

**Attention Response Functions:
Characterizing Brain Areas Using fMRI
Activation during Parametric Variations
of Attentional Load**

Intro

- Examine attention response functions
 - Compare an attention-demanding task to a non-attentional control task
- Examine how activation in different regions is affected by additional increases in attentional load
 - Parametric design (vs. subtraction)

Parametric vs. subtraction design

- Subtraction:

- Requires inclusion/exclusion of a single mental process – concept of “pure insertion”
- **BALANCE** the “off” and “on” blocks so only **one thing** is altered

- Assumptions:

- Neural structures supporting cognitive and behavioral processes combine in a simple additive manner
- “Pure insertion”: a new cognitive component can be purely inserted without affecting the expression of previous ones
- **BUT** processes probably combine in a non-additive/interactive fashion

- **Parametric design:**

- Examine the brain responses to increasing frequency of stimulus presentation in different contexts and look for a differential sensitivity to increasing presentation rate.

Major goal of study

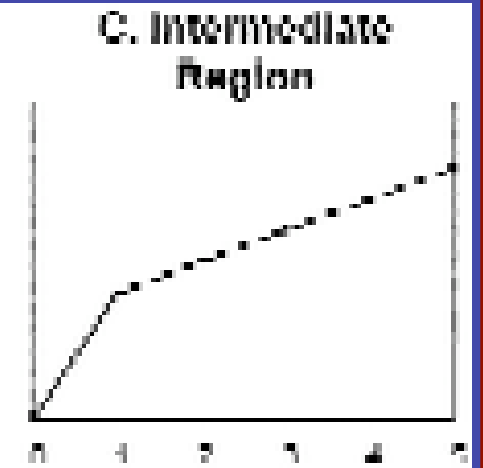
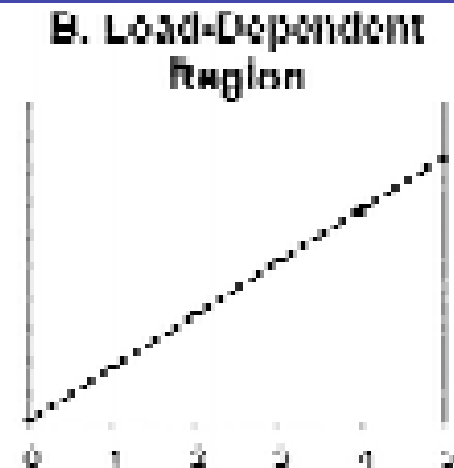
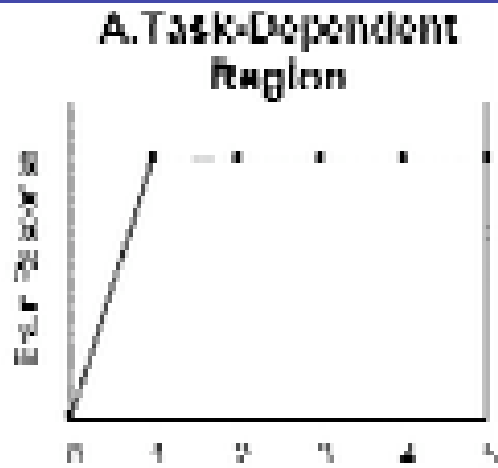
- Use a parametric load manipulation to disentangle the functions of the cortical regions that have been shown to be activated by both attention and eye movements

Hypothesis

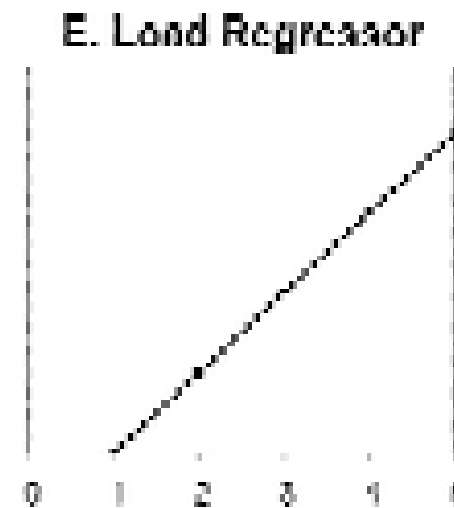
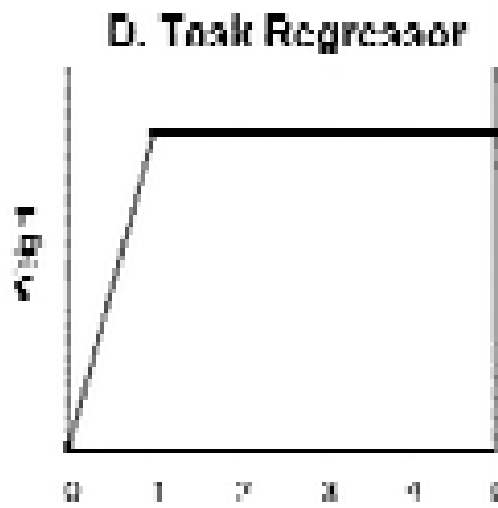
- Areas directly involved in attentional processing would show steadily increasing activation as attentional load is increased
- Regions with activation due to eye movement factors would be activated by attention to one target but would show no further response gains as more targets were added

- Specifically interested in the activation function of the frontal eye fields (FEF)
 - Are reliably activated by attentional tasks
 - But have been postulated by some to serve purely oculomotor functions and remain largely unaffected by cognitive factors

Hypothetical
Attention
Response
Functions



Hypothetical-
Driven
Regressors



Number of Allocated Resources

- Hypothetical data

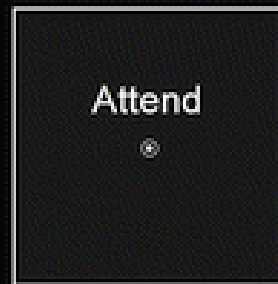
- “Task-only” regions that are not directly involved in attentional performance would show a task effect with no further increase in activation as task difficulty increases
- Regions that are directly involved in attentional performance would show “load-dependent” activity that increases with attentional demands, being greater at high loads than low loads only regions not directly

