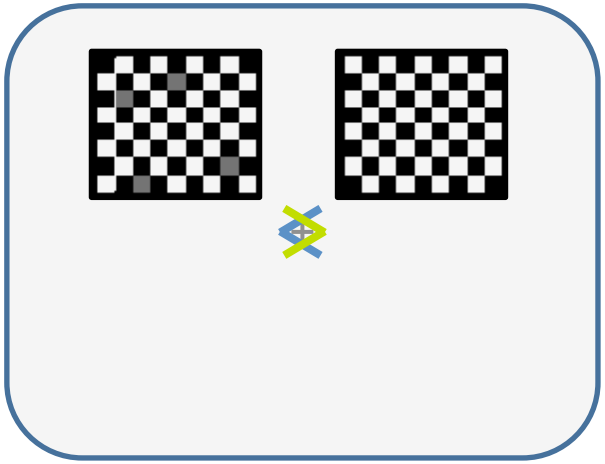
What is attention ?

Every one knows what attention is. It is the taking possession of the mind, in clear and vivid form, of one out of what seem several simultaneously possible objects or trains of thought. Focalization, concentration, of consciousness are of its essence. It implies withdrawal from some things in order to deal effectively with others and is a condition which has a real opposite in the confused, dazed, scatterbrained state which in French is called *distraction*, and *Zerstreutheit* in German.

William James: The Principles of Psychology 1890

Hopfinger *et al.* (2000) [1] Mechanisms of top-down control in spatial attention (human fMRI)



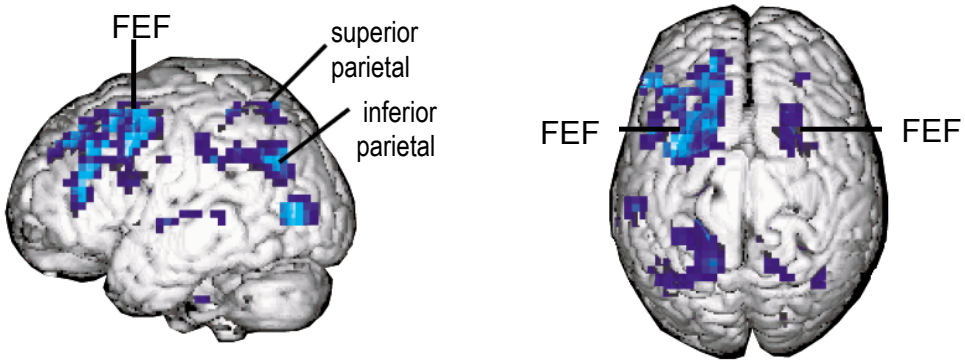
TASK:
Attend in direction of blue arrow cue & report presence/absence of grey squares in grid (cue alternates left & right across trials).

OBSERVE:
Activity in frontoparietal areas (including FEF) after cue but preceding onset of grids.

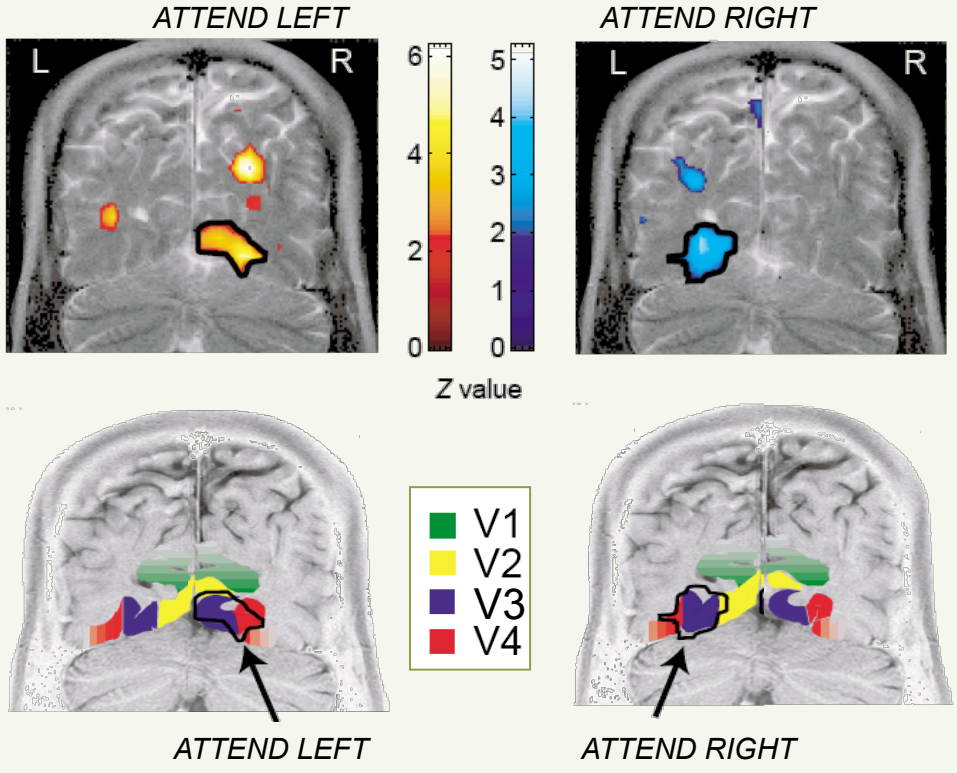
After grid onset, there is enhanced activity in visual cortex contralateral to attended grid (illustration shows the *difference* in activity between attend left & attend right conditions.

CONCLUDE:
There is a frontoparietal network of areas for controlling spatial attention, activated by a cue, that enhances visual cortex response to the target grid.

Source of attentional control (frontoparietal network)



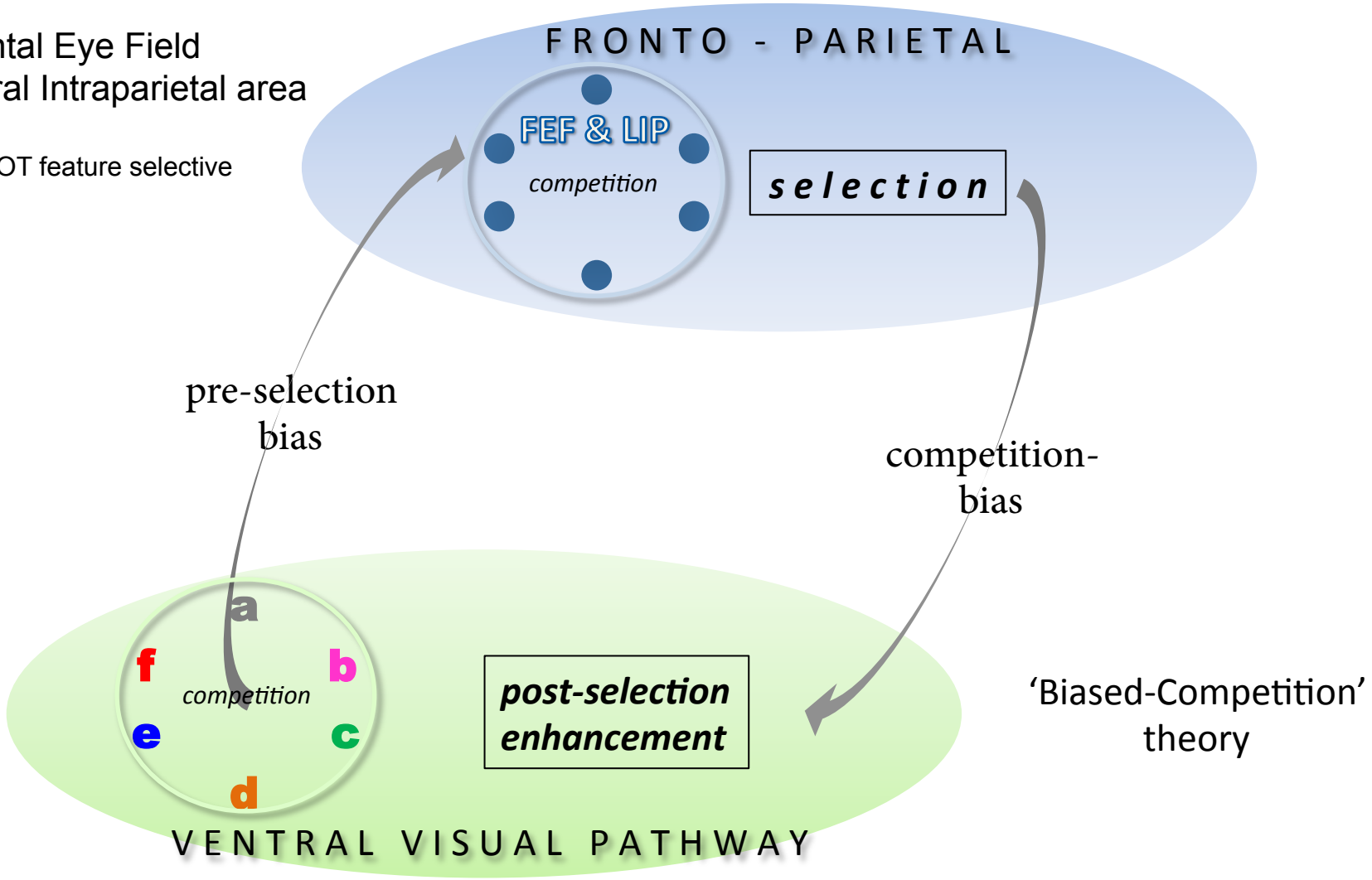
Site of attentional action (visual cortex)



