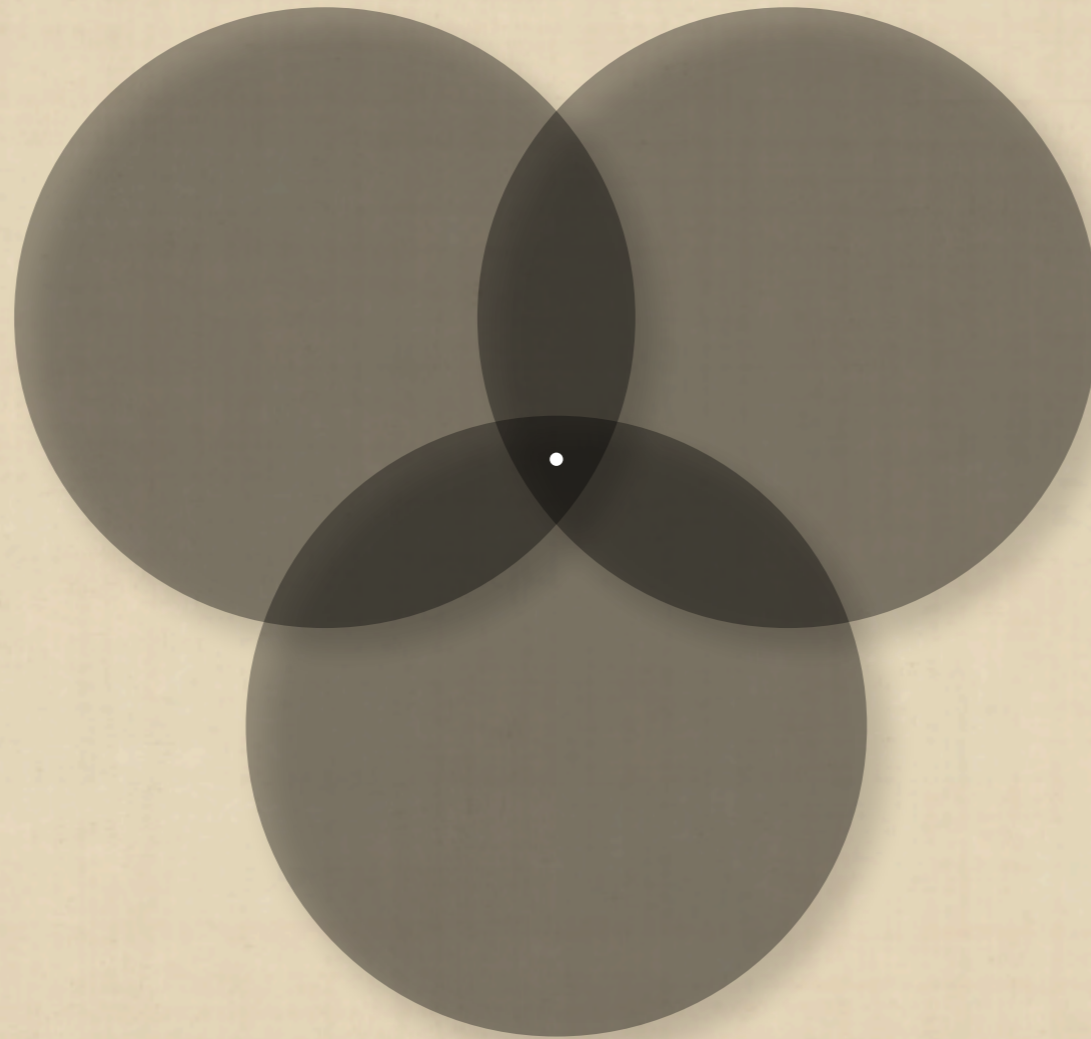


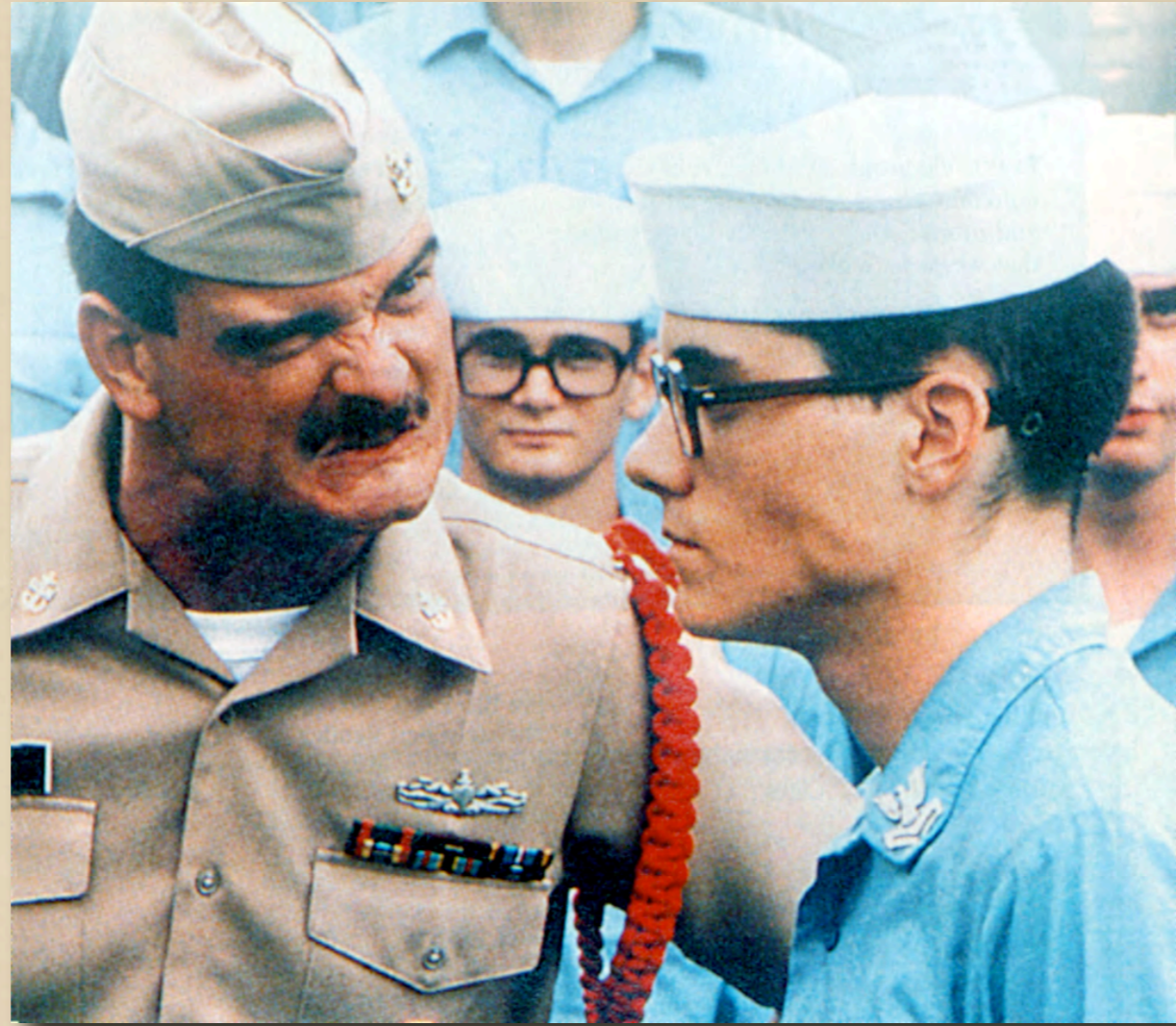
Attention

March 4, 2009

John Maunsell



Mitchell, JF, Sundberg, KA, Reynolds, JH (2007) Differential attention-dependent response modulation across cell classes in macaque visual area V4. *Neuron*, 55:131–141.

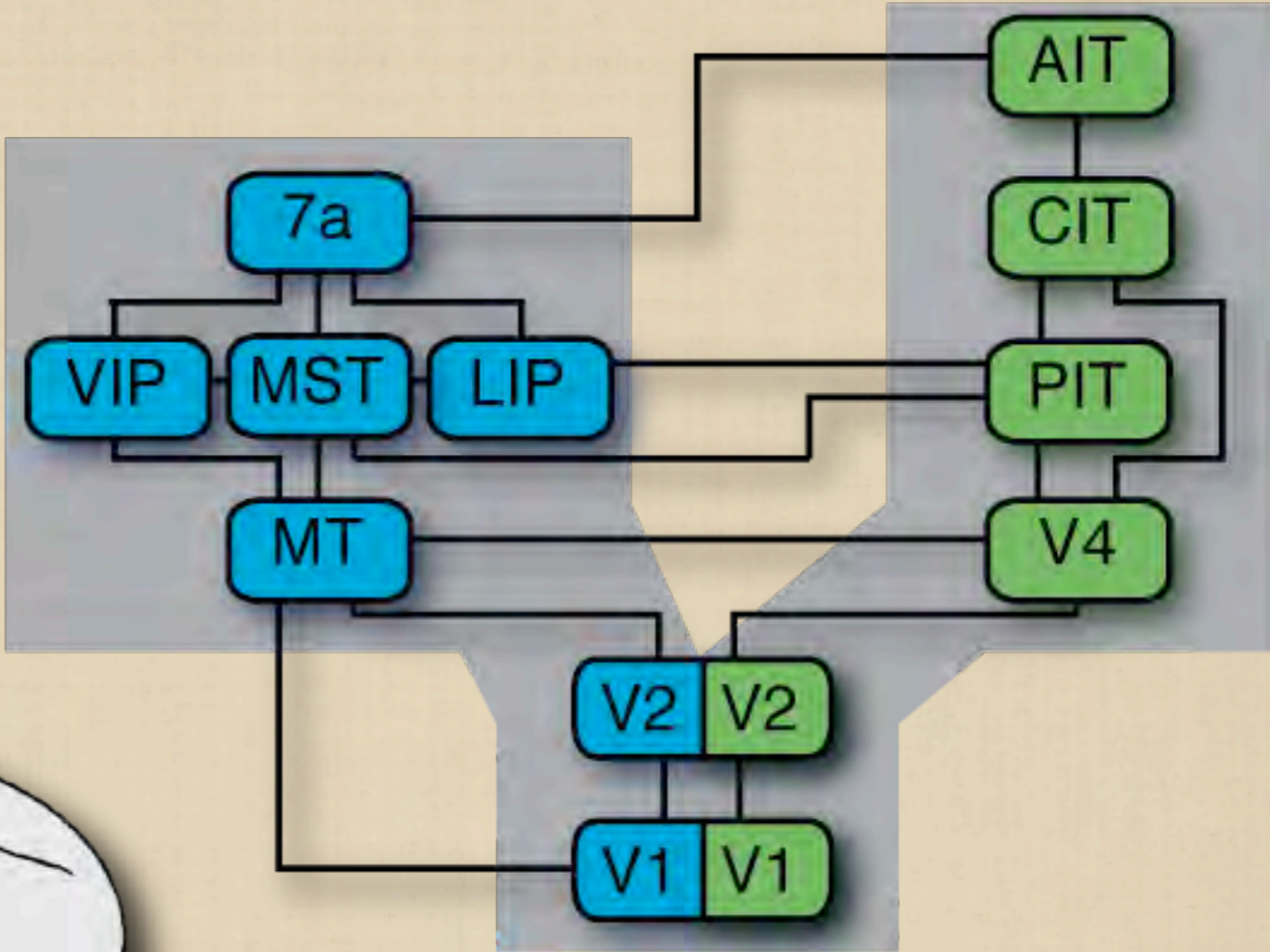




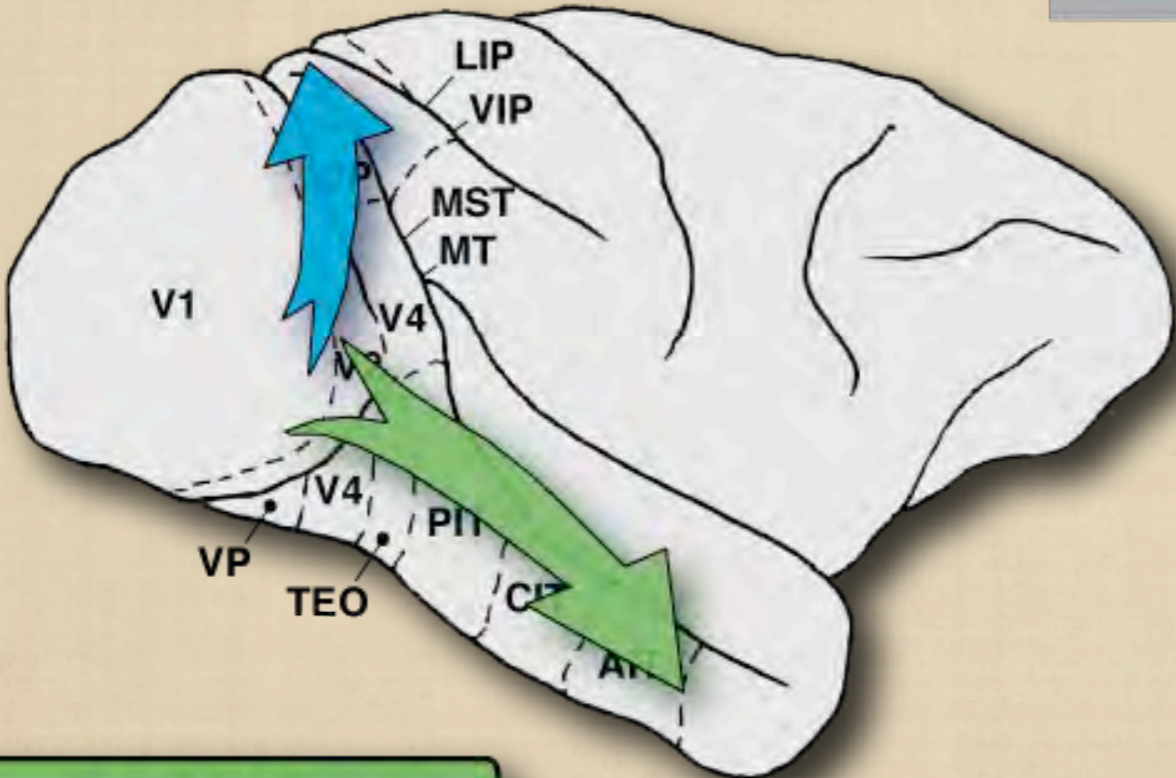
Moore et al.

Parietal Pathway

Temporal Pathway

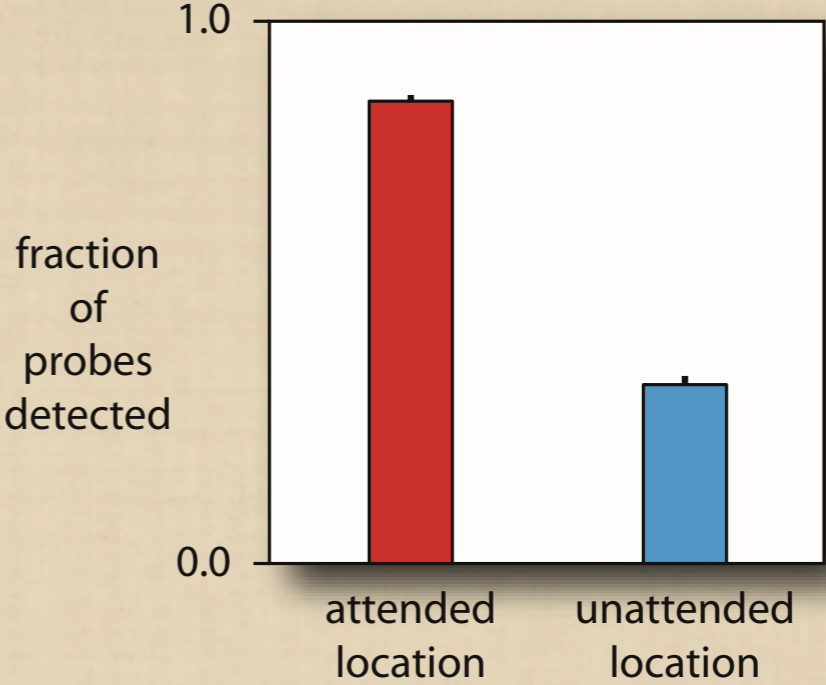
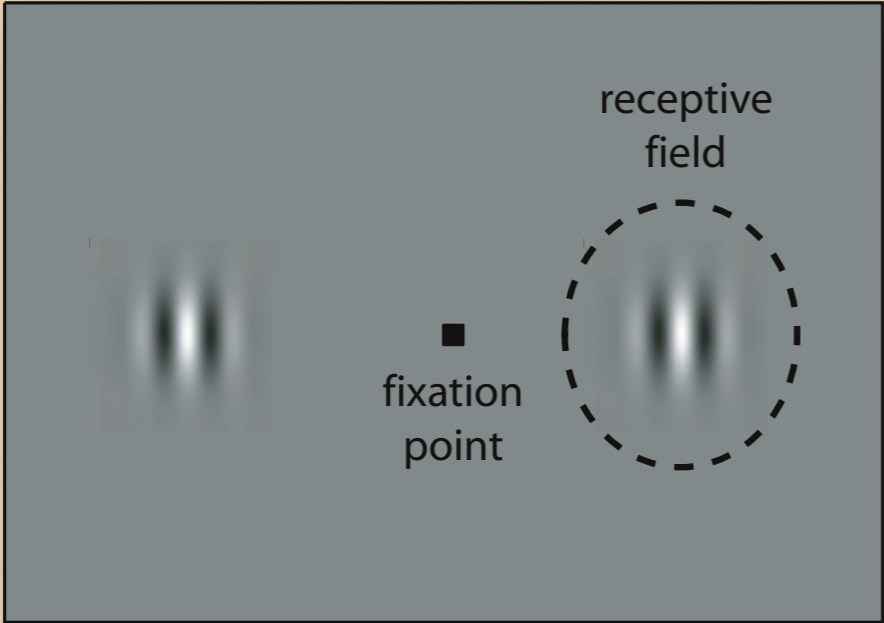


Parietal Pathway

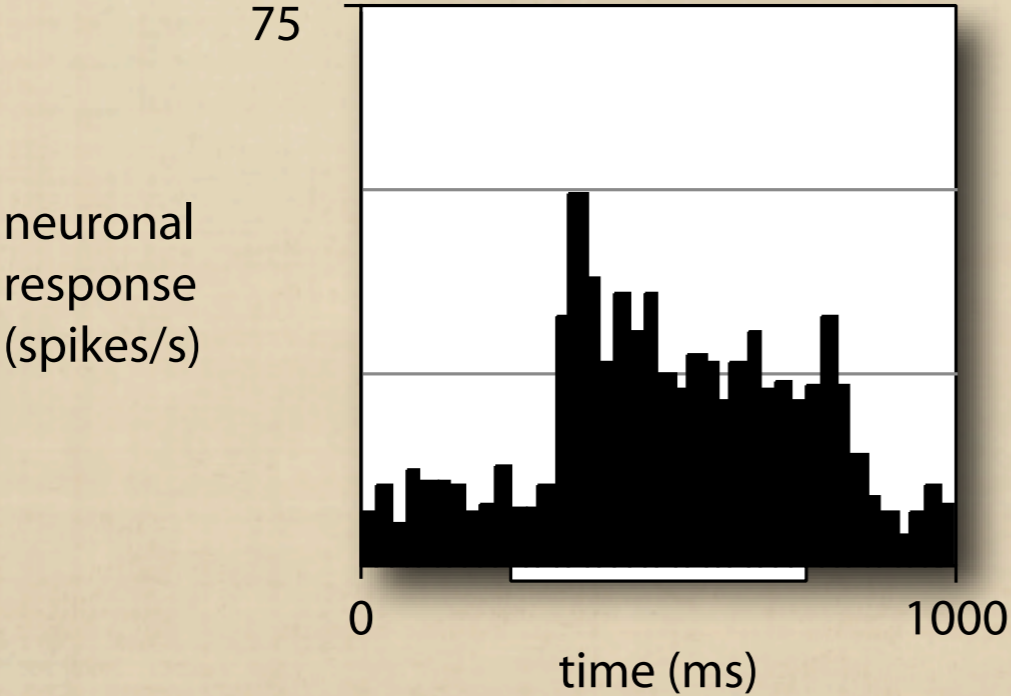


Temporal Pathway

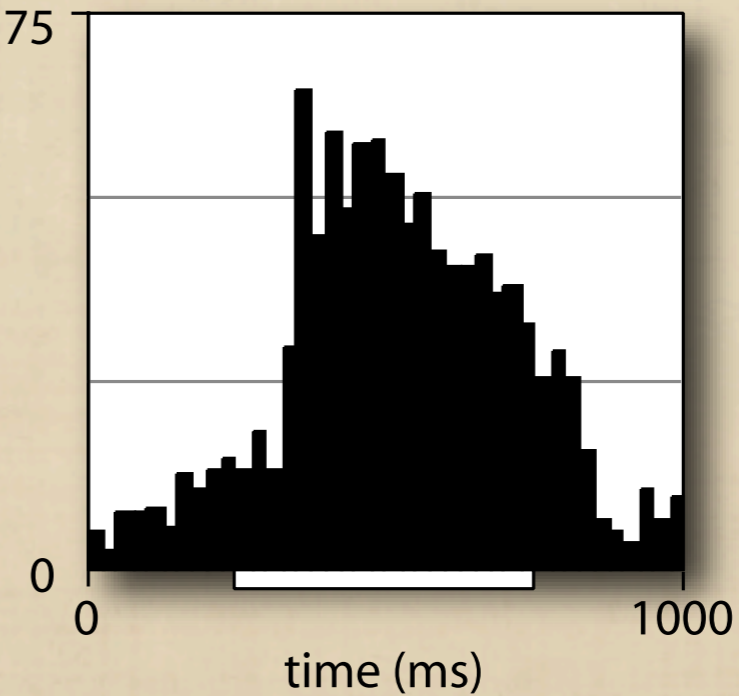
Spatial attention task



attend to other stimulus

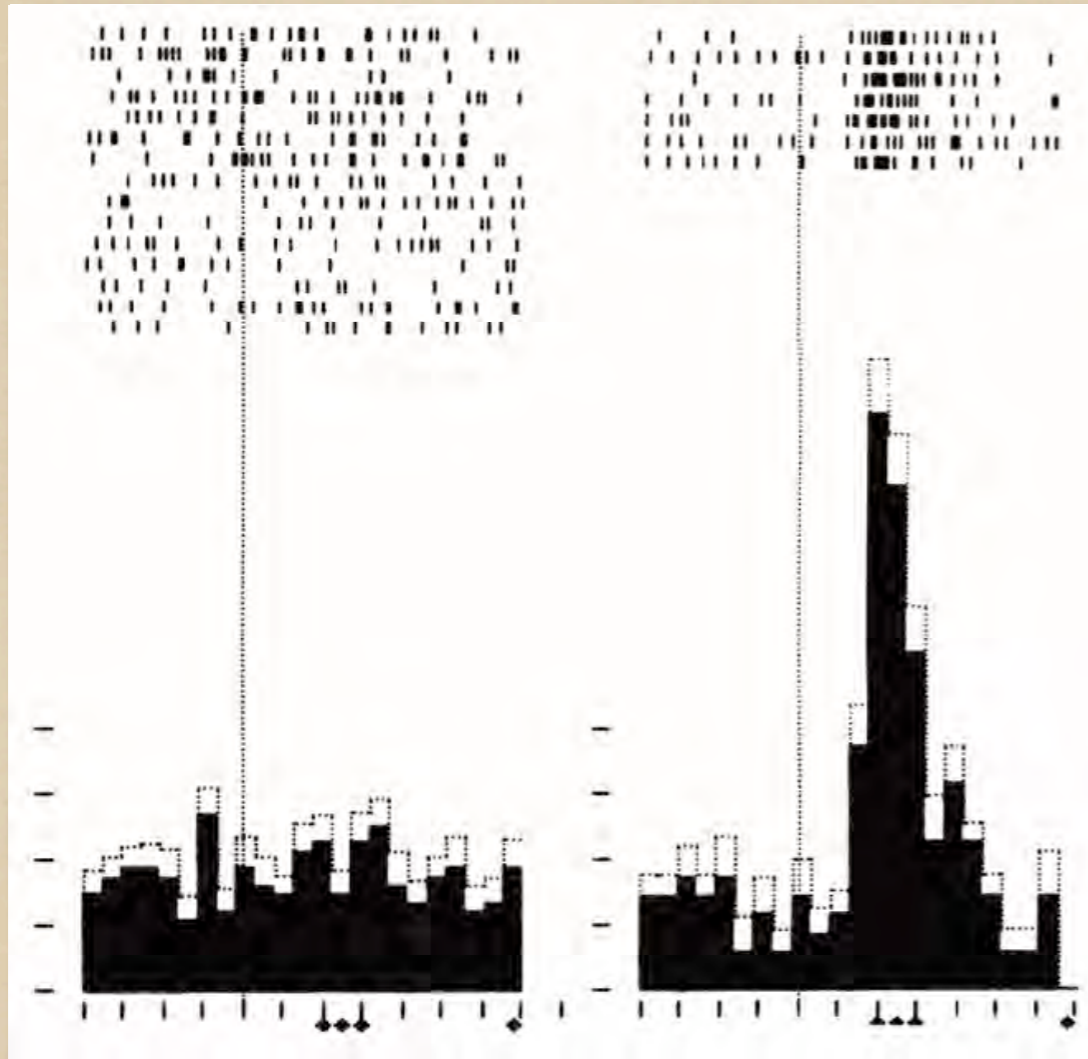


attend to receptive field stimulus

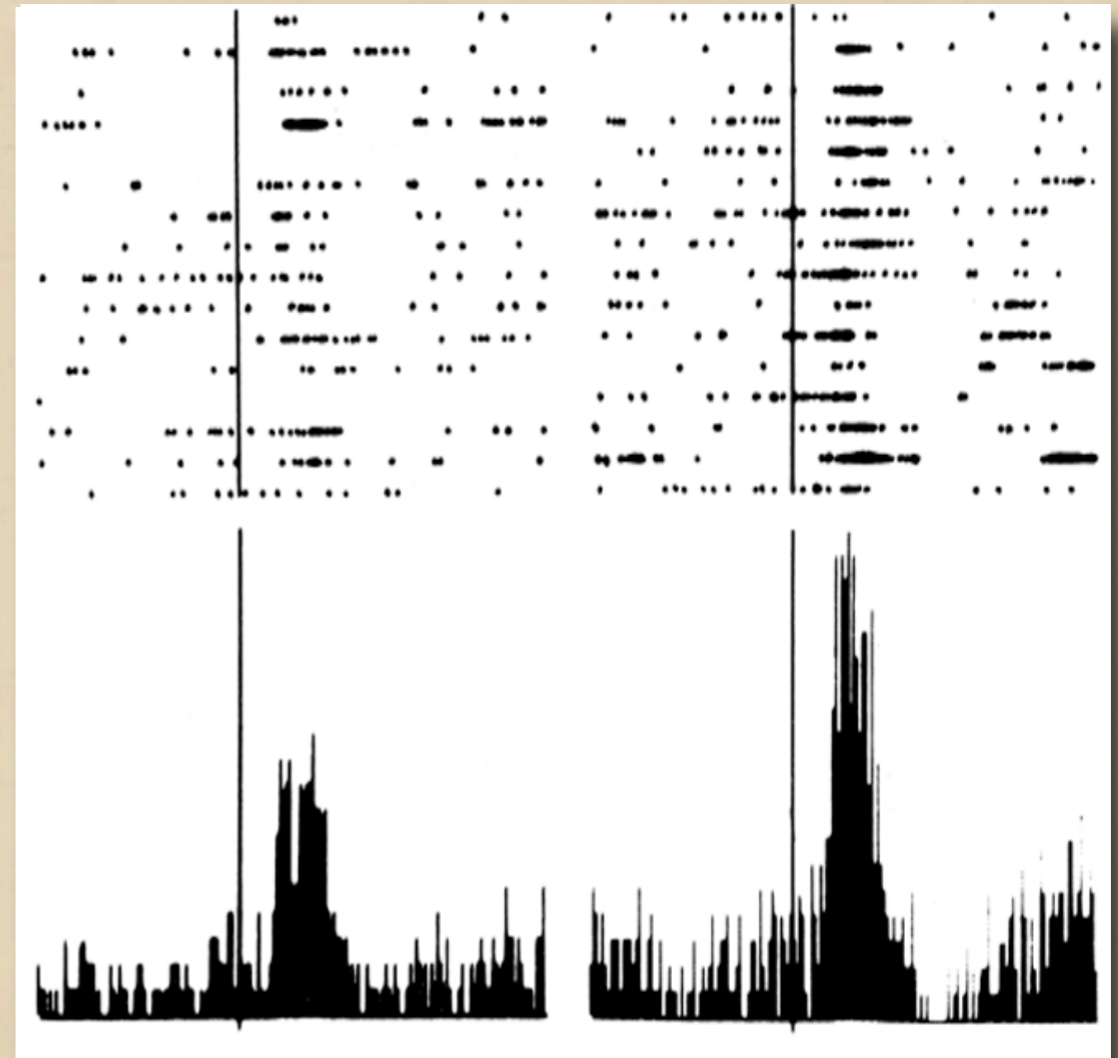


Effect of behavioral state in Area 7a

Mountcastle, Andersen & Motter 1981

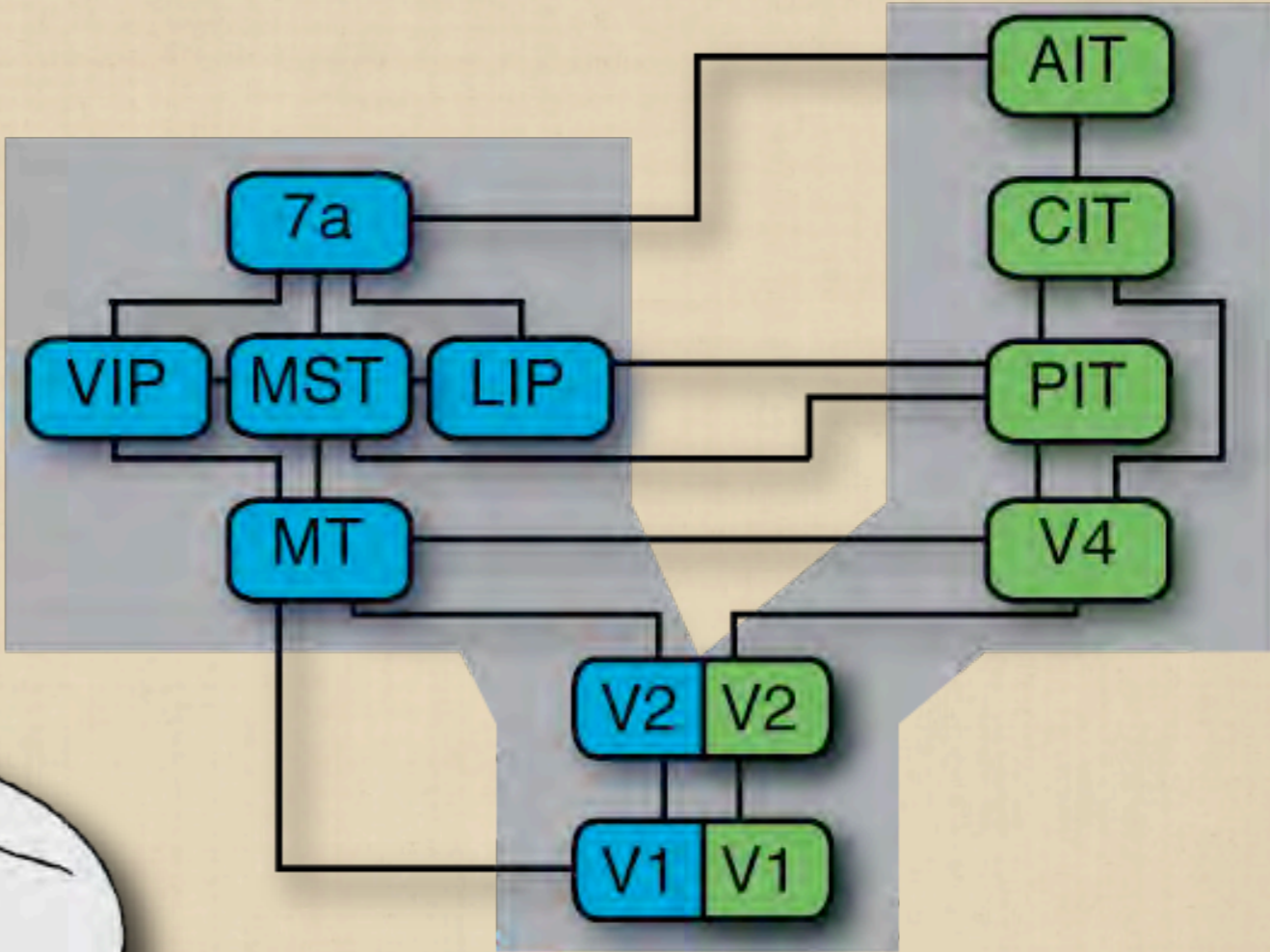


Bushnell, Goldberg & Robinson 1981

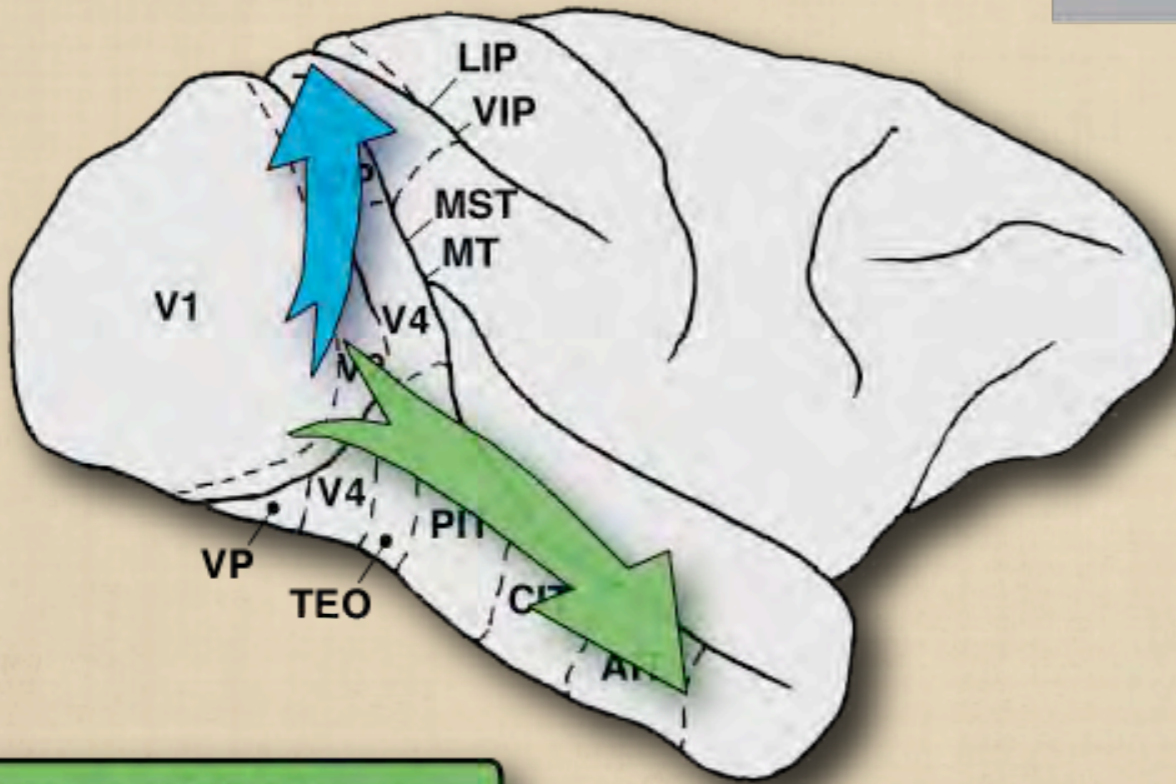


Parietal Pathway

Temporal Pathway



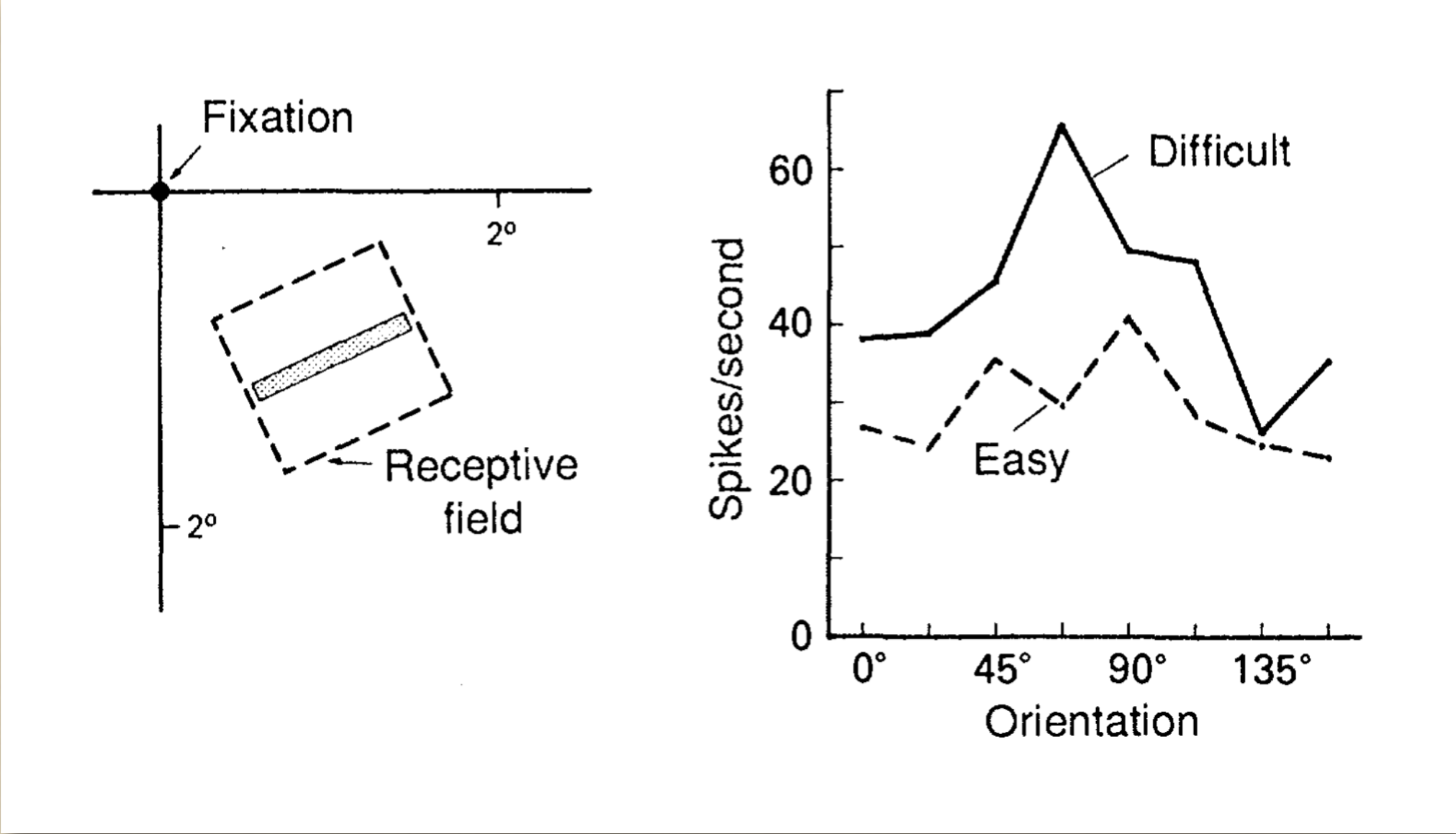
Parietal Pathway



Temporal Pathway

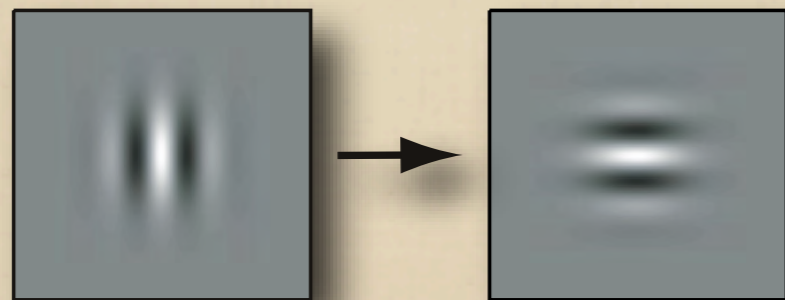
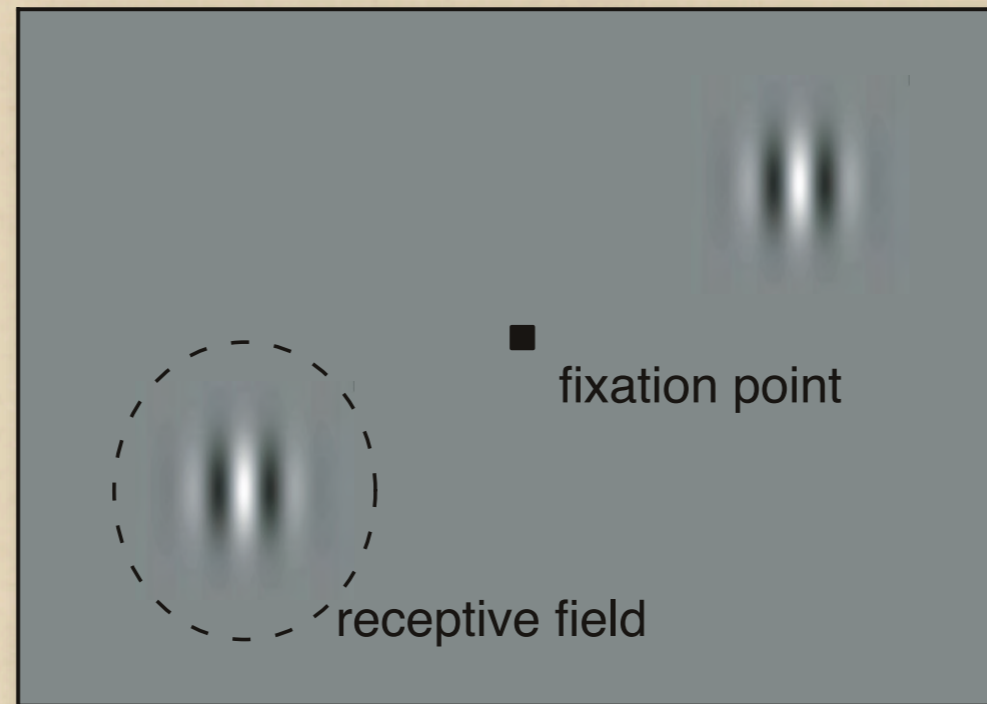
Task difficulty modulates neuronal responses in Area V4