Experimental Design

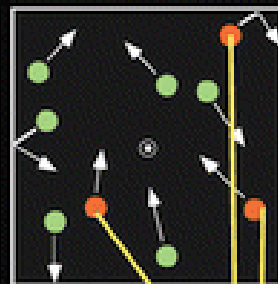
- 9 balls move randomly
- Subjects fixate on center point
- Attentive tracking epochs
 - A subset of 1 – 5 balls turn red for 2 s then turn green
 - Subject track the cued balls for 17 s
- Passive epochs – 11 s
 - No balls are cued
 - Passively watch the display without paying attention to any particular balls

A. Attentive Tracking

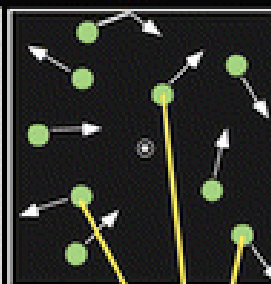
1 sec



2 sec



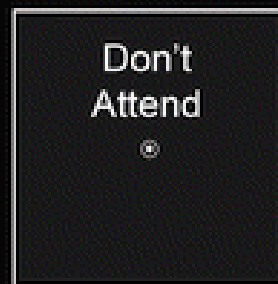
17 sec



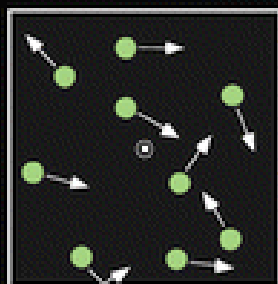
tracked items
(variable number: 1 to 5)

B. Passive Viewing

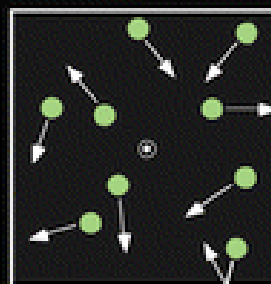
1 sec



2 sec



9 sec



0 tracked items

Demo – track 3 balls

http://defiant.ssc.uwo.ca/Jody_web/share/ARF_Neuron/attentive_tracking_demo.htm

- 8 Subjects

- Test trials – after done attentive tracking, a single ball turned white and the subject had to indicate whether the white ball was a tracked target or not

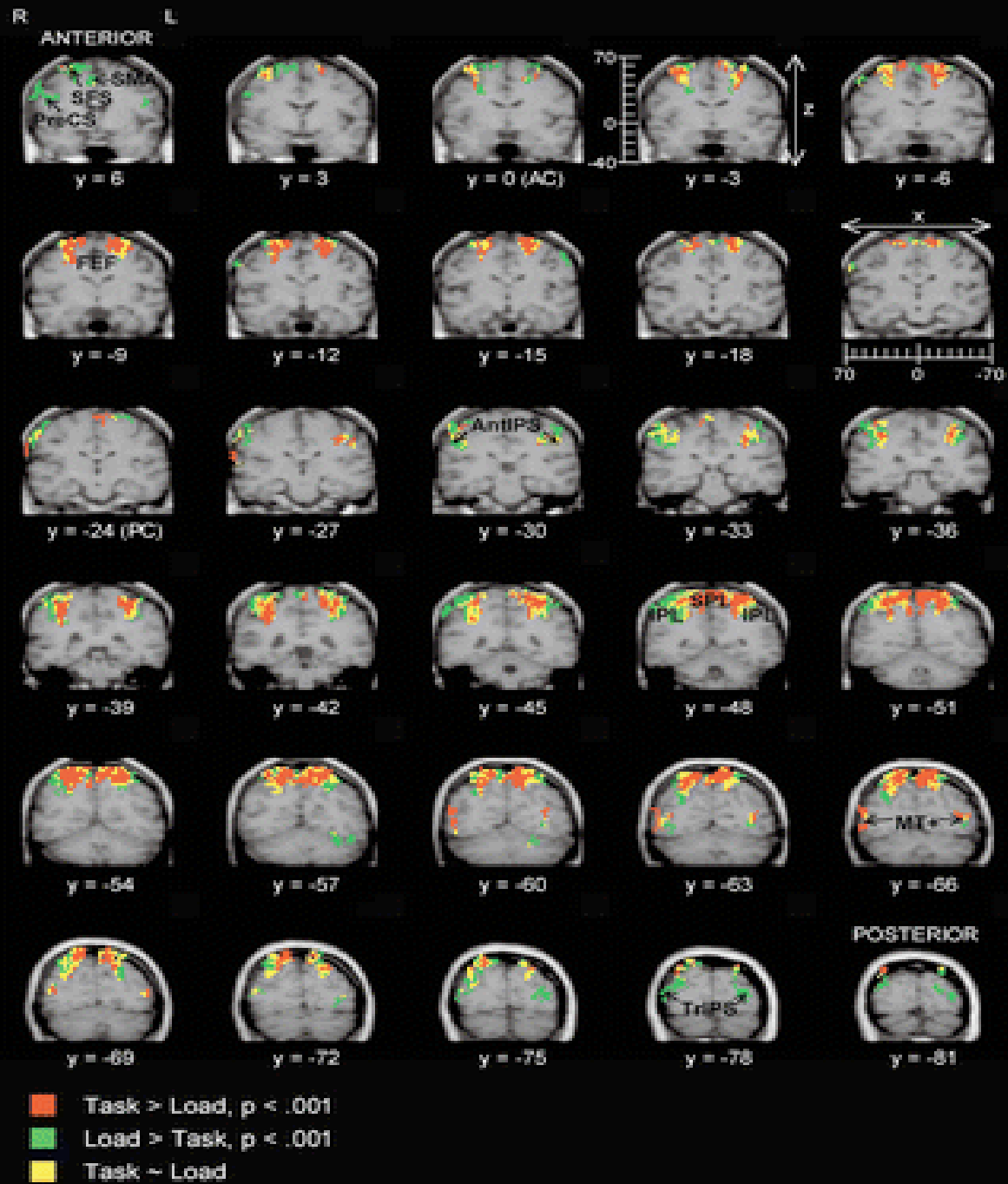
- MRI

- 1.5 T
- Asymmetric spin echo pulse

Data Analysis

- Two components/contrasts
 - Task-related activation = ***task effect***
 - Compared all attentive tracking tasks (equally weighted) to baseline
 - Activation that increased with attentional load during the task = ***load effect***
 - Estimated the degree to which activation increased with task load
 - (Group-averaged data)