Neural interpretation of attention

FEF – Frontal Eye Field
LIP – Lateral Intraparietal area

neurons are NOT feature selective



'Biased-Competition' theory

Top-down and bottom-up mechanisms in biasing competition in the human brain. (Beck & Kastner (2009) [GENERAL READING NO. 30]

2. Multiple stimuli compete for neural representation in visual cortex. The first and most fundamental prediction of biased competition theory is that objects compete for neural representation in visual cortex.

3. Competition is greatest at the level of the RF
… If stimuli are competing for representation by a particular neuron, then the competitive interactions should be most apparent when the stimuli fall within the RF of that same neuron.

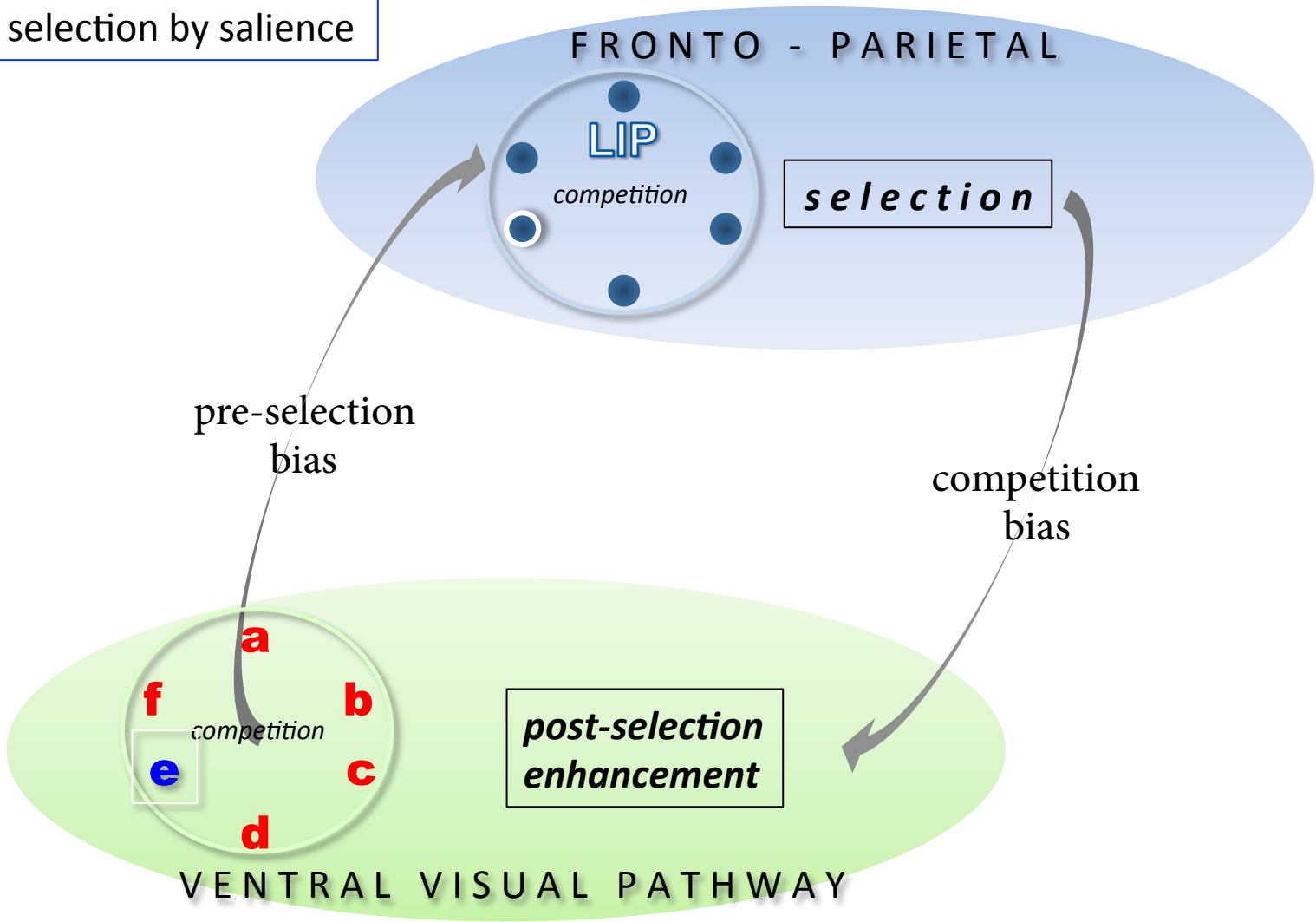
4.1.1. Filtering of unwanted information
When a monkey directed attention to one of two competing stimuli within a RF, the responses in extrastriate areas V2, V4, and MT to the pair of stimuli were heavily weighted in favor of the attended stimulus; … In other words, attention counteracted the suppressive influence of the competing stimulus.

NO ! Objects/stimuli do not compete !

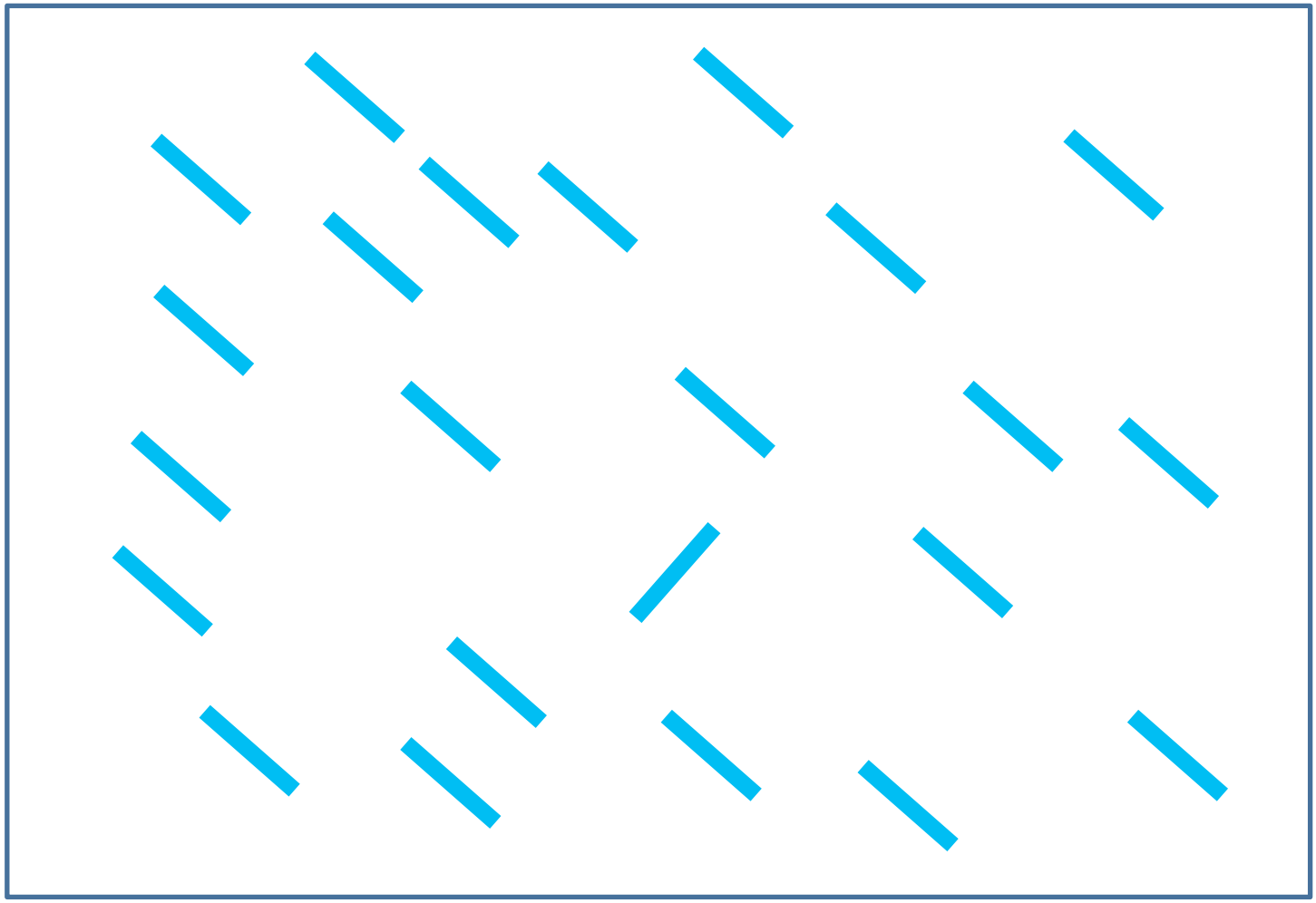
The competition is between neurons dedicated to representing one of the alternative stimuli.