Spitzer, Moran & Desimone 1988

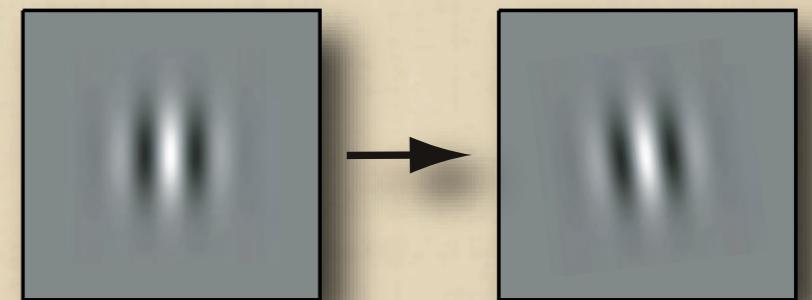


Detecting orientation change

Boudreau et al. (2006)



easy mode (90°)

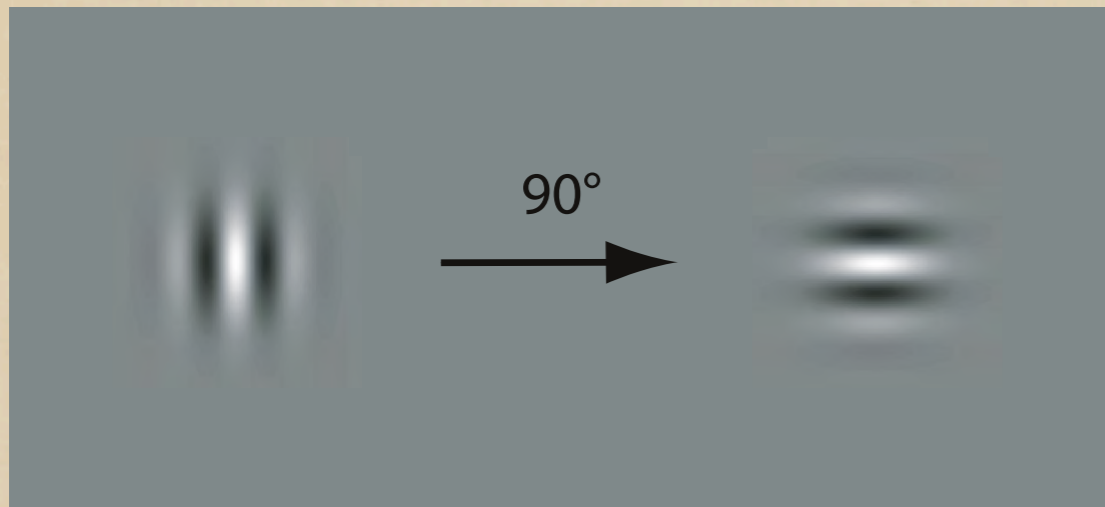


difficult mode ($\sim 10^\circ$)

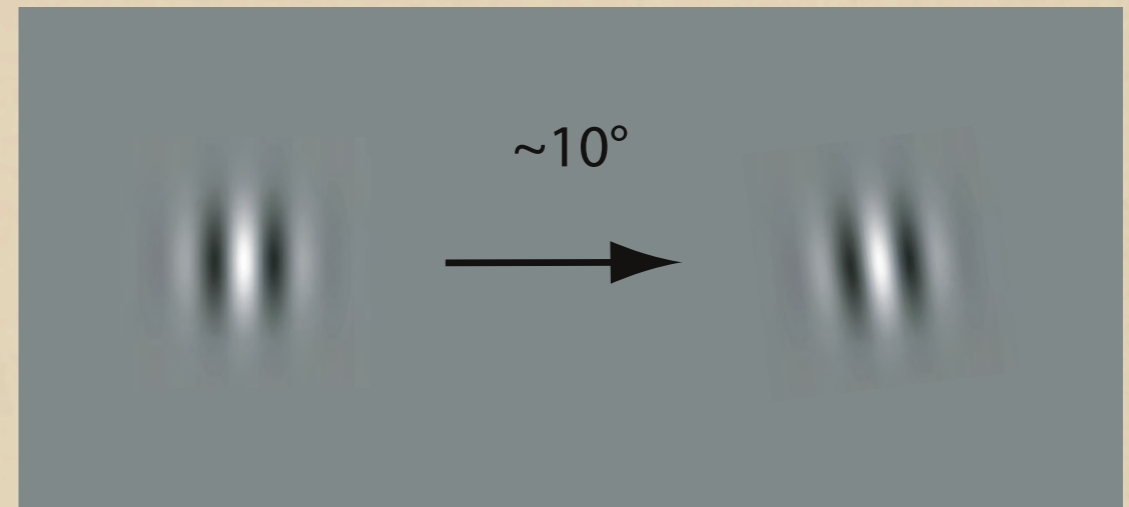
Task difficulty is determined by the size of orientation change

Boudreau et al. (2006)

easy



difficult



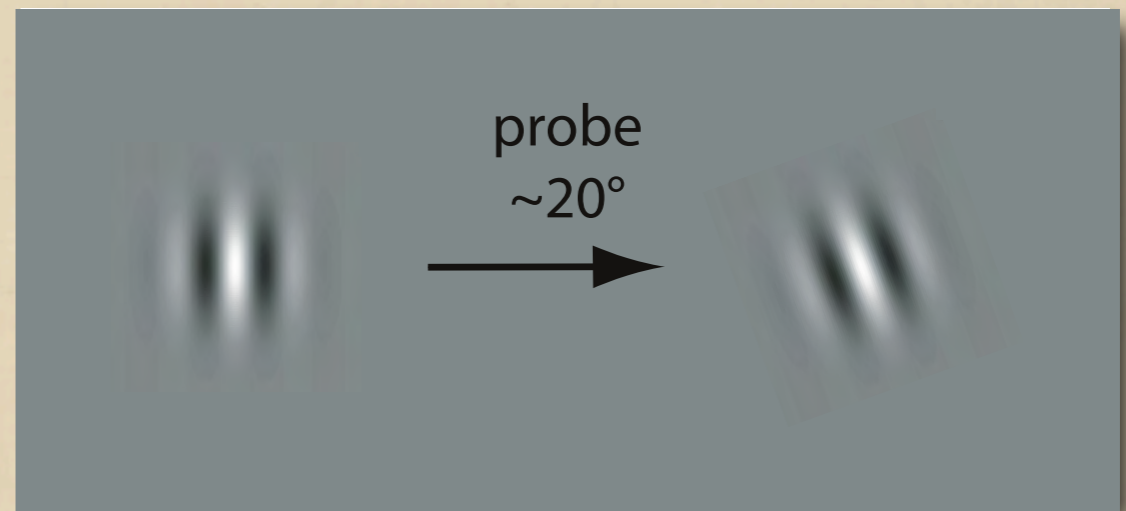
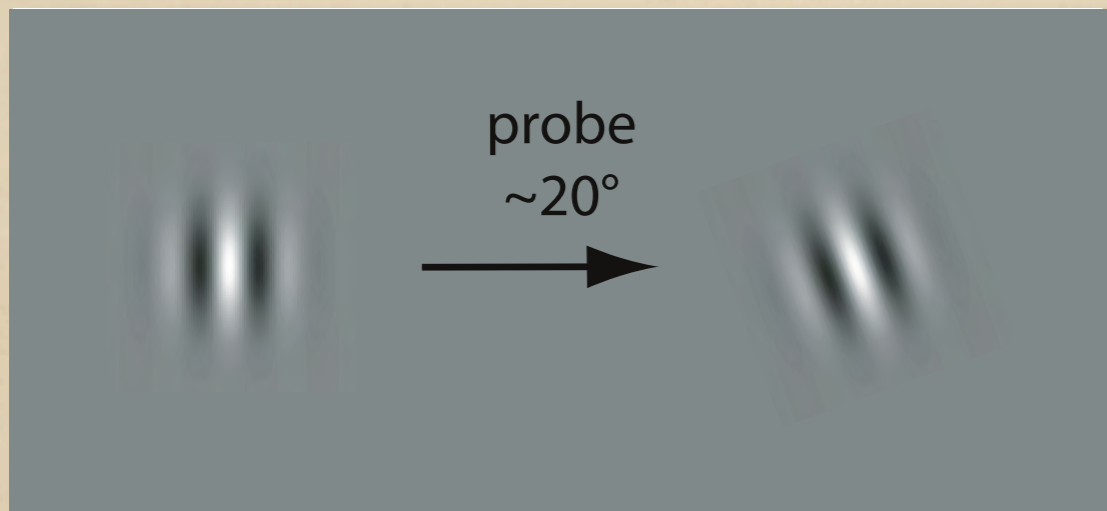
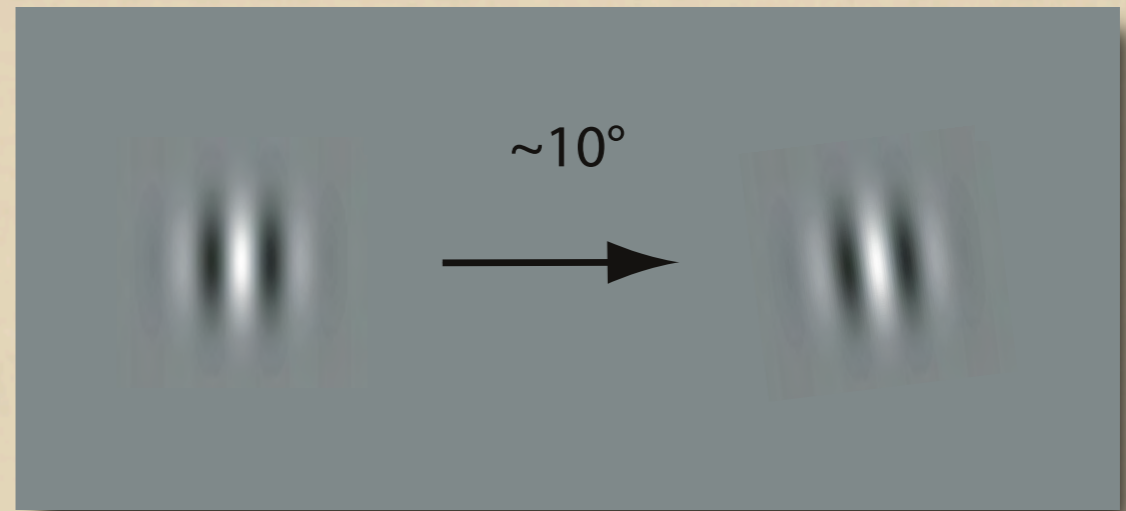
Task difficulty is determined by the size of orientation change

Boudreau et al. (2006)

easy



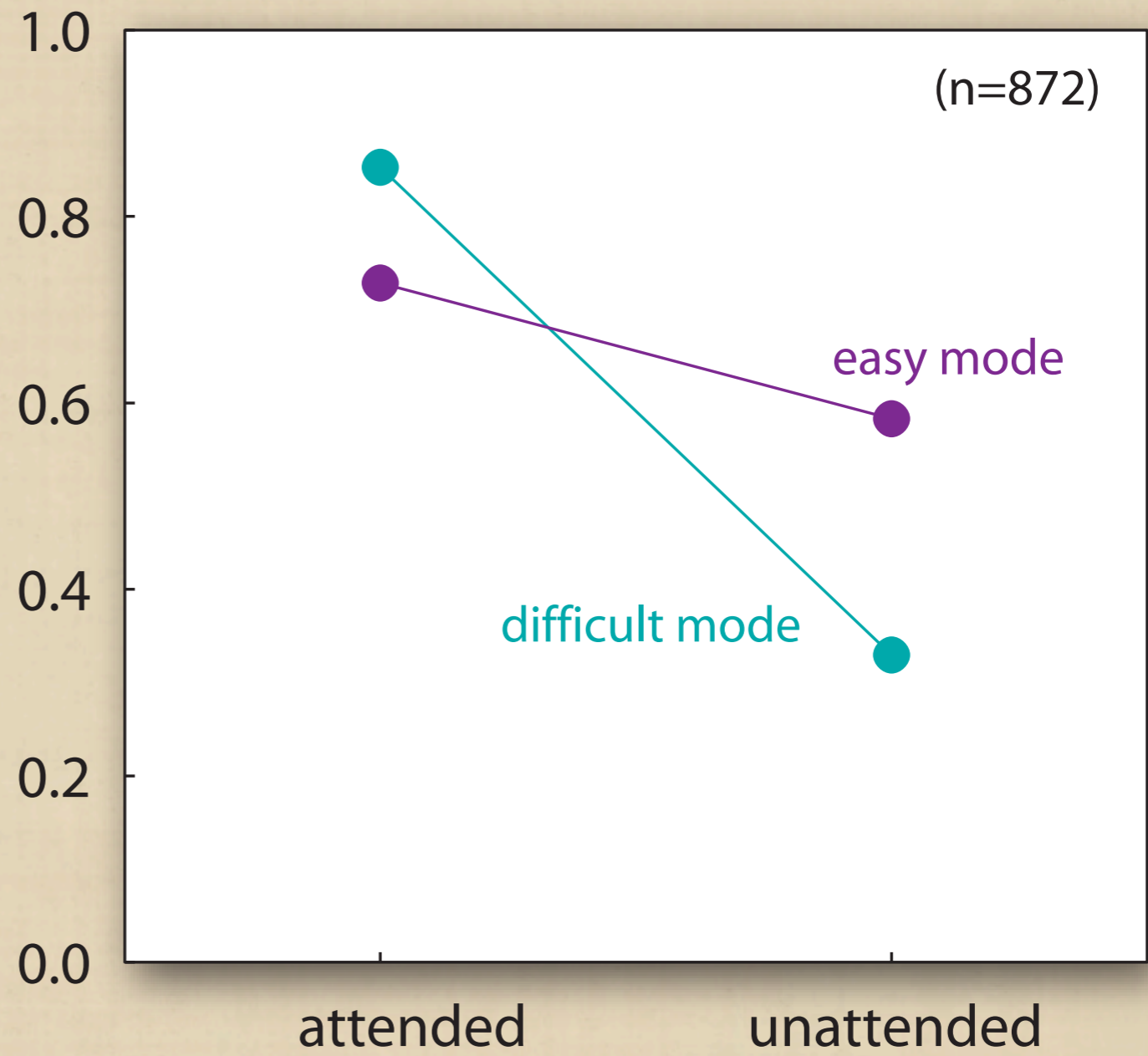
difficult



Behavioral performance

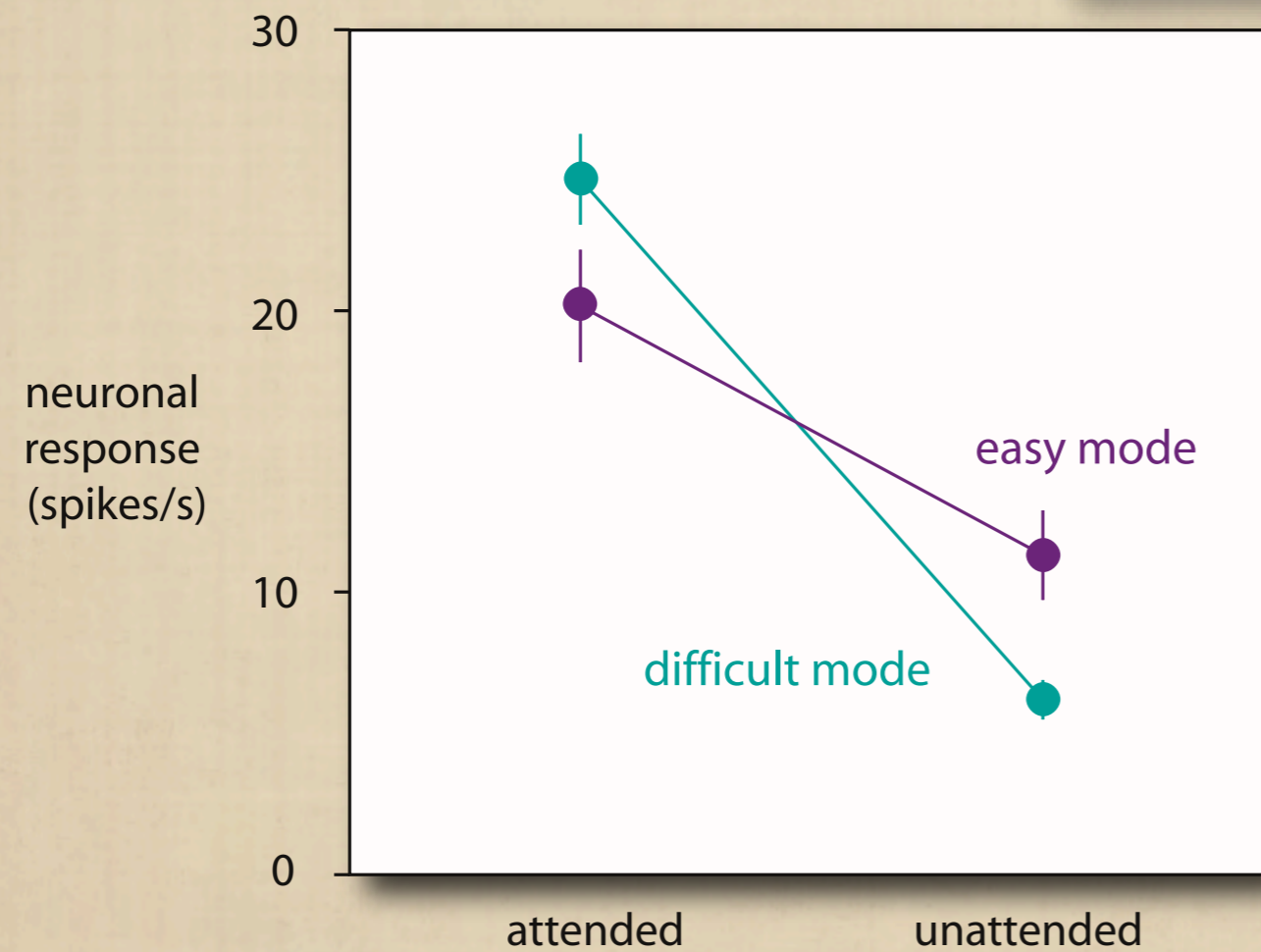
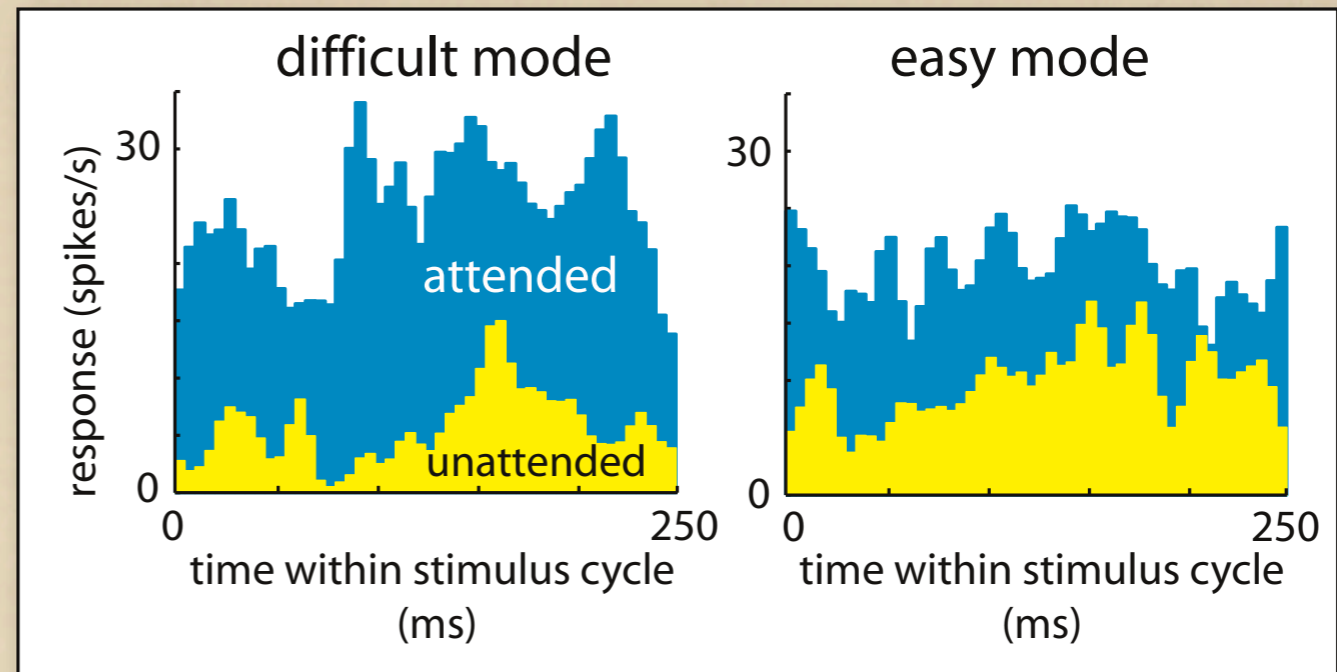
Boudreau et al. (2006)

performance on probes
(proportion correct)



Example V4 neuron response to preferred orientation

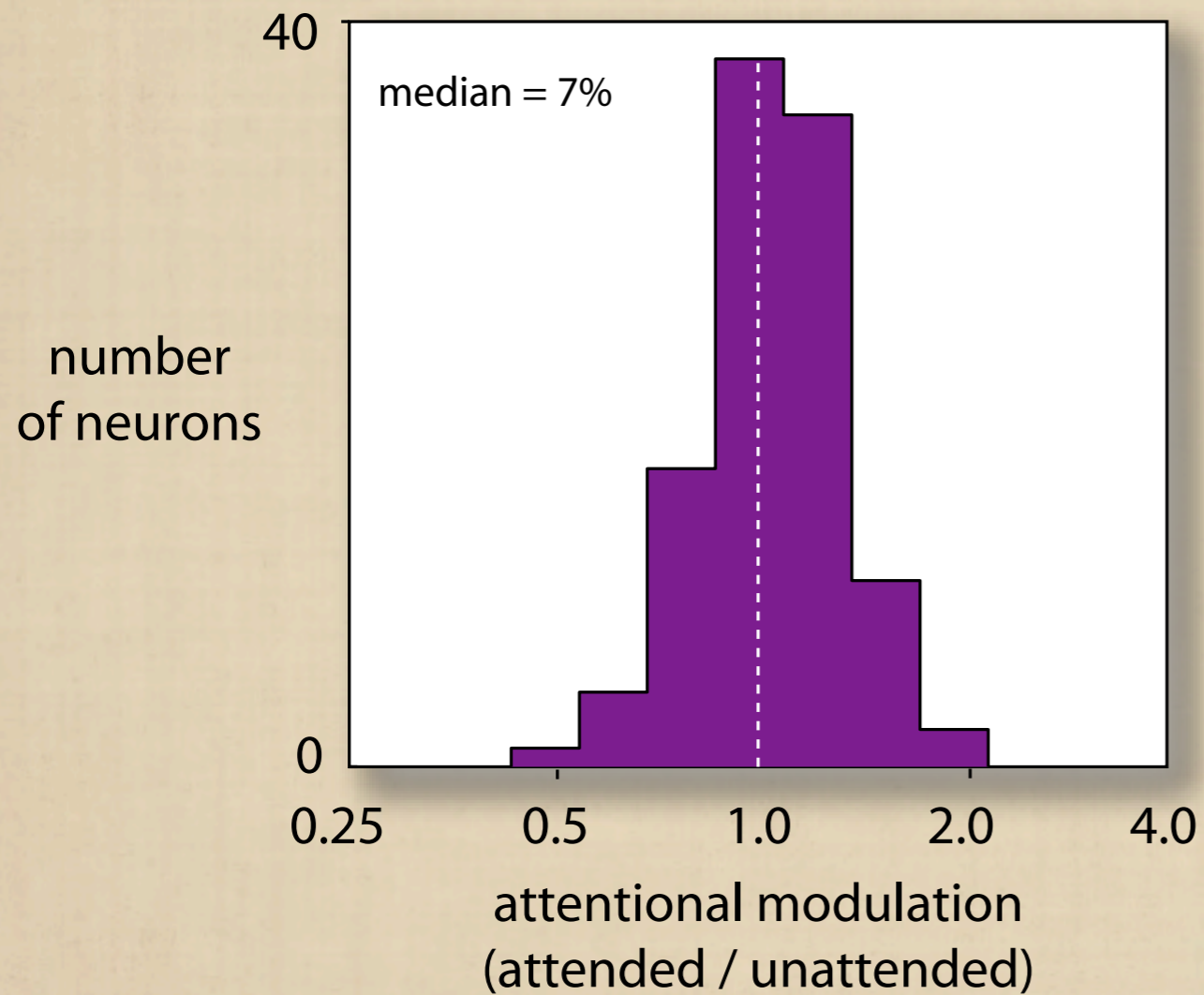
Boudreau et al. (2006)



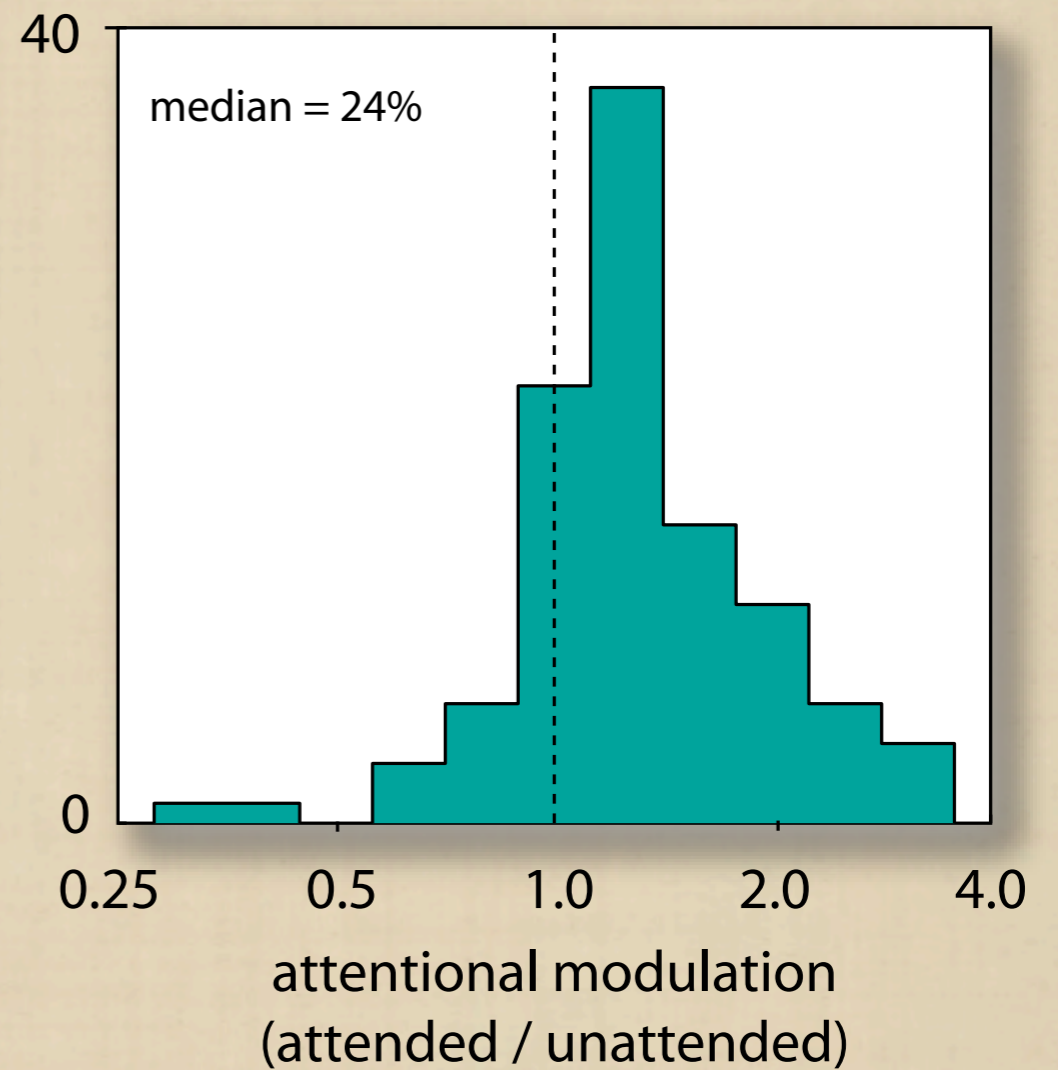
Distribution of attentional modulation in V4

Boudreau et al. (2006)

easy mode



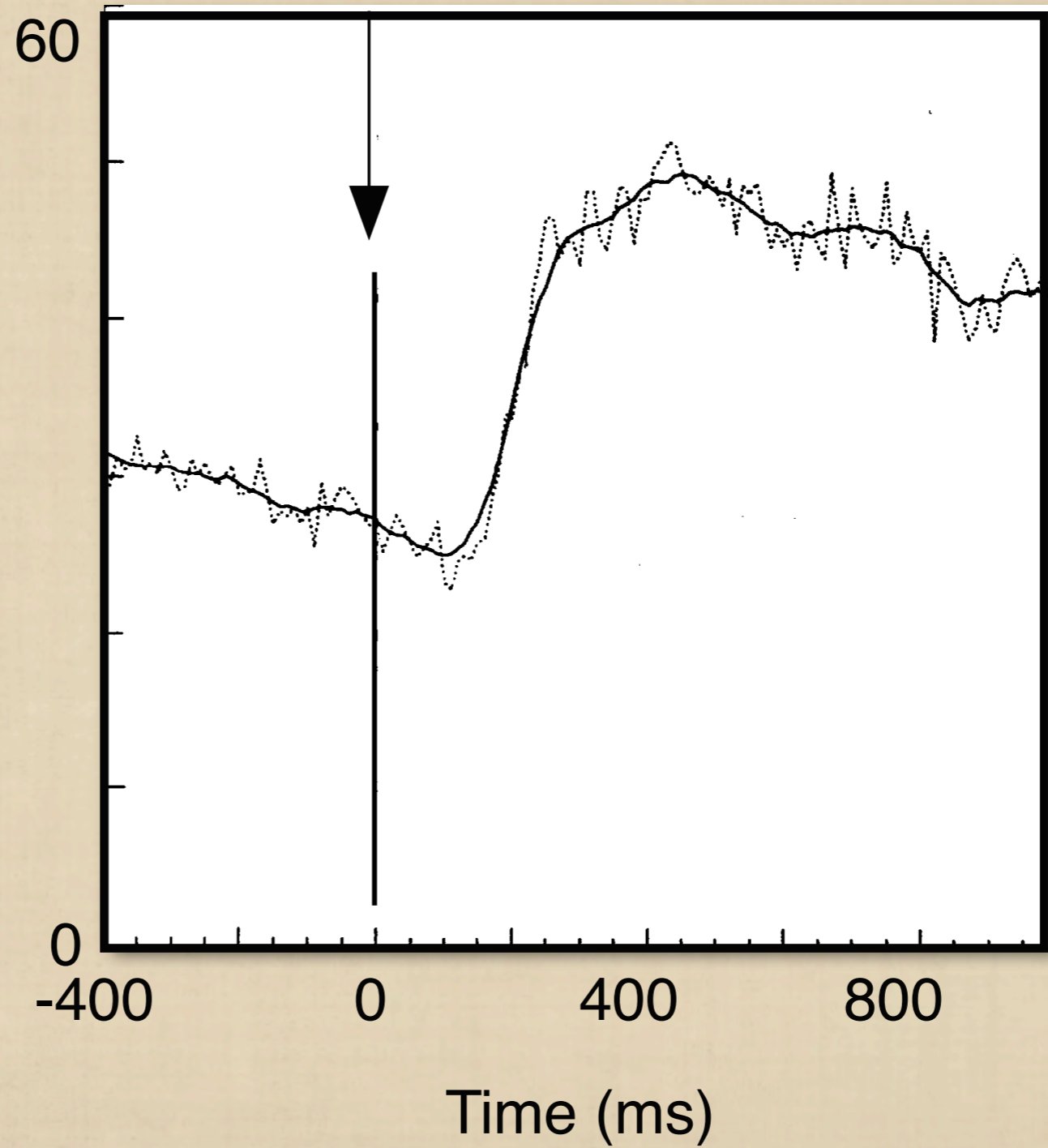
difficult mode



Motter (1994)