- Voxels in which the task regressor contributed significantly more than the load regressor ($p < .001$) are **red**
- Voxels in which the load regressor contributed significantly more than the task regressor ($p < .001$) are **green**
- Voxels with no significant difference between the two regressors are **yellow**

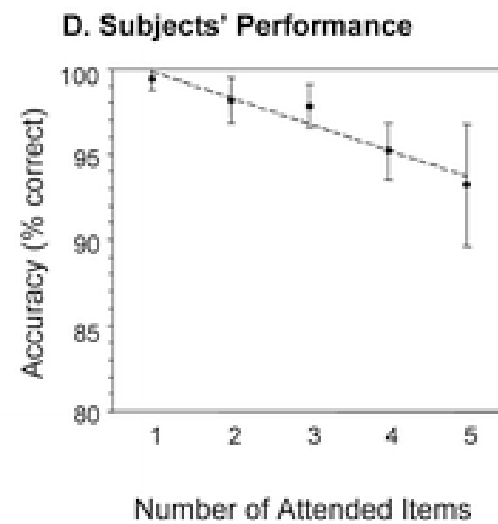
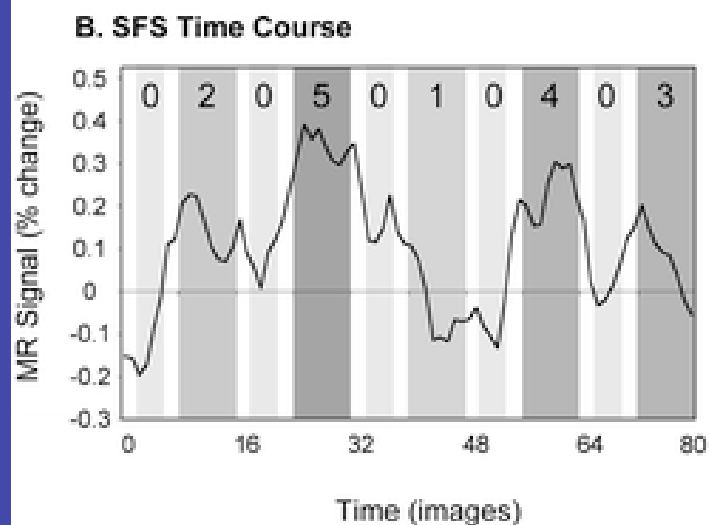
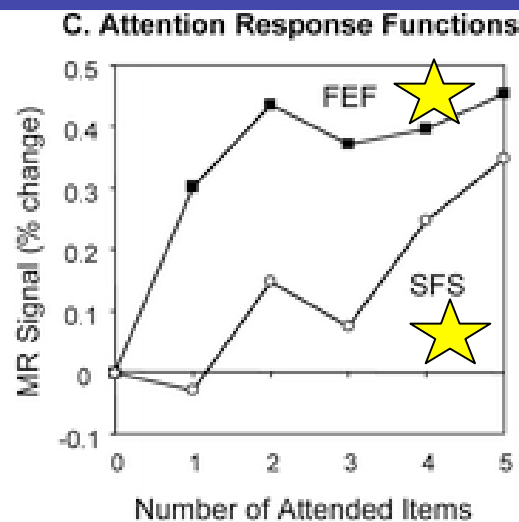
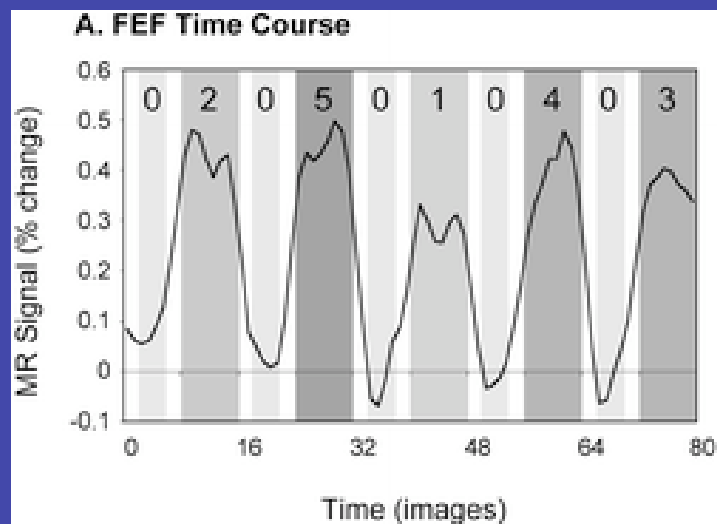


- Task regressor > load regressor (**red**)
 - FEF
 - SPL
 - Medial precuneus
 - MT+ complex

- Load regressor > task regressor (green)
 - SFS – superior frontal sulcus
 - PreCS – precentral sulcus
 - SMA
 - AntIPS – anterior intraparietal sulcus
 - IPS – posterior intraparietal sulcus
 - IPL – inferior parietal lobule
 - TrIPS – transverse occipital sulcus

- Voxels with no significant difference between the two regressors are **yellow**
 - Transition zones – possibly due to blurring when Talairach averaging

Time courses and attention response functions



Discussion

- Task-specific functions not affected by increasing demands on attention
- Attention-specific functions become more engaged as attentional demand increases

Task-specific

- Gain in activation between active and passive conditions – but no additional gain as more items are added
 - Not driven by attention per se (not involved in multiple object tracking)
 - More likely basic support functions of the task
 - Planning a saccade
 - Suppressing eye movements

Attention-specific/Load-dependent

- Load-related increase – these areas play a role in task performance
 - IPS – may be involved in spatial attention and working memory
 - SFS – working memory
 - PreCS – visual working memory and cognitive set switching
 - TrIPS – motion-selective – attentional tracking of moving targets