Neural interpretation of attention

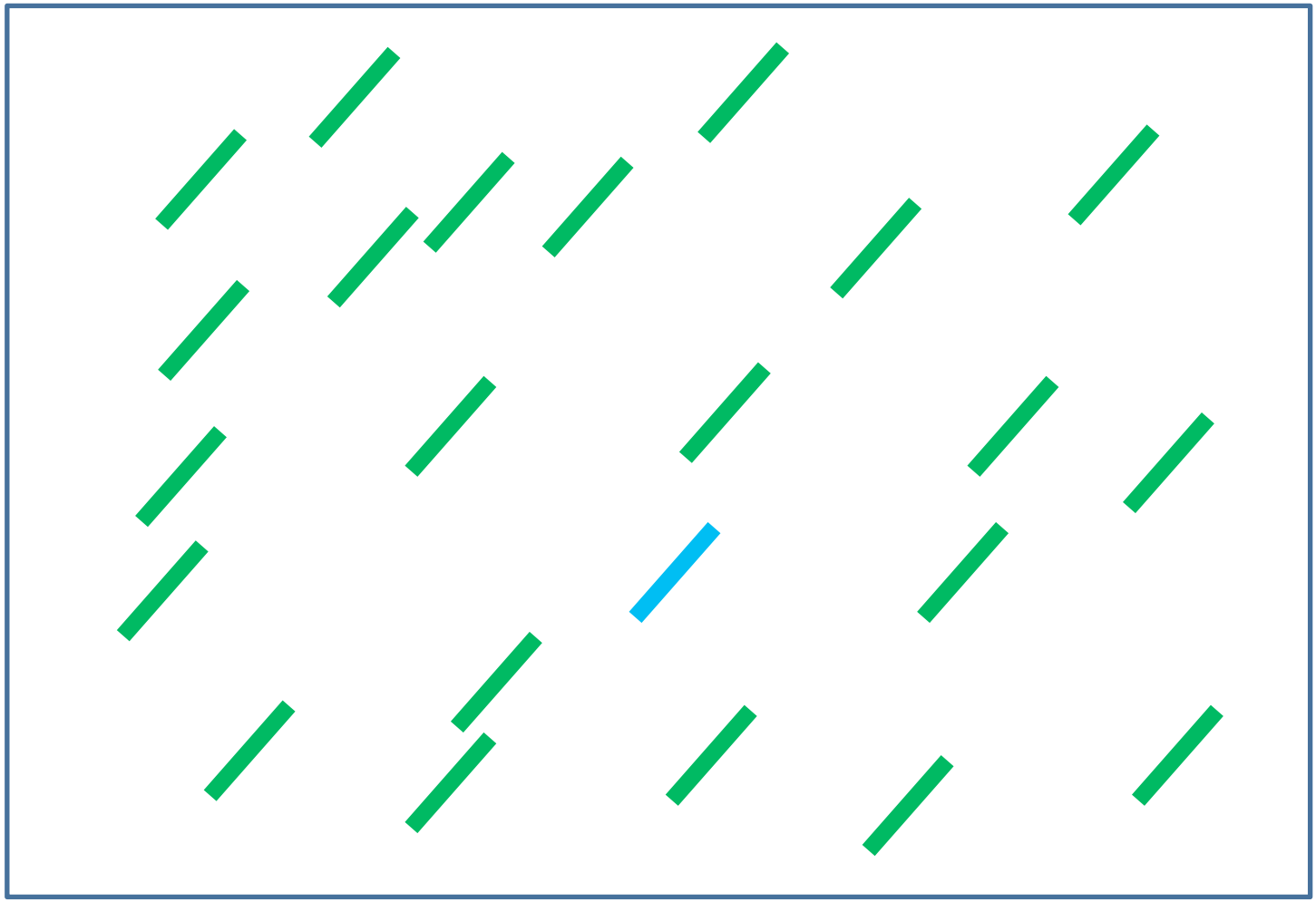
'Bottom-up':
selection by salience



Feature search task (or ‘pop-out’ task)



Feature search task (or ‘pop-out’ task)