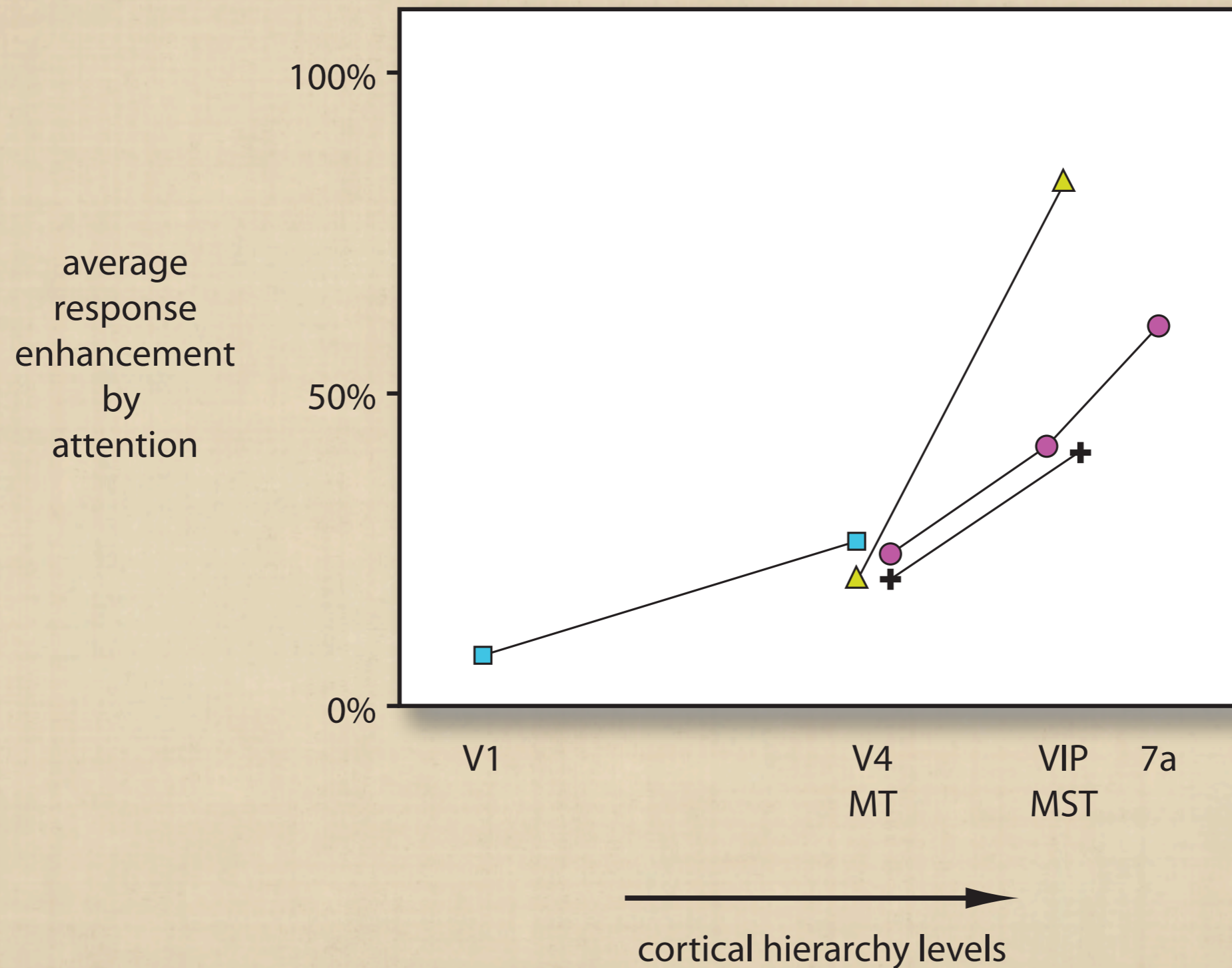
instruction
to shift
attention

Average
response
(spikes/s)

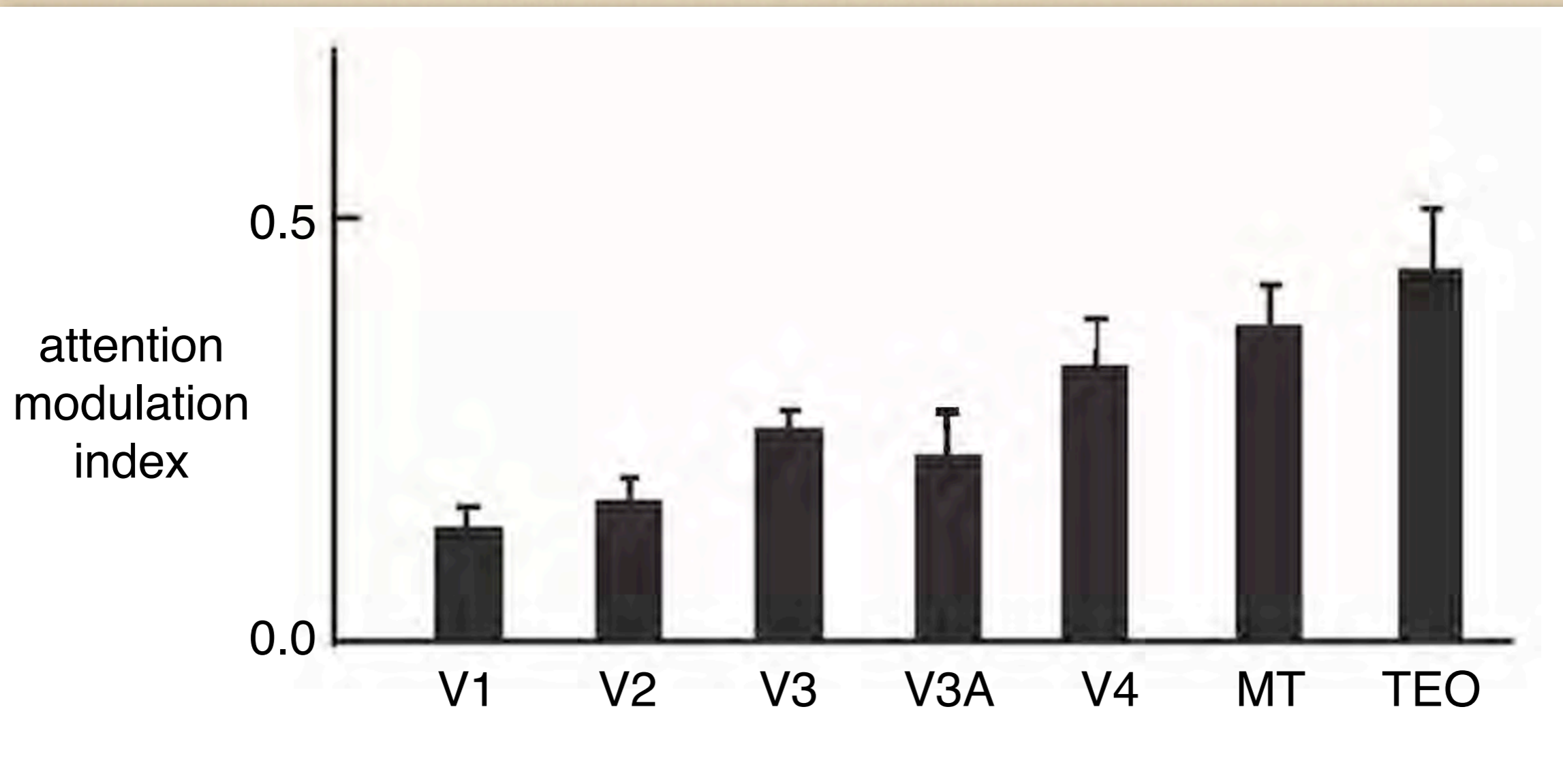


Average attention modulation of single unit responses at different cortical levels

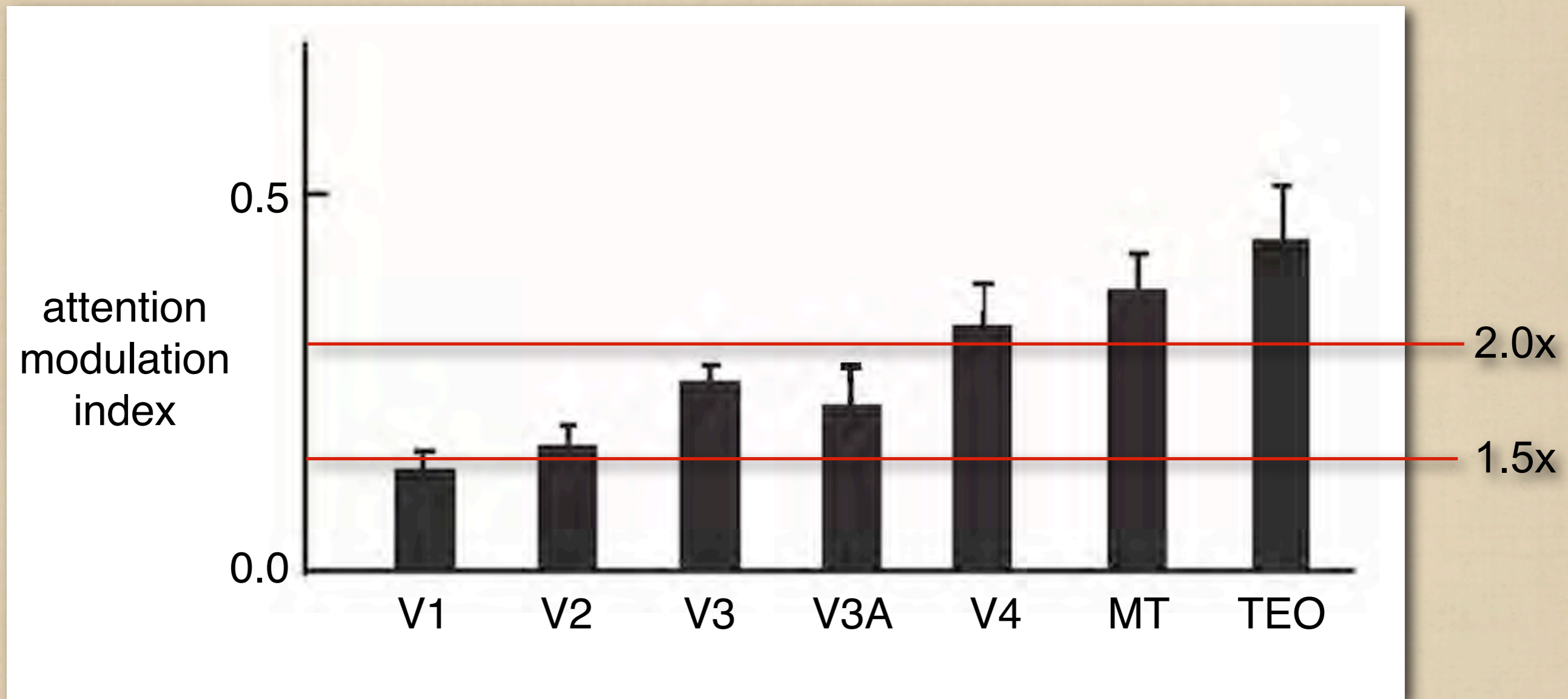
Cook & Maunsell (2002)



Size of modulation spatial attention of fMRI signal in different visual areas
O'Connor, Fukui, Pinsk, & Kastner (2002)

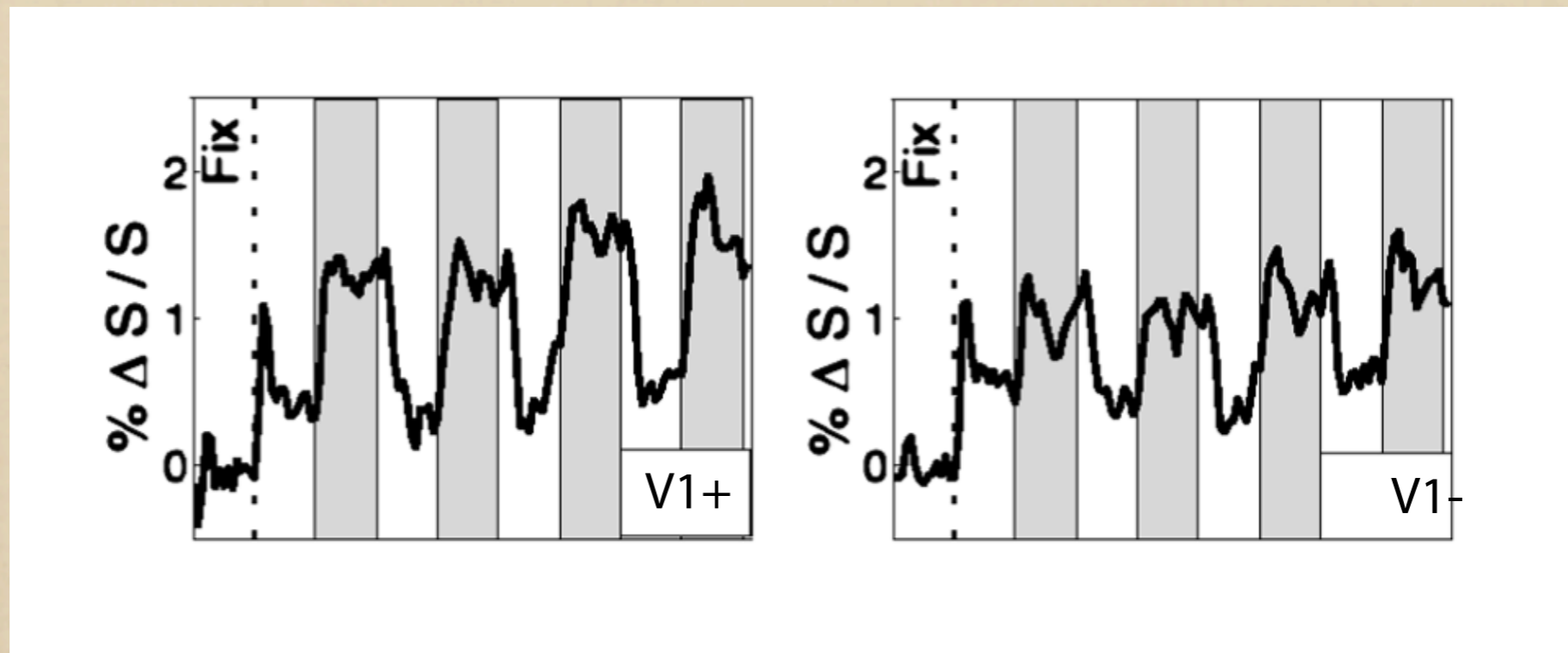
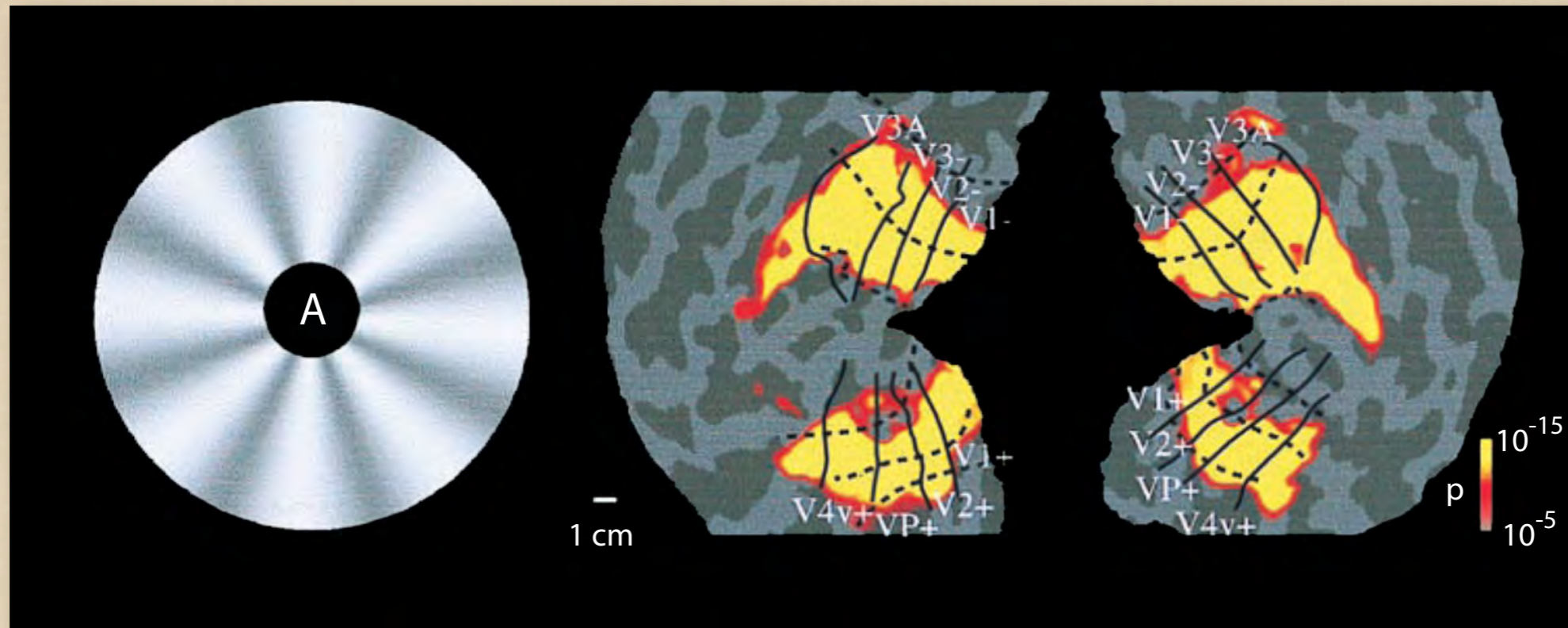


Size of modulation spatial attention of fMRI signal in different visual areas
O'Connor, Fukui, Pinsk, & Kastner (2002)



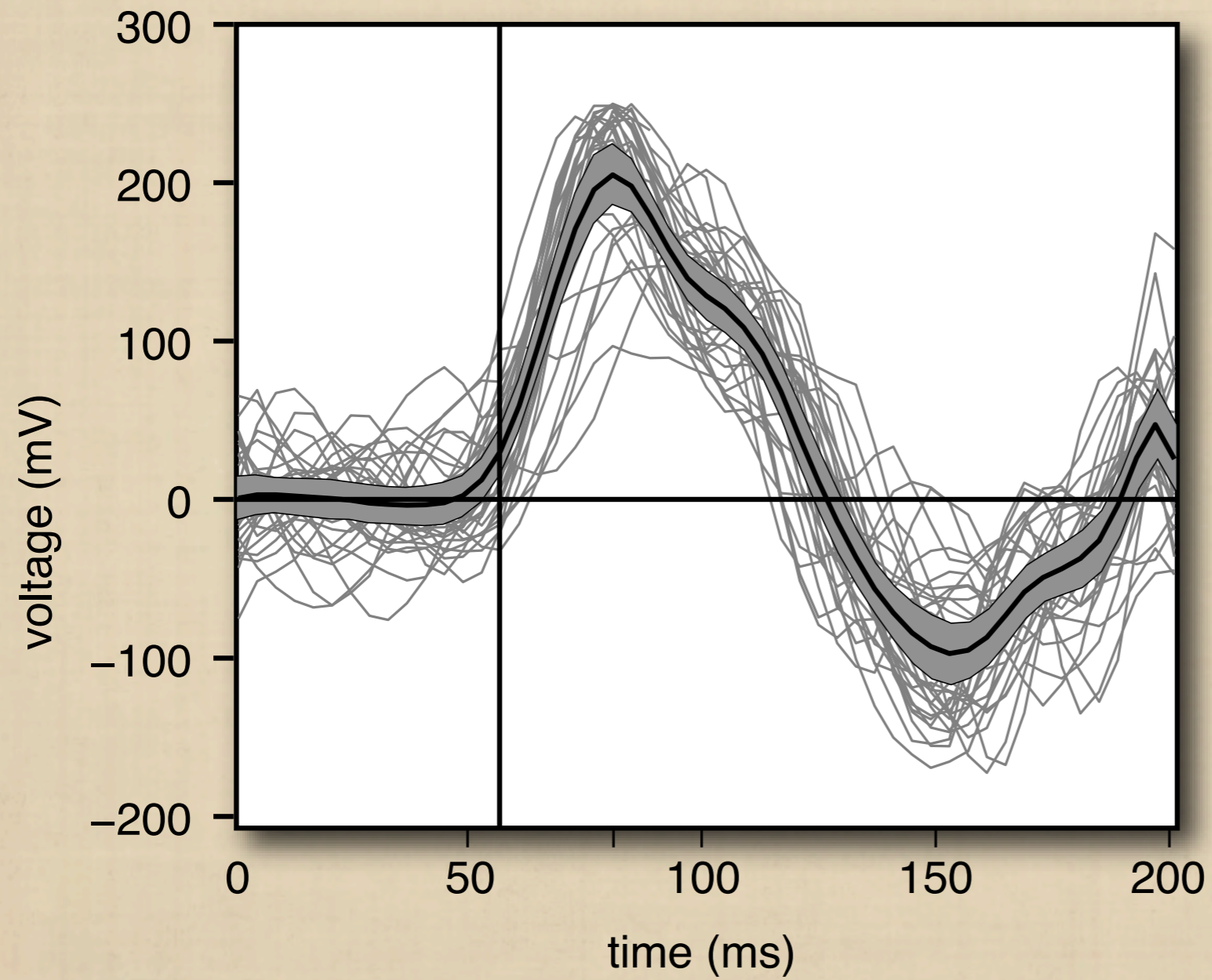
Modulation of V1 fMRI BOLD signal by attention

Somers et al. 1999



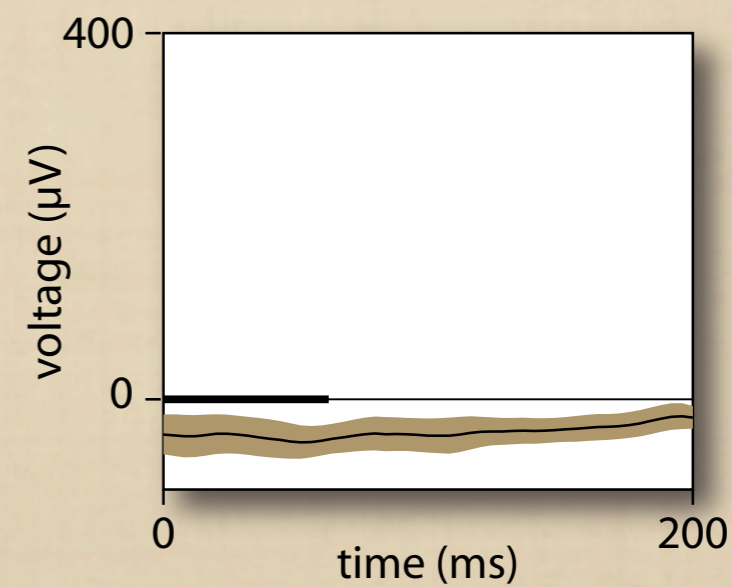
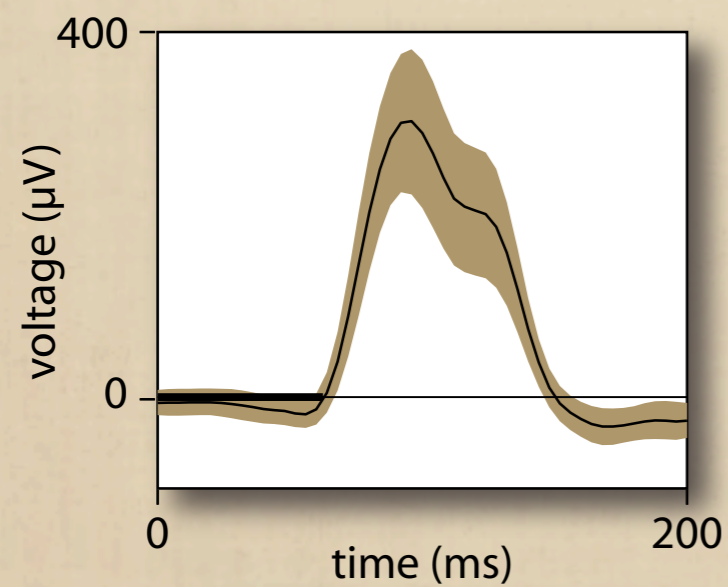
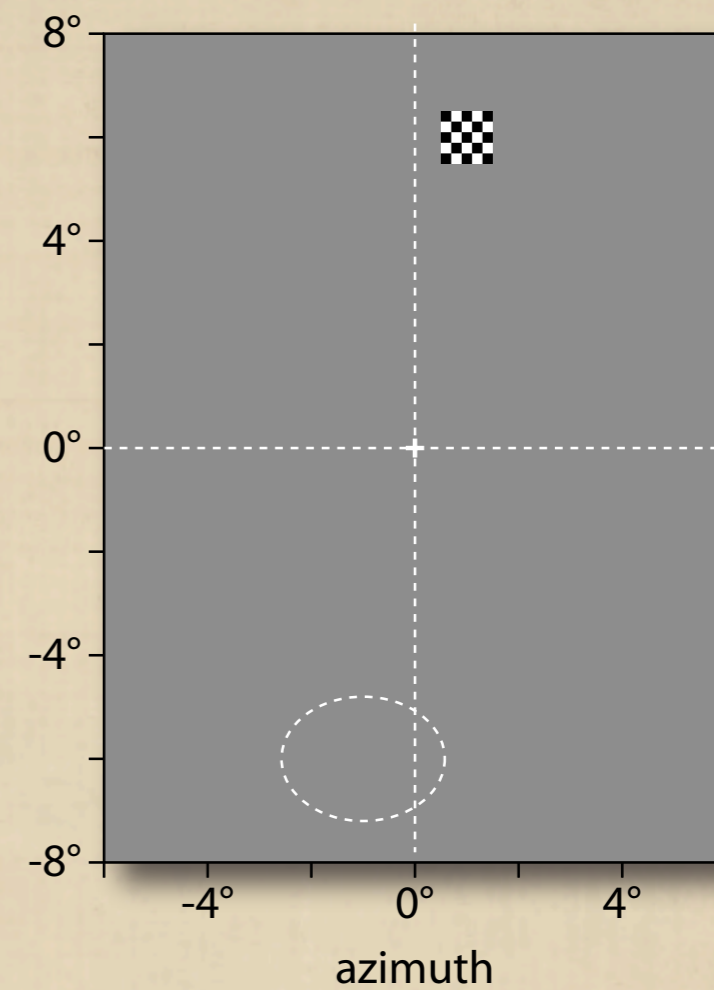
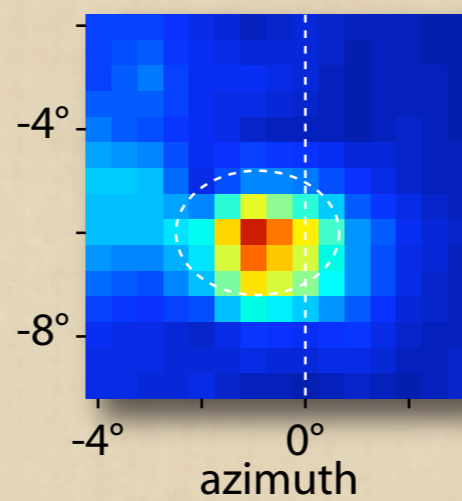
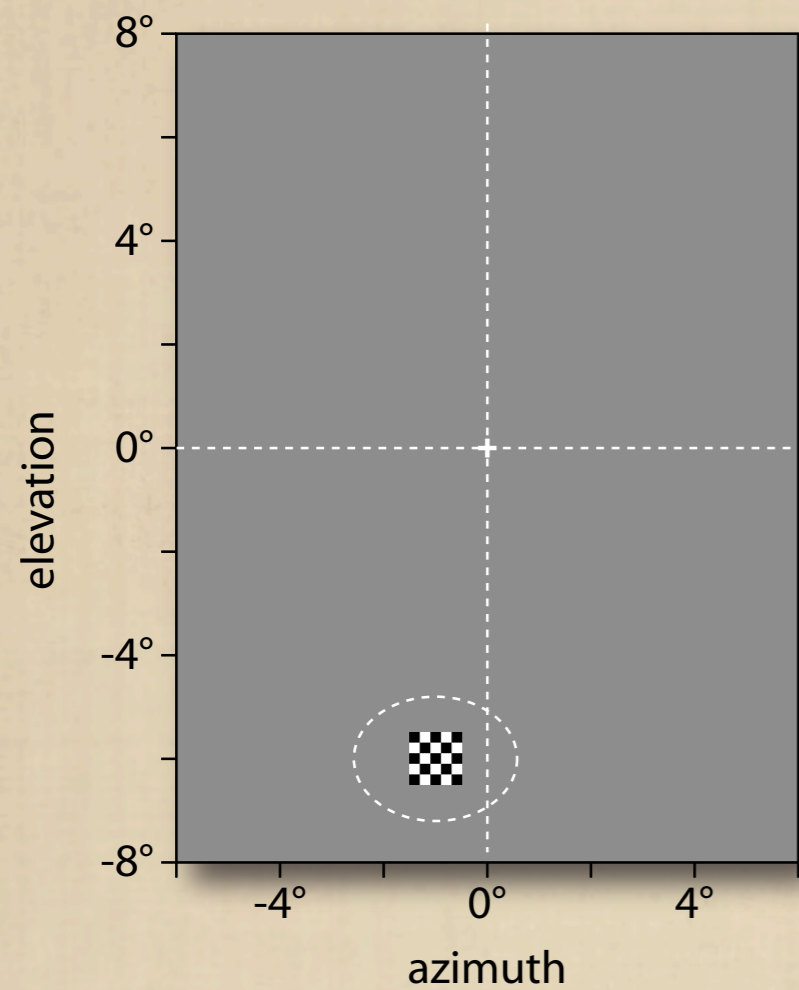
Recording from human visual cortex

Yoshor et al. 2007



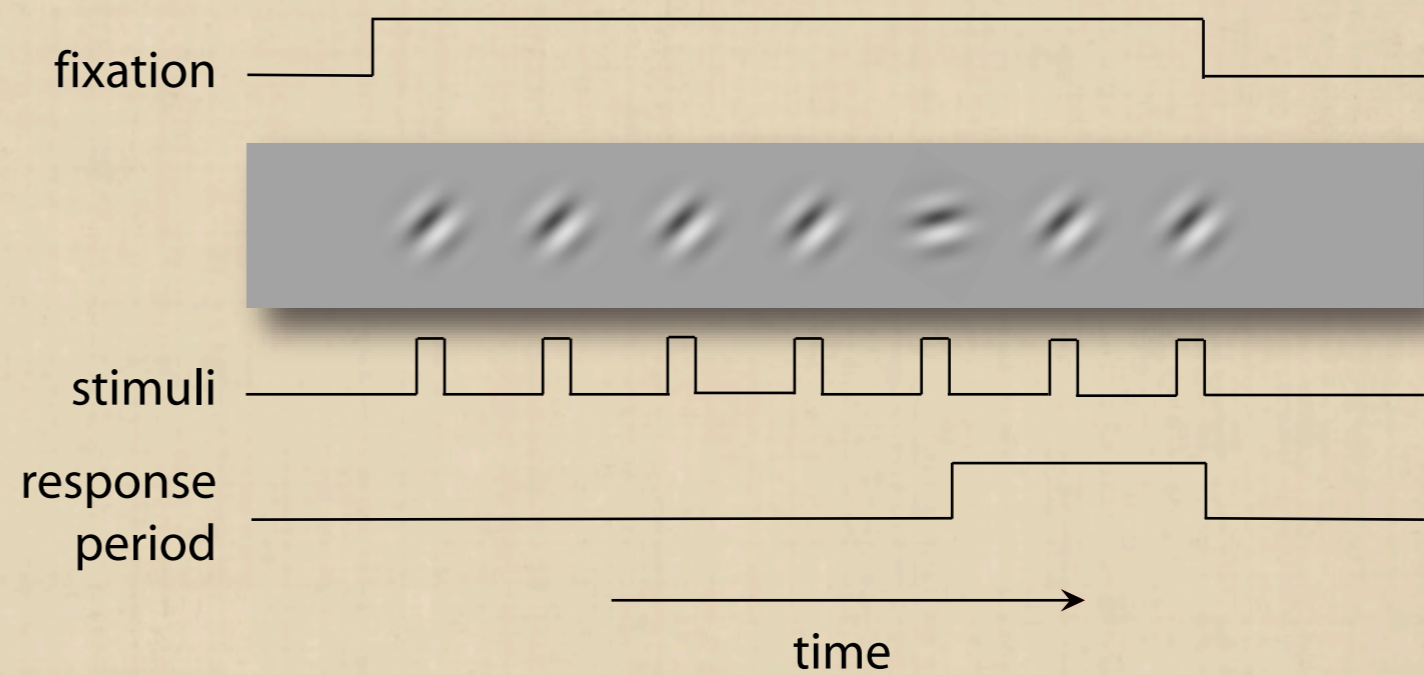
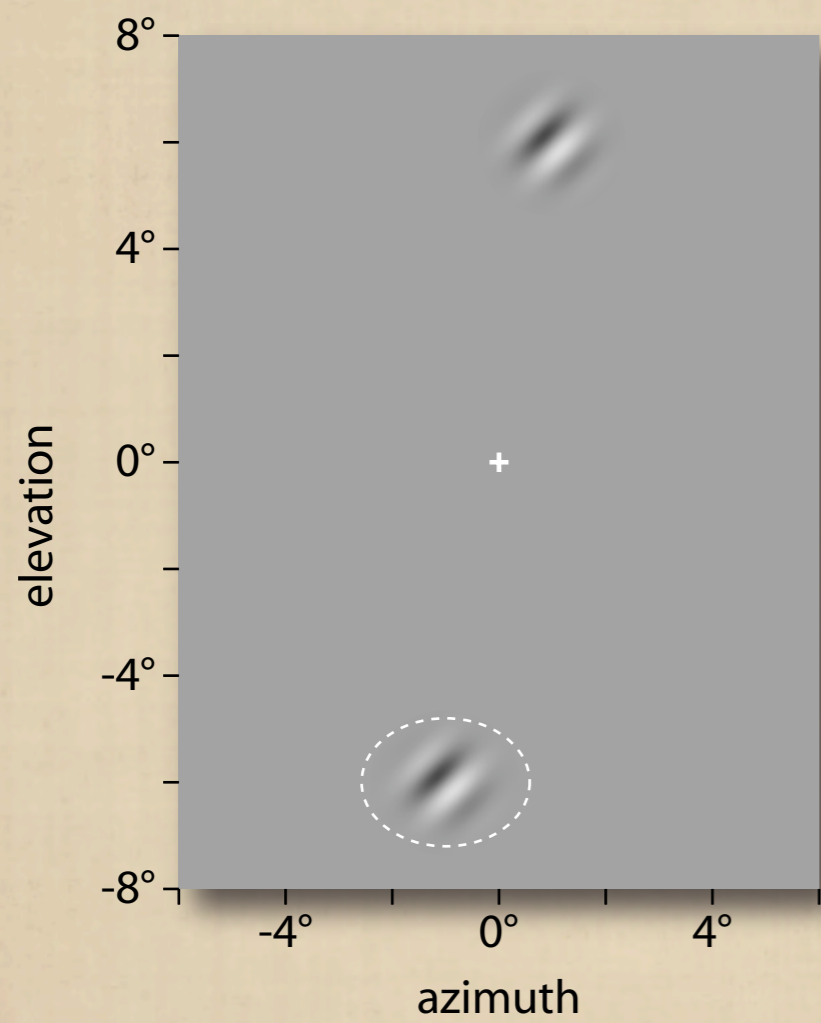
Responsive and unresponsive locations