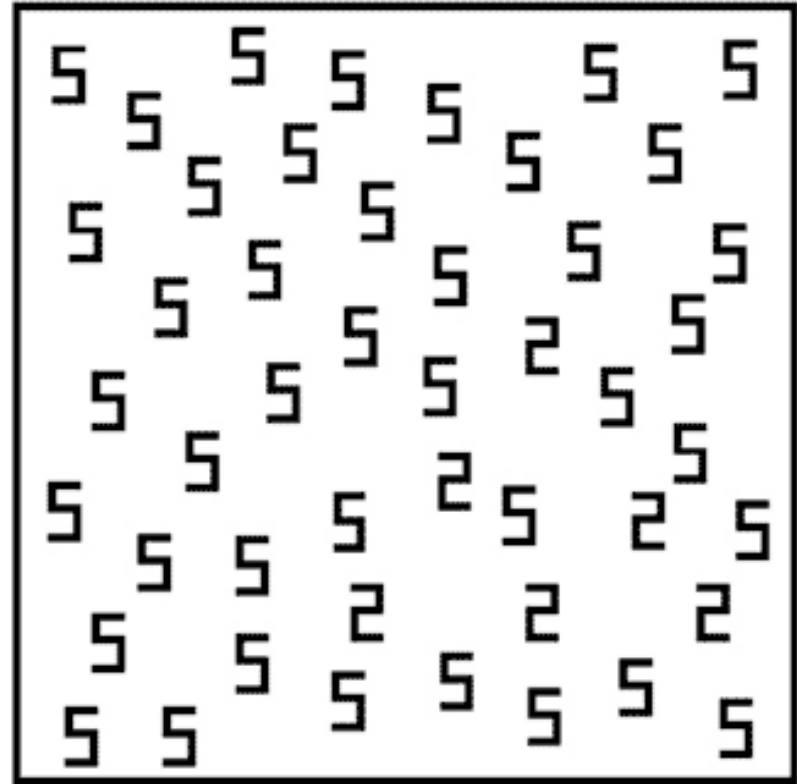
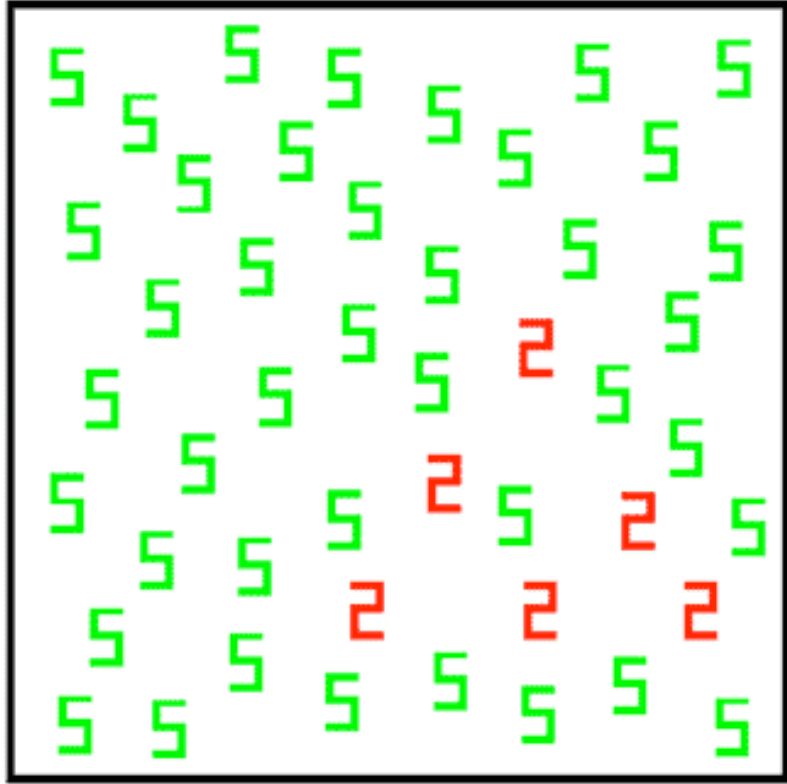
General conclusions

- Task functions – support overall performance
- Load functions – directly involved in handling increased load
- Parametric design – may have not seen these functional differences had a simple subtraction paradigm been used

Effect of Spatial Attention on the Responses of Area MT Neurons

Introduction

- Bottom-up vs. Top-down attention
 - **Bottom-up** = automatic – pop-out effects
 - **Top-down** = voluntary, goal-directed – flexibility in directing attention to different stimuli in the same visual scene



- Where is attention modulated in the brain?
- Bottom-up – assumed to be at very early processing stages
- Top-down – early vs. late selection

- Early selection

- Attention influences early stages of the visual system to allow for more efficient use of limited capacities at all subsequent stages

- Late selection

- Top-down mechanisms filter out irrelevant info only at late processing stages – after perception but before behavioral responses

Treue and Maunsell (1996) study

- Very strong attentional modulation in MT
 - Monkey had to attend to one moving target among distracter targets
 - Report when target changed speed
 - When two targets moved in opposite directions in the RF of an MT or MST neuron, response dominated by the attended target
 - Strong response when attended target moved in cell's preferred direction (>80%)
 - Weak response when attended target moved in null direction

