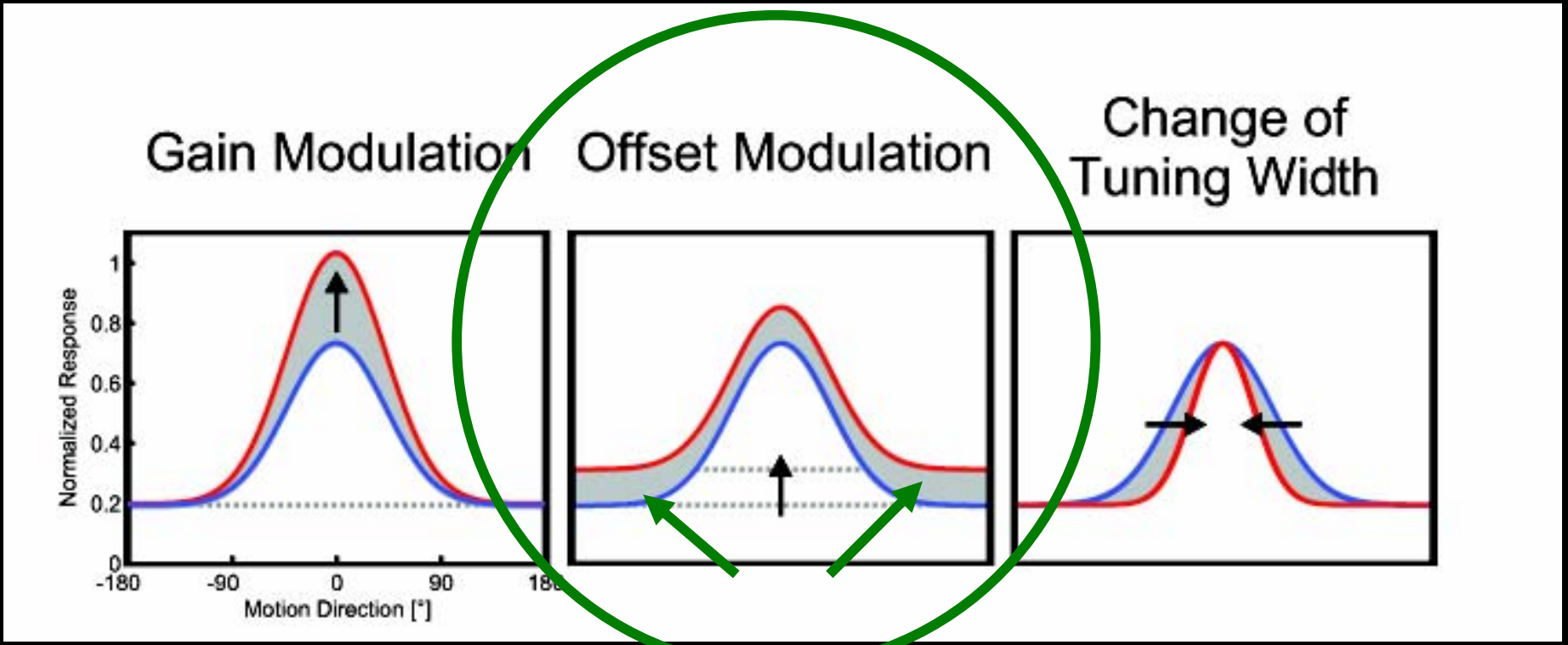
Blue = unattended; Red = attended.



1a. McAdams & Maunsell (1999): (multiplicative) gain modulation in V4.

Firing Rate Effects

1. Possible effects of Attention on neural Response:



Blue = unattended; Red = attended.