Yoshor et al. 2007



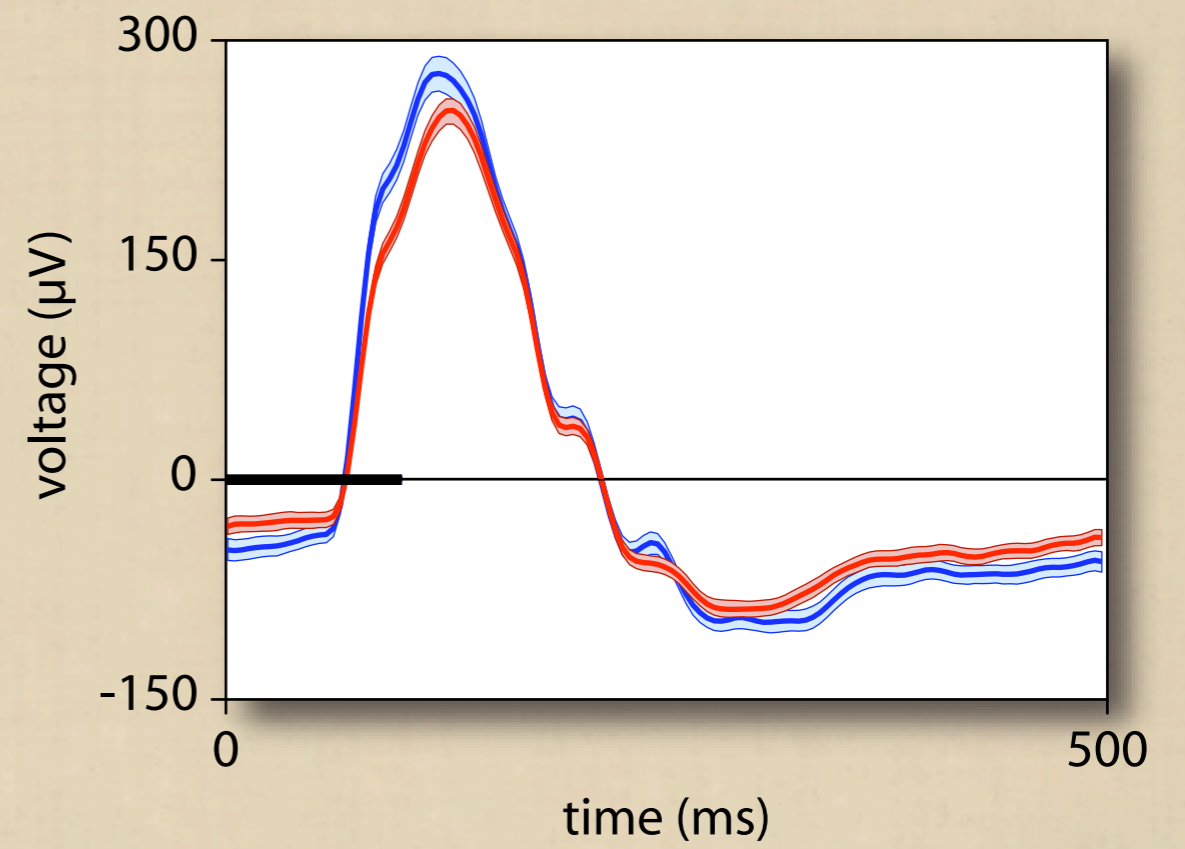
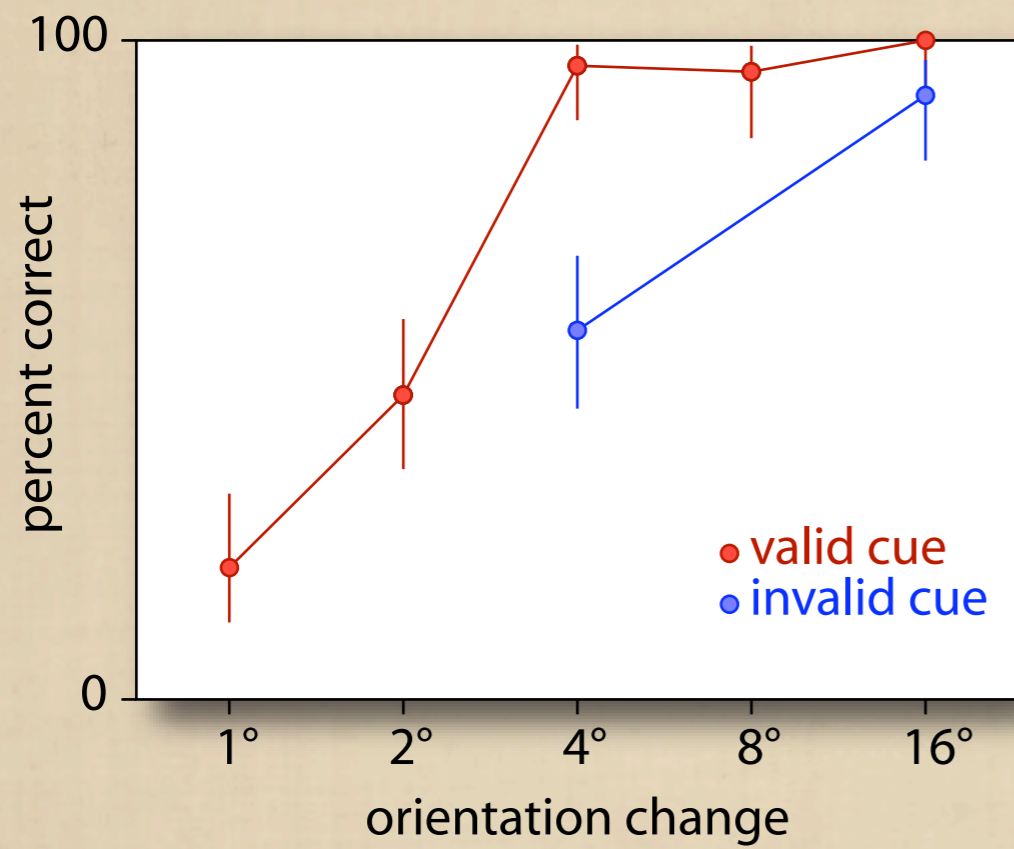
Spatial attention task

Yoshor et al. 2007

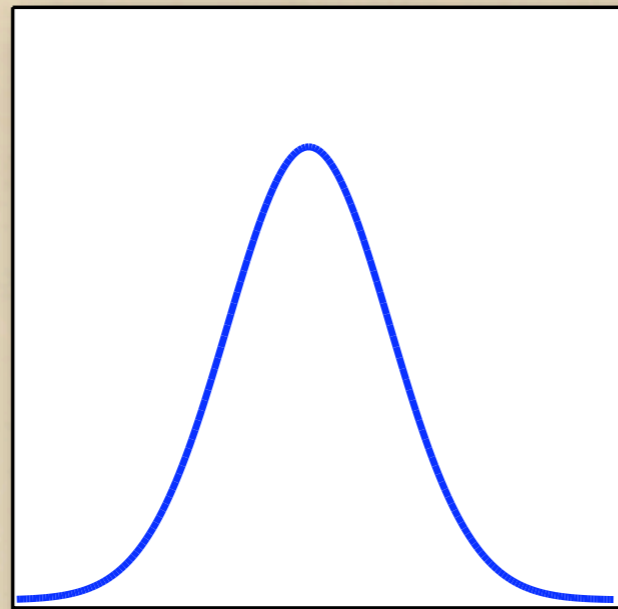


Effect of attention on human LFP

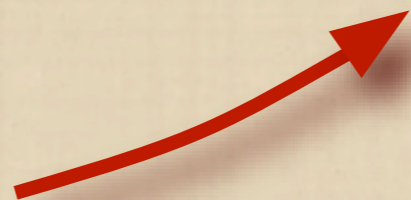
Yoshor et al. 2007



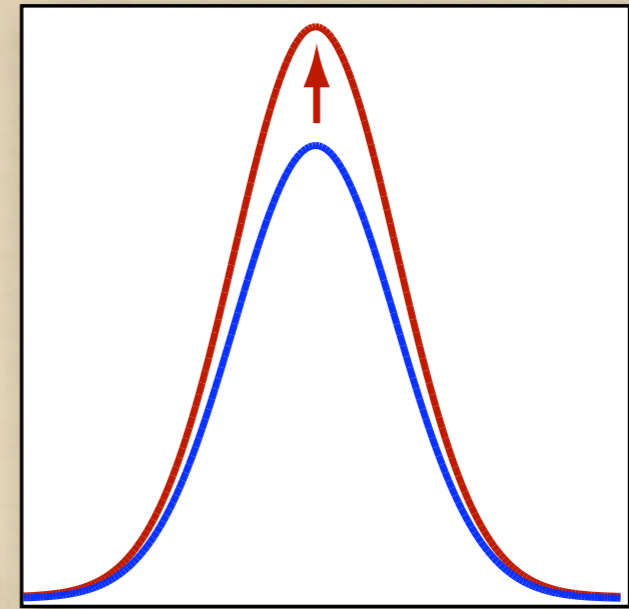
response



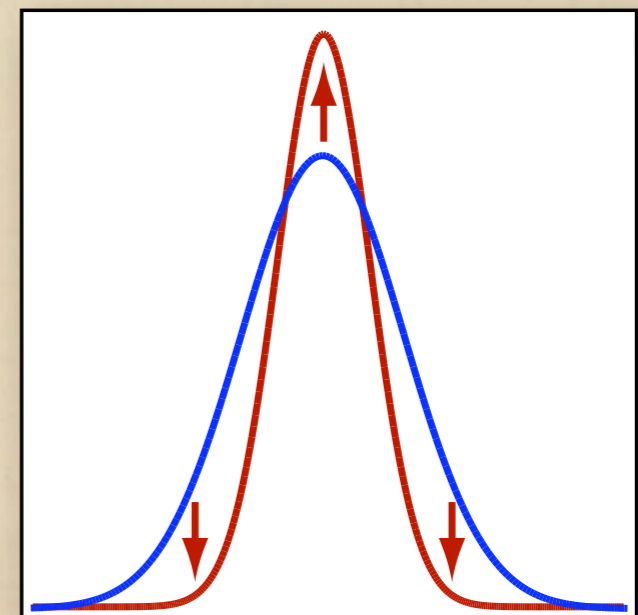
orientation



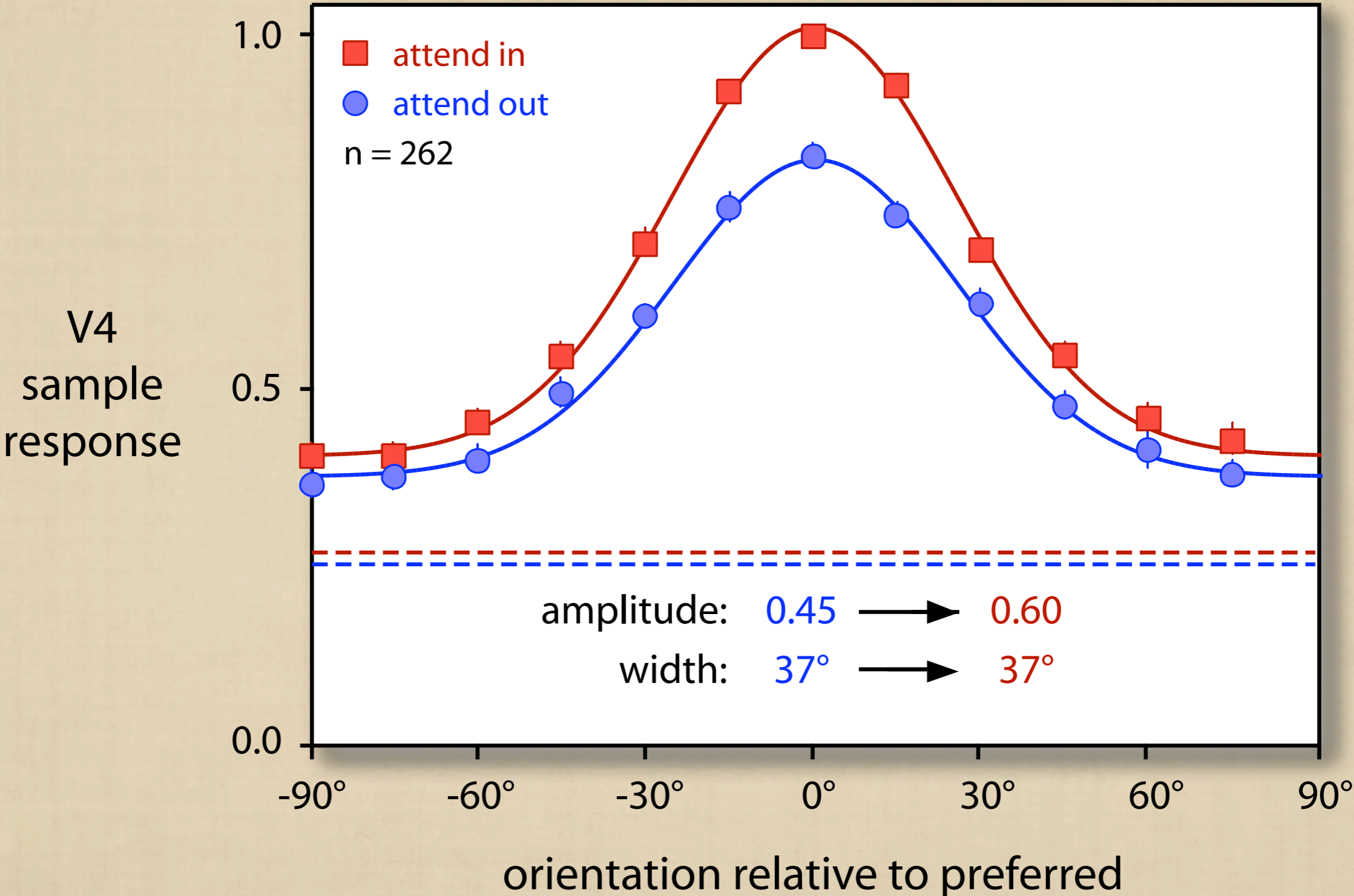
stronger response



stronger response & increased selectivity

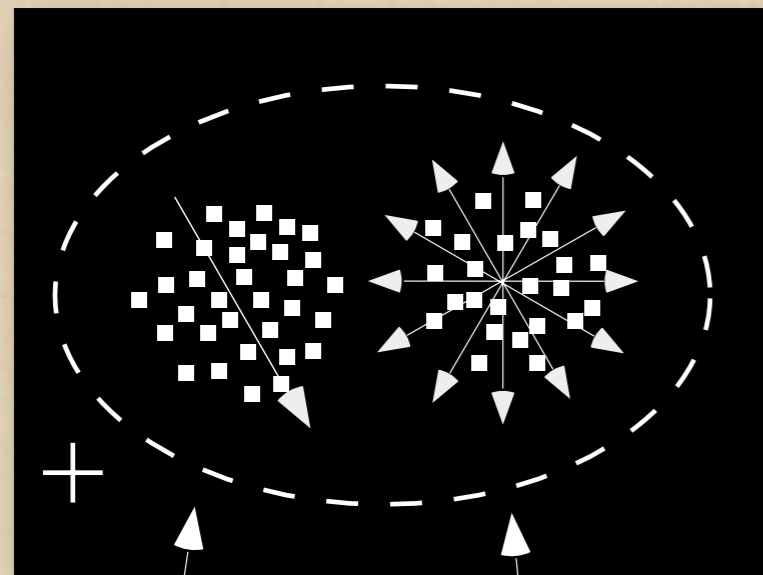


Change in average V4 orientation tuning by attention



Attention does not sharpen direction tuning in MT

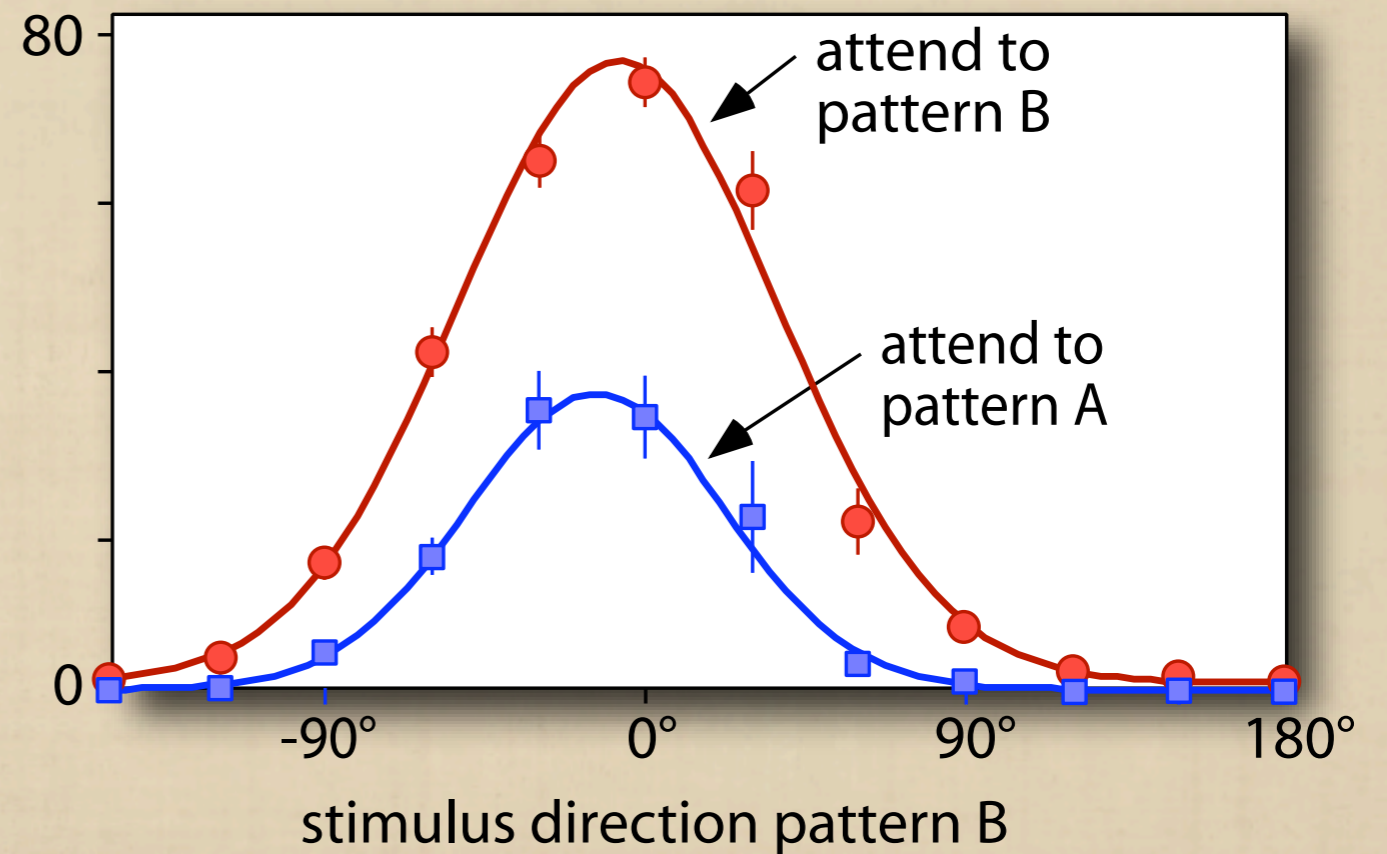
Treue & Martinez-Trujillo 1999



pattern A

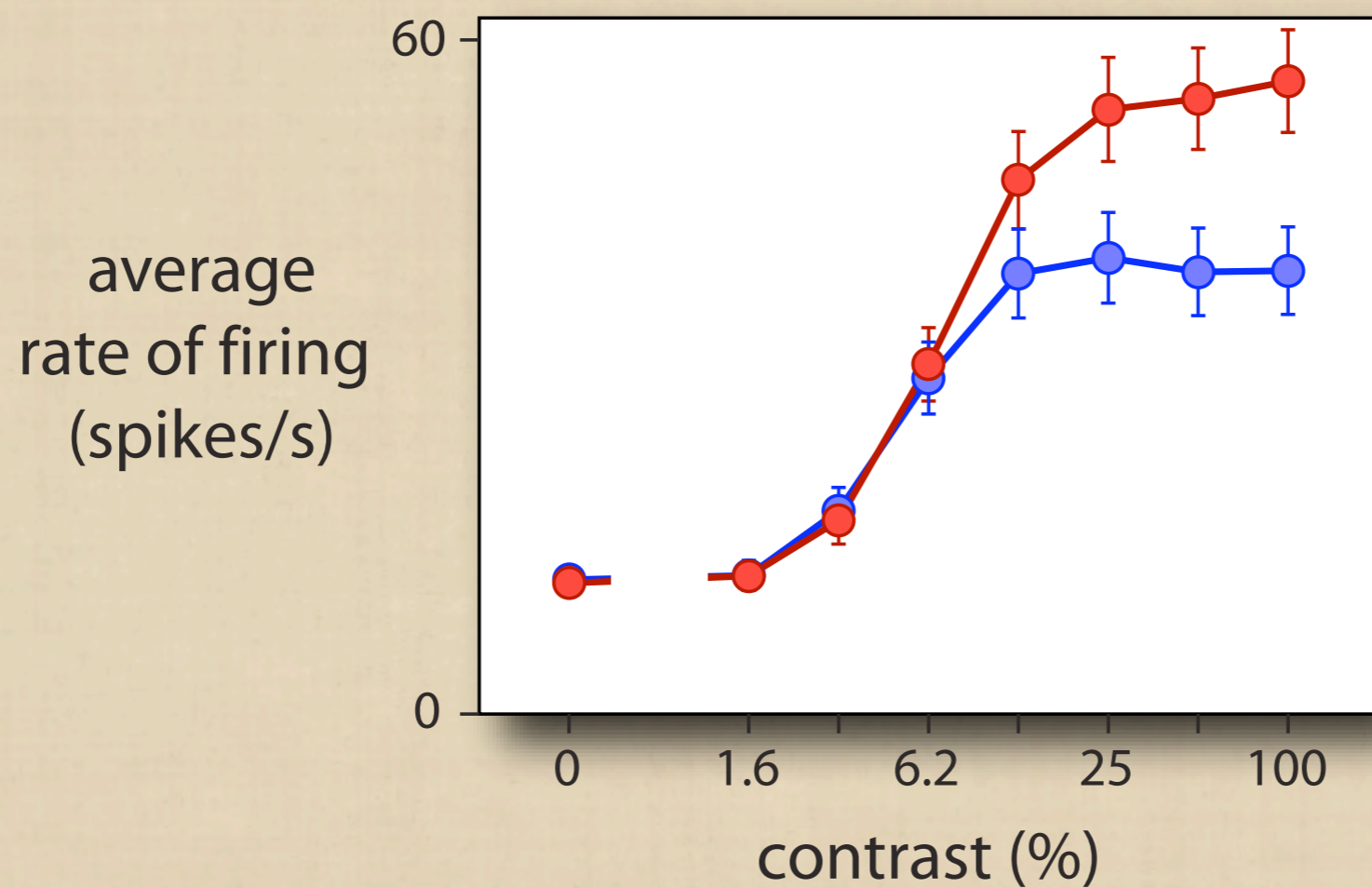
pattern B

response
(spikes/s)



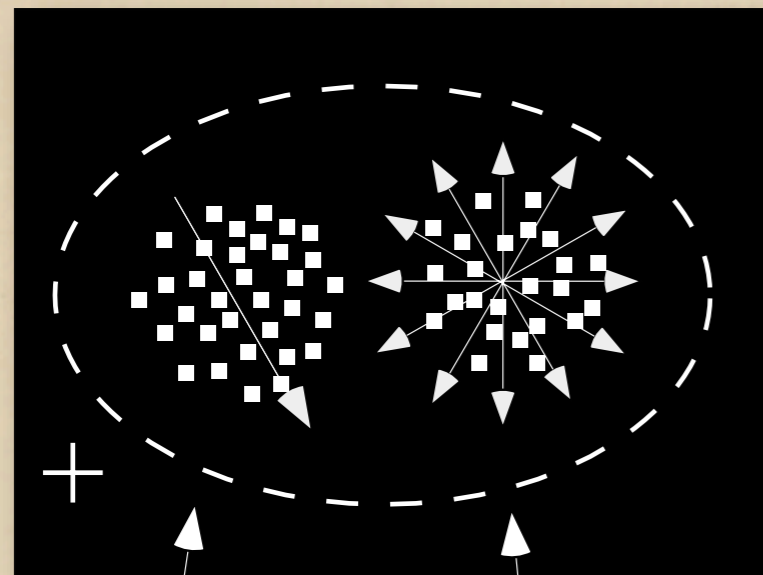
Average MT contrast response functions

(n = 56)



Attention does not sharpen direction tuning in MT

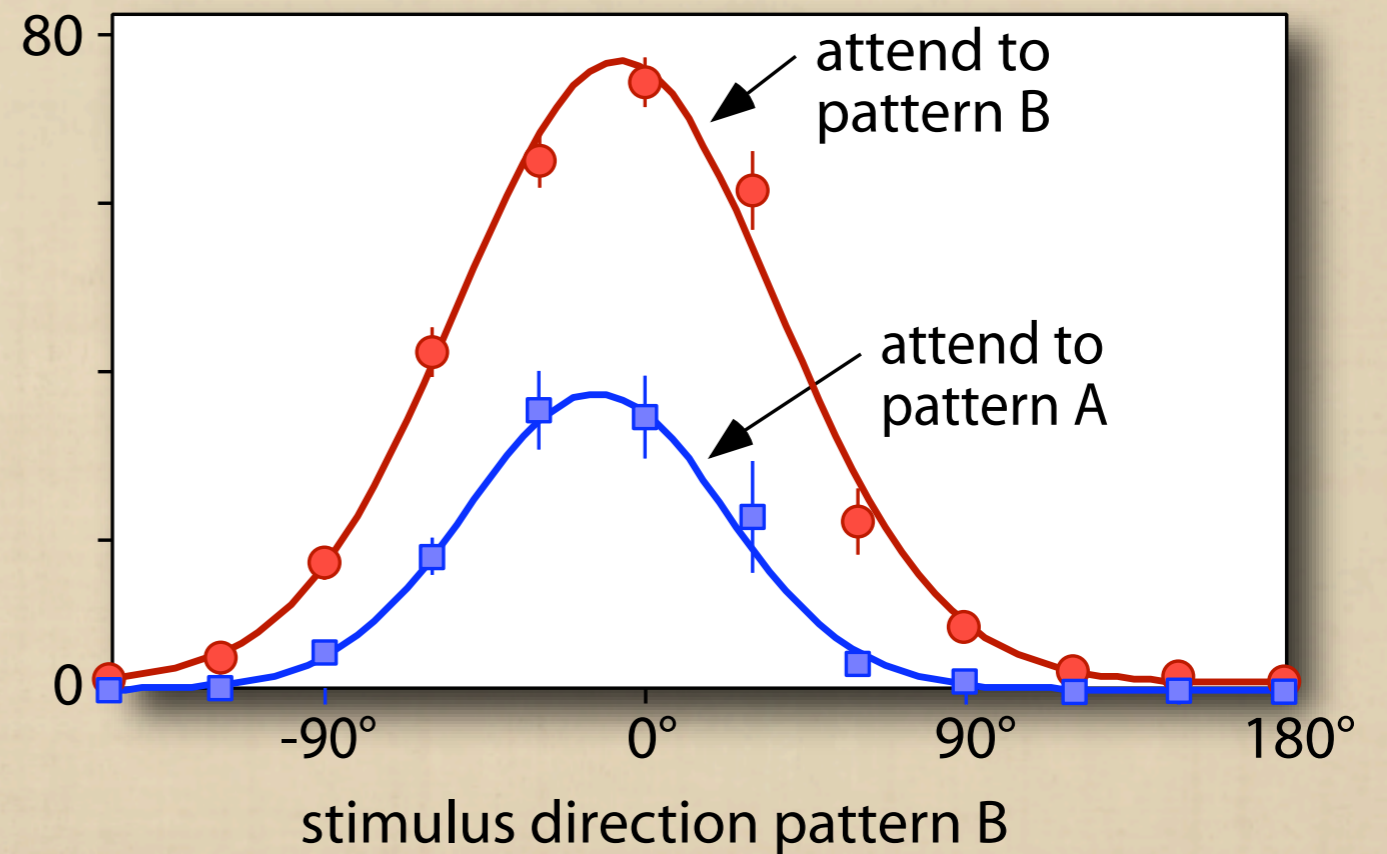
Treue & Martinez-Trujillo 1999



pattern A

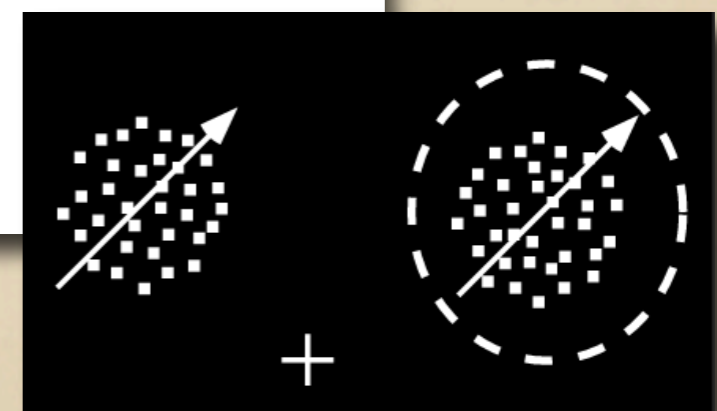
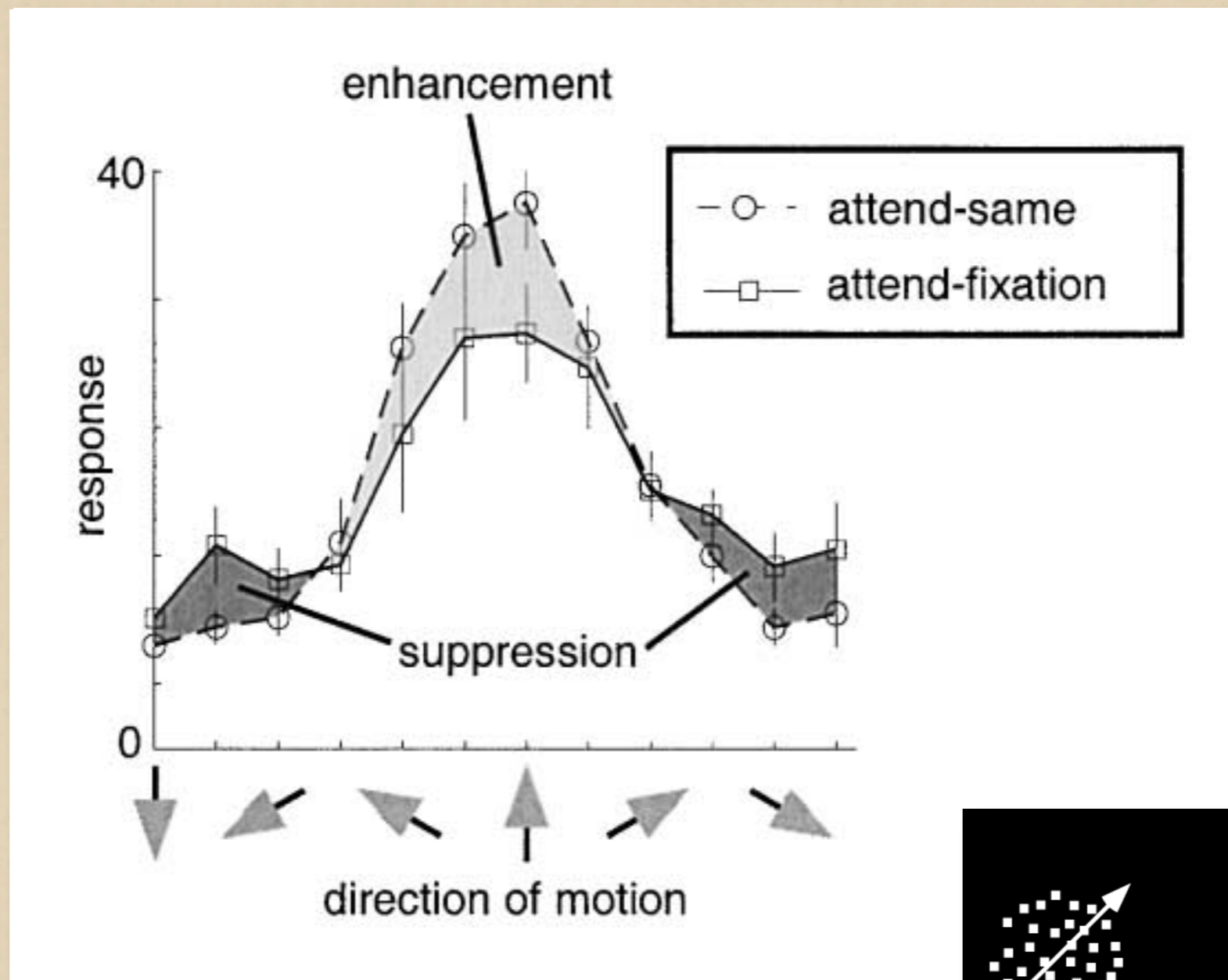
pattern B

response
(spikes/s)



Attention can sharpen the tuning of a population response

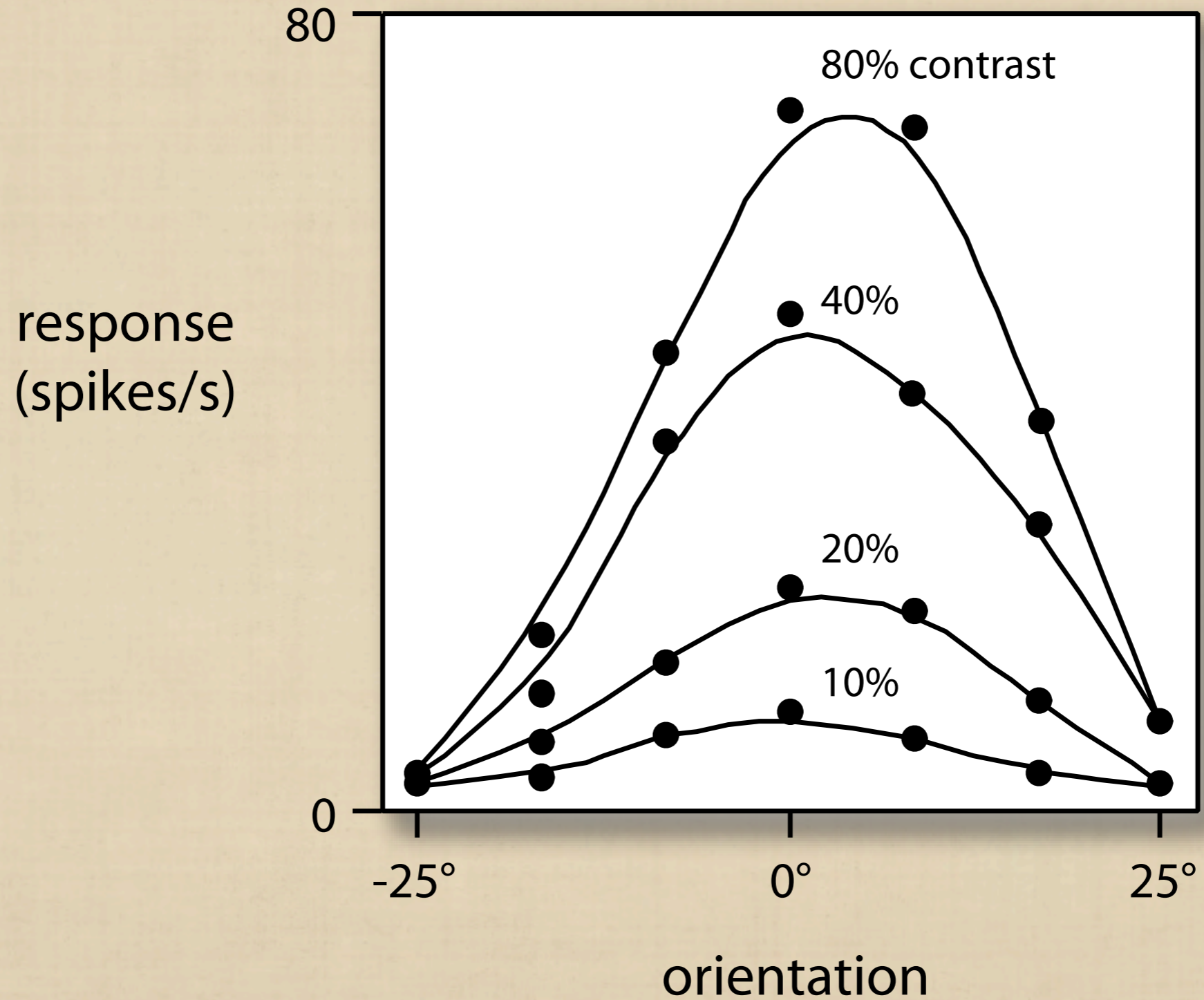
Martinez-Trujillo & Treue 2004



Orientation tuning measured with different contrasts

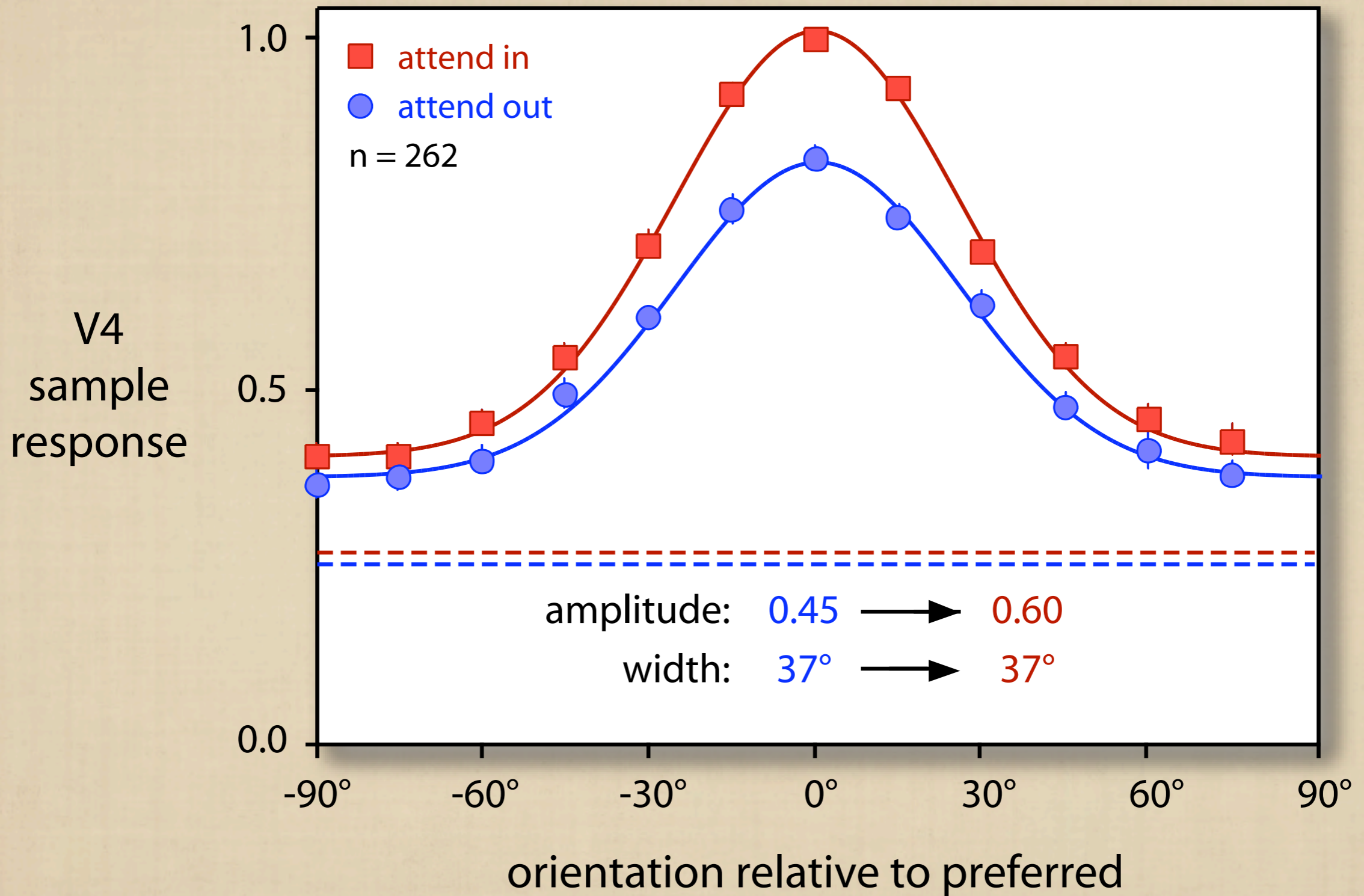
Cat V1

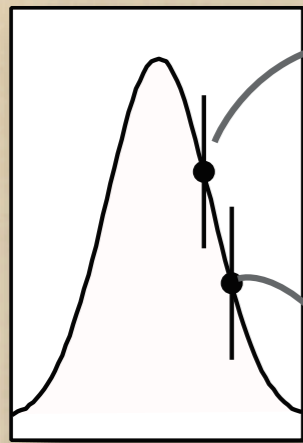
Sclar & Freeman 1982



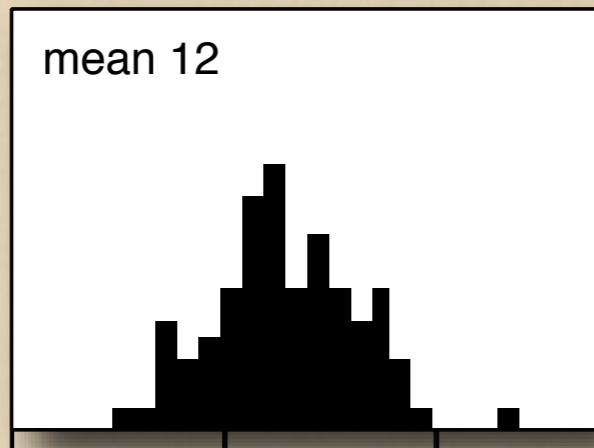
Change in average V4 orientation tuning by attention