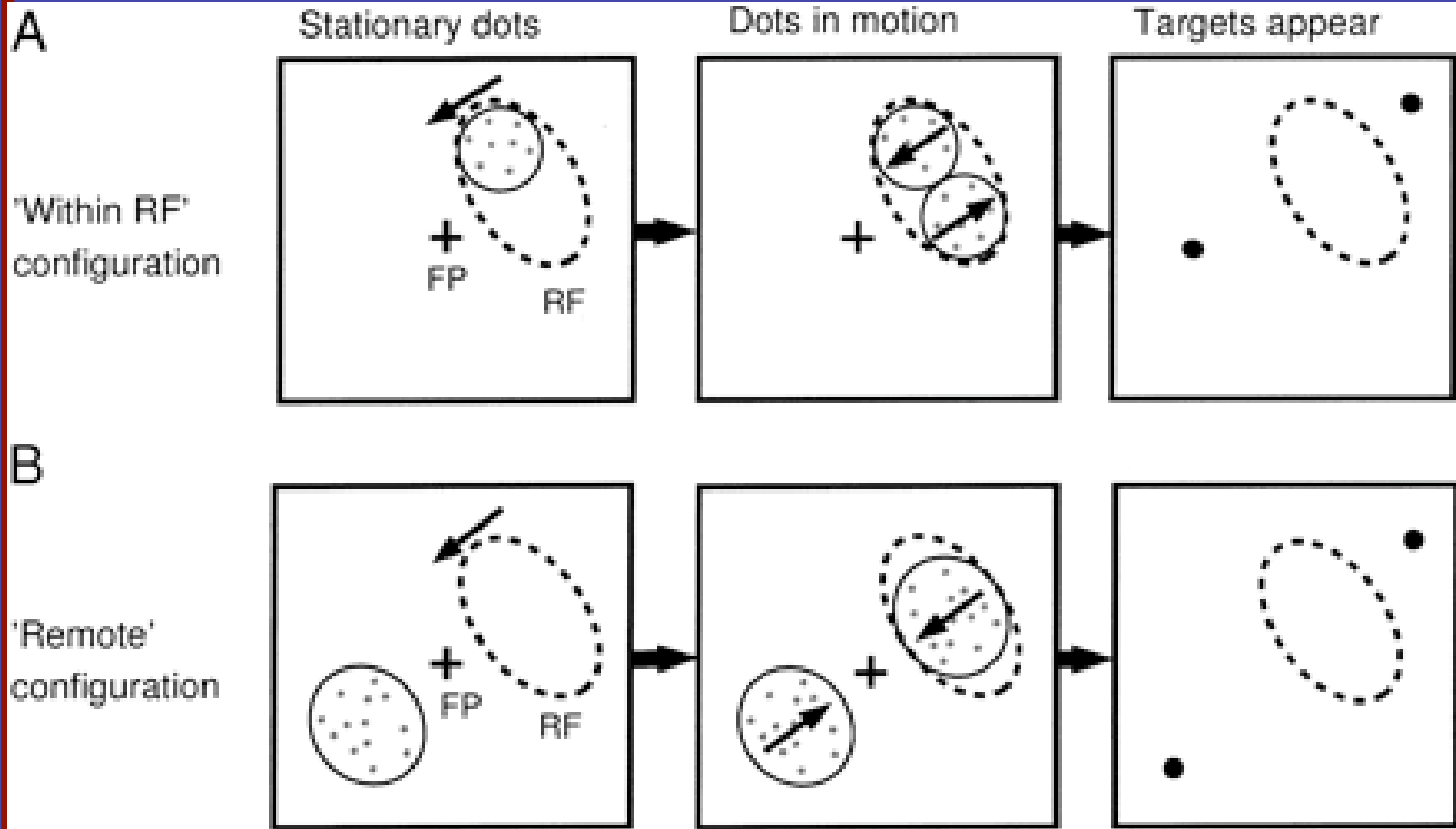
- These results vary from previous studies that failed to find substantial attentional effects in MT

- To test see if this could be replicated – this study recorded from MT neurons while monkey performed a spatial attention task



Methods

- On each trial, two apertures of random-dot stimuli appeared simultaneously in two spatially separated locations
- The monkey was required to discriminate the direction of motion in one aperture while ignoring the direction of motion in the other (distracter) aperture



The apertures could be within the same RF (A) or large and spatially remote (B)

- Each trial starts with Fixation
- After fixation, a circular aperture of stationary dots appears at one of two possible locations
- Stationary dots inform the monkey which aperture location to attend

- After stationary dots disappear, 2 circular apertures of random dots appear in the 2 spatial locations
- In each aperture, a fraction of the dots move coherently in 1 of 2 possible directions (preferred or null) while the other dots are re-plotted at random locations
- Monkey was required to discriminate the direction of motion at the attended location (cued by the stationary dots) and ignore motion at the other location

- After offset of the random-dot stimulus, 2 saccade targets appear
- Monkey indicates the perceived direction of motion at the attended location by making a saccadic eye movement to the corresponding target