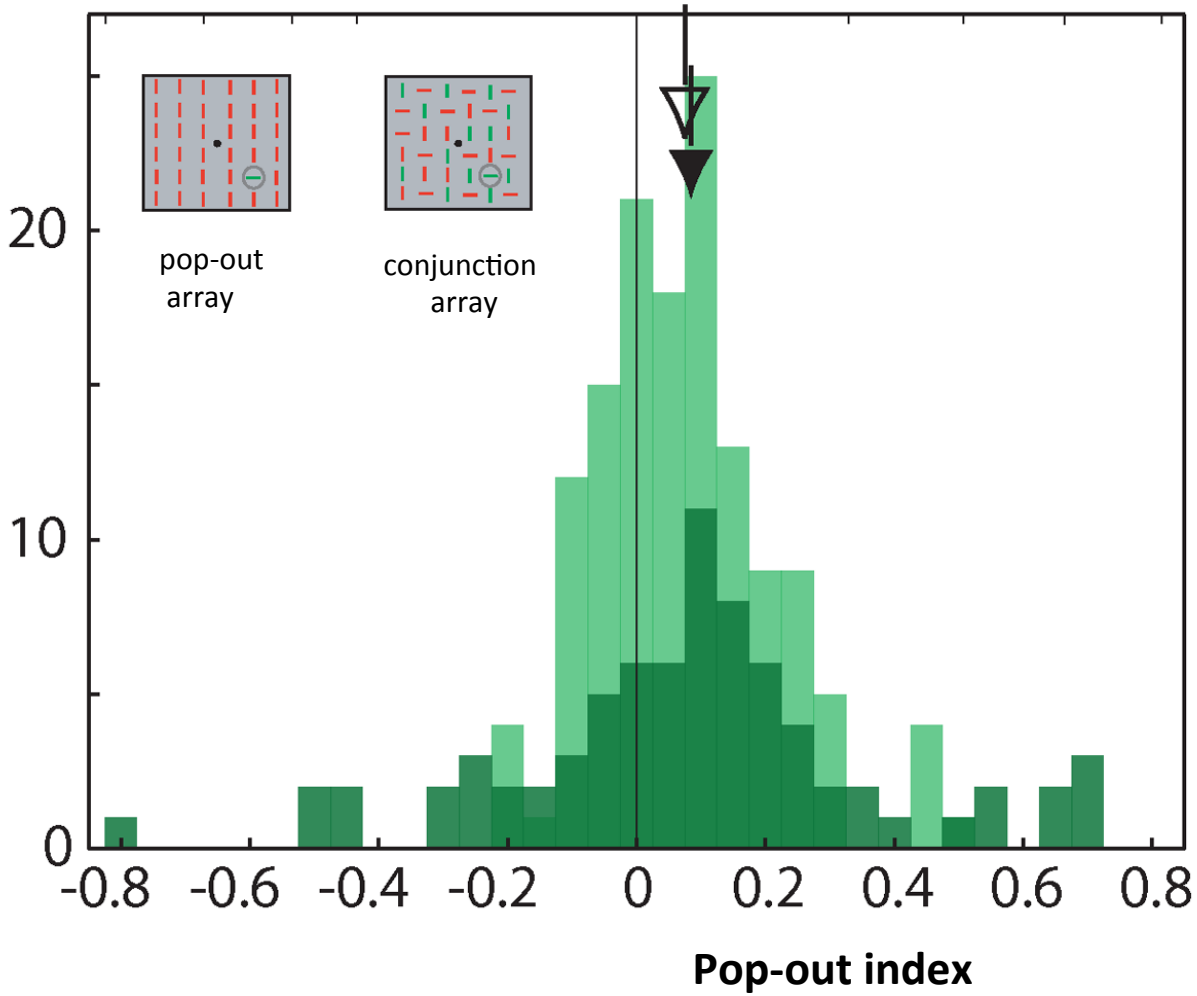


Burrows & Moore (2009)[2] Response of V4 neurons to salient bars (colour & orientation pop-out)

TASK:
Maintain fixation;
i.e. no requirement to identify or select the unique array item in either the pop-out or conjunction display.

RESULT:
The majority of neurons show a significantly greater response to the pop-out array, when the array item placed in their RF is identical.

CONCLUSION:
Salience modulates the response of V4 neurons; (the experiment did not attempt to distinguish between pre- and post-selective mechanisms).

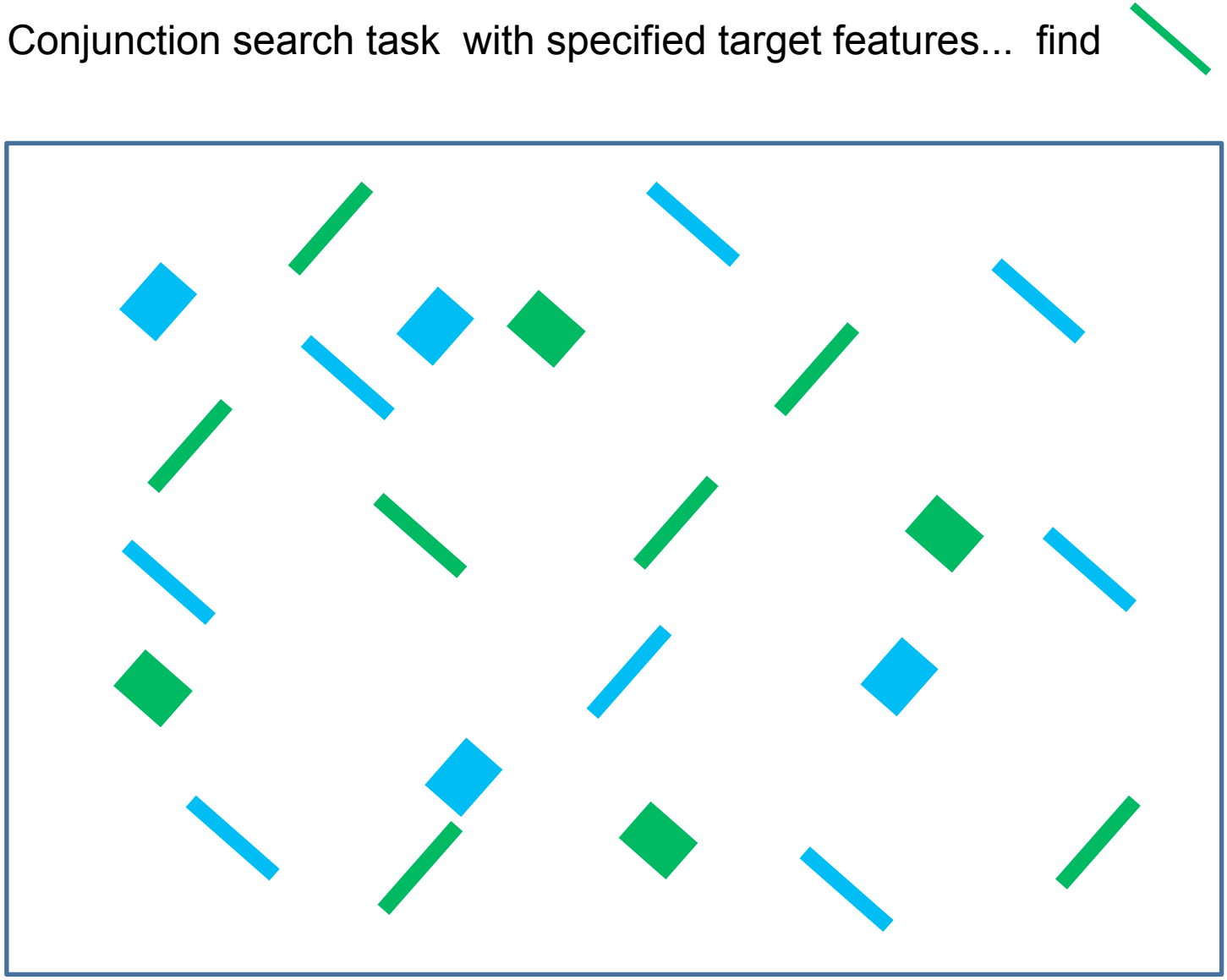


$$\text{Pop-out index} = \frac{\text{response}^{\text{POPOUT}} - \text{response}^{\text{CONJUNCTION}}}{\text{response}^{\text{POPOUT}} + \text{response}^{\text{CONJUNCTION}}}$$

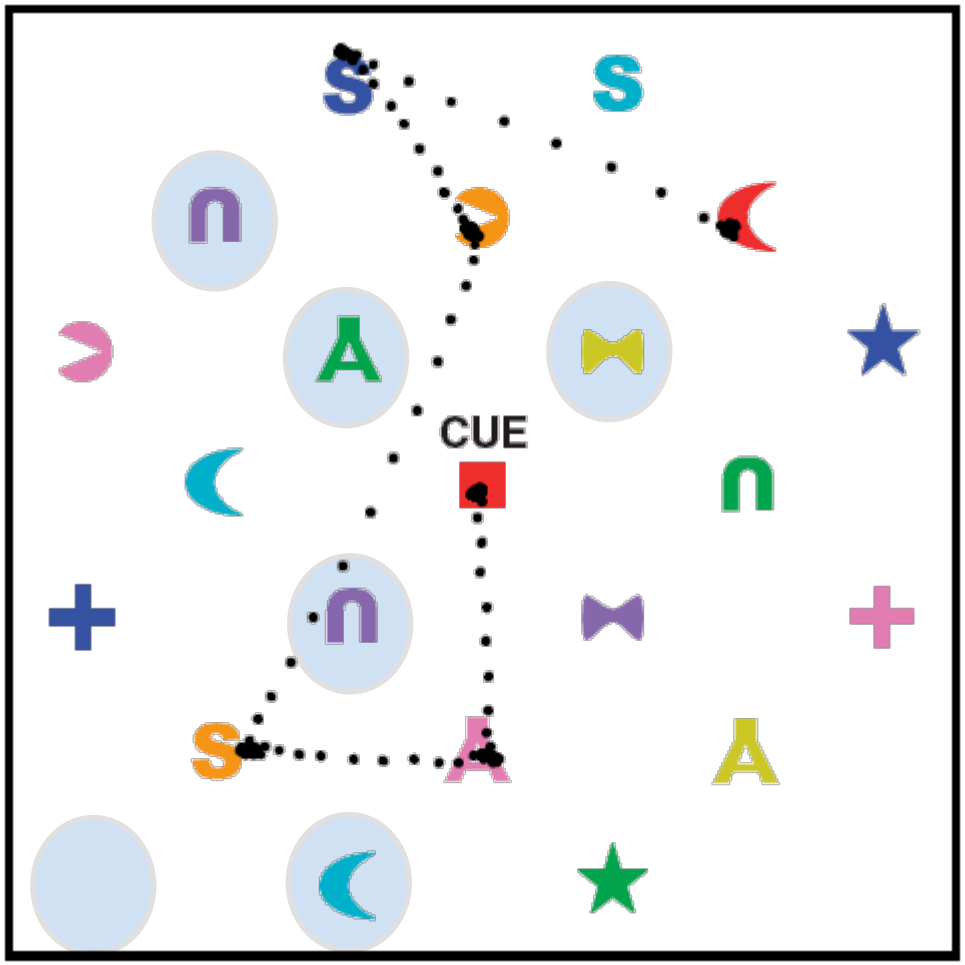
137 neurons: PI index calculated from the 'raw' response to array + target bar within RF