McAdams & Maunsell (1999)





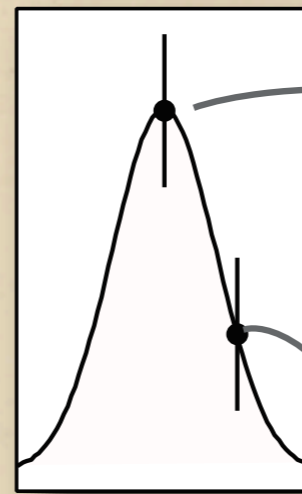
orientation



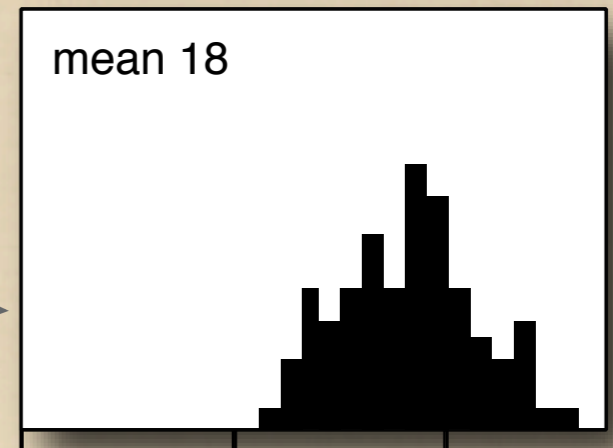
mean 12

0 10 20

spikes per stimulus



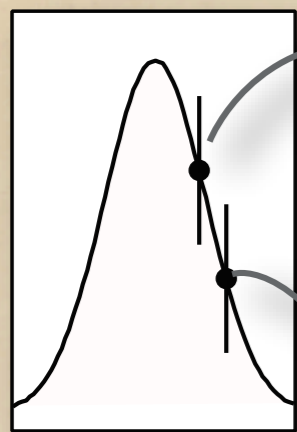
orientation



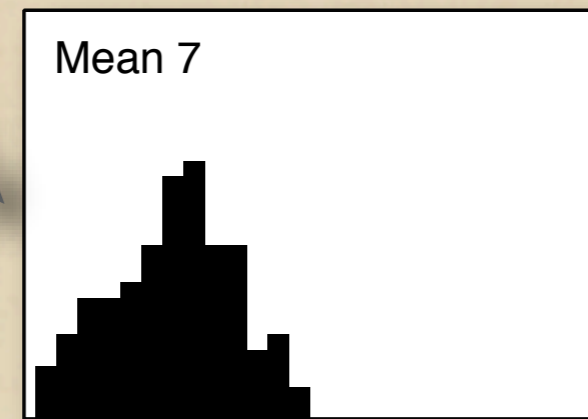
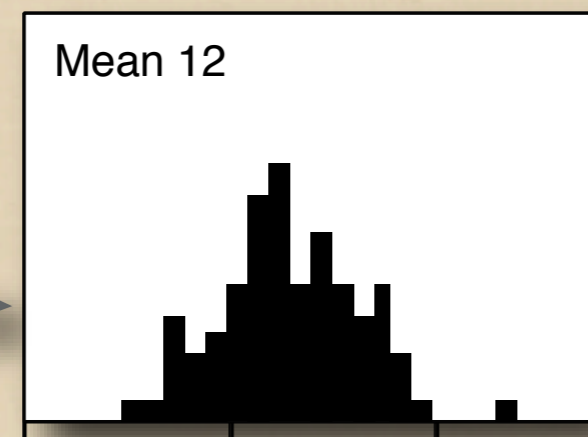
mean 18

0 10 20

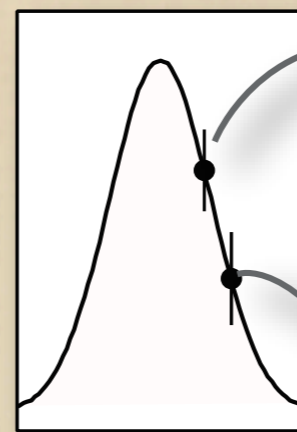
spikes per stimulus



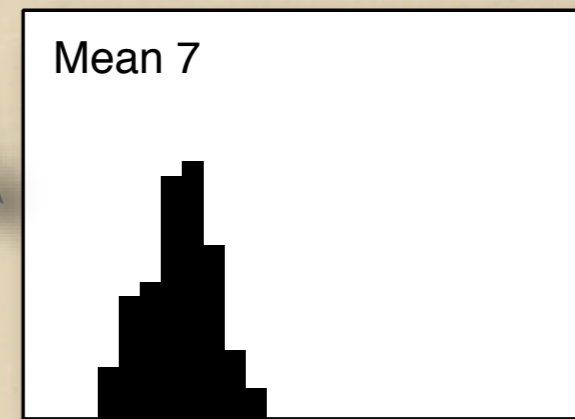
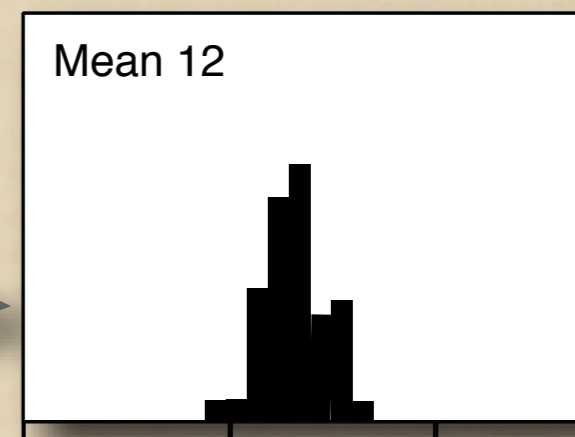
Orientation



0 10 20
Spikes Per Stimulus



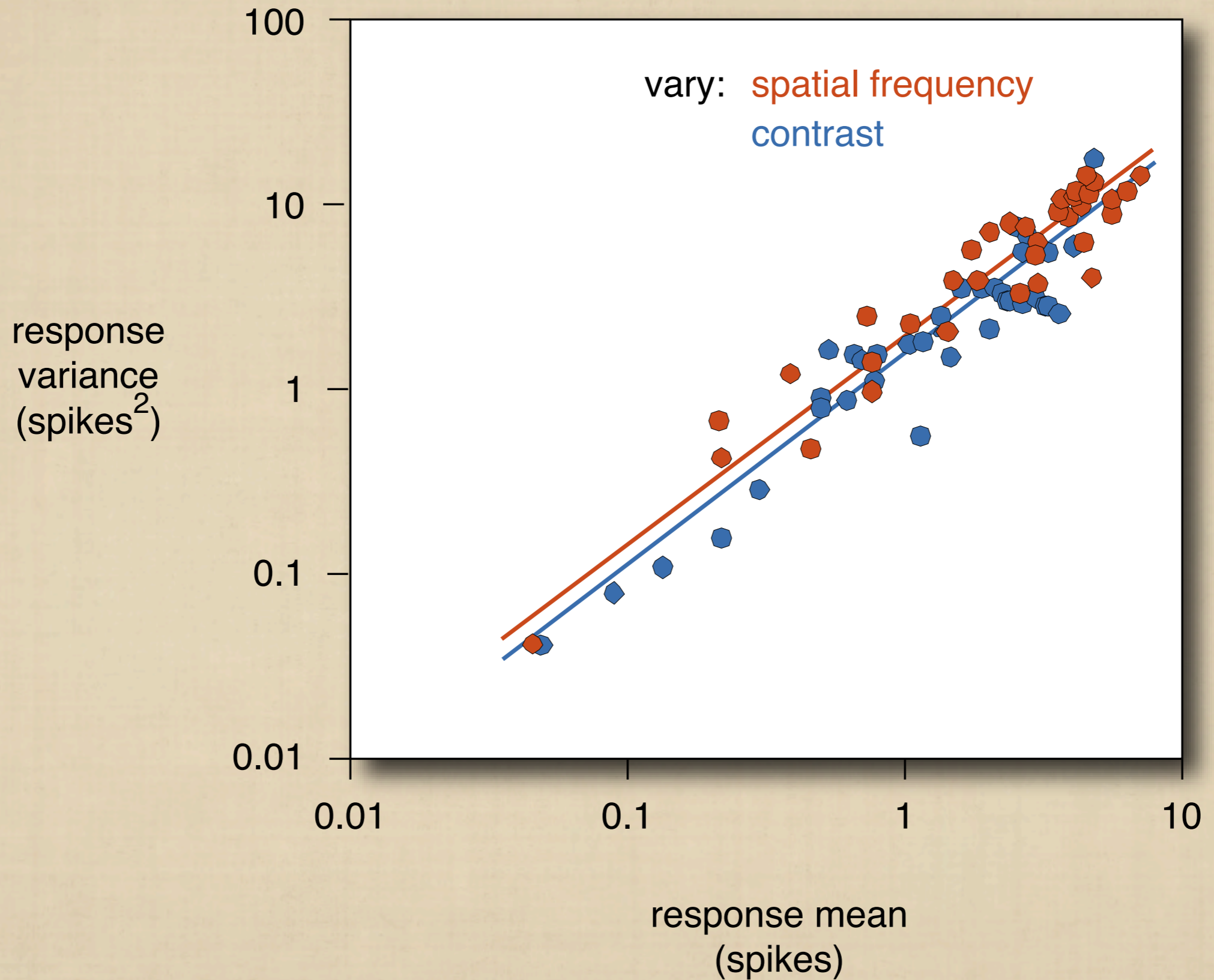
Orientation



0 10 20
Spikes Per Stimulus

Variance of cat V1 neuron response

Dean 1981

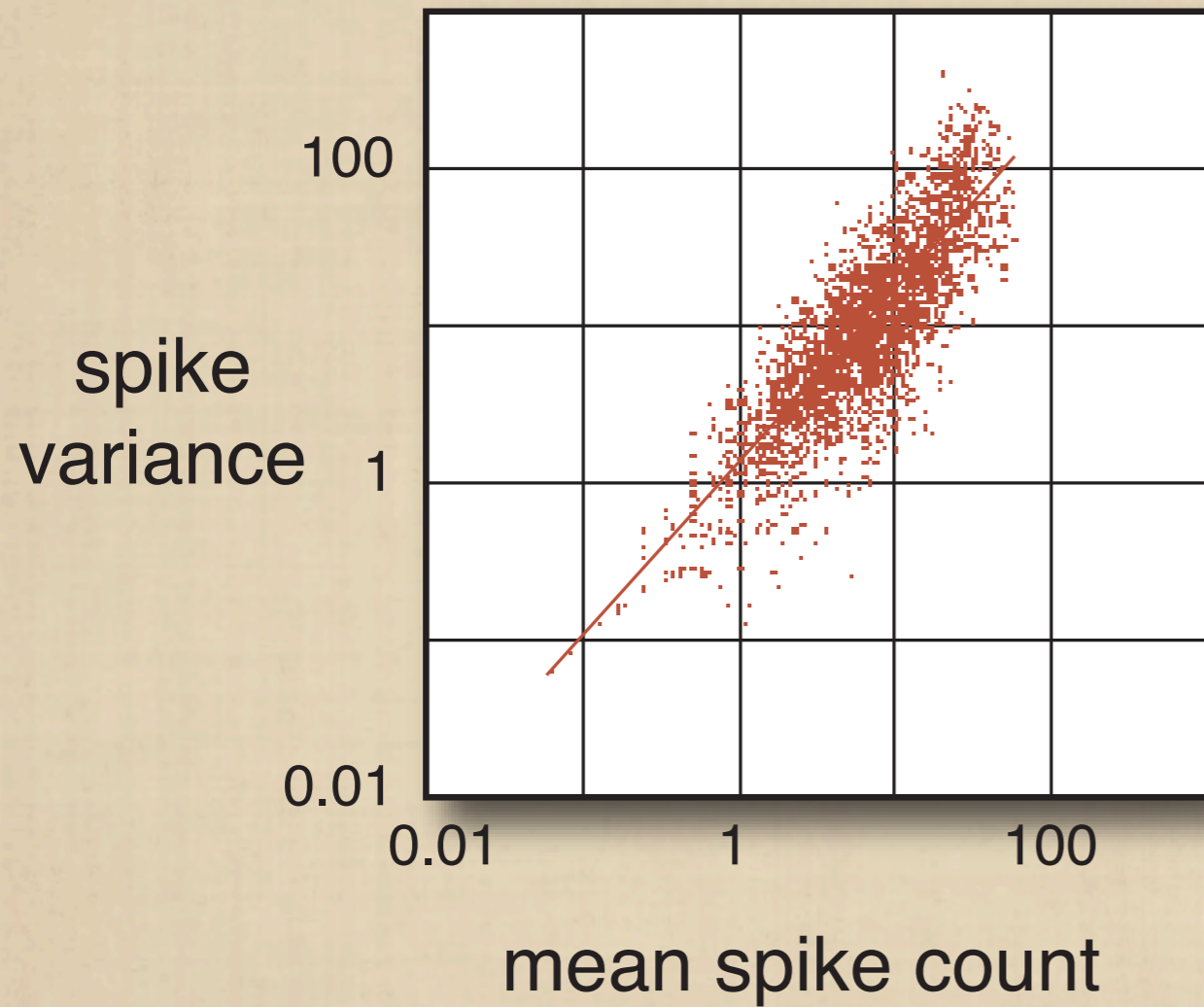


V4 sample counts-variance functions

McAdams & Maunsell (1999)

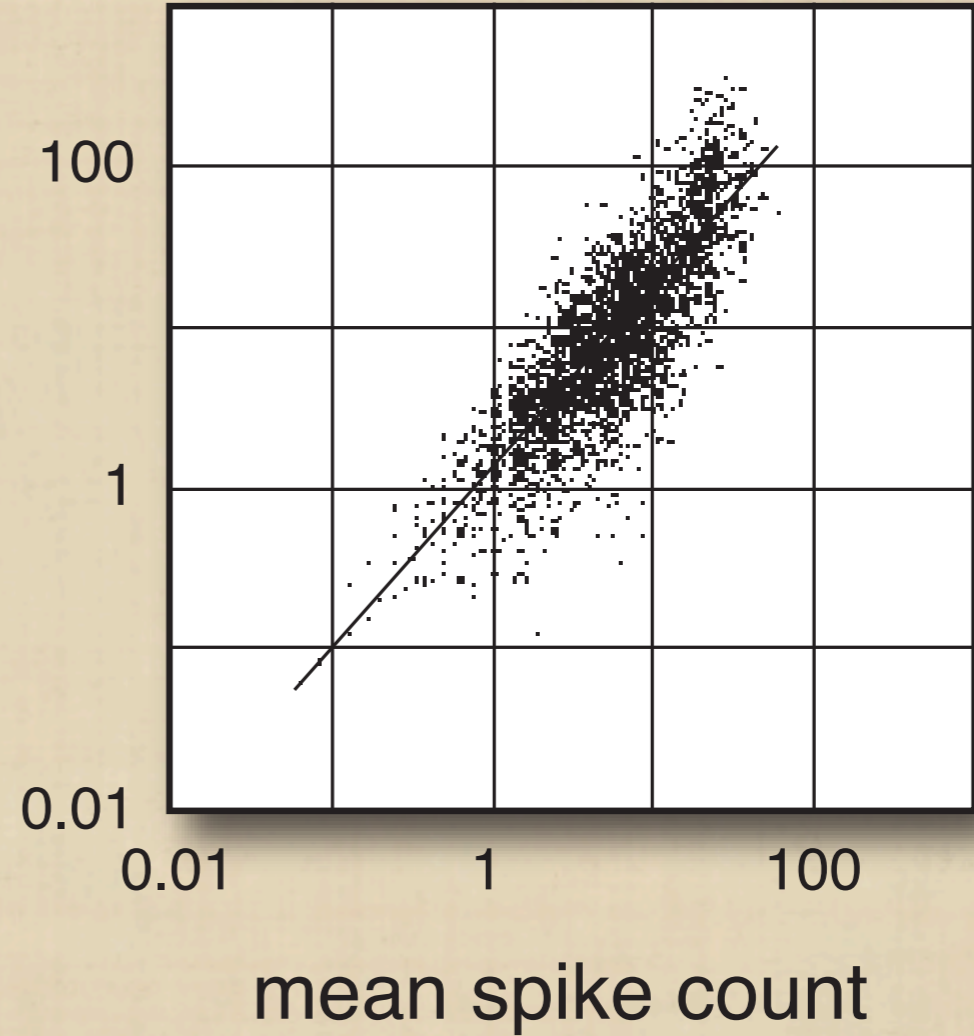
with attention

$$\text{variance} = 1.2 * \text{counts}^{1.1}$$

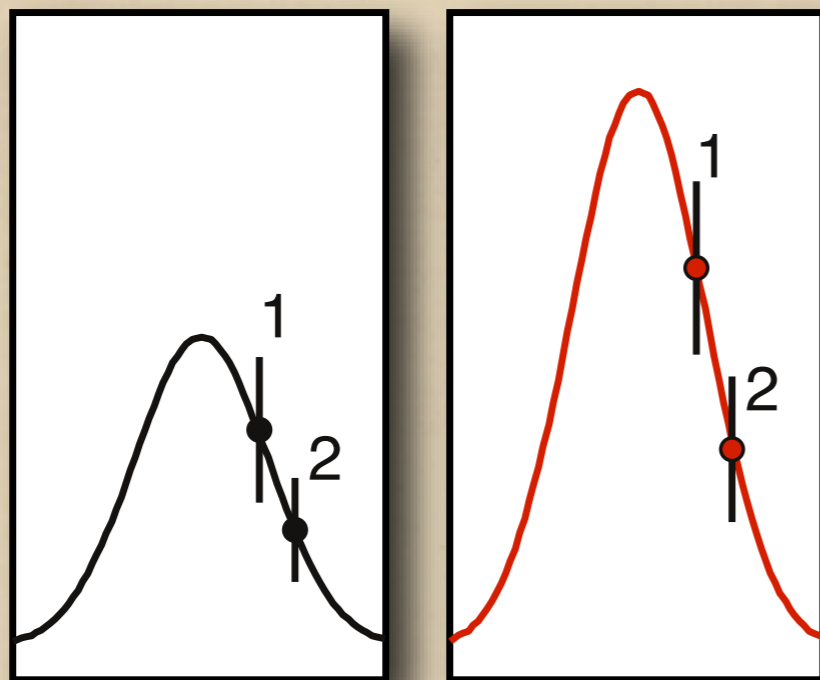


without attention

$$\text{variance} = 1.3 * \text{counts}^{1.1}$$

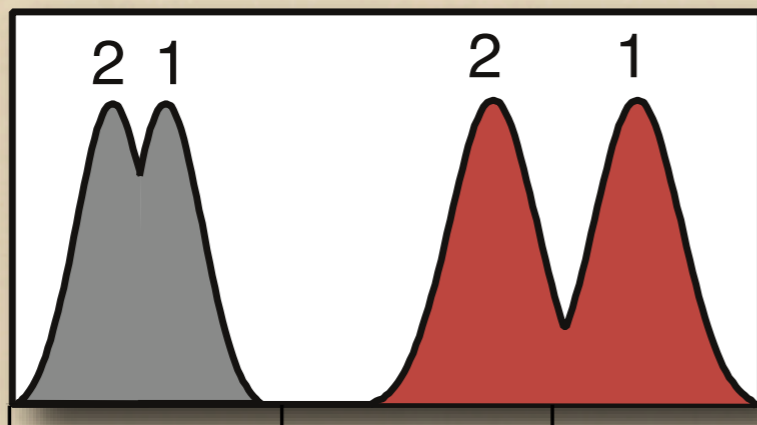


response

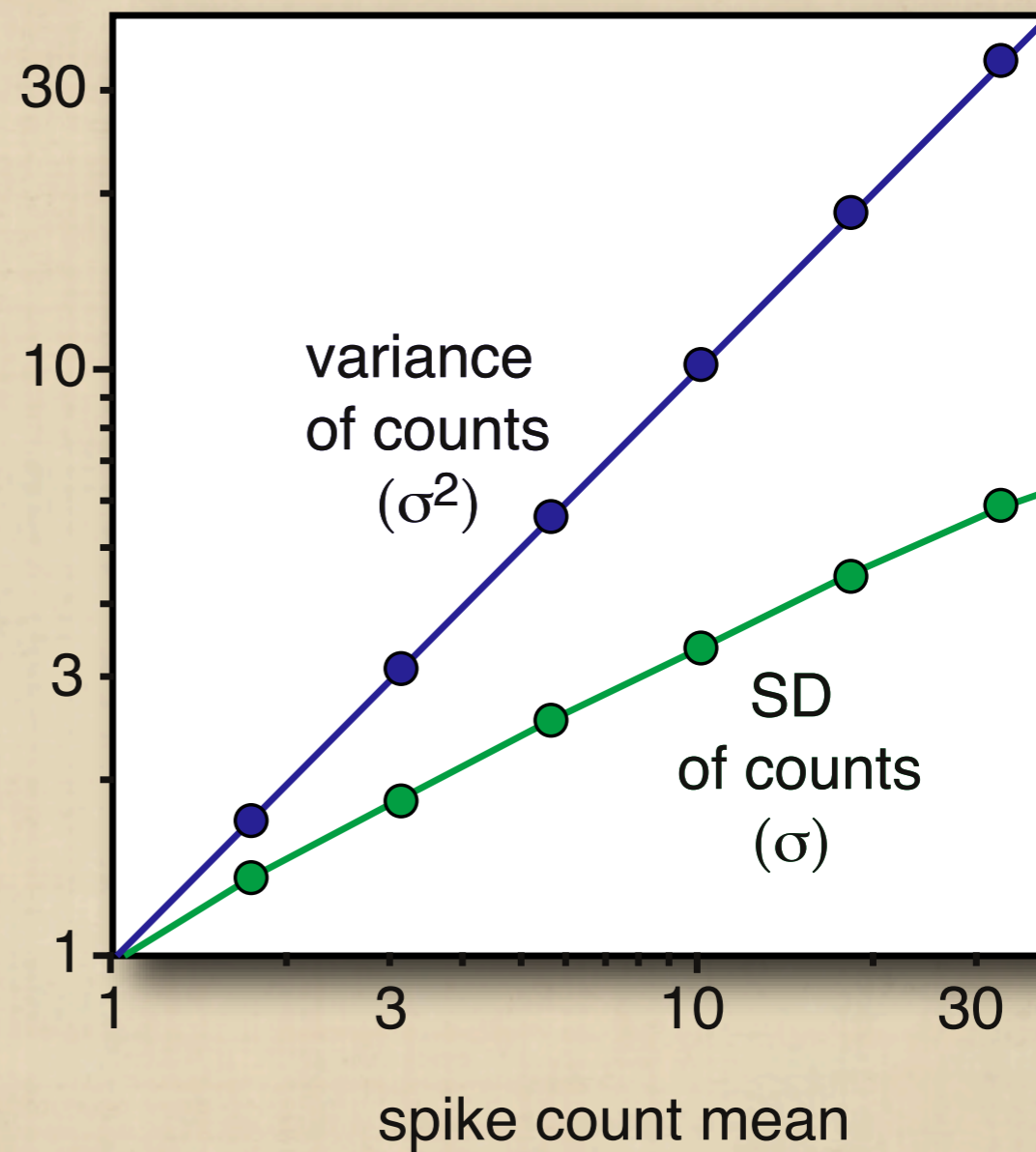


orientation

orientation



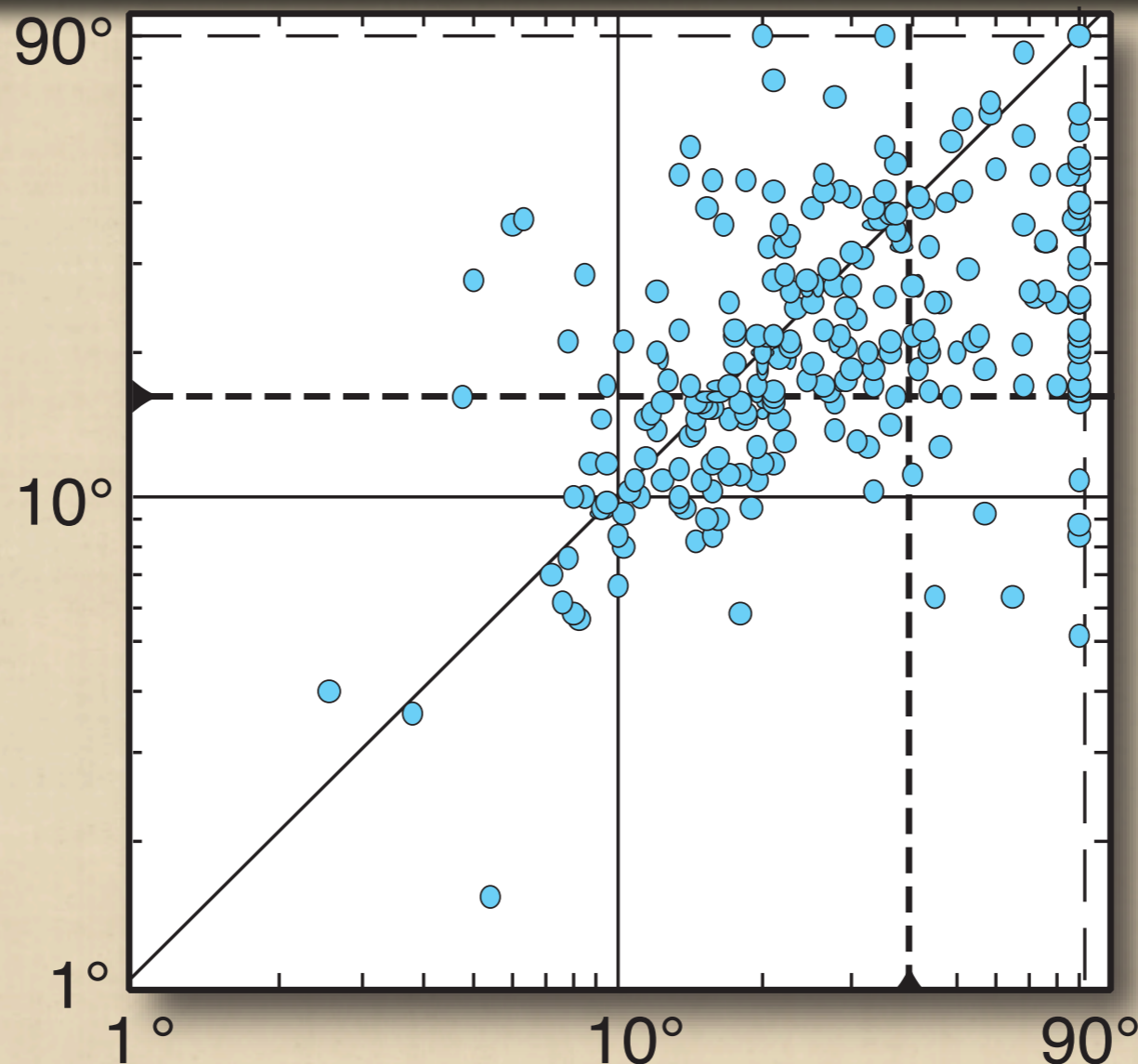
spikes per stimulus



Effect of attention on orientation discriminability



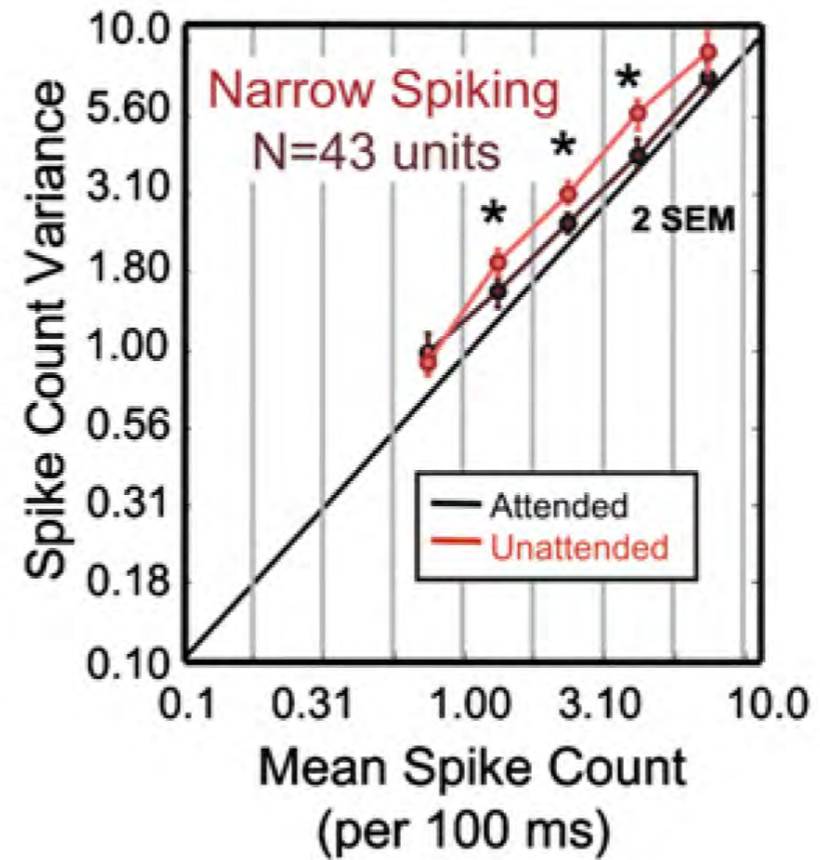
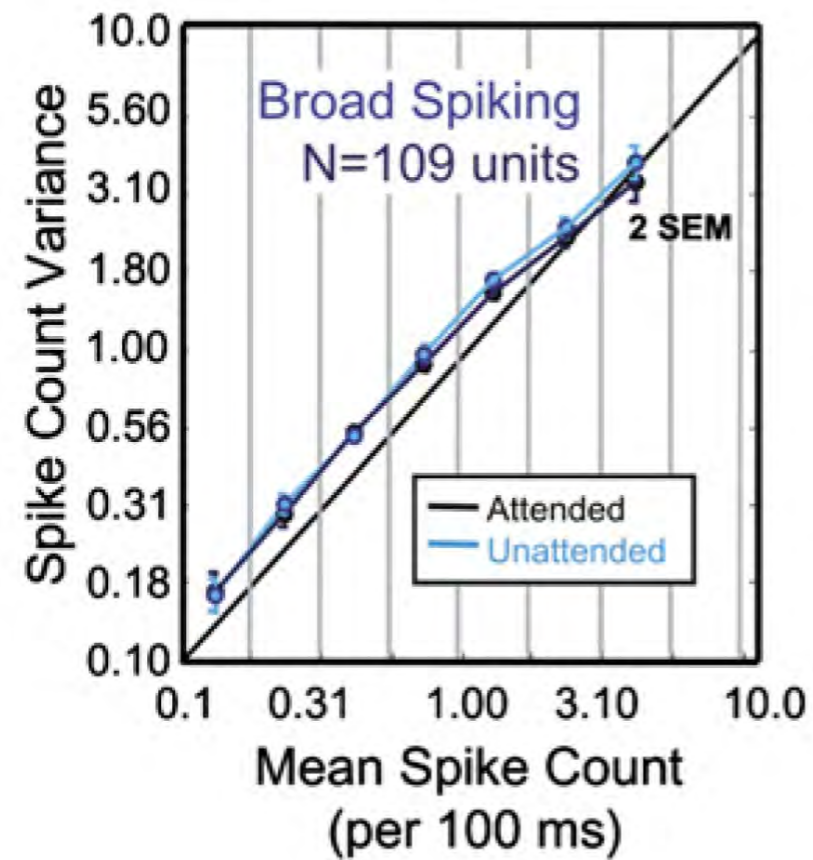
discriminability
attending to target



discriminability
ignoring target

Attention affects Fano factor in Area V4

Mitchell et al. 2007

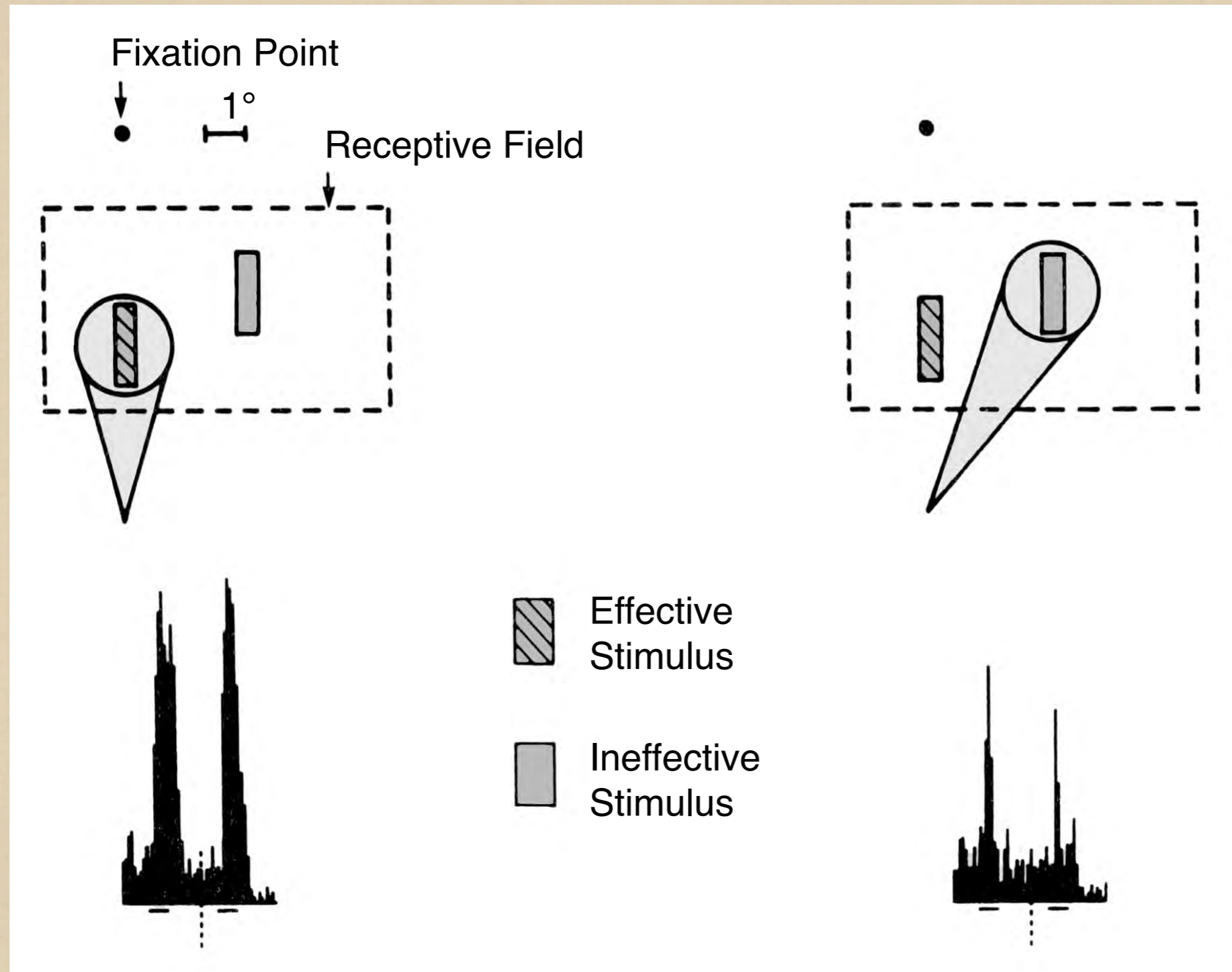






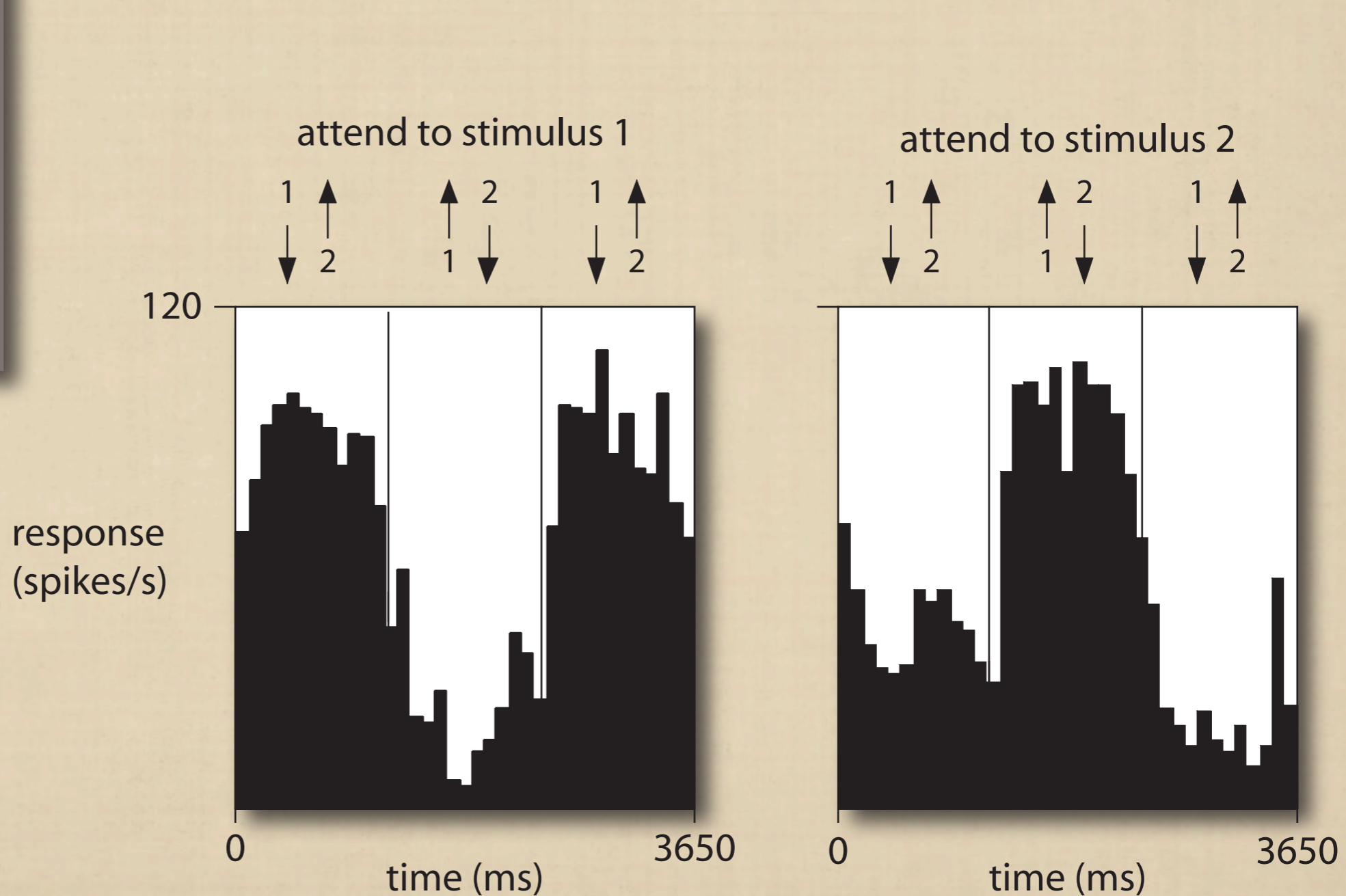
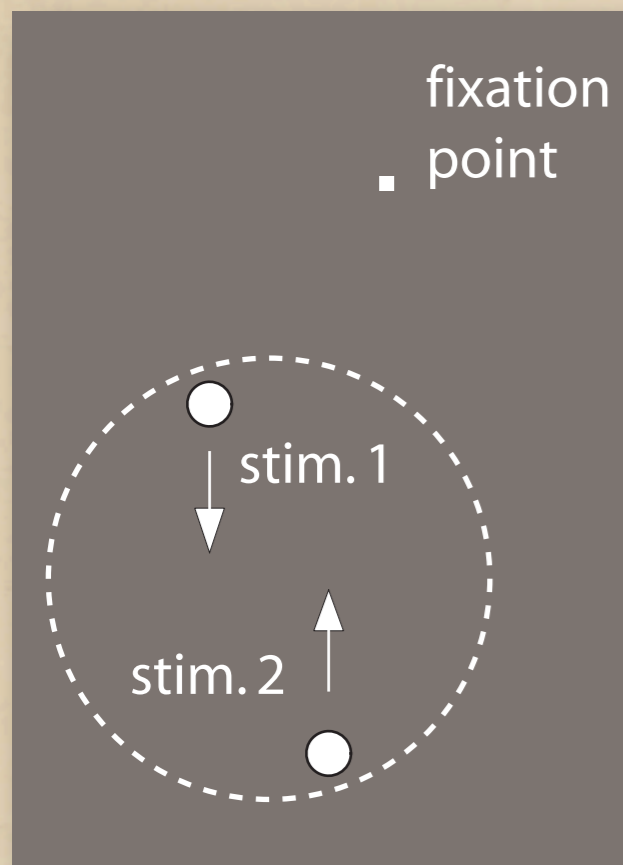
Attention to Stimuli within a V4 Receptive Field