Data analysis

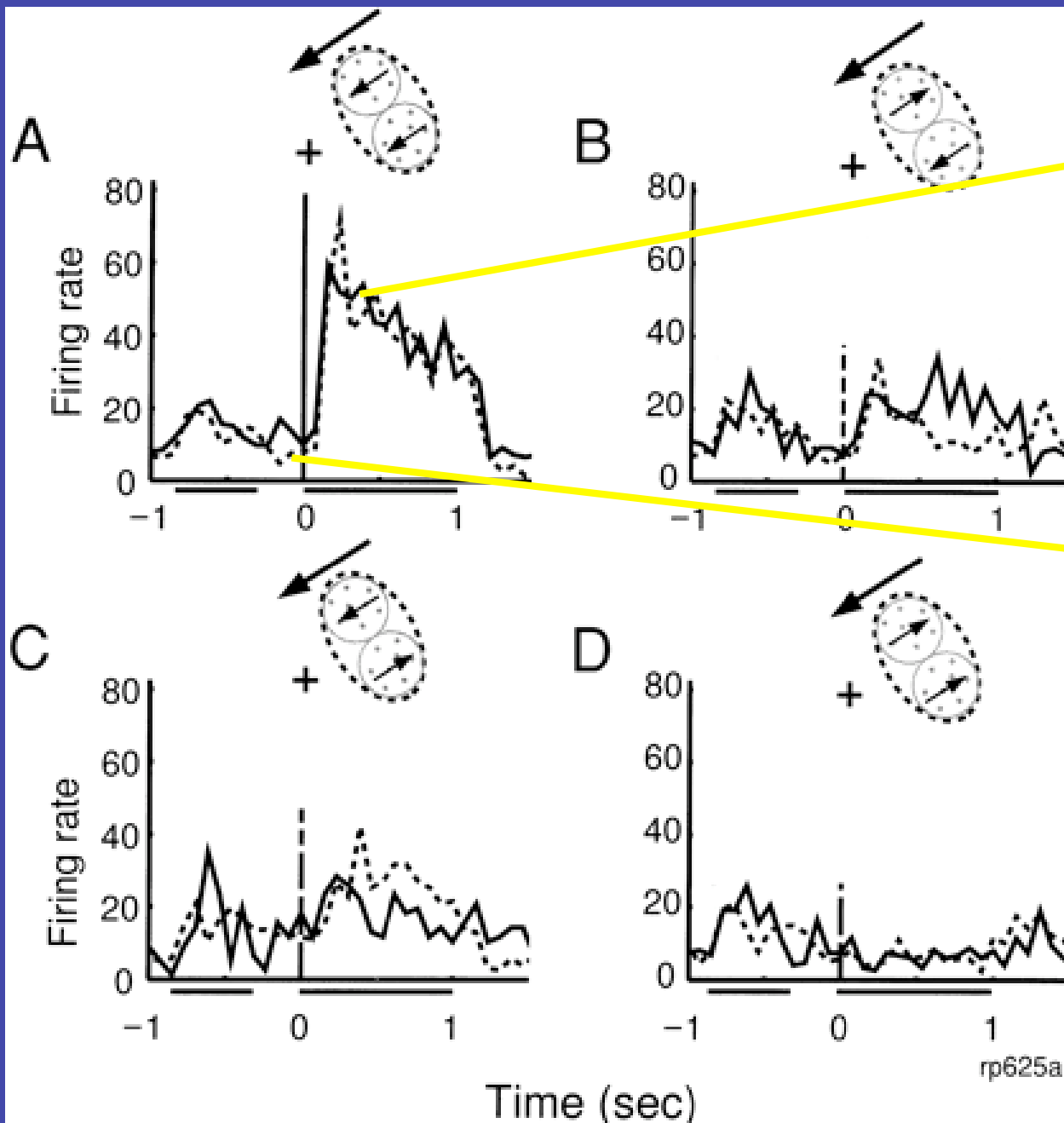
- Recorded from MT neurons
- Quantify attentional effect by comparing the responses of individual MT neurons to identical visual display conditions when the monkey was instructed to attend to one or the other aperture
- Neuronal responses were measured as the number of spikes that the cell fired during the 1-s presentation of the motion stimuli

- For each of the four visual display conditions, compared the mean response in the two attentional states using a selectivity ratio (SR) index

- The SR can assume values between - 1 and 1
 - A value of 0.33 indicates that the responses are modulated by the attentional state
 - A value close to zero implies that the responses of the neuron are not modulated by spatial attention.

Results – effect of spatial attention on responses of MT neurons

- Predict: attentional effect to be maximized when both apertures are presented within the RF and effects to be strongest when attending to preferred direction of motion (based on previous studies...)
- Aperture problem link:
http://www.psico.univ.trieste.it/labs/perclab/integration/english_version/aperture.php3