76 neurons: PI index calculated once the response to array *lacking* the target bar within RF is subtracted from the raw response

Conjunction search task with specified target features... find



Bichot *et al.* (2005) Feature attention in area V4 neurons during a colour (or shape) search task [REF 3]

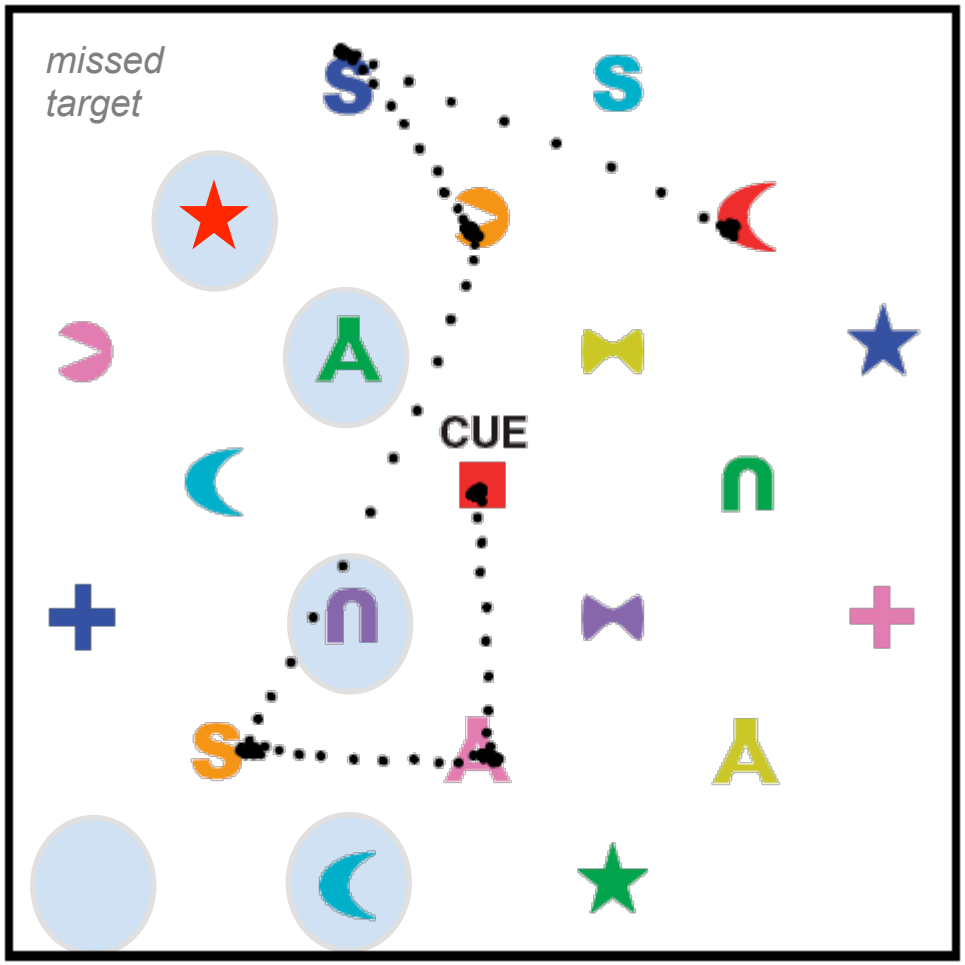


Fovea

Receptive field of neuron being studied

- 4 inspections before finding target;
- 5 saccades in total;
- Average was 6.3 saccades;
- Expected average = 10.5;
- Conclude that search is efficient: ‘GUIDED SEARCH’

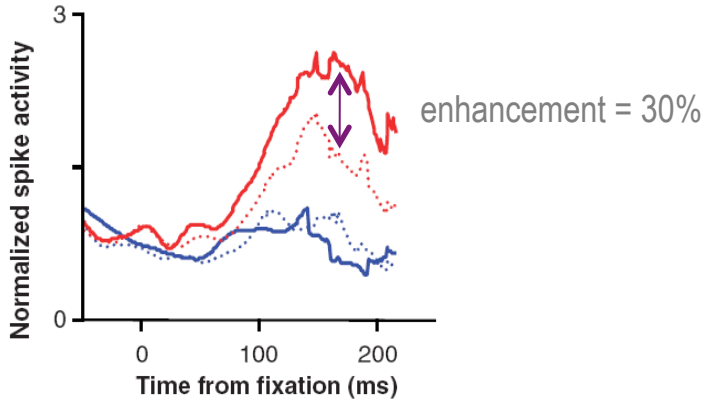
Bichot *et al.* (2005) Feature attention in area V4 neurons during a colour (or shape) search task [REF 3]



COLOUR SEARCH TASK

Receptive field of
neuron being studied

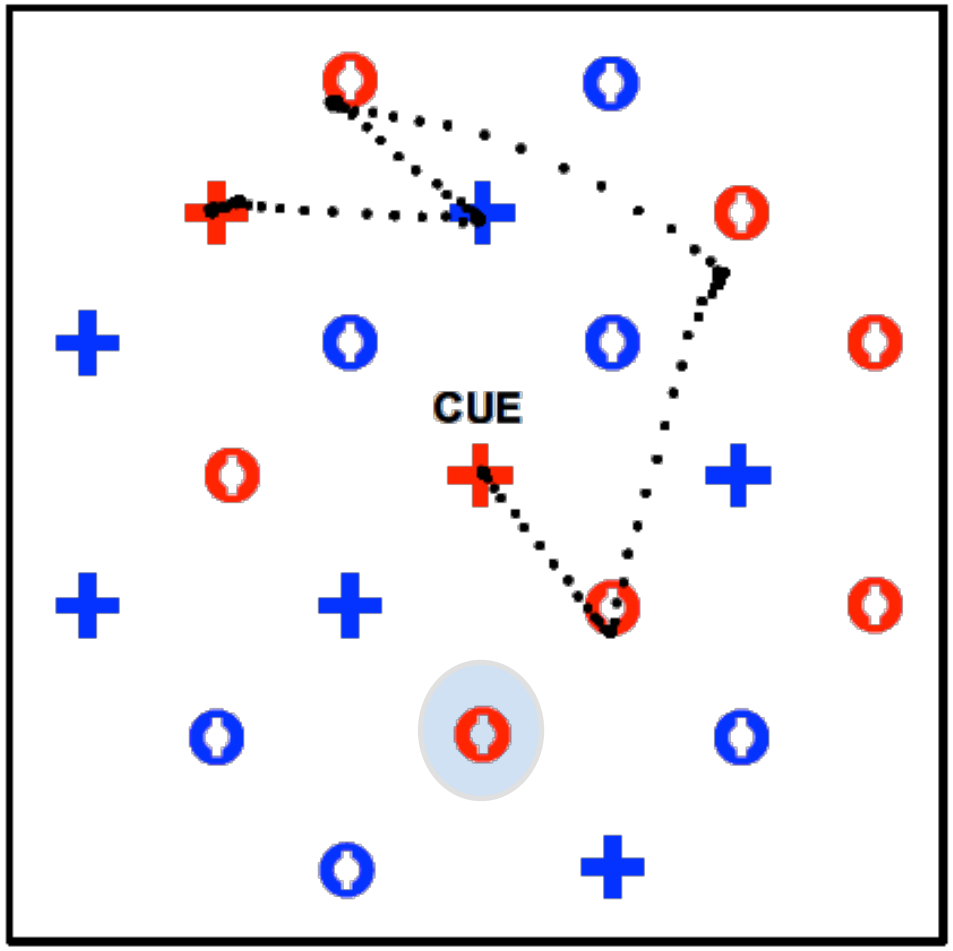
AVERAGED RESPONSE OF ALL TESTED NEURONS



Cue colour	Item colour (within RF)	Enhanced response ?
preferred	preferred	YES
non-preferred	preferred	
preferred	non-preferred	NO
non-preferred	non-preferred	