Moran and Desimone 1985



MT responses with attention to one of two receptive field stimuli

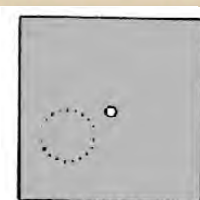
Treue & Maunsell, 1996



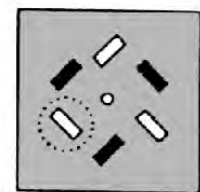
Attention to Grouped Stimuli

Motter 1994

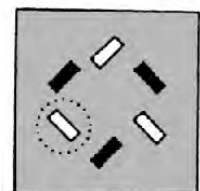
Fixation



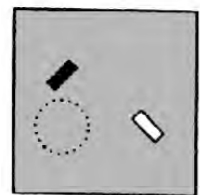
Stimuli



Cue Removed



Decision



M

NM

M

NM

M

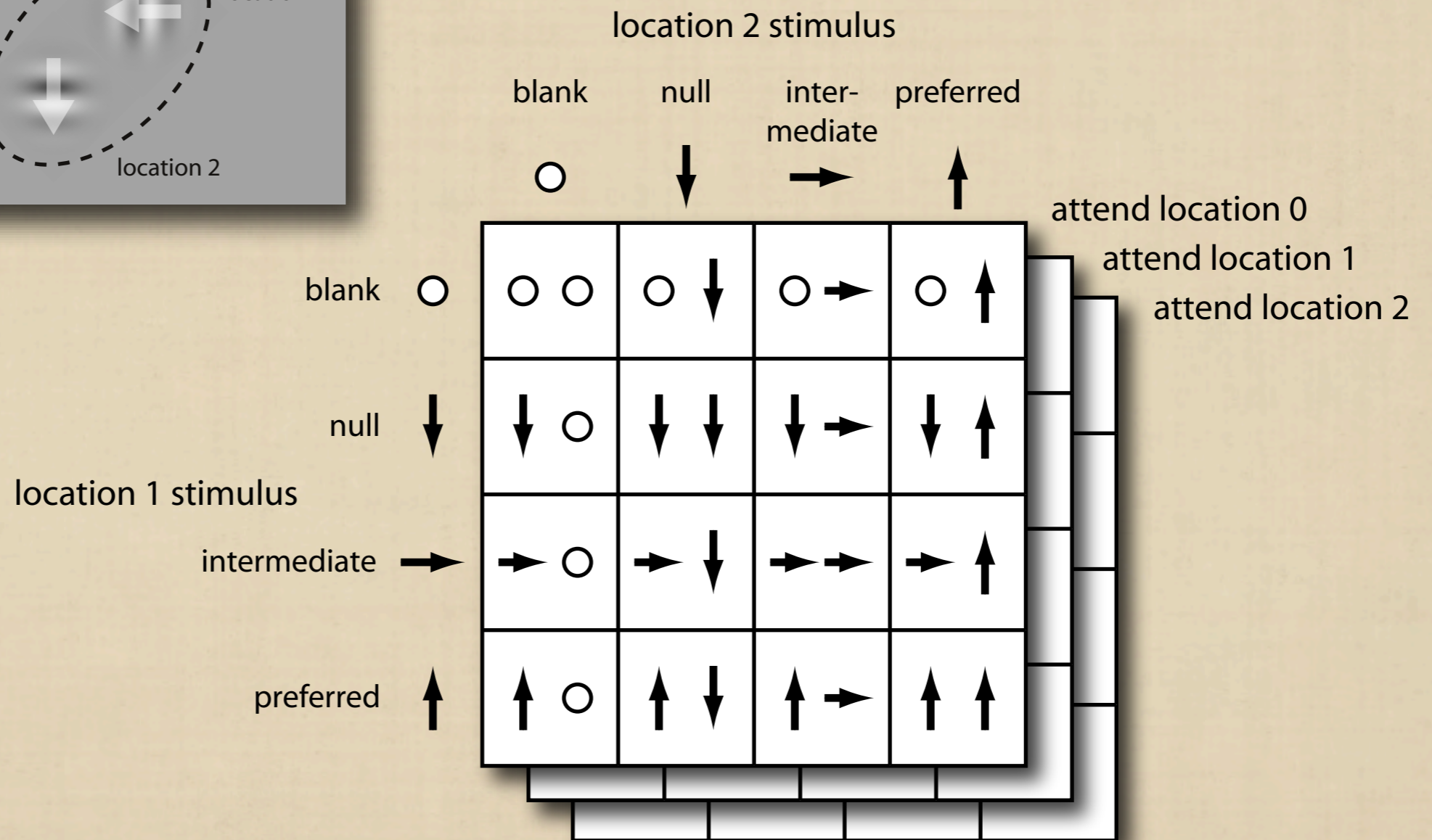
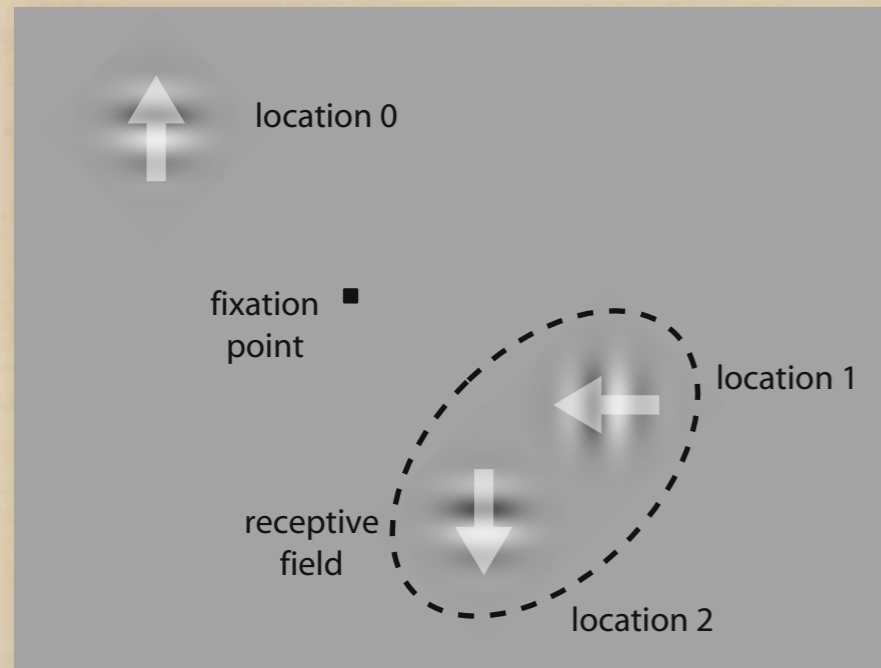
NM

M

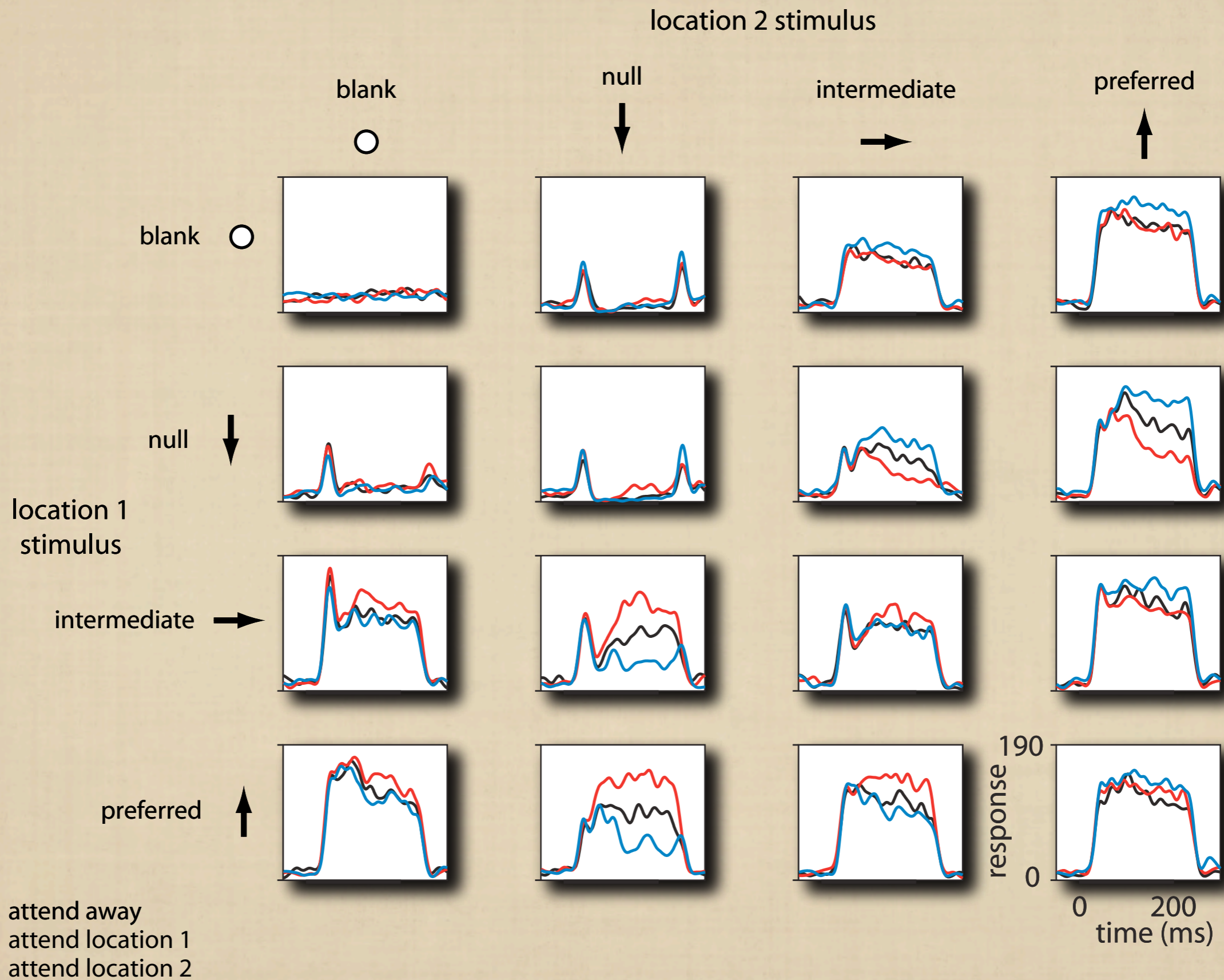
NM

300 ms/div

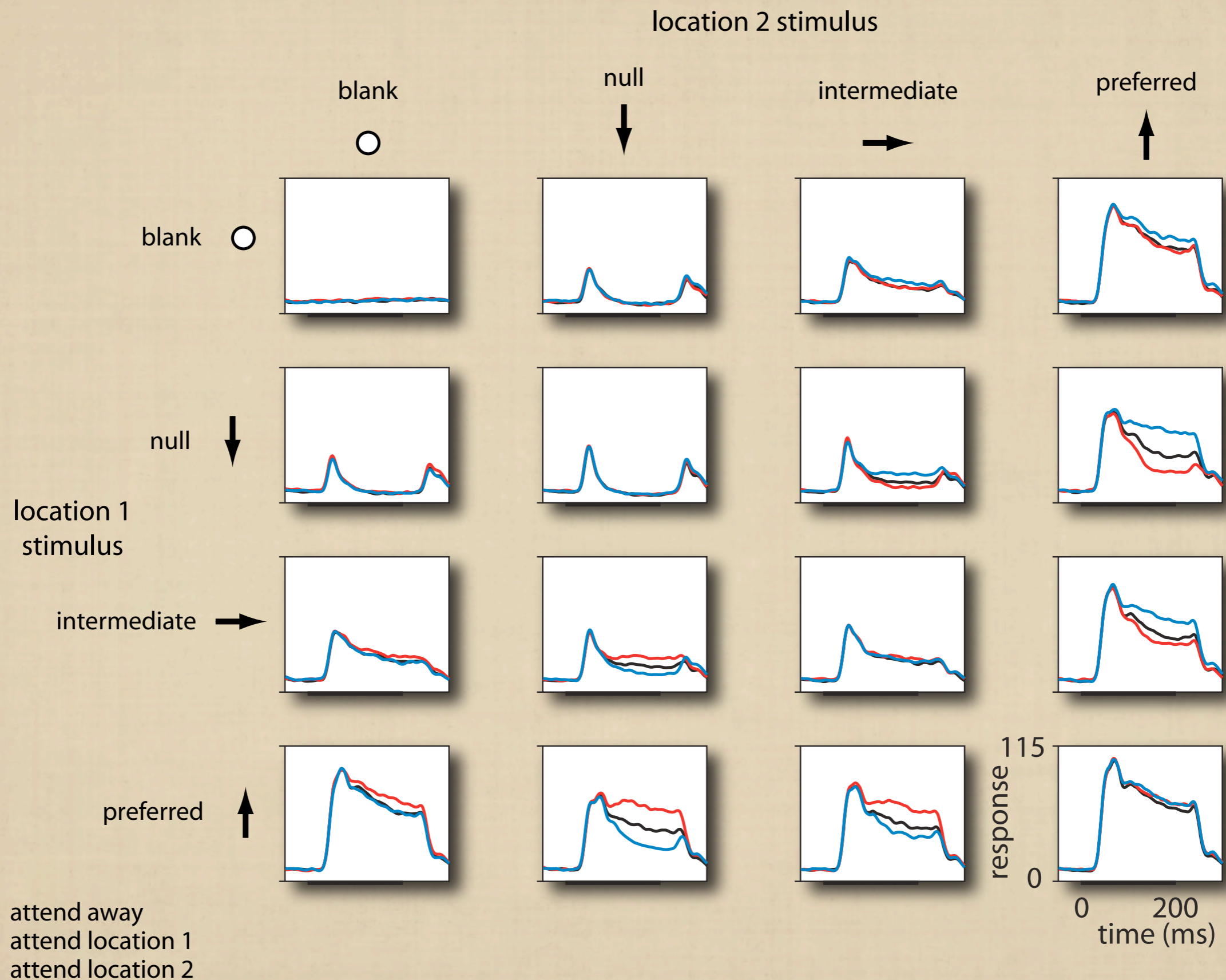
Shifting attention between two stimuli inside the receptive field of a neuron in MT



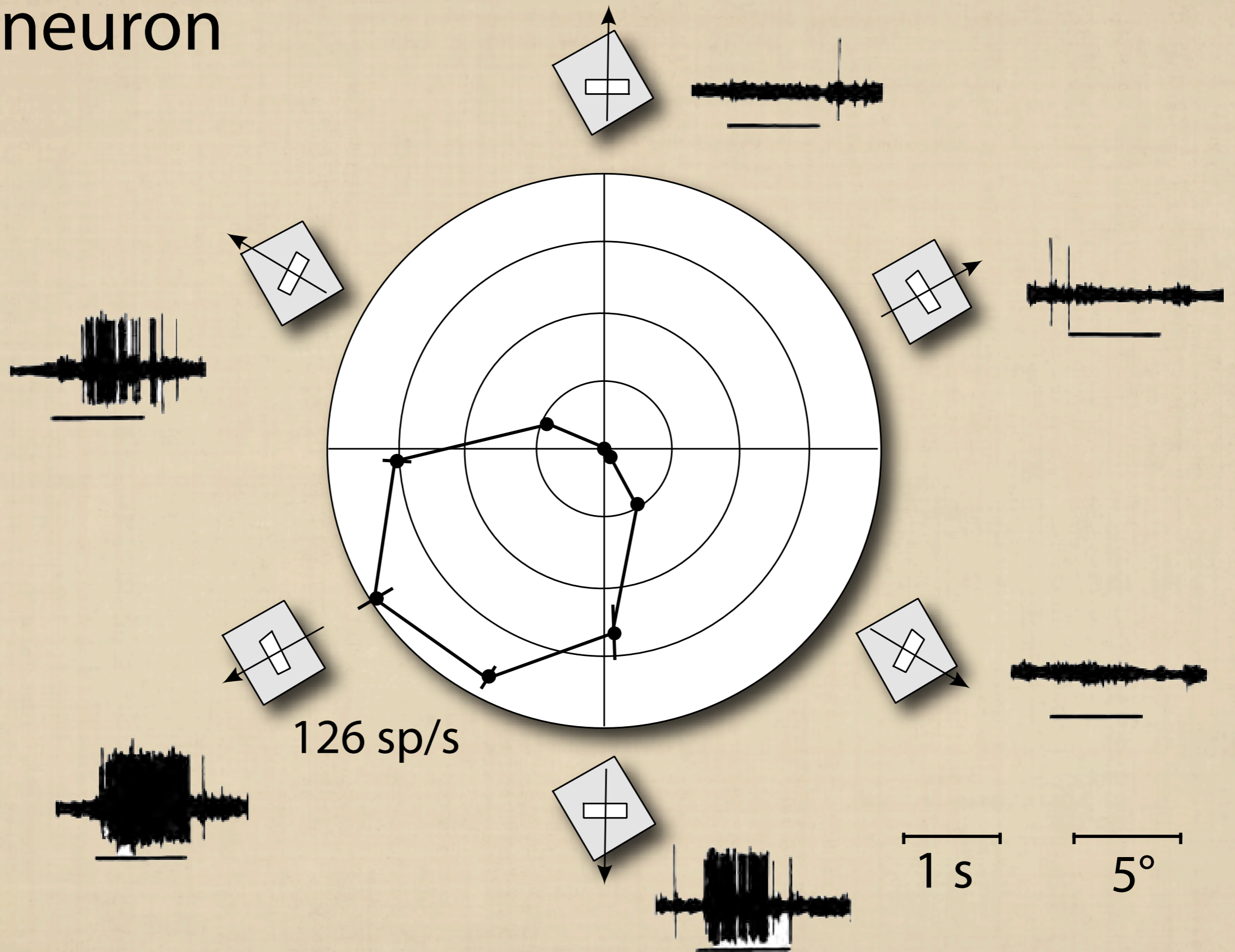
Responses of an MT neuron to different stimulus pairings and attentional states



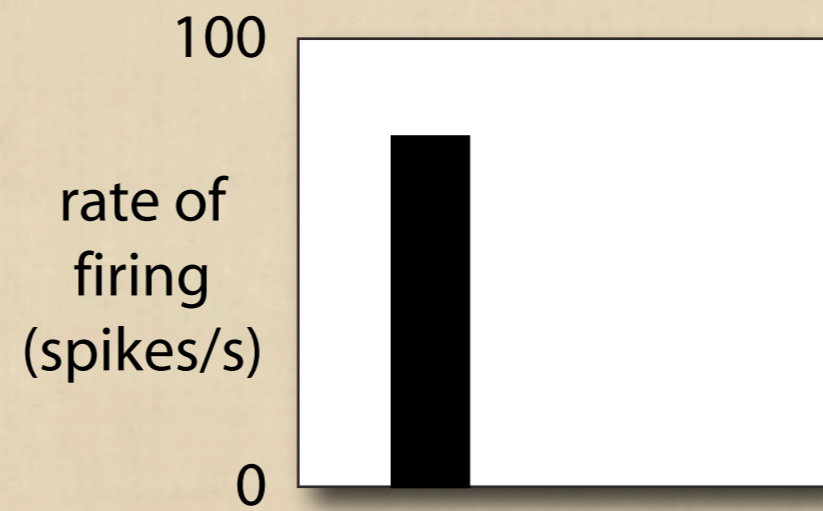
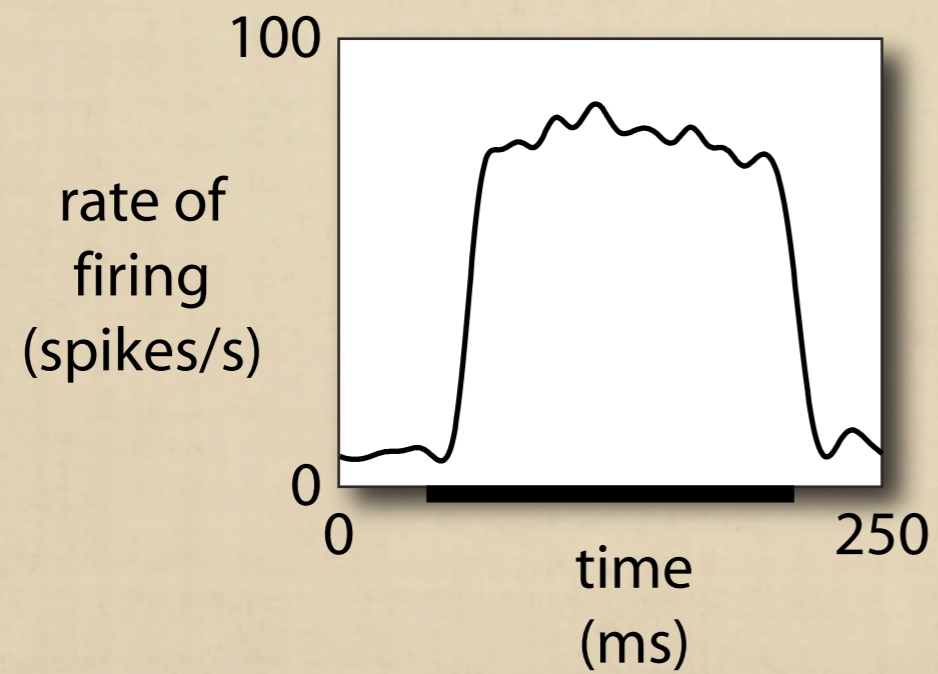
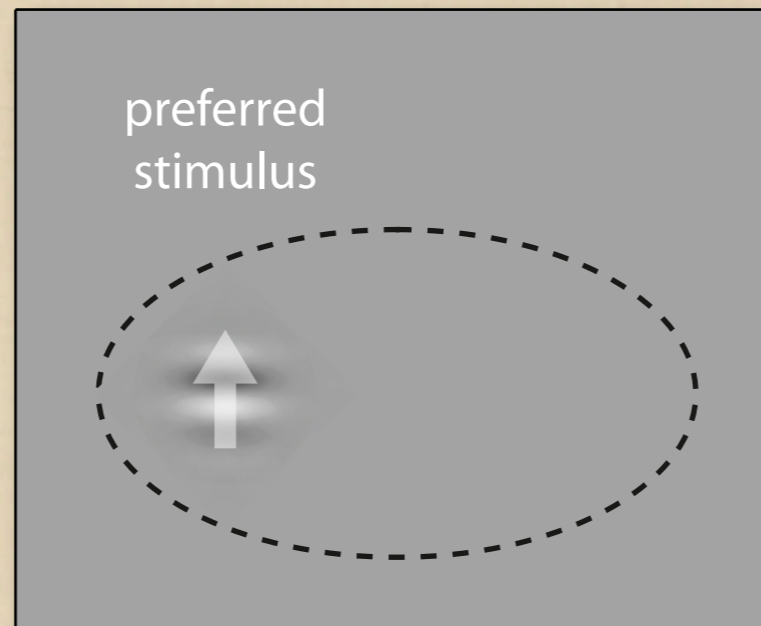
MT population average responses to different stimulus pairings and attentional states



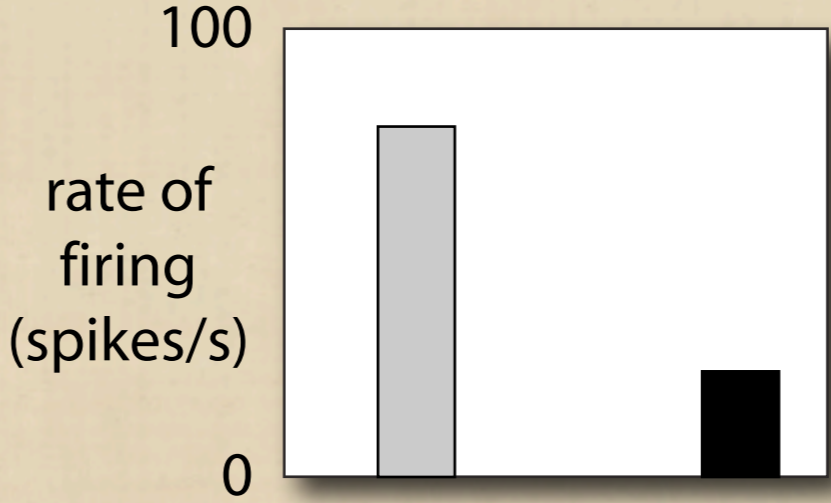
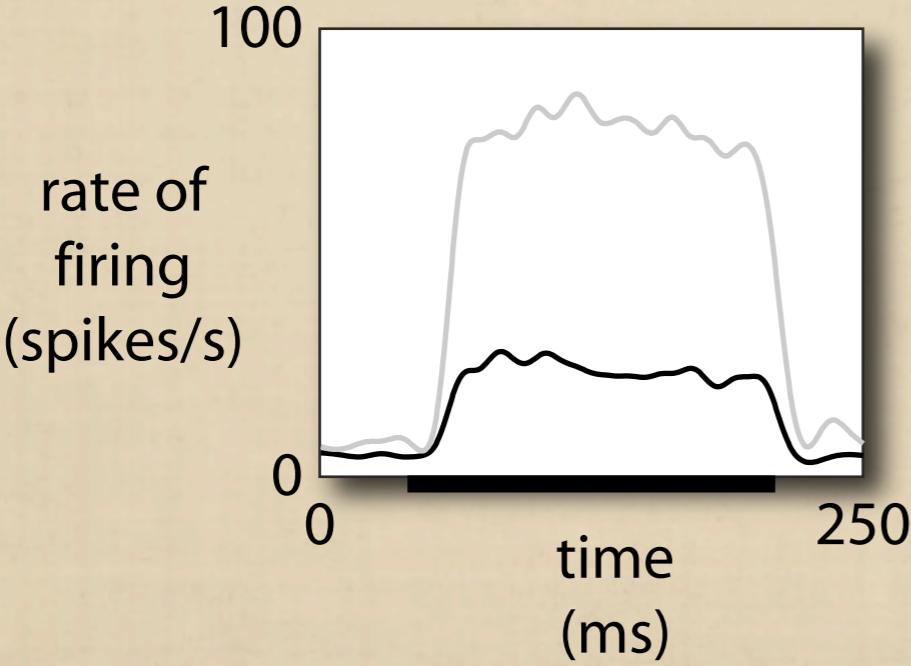
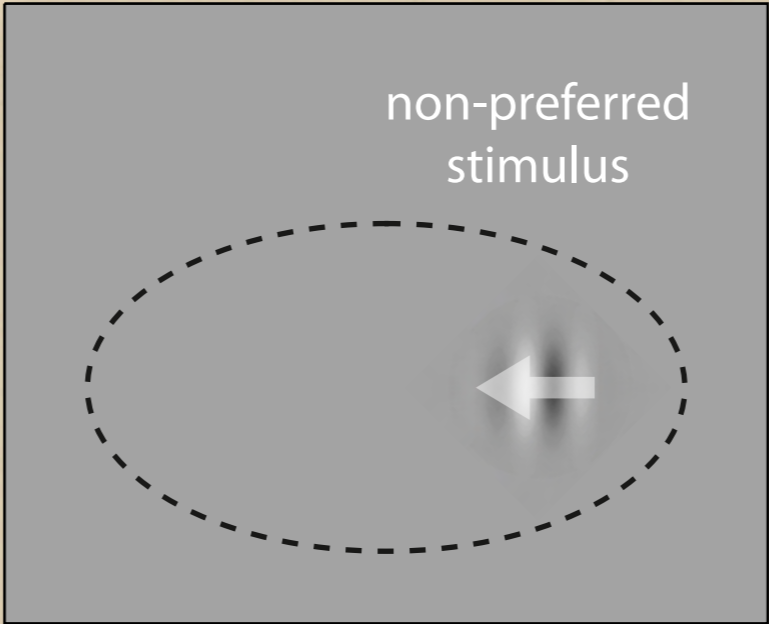
MT neuron



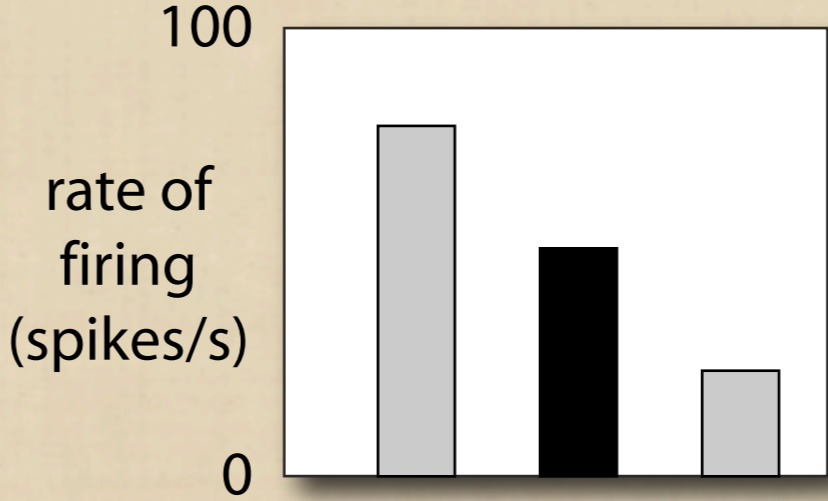
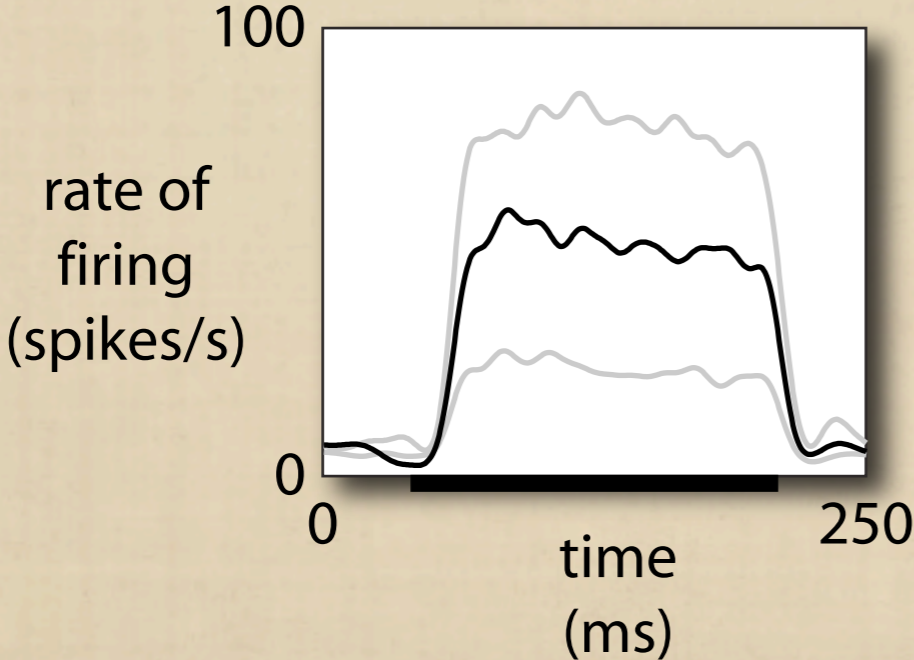
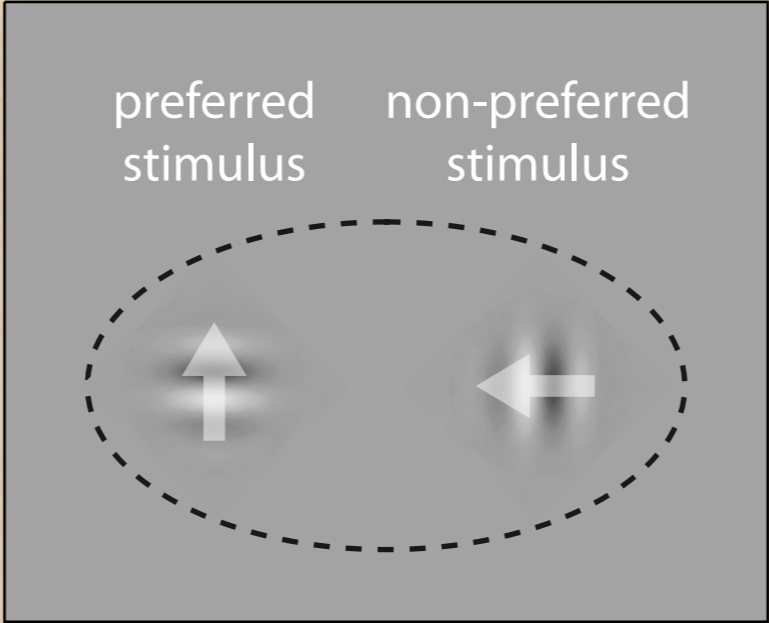
Normalization of neuronal responses