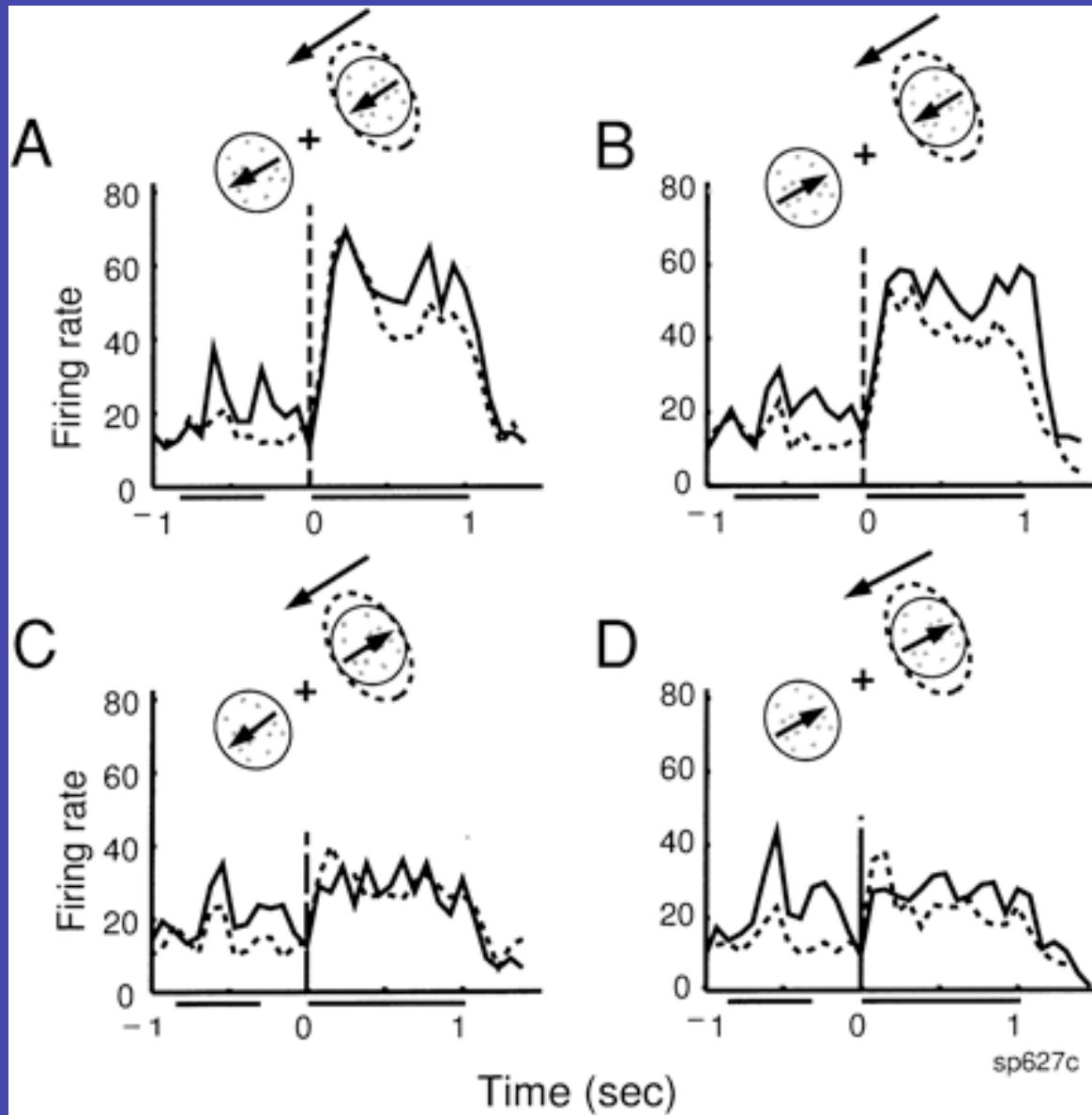
— Attend lower

..... Attend upper

- Four possible stimulus configurations are shown in the 4 panels (*A-D*)
 - A – response strongest when both apertures moved in preferred direction
 - B, C – responses were intermediate when apertures moved in opposite directions
 - D – weakest when both apertures moved in null directions

- Data from one of the largest attentional effects observed in the within RF configuration:
- B and C – the response differed between the two attentional states
 - B – 44% stronger when attend to lower apertures – preferred direction
 - C – 50% stronger when instructed to attend to upper aperture – preferred direction
 - ***The responses of the cell to identical visual displays conditions were modulated by the spatial location to which the monkey attended***

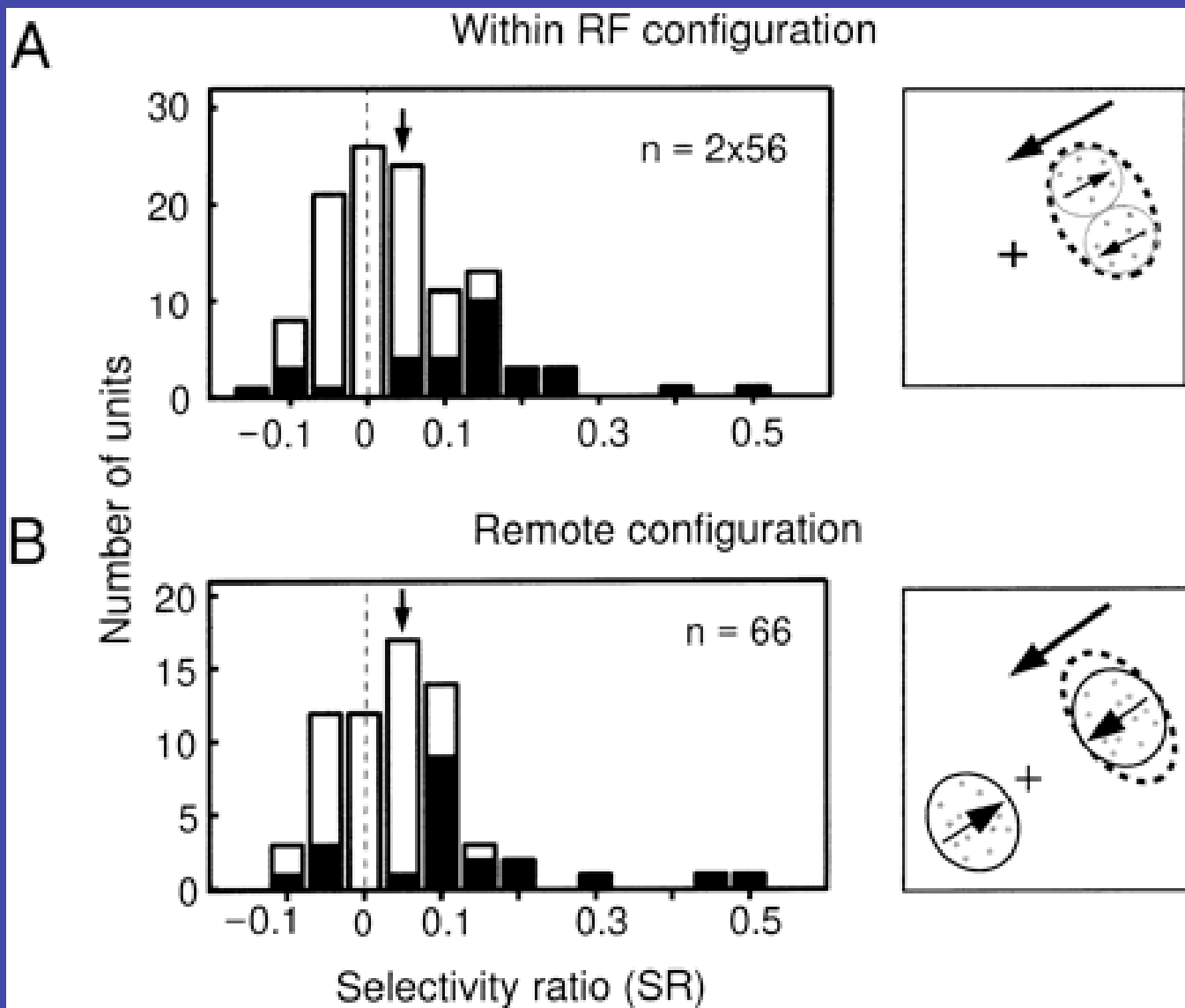
Remote condition



—————
Attend RF aperture

.....
Attend remote aperture

- If spatial attention influences MT neurons in the remote config – expect the responses to be stronger when the monkey is instructed to attend to the stim within the RF
 - A and B – 11% and 23% modulation
 - No significant attentional modulation when null direction motion appeared in the RF (C and D)