Bichot *et al.* (2005) Feature attention in area V4 neurons during a conjunction search task [REF 3]

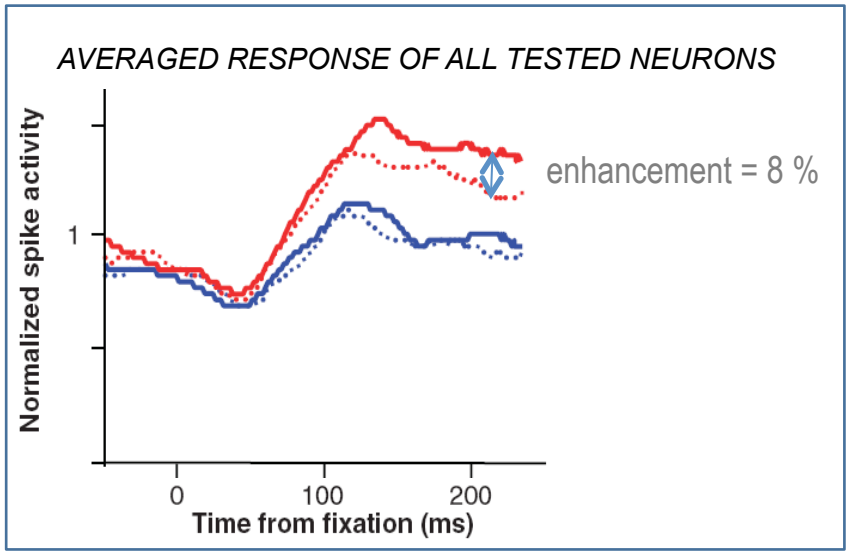
Target =



COLOUR /SHAPE CONJUNCTION SEARCH TASK

Fovea

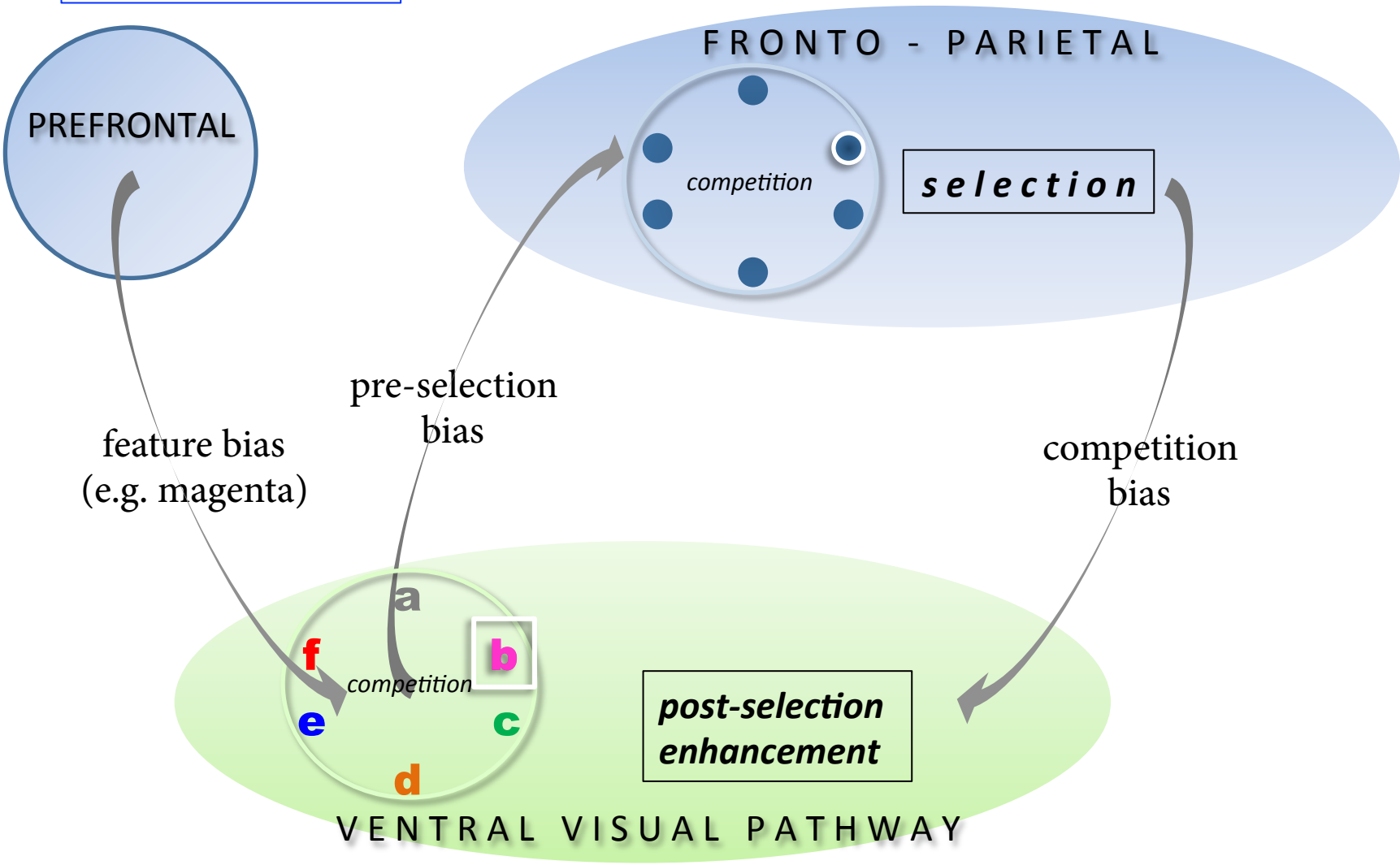
Receptive field of neuron being studied



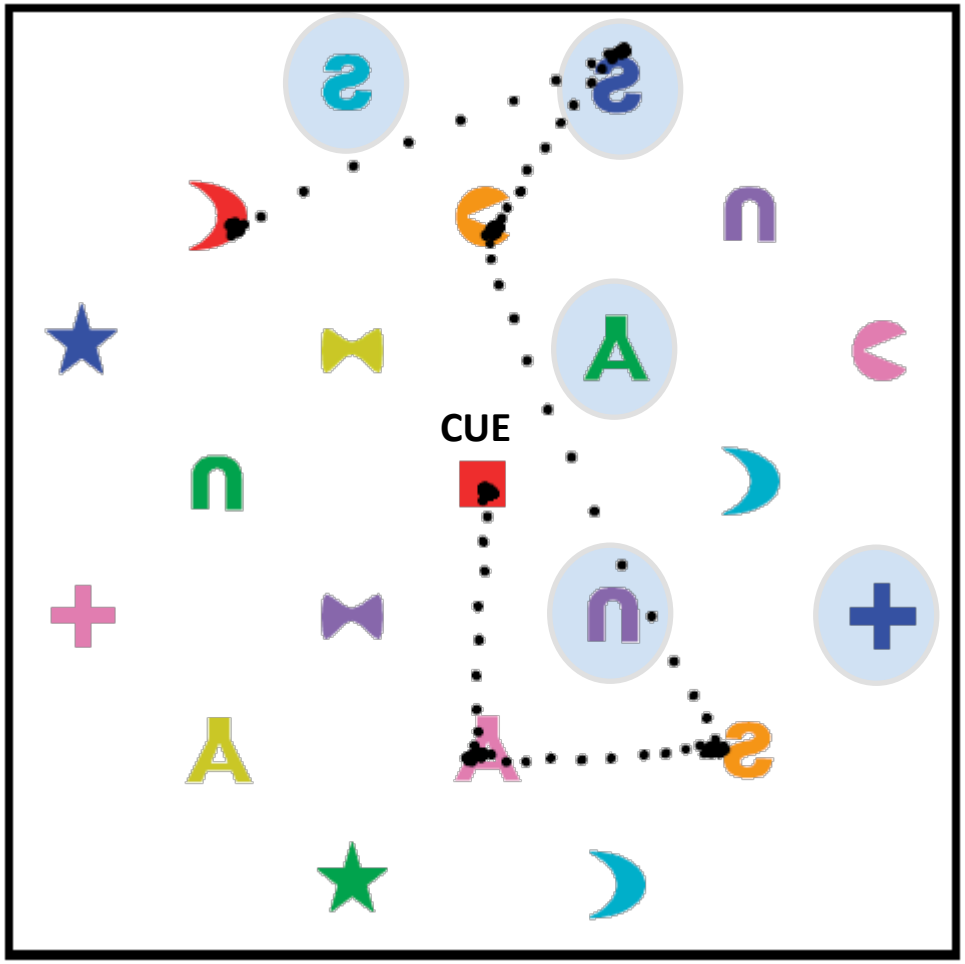
Cue colour	Item colour	Enhanced response ?
preferred	preferred	YES
non-preferred	preferred	
preferred	non-preferred	NO
non-preferred	non-preferred	