1. Possible effects of Attention Neural Response:

b. Offset Modulation (= Baseline Shift)

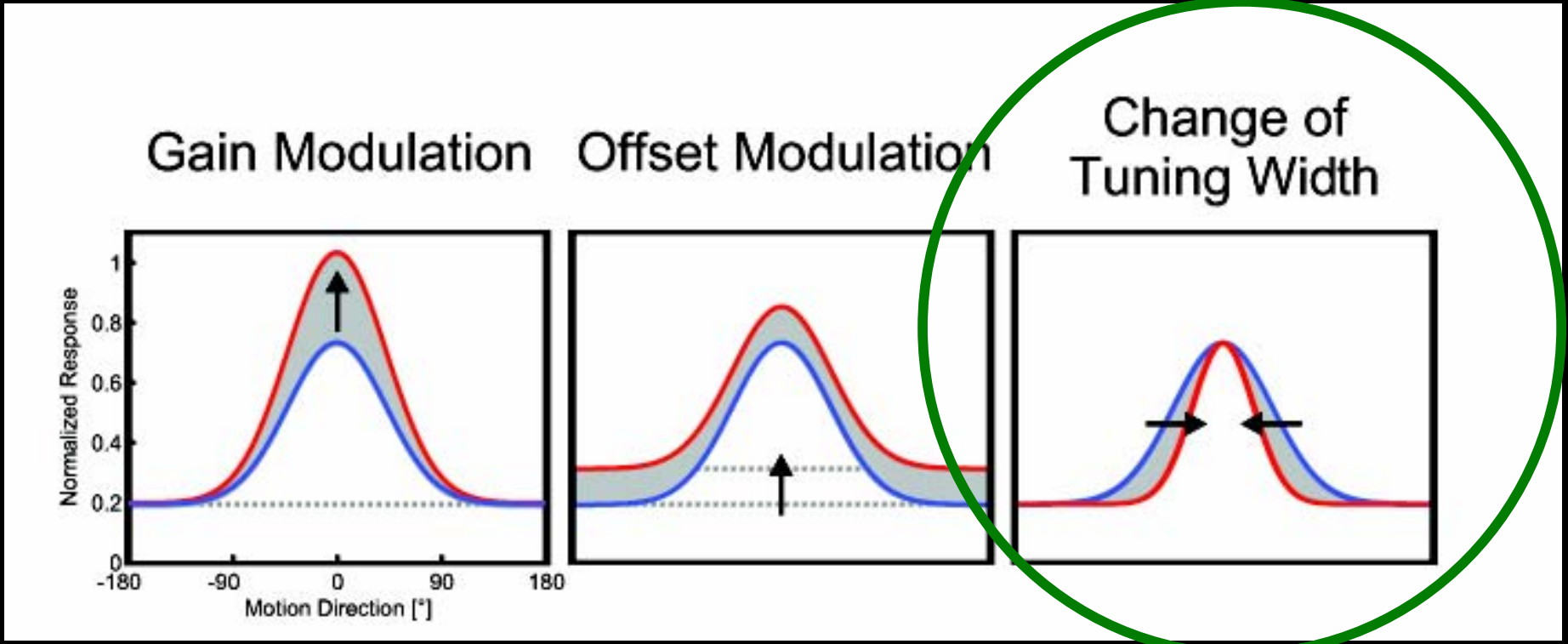
Ress, Backus & Heeger (2000):
stim-independent activity in V1.

Why can't this be gain modulation or change of tuning width?

Firing Rate Effects

1. Possible effects of Attention on Neural Response:

Blue = unattended; Red = attended.