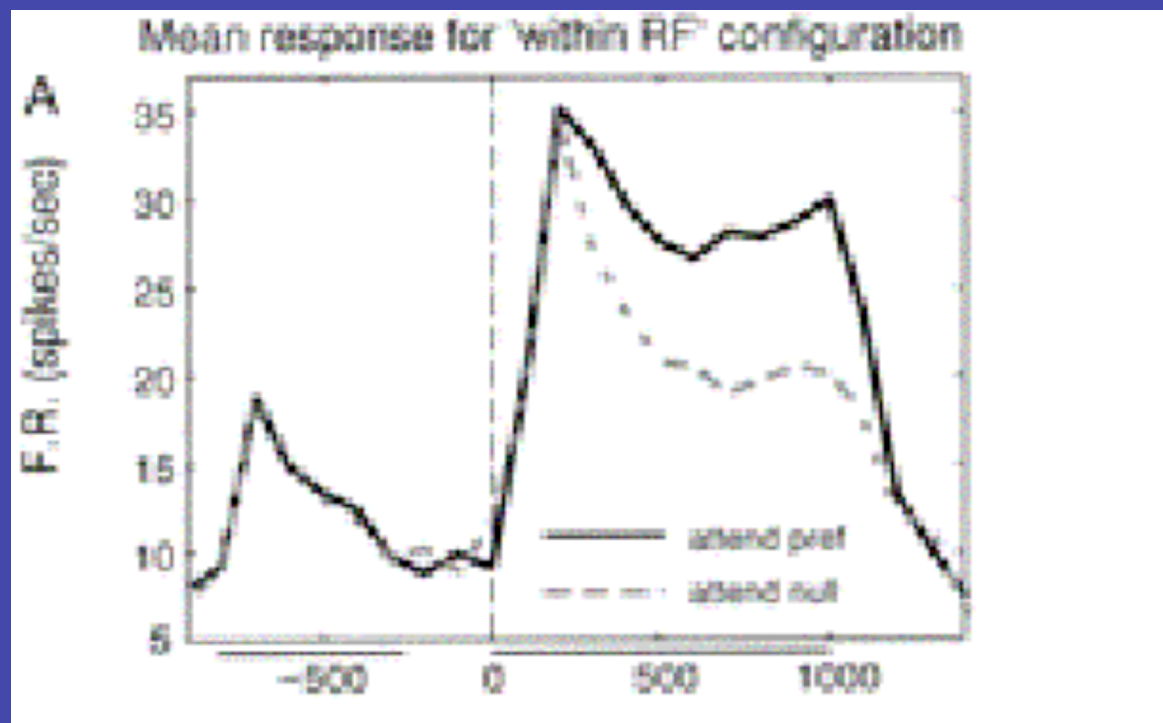
- Distribution of the selectivity ratio index combined over the 2 monkeys

- **4 A – within RF – (Figure 2 B, C)**
- The distribution of the SRs is shifted to the right of zero
 - Indicates that MT neurons responded to identical visual stimuli more strongly when the monkey attended to the spatial location that contained the preferred direction of motion
- The magnitude of this effect is significant (*t*-test, $P < 0.00005$)
- The average SR is 0.042
 - Corresponds to an 8.7% increase in firing rate when monkeys attended to preferred stim

- **4 B – remote configuration (figure 3B)**
- Distribution is also shifted to the right of zero (*t*-test, $P < 0.001$)
- Indicates that MT neurons responded more strongly to identical visual display conditions when the monkey was instructed to attend to a preferred stimulus within the RF
- The average SR was 0.047
- Corresponds to a 9.9% increase in firing rate

Time course of the attentional effect within single trials

- Time course information can yield useful insights concerning mechanisms that might underlie the attentional effects



■ 7 A

- On trials with preferred direction motion (solid line), the average response remained high throughout the stimulus presentation interval
- For the *identical* visual display condition, the response declined throughout the stimulus presentation interval for the null direction motion (dashed line)

- Summary of results:
 - Observed weak effects of spatial attention in MT
 - Responses were ~8% stronger, on average, when the monkey attended to the aperture containing preferred direction motion
 - Attentional response modulations were similar in the within RF and remote configurations

Discussion

- Goal - measure the effect of spatial attention on the responses of MT neurons
- Found systematic differences between the responses of MT neurons to identical visual display conditions in the two attentional states
- Suggests that spatial attention indeed modulates the responses of MT neurons
- On average, responses were 8.7% stronger when monkey attended to the aperture containing preferred direction motion

Primary findings

1. Attentional modulations were similar in magnitude in the within RF and remote configurations
 - The mechanism that mediates spatial attention in our experiments is not likely to be based on local competitive interactions

2. Attentional modulations in our paradigm develop slowly

- Begin ~250-300 ms after stimulus onset and increase gradually throughout the trial, peaking near the time of stimulus offset
- This is compatible with slow, top-down attentional mechanisms that are likely to be mediated by the extensive feedback connections to MT from higher areas

3. Effects observed (8.7% in the within RF configuration) are an order of magnitude smaller than the attentional effects measured by Treue and Maunsell (1996) (>80%) even though both studies required similar tasks
- This difference between the two studies provides important clues about the neural mechanisms underlying visual attention

- Differences between these results and those of Treue and Maunsell are not likely to be due to differences in either the *amount* of attentional demand or in the selectivity of MT neurons for the stimuli used in the two studies

- Attention may be acting at different *sites* in the two paradigms
 - In this study, attention appears to exert its primary effects downstream from MT, consistent with "late selection" models of visual attention
 - In the paradigm of Treue and Maunsell attention exerts pronounced effects at, or before, the level of MT

- A key question remains: what difference(s) between the two paradigms could be responsible for such a dramatic difference in the effects of attention in MT?

Potential sources for the contrasting results

- The tasks differ in at least four important ways ...

- May be that attentional mechanisms can modulate the responses of MT neurons more effectively with reference to a combination of direction and space (Treue and Maunsell) than to space alone (this study)
 - Feature-based attentional mechanisms (direction of motion as feature) may contribute to the attentional modulations observed by Treue and Maunsell

- The current contrasting results suggest that attentional mechanisms can act at multiple levels within the hierarchy of visual areas
 - "Early" selection may be optimal under some circumstances
 - And an unbiased representation in the early visual areas might be preferable under other circumstances - attentional mechanisms must operate at later processing stages downstream from MT

- In exploiting the advantages of early and late selection mechanisms, therefore, the brain may get the best of both worlds, switching from one strategy to the other depending on subtle aspects of the task