Neural interpretation of attention

'Feature attention'



Bichot *et al.* (2005) Feature attention in area V4 neurons during a colour (or shape) search task:
What happens when an item is selected for attention? [REF 3]



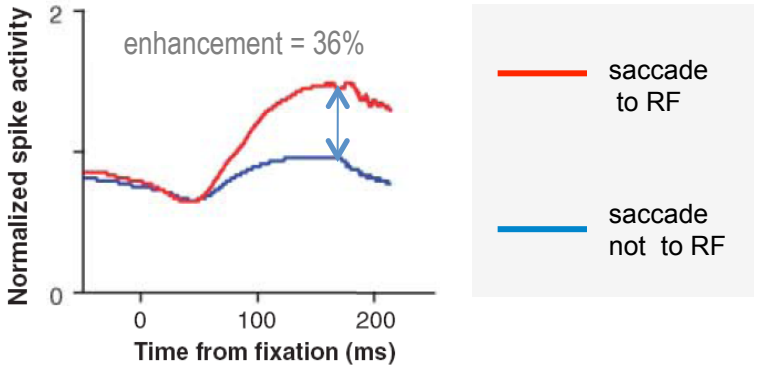
COLOUR SEARCH TASK

covert versus ***overt*** spatial attention

Receptive field of neuron being studied

Fovea

AVERAGED RESPONSE OF ALL TESTED NEURONS

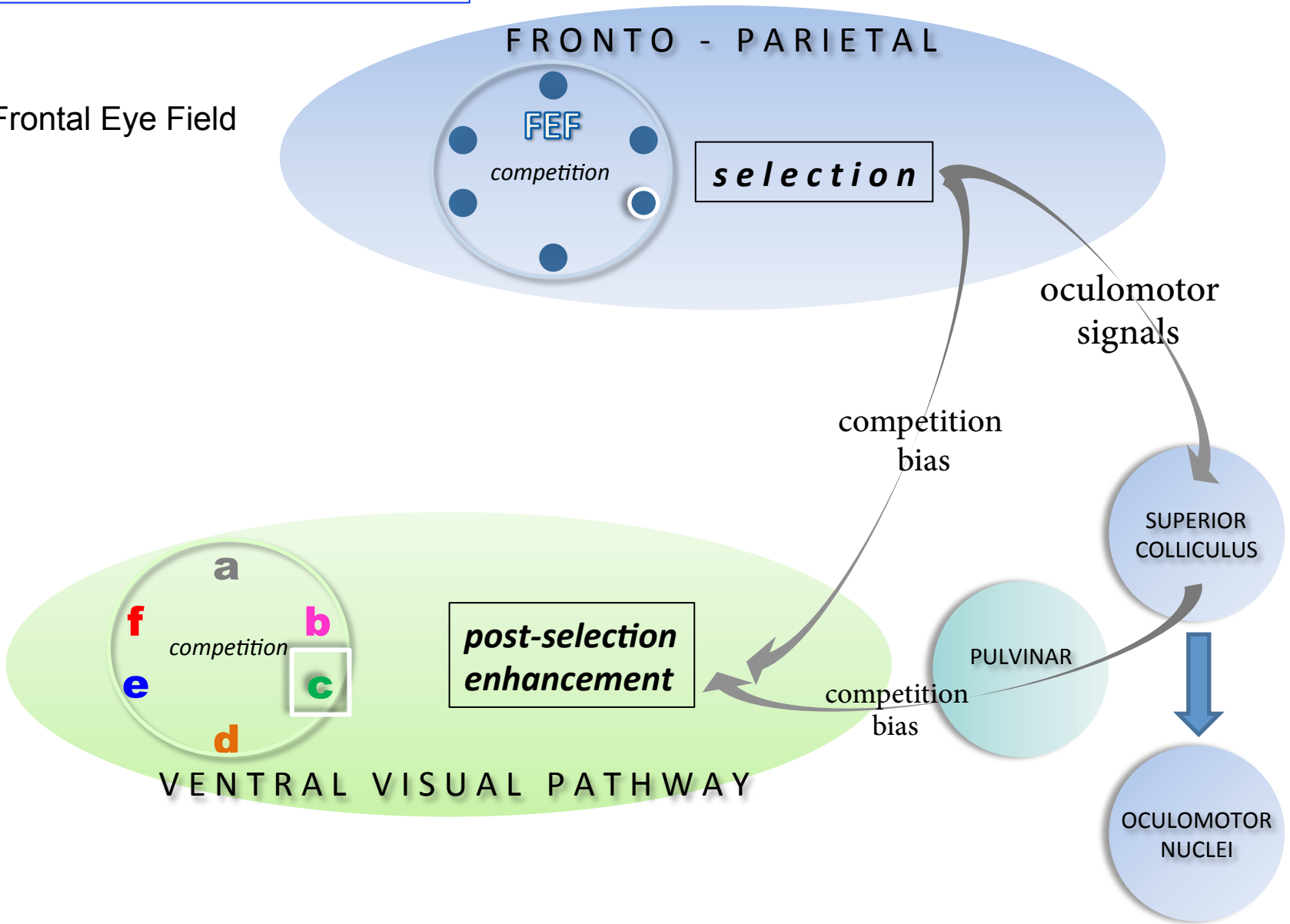


- 70% of neurons show an effect of this 'spatial' selection;
- For the majority, the selected item would not match the preferred colour (or shape) of the neuron – *but the report fails to specify these details.*

Neural interpretation of attention

'Premotor (or visuomotor) theory of attention'