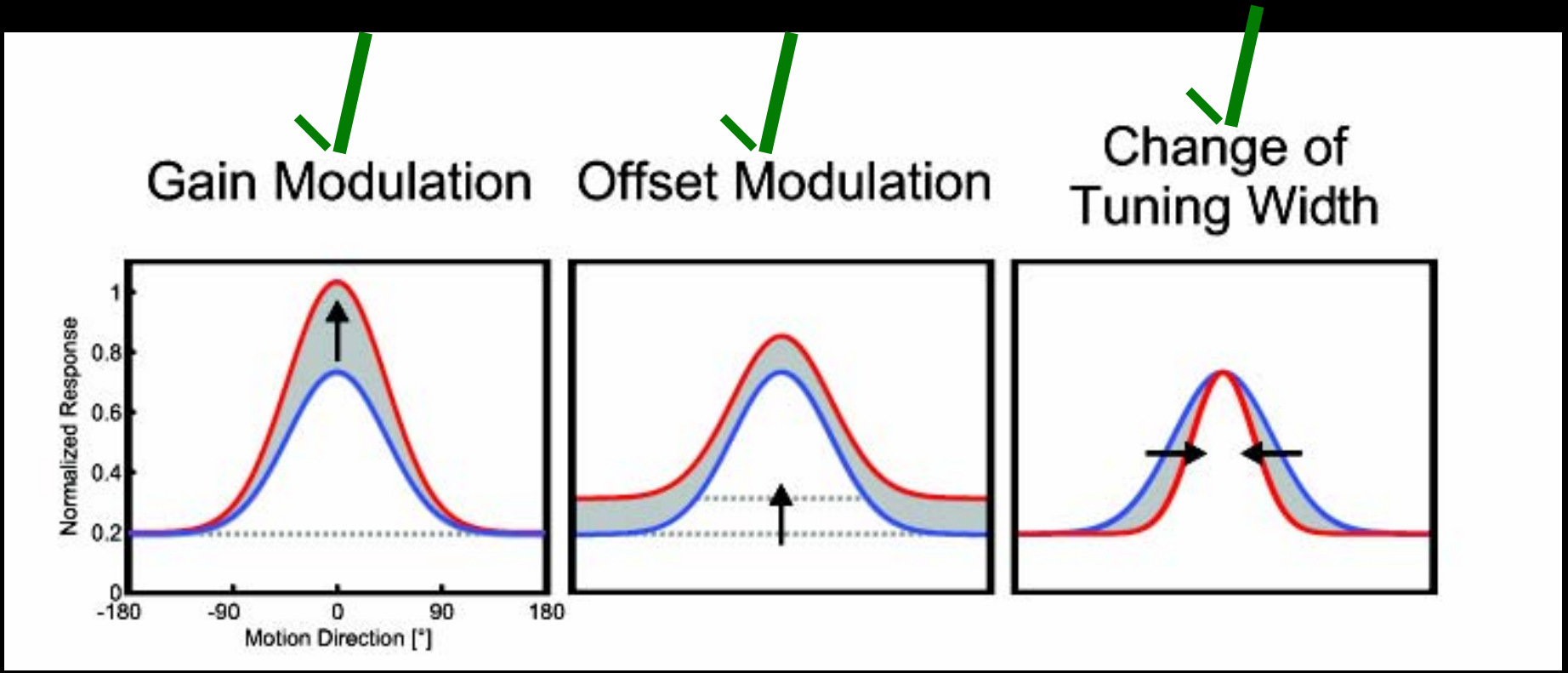


 Source: Friewald, W. and N. Kanwisher. "Visual Selective Attention: Insights from Brain Imaging and Neurophysiology." In *The Cognitive Neurosciences*. 3rd ed. Edited by Michael S.Gazzaniga. Cambridge, MA: MIT Press, 2004.

Neurophysiologists can study this by directly measuring the tuning function of individual neurons. What fMRI method would you use?

Firing Rate Effects

1. Observed effects of Attention on Neural Response:



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What Have we Learned about Attention?

1. How "early" is attentional selection?
   - Anatomically *very* early: LGN
   - Temporally not necessarily so early - may occur only after initial feedforward pass up the system.
     But: baseline shifts = very early….

2. What are the units of attentional selection?
   locations, features, *and* objects

3. How exactly does attention affect neural responses?
   synchrony of firing, gain modulation, & baseline shifts
   sharpening of tuning