Normalization of neuronal responses

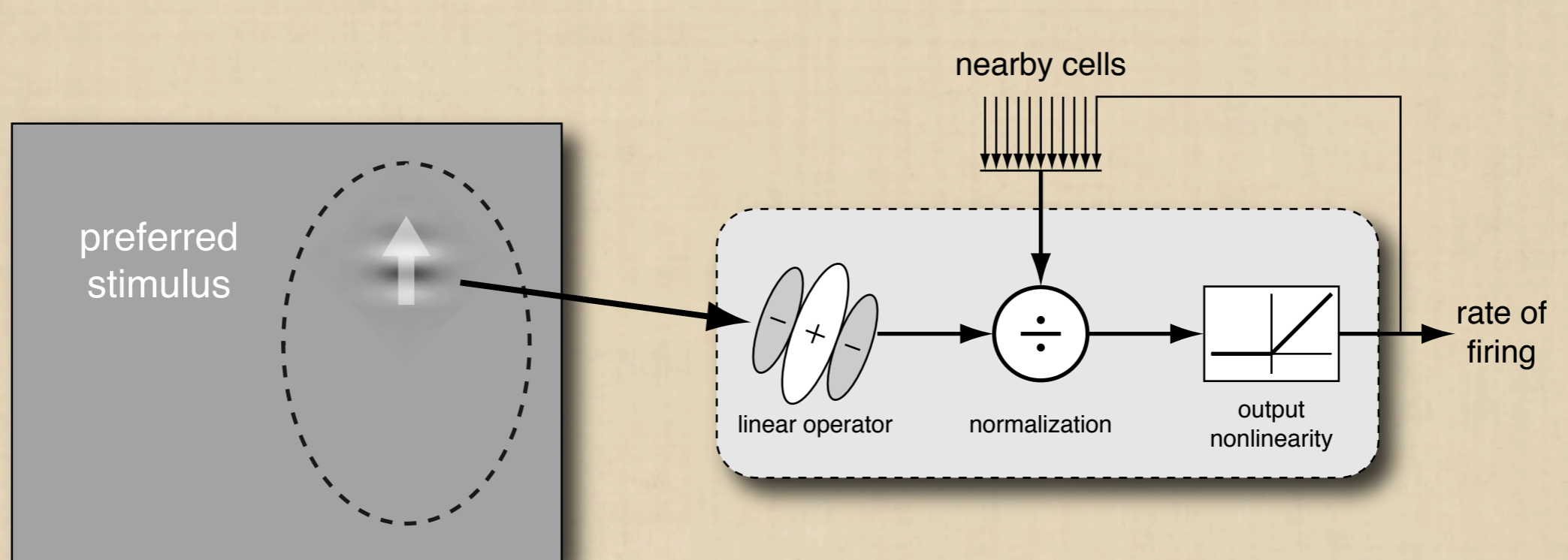


Normalization of neuronal responses



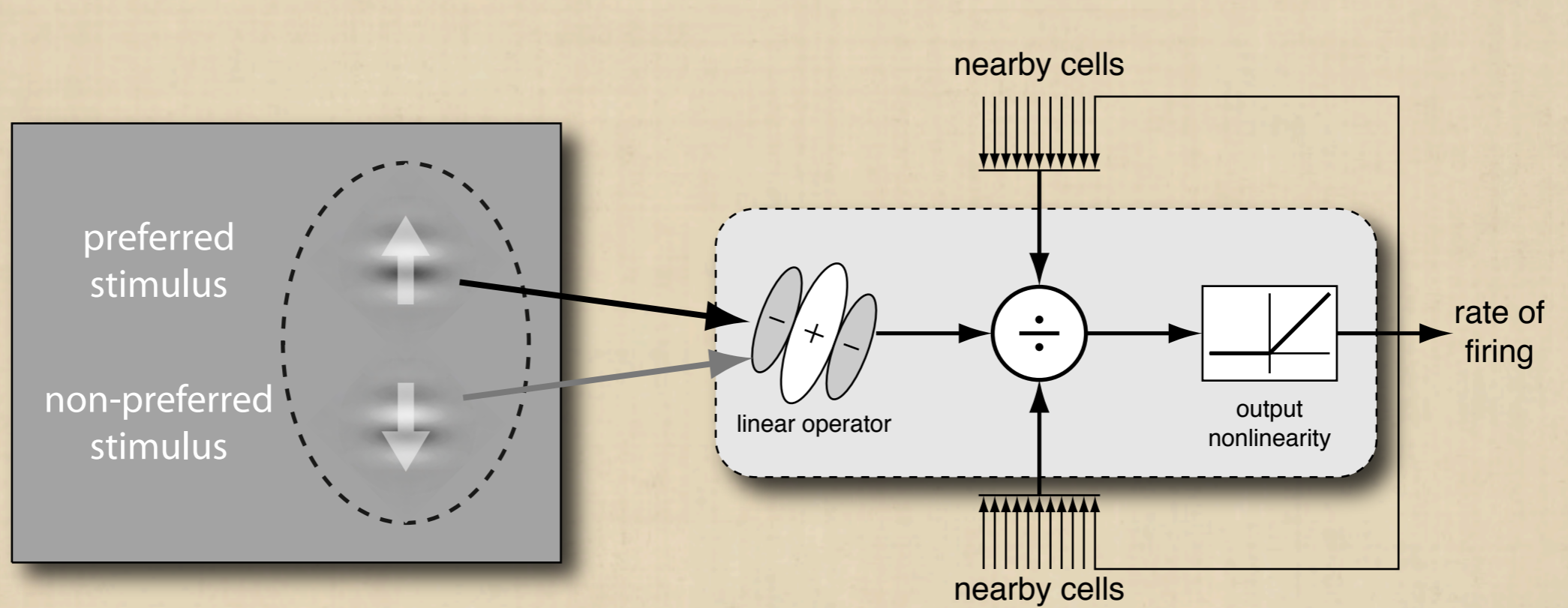
Normalization of neuronal responses

Heeger et al. 1996



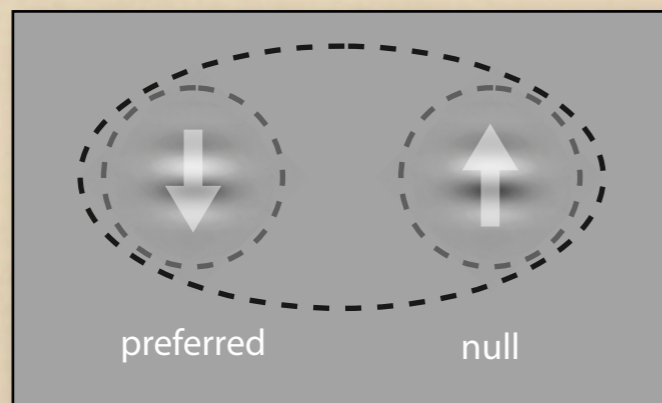
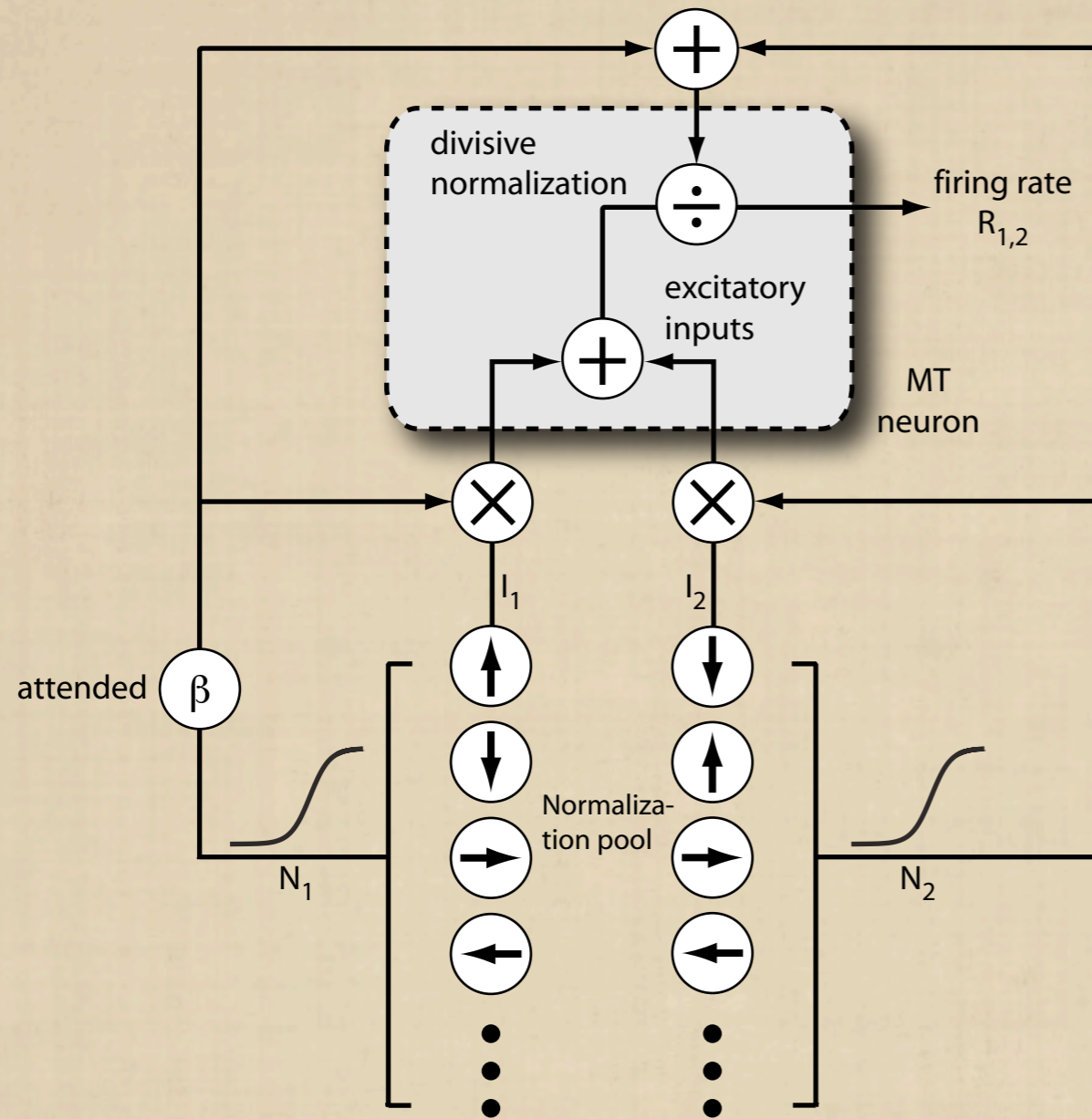
Normalization of neuronal responses

Heeger et al. 1996



Attention Normalization Model

Lee & Maunsell (2009)



$$R_{1,2} = \left(\left(\frac{I_1 \cdot N_1}{N_1 + N_2} \right)^n + \left(\frac{I_2 \cdot N_2}{N_1 + N_2} \right)^n \right)^{\frac{1}{n}}$$

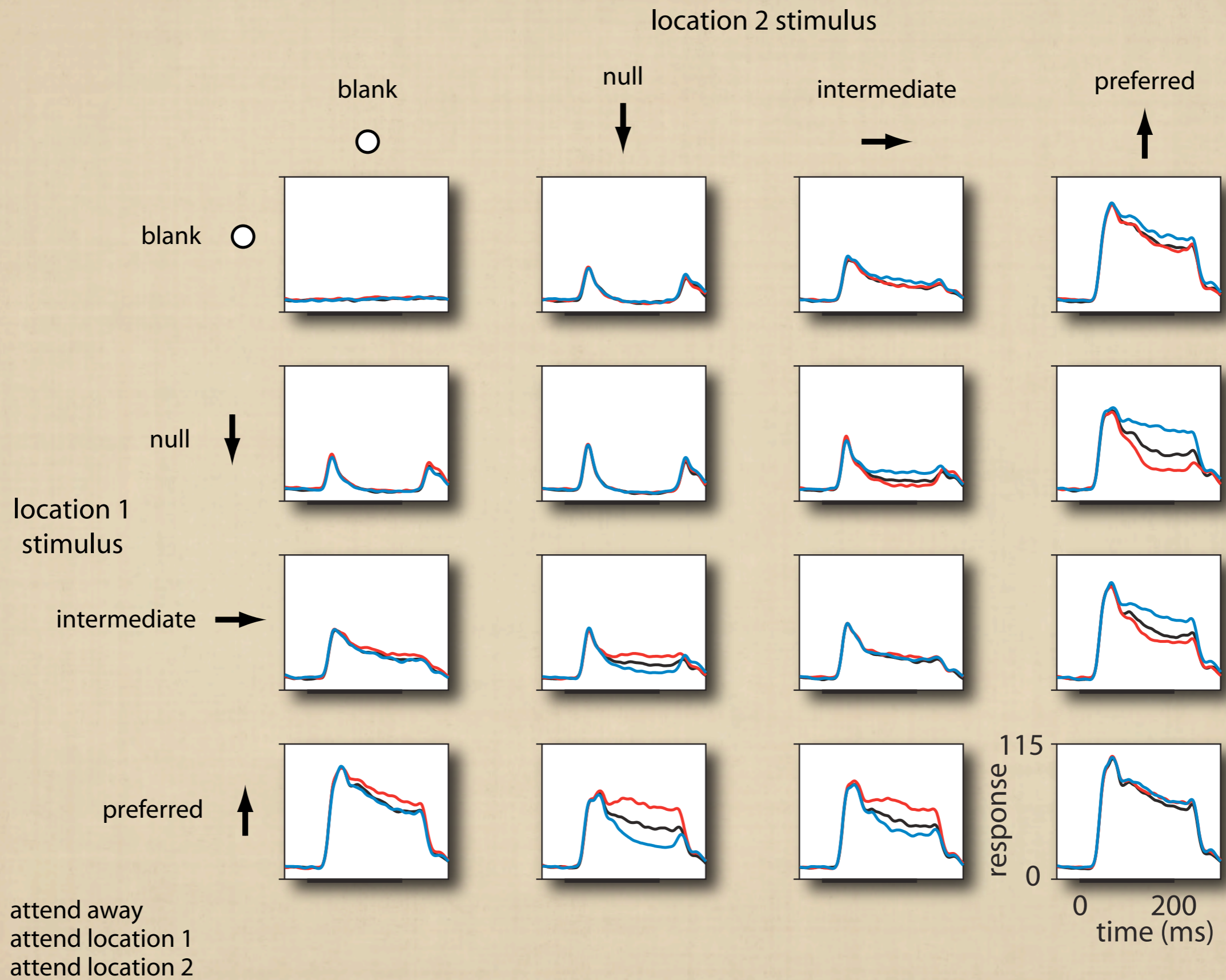
attended:

$$N = s + (1 - s) \cdot (1 - e^{-c\alpha\beta})$$

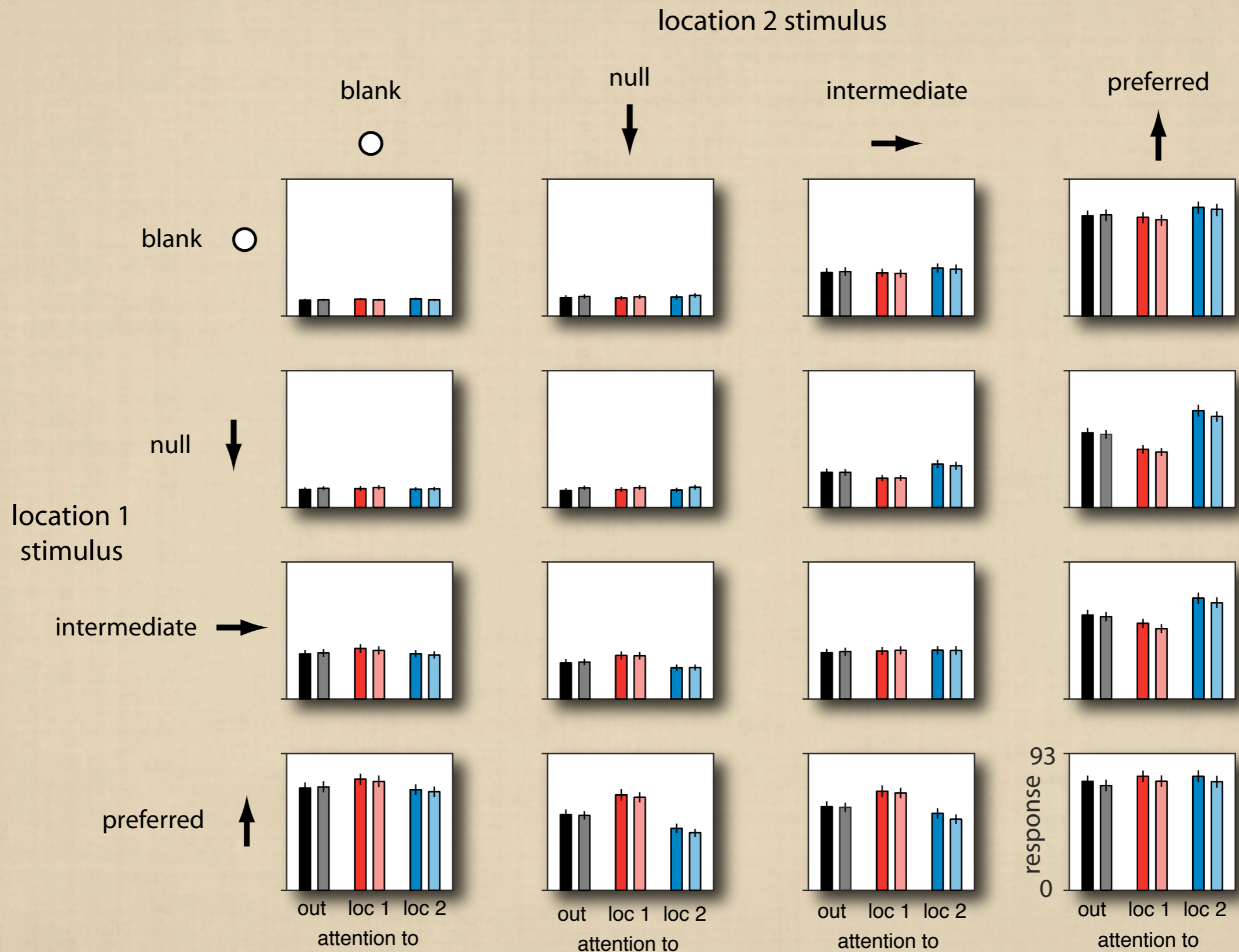
ignored:

$$N = s + (1 - s) \cdot (1 - e^{-c\alpha})$$

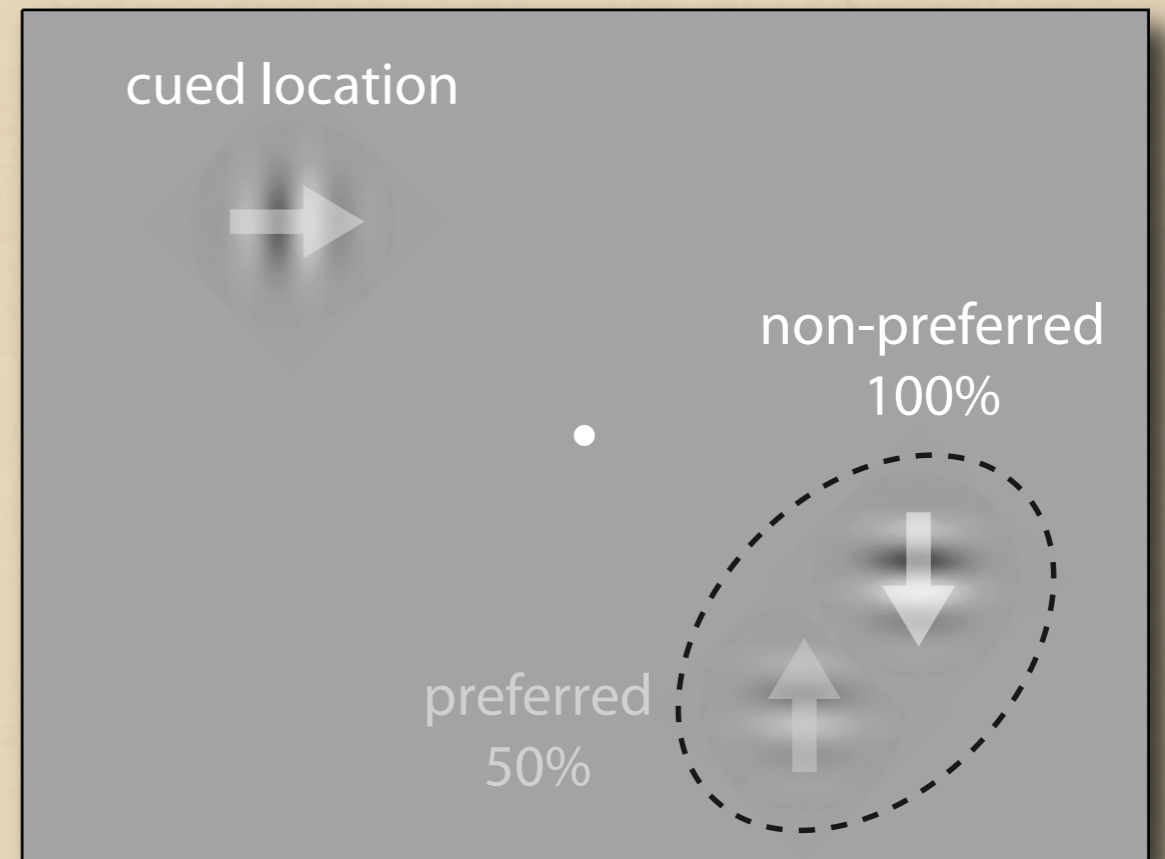
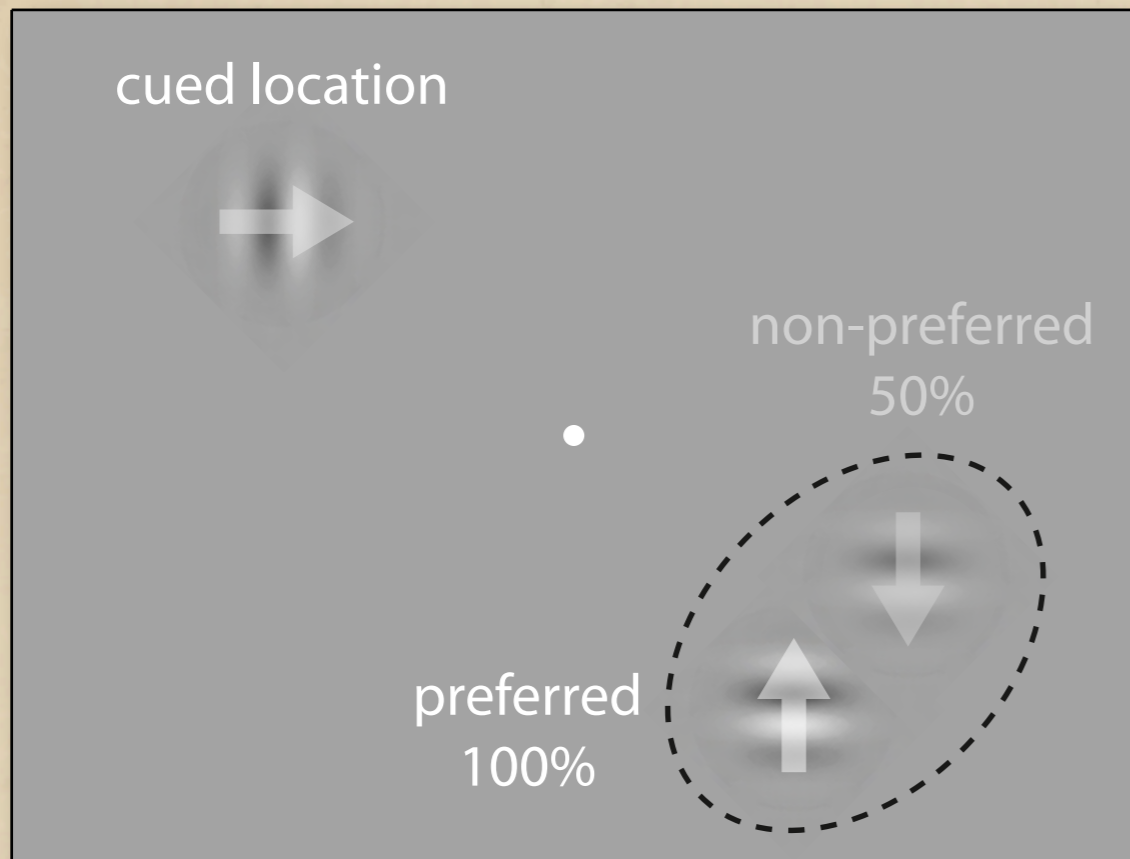
MT population average responses to different stimulus pairings and attentional states



Responses of an MT neuron and fit of normalization model

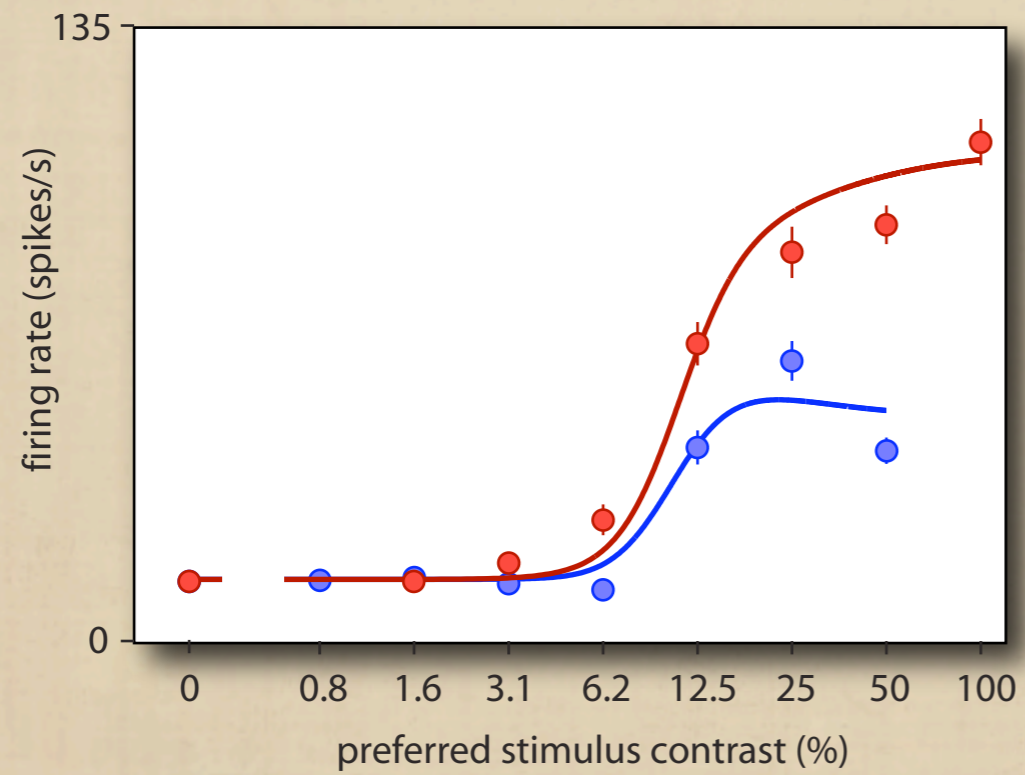
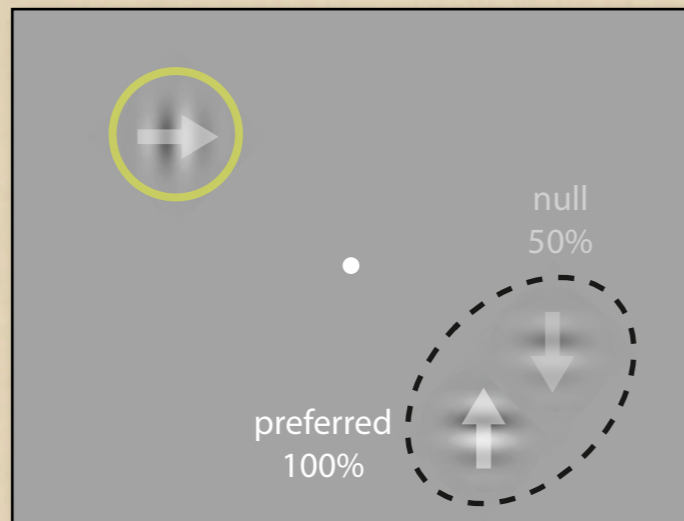


Two stimuli in the receptive field with different contrasts



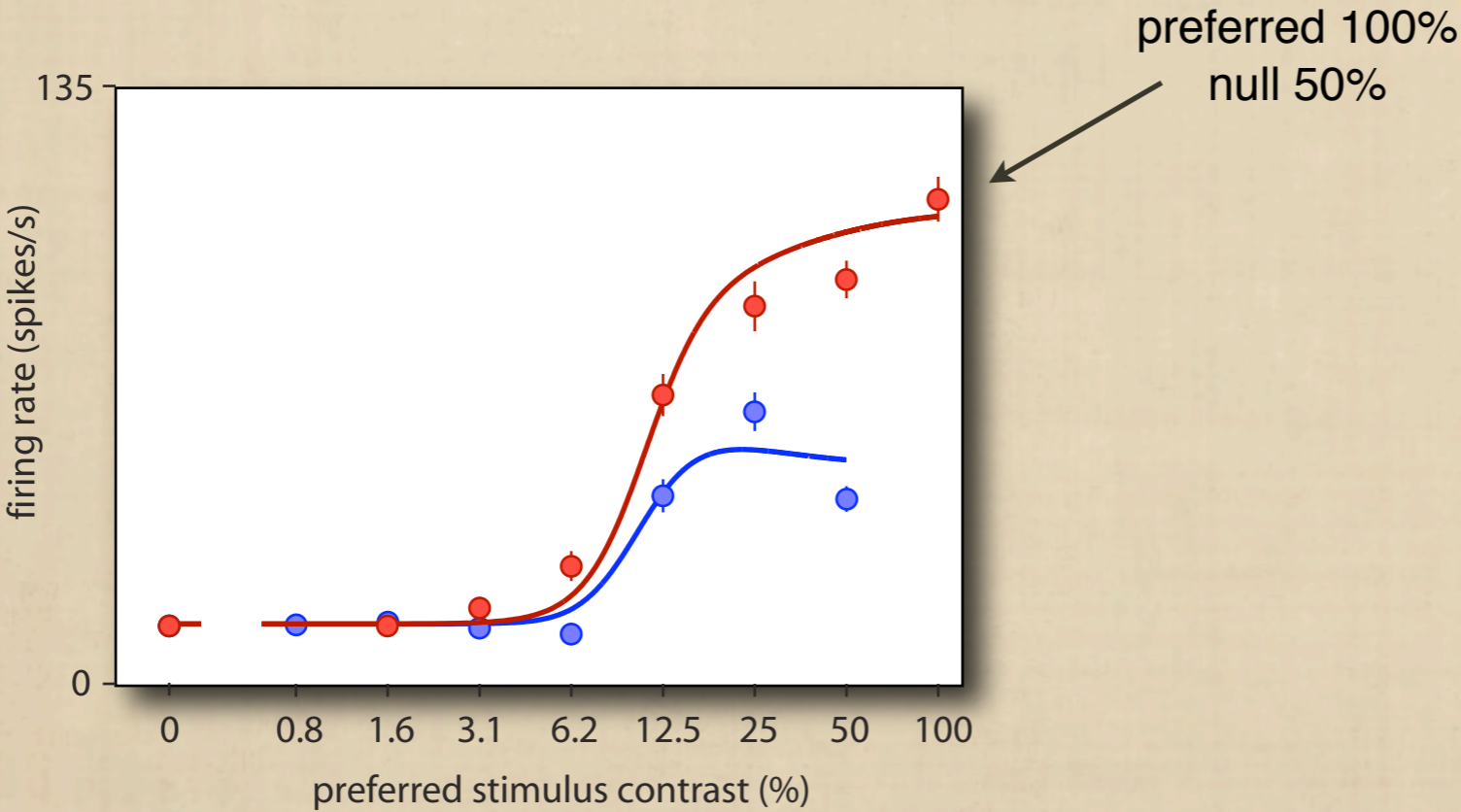
Effect of contrast offset on the response functions of an MT neuron

attention fixed
relative contrast varied



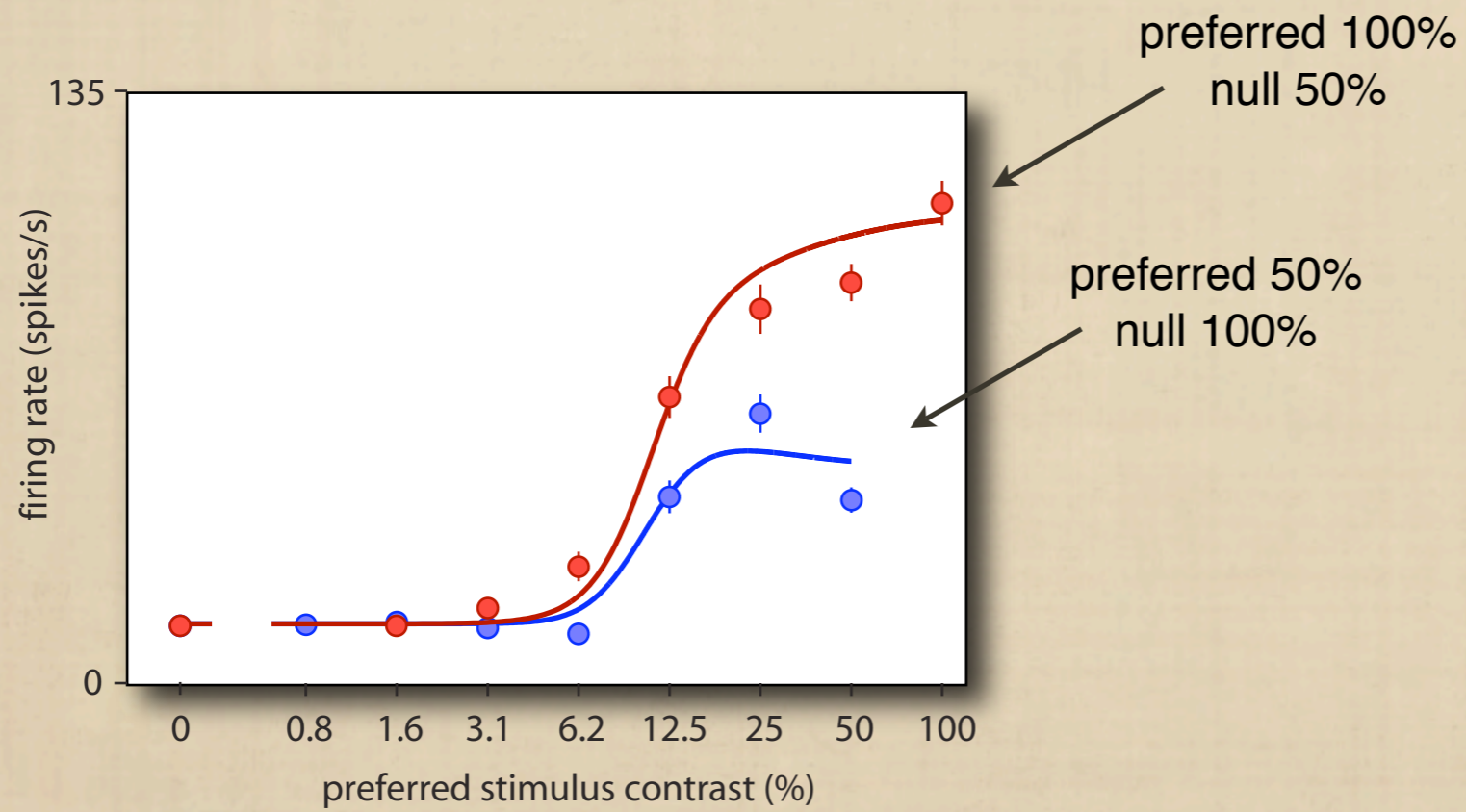
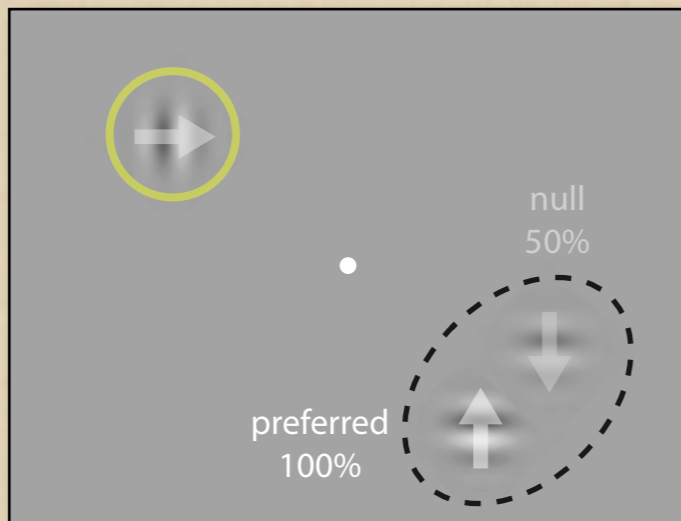
Effect of contrast offset on the response functions of an MT neuron

attention fixed
relative contrast varied



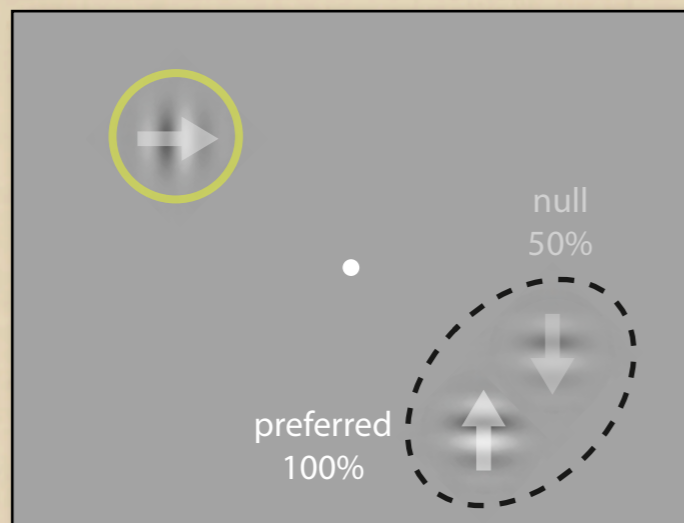
Effect of contrast offset on the response functions of an MT neuron

attention fixed
relative contrast varied

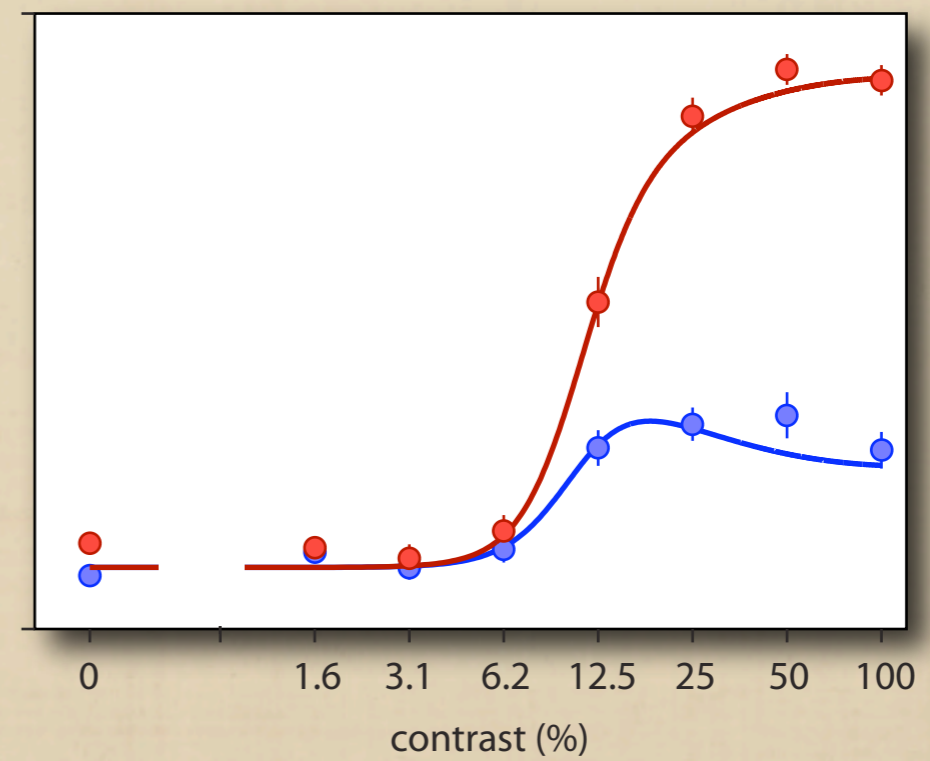
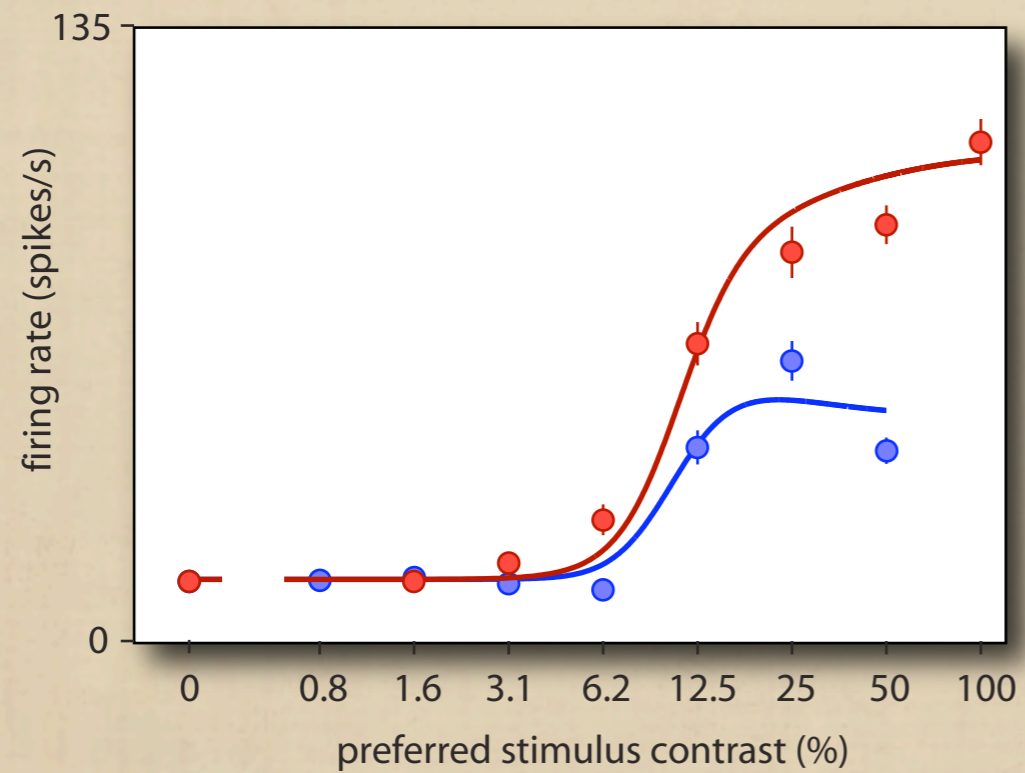
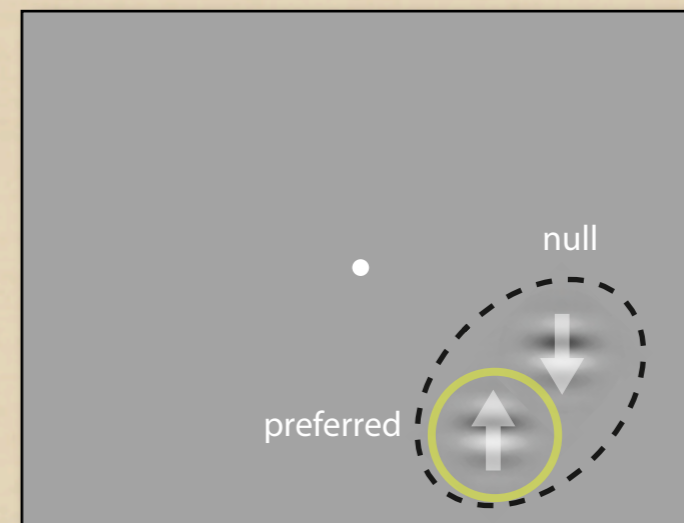


Contrast response functions of an MT neuron with strong modulation

attention fixed
relative contrast varied

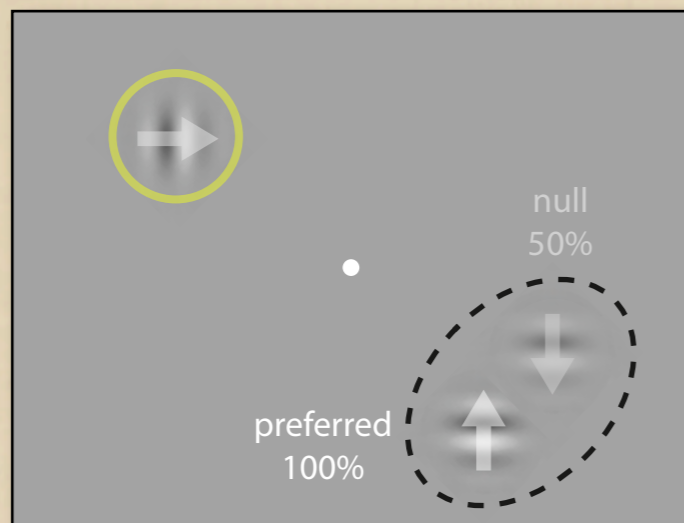


attention varied
relative contrast fixed

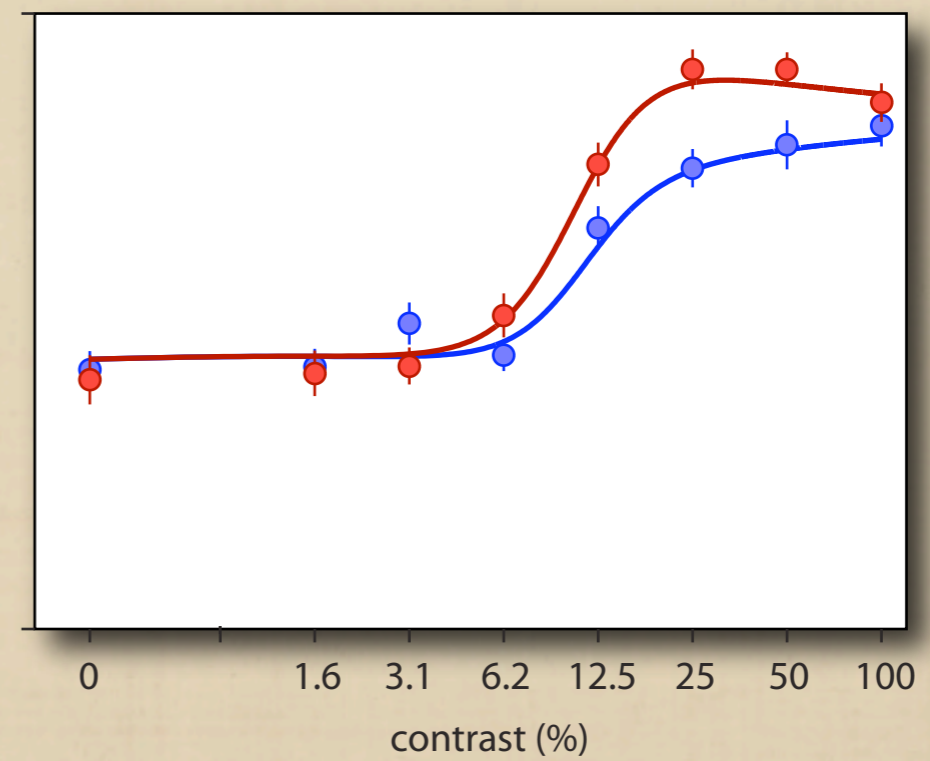
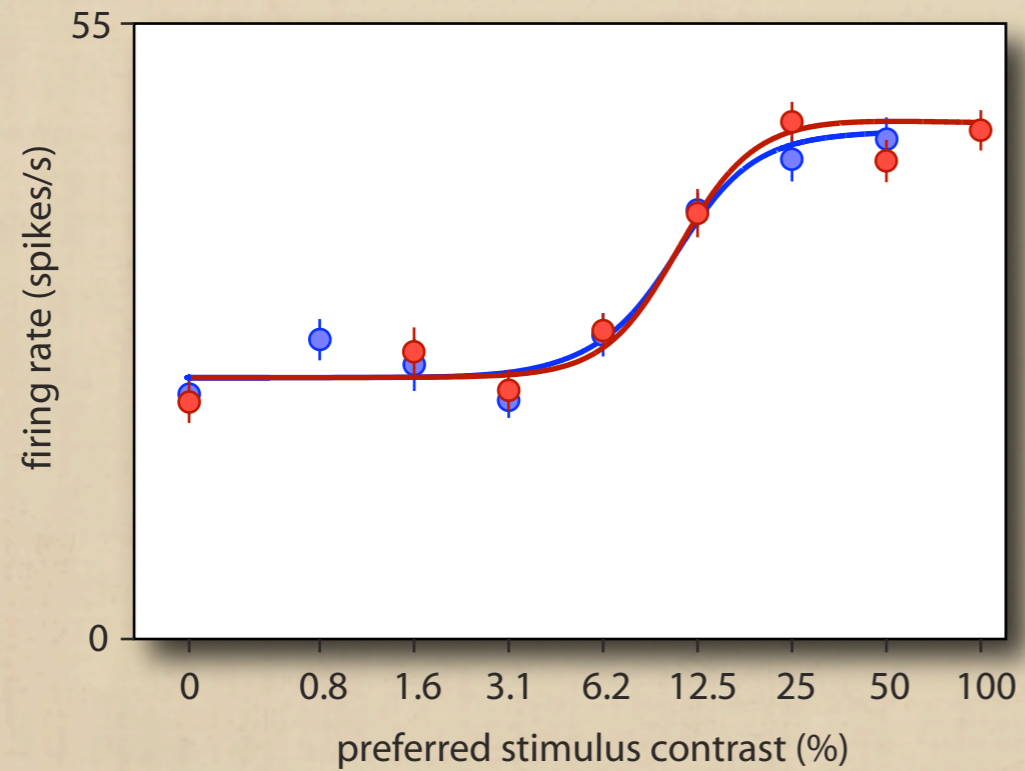
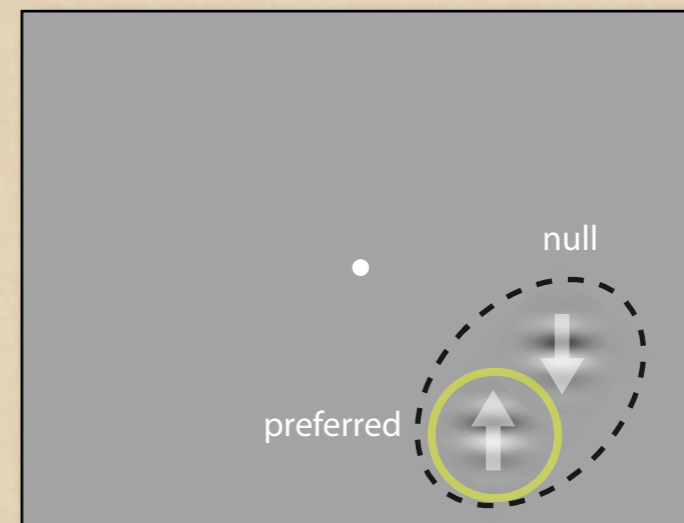


Contrast response functions of an MT neuron with weak modulation

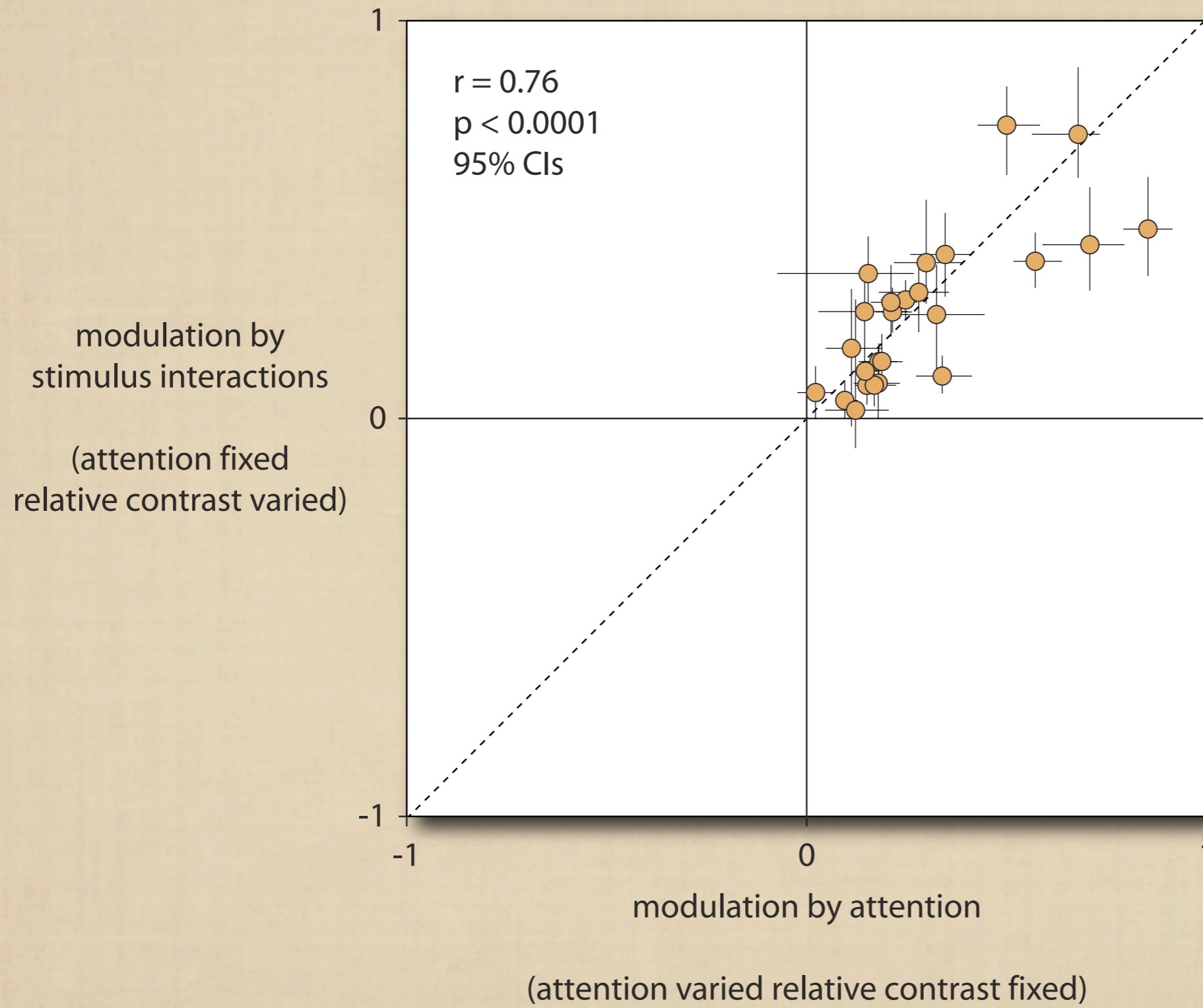
attention fixed
relative contrast varied



attention varied
relative contrast fixed



Modulation by attention is correlated to modulation by stimulus interactions

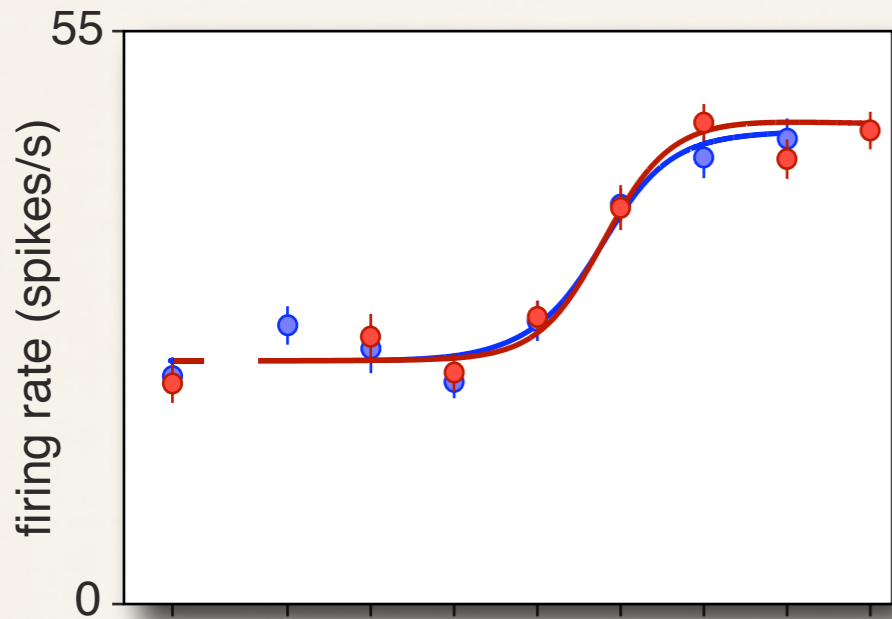


Modeling attentional normalization

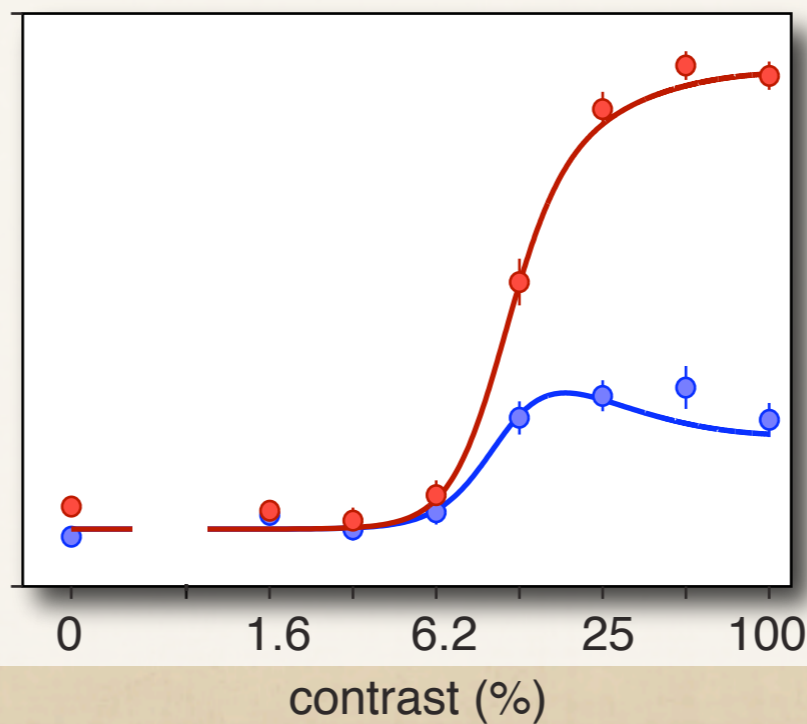
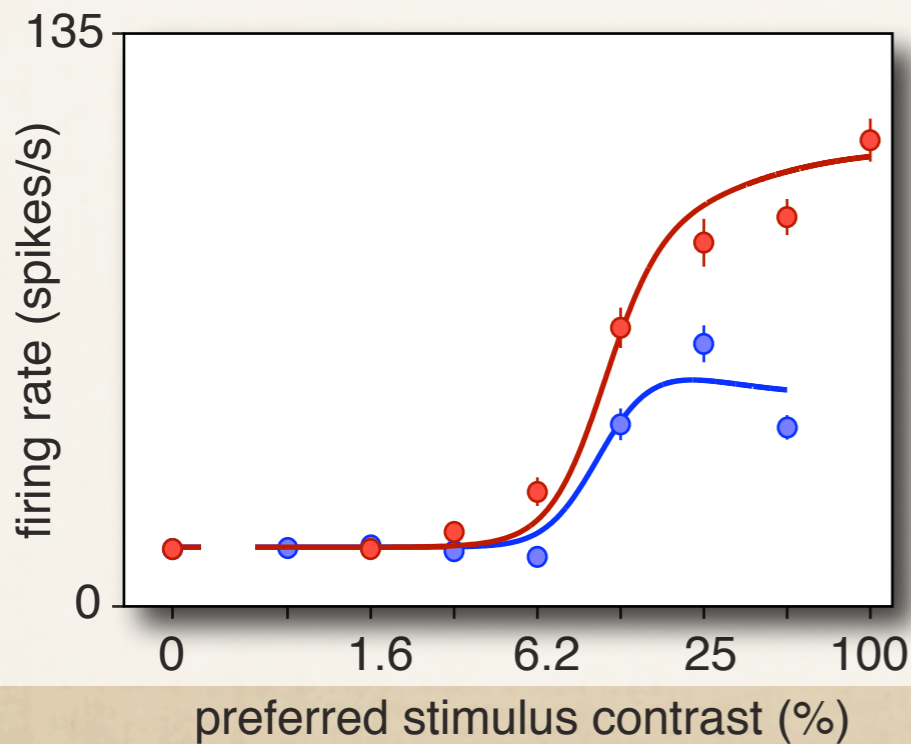
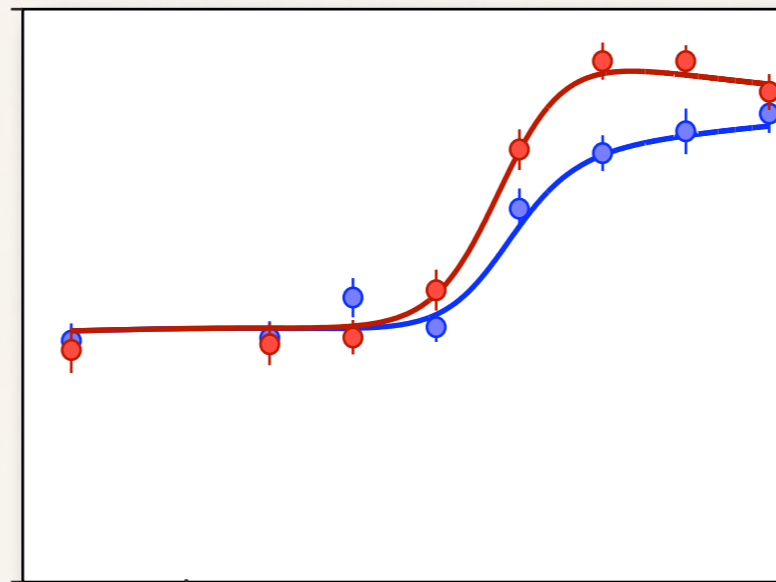
$$R_{1,2} = \left(\left(\frac{I_1 \cdot N_1}{N_1 + N_2} \right)^n + \left(\frac{I_2 \cdot N_2}{N_1 + N_2} \right)^n \right)^{\frac{1}{n}}$$

$$N = s + (1 - s) \cdot (1 - e^{-c\alpha\beta})$$

attention fixed
relative contrast varied

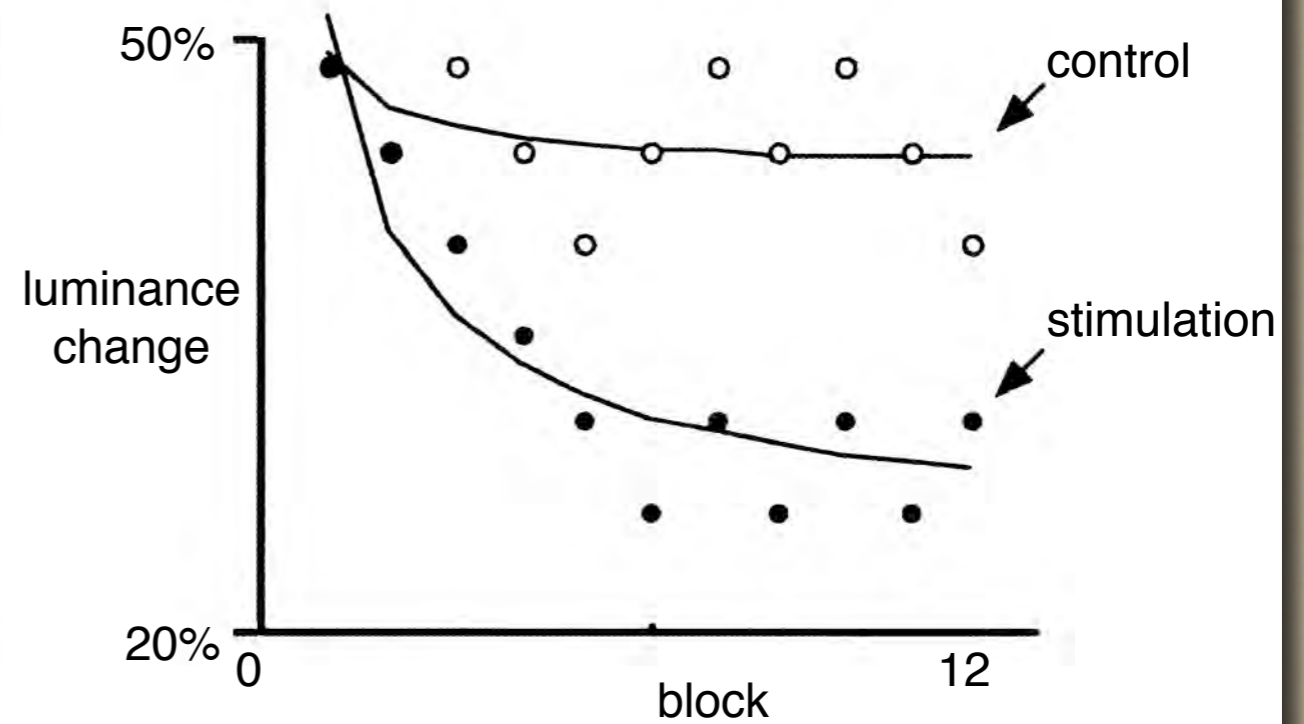
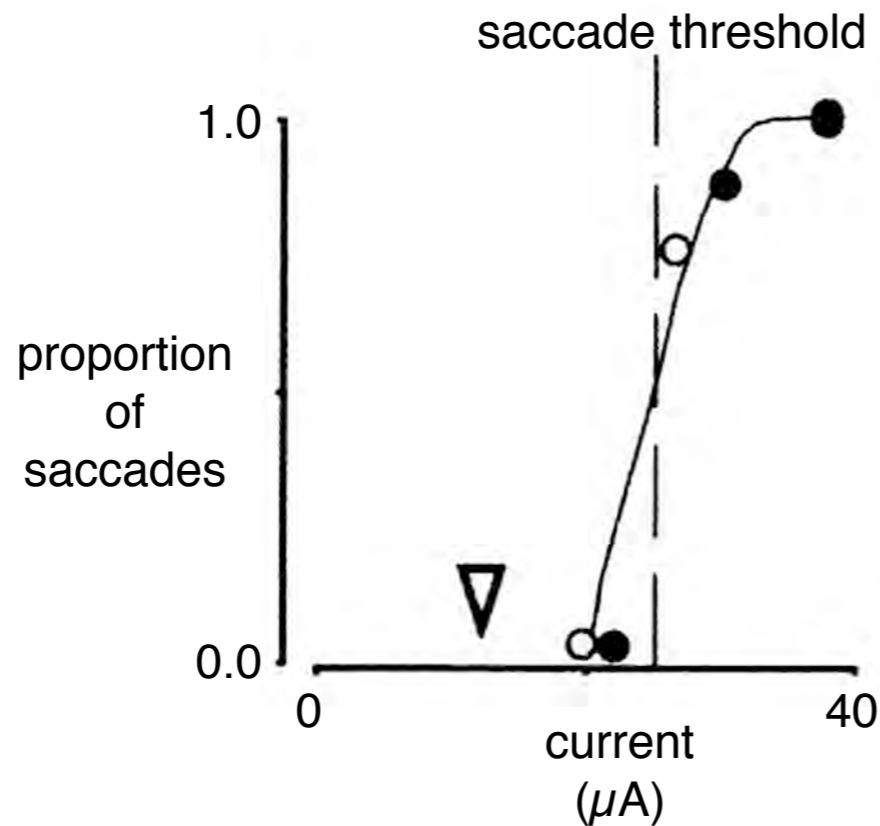
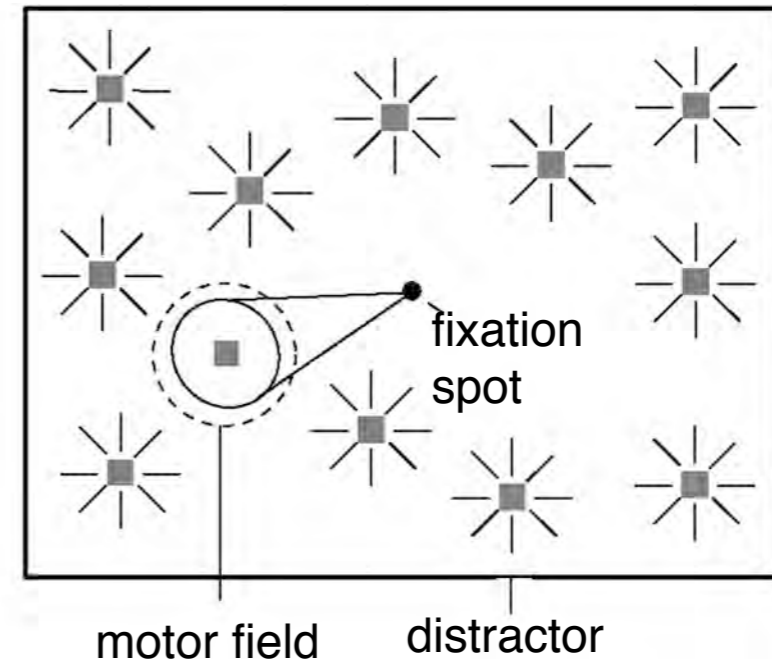
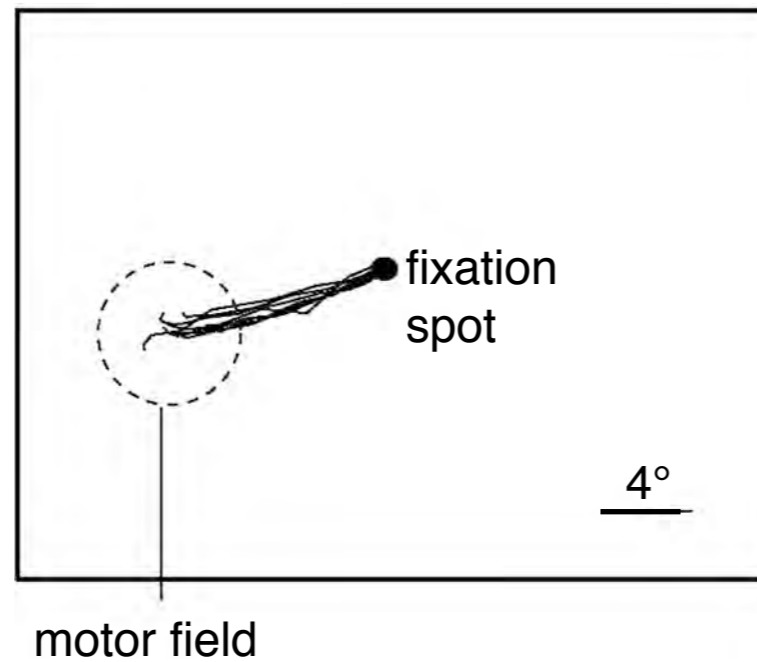


attention varied
relative contrast fixed



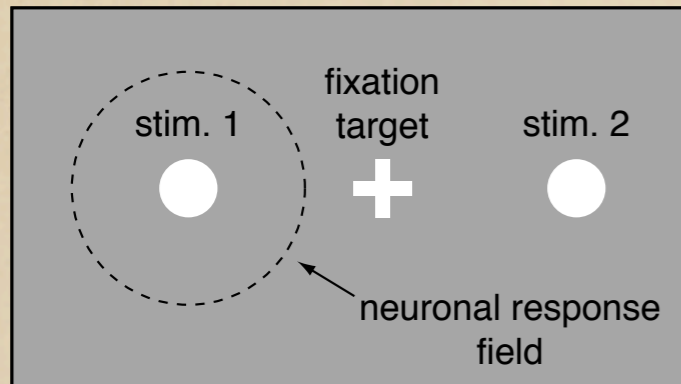
Subthreshold FEF electrical stimulation locally improves detection of a luminance change

Moore & Fallah 2001, 2004



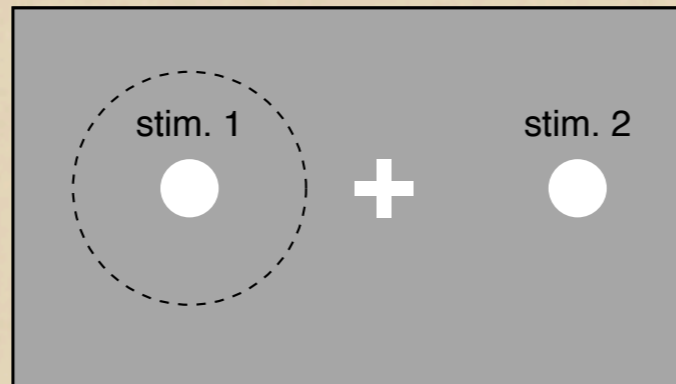
Representative reward and attention tasks

A. Reward size



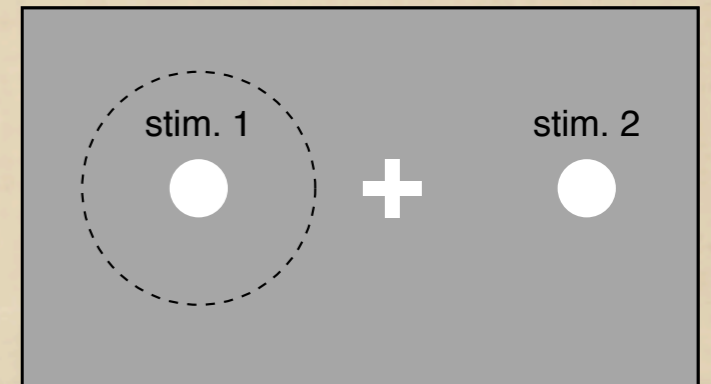
stim. 1 reward		stim. 2 reward		neuronal activity
size	prob.	size	prob.	
8	0.5	2	0.5	high
2	0.5	8	0.5	low

B. Reward probability



stim. 1 reward		stim. 2 reward		neuronal activity
size	prob.	size	prob.	
5	0.8	5	0.2	high
5	0.2	5	0.8	low

C. Spatial attention



stim. 1 reward		stim. 2 reward		neuronal activity
size	prob.	size	prob.	
5	1.0	0	0.0	high
0	0.0	5	1.0	low