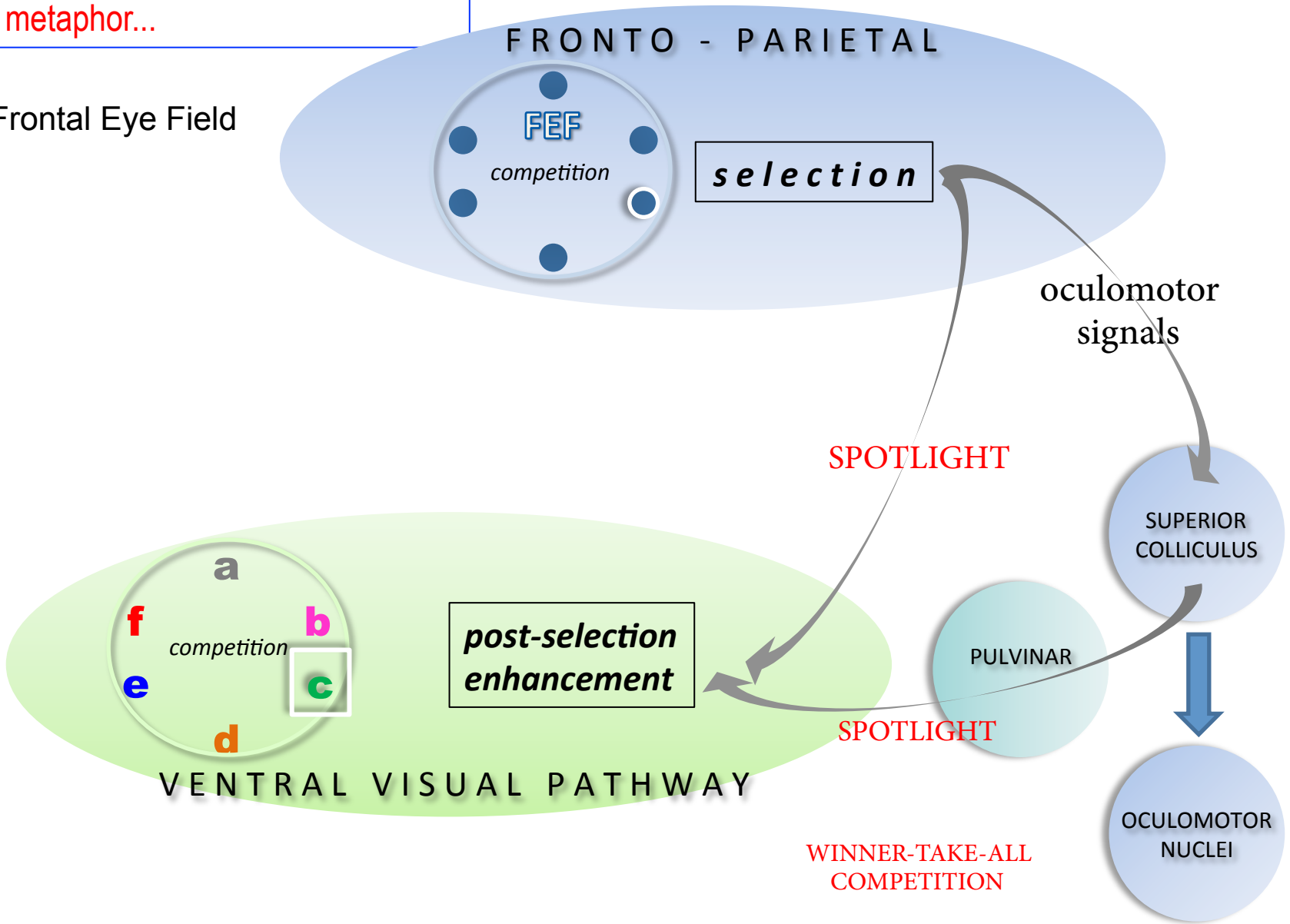
FEF – Frontal Eye Field



Neural interpretation of attention

'Premotor (or visuomotor) theory of attention'
...'spotlight' metaphor...

FEF – Frontal Eye Field



The ‘premotor’ (or visuomotor) theory of attention

The focus of spatial attention can be shifted without moving the eyes - sometimes referred to as the ‘mind’s eye’ or the ‘spotlight’ of attention.

Attending to a location other than the fixation point is known as ‘covert attention’.

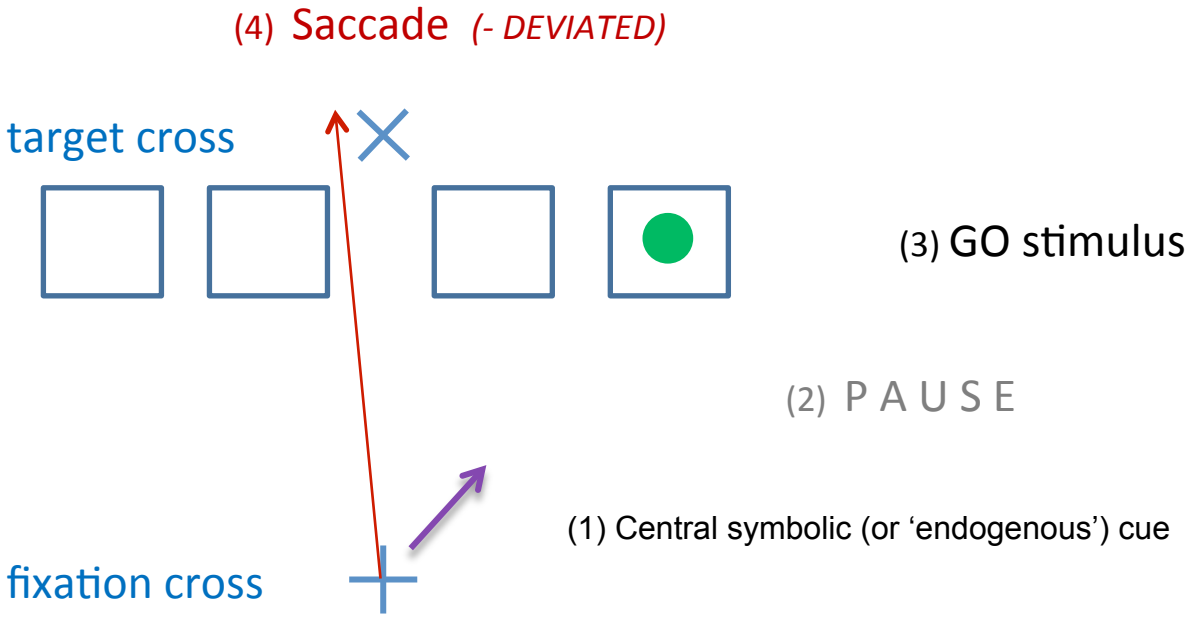
The premotor theory holds that the neural apparatus for shifting attention overlaps extensively with the forebrain oculomotor centres.

Evidence from:

1. Psychophysics (human)
2. Functional imaging (human)
3. Neurophysiology of FEF neurons (macaque)
4. Stimulation of FEF

Sheliga, Rizzolatti *et al.* (1994) Evidence from deviated eye movements [REF 6]

Evidence from:
1. Psychophysics (human)
2. Functional imaging (human & macaque)
3. Neurophysiology of FEF neurons (macaque)
4. Stimulation of FEF



TASK:
Task is to saccade from fixation to target cross when instructed by GO stimulus appearing in 1 of 4 boxes; location of GO stimulus is revealed in advance by an arrow cue.

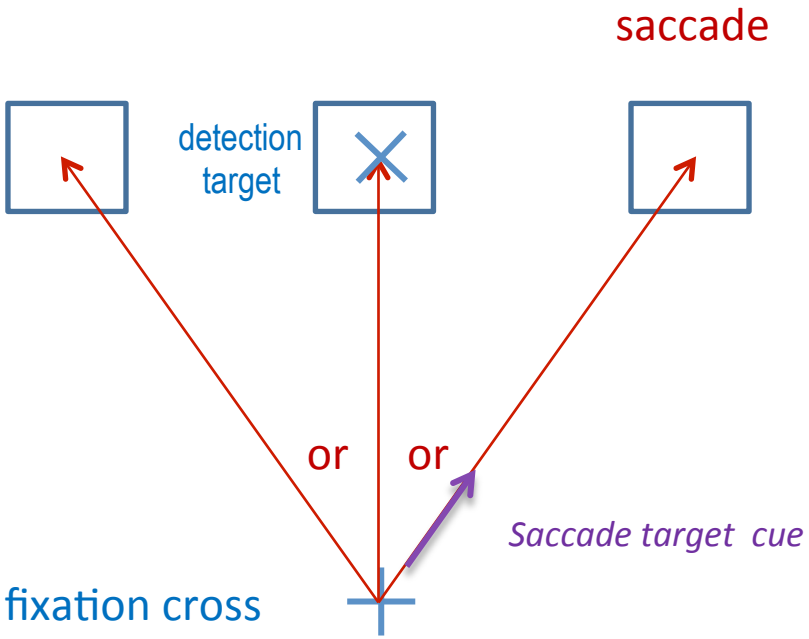
RESULT:
saccades deviate into hemifield contralateral to GO stimulus.

CONCLUSION:
"Allocation of spatial attention leads to an activation of oculomotor circuits, in spite of eye immobility".
i.e. covert attention involves a saccade plan, even though there is never a conscious intention to look directly at the GO cue.

RATIONALE:
Period of spatial attention to predicted GO stimulus location habituates neurons (e.g. in FEF or SC) that are also involved in controlling saccades. When the saccade is instructed, neural population activity is subtly altered, producing a modest error in trajectory.

Kowler *et al.* (1995) Evidence from impairment of target detection by saccade planning [REF 5]

Evidence from:
1. Psychophysics (human)
2. Functional imaging (human)
3. Neurophysiology of FEF neurons (macaque)
4. Stimulation of FEF (macaque & human)



TASK:
Task is to saccade from fixation to a prespecified location when instructed by an auditory 'GO' cue; also to detect a stimulus presented briefly beforehand, at same or different location to saccade target.

RESULT:
Detection performance is better when detection target is in same location as saccade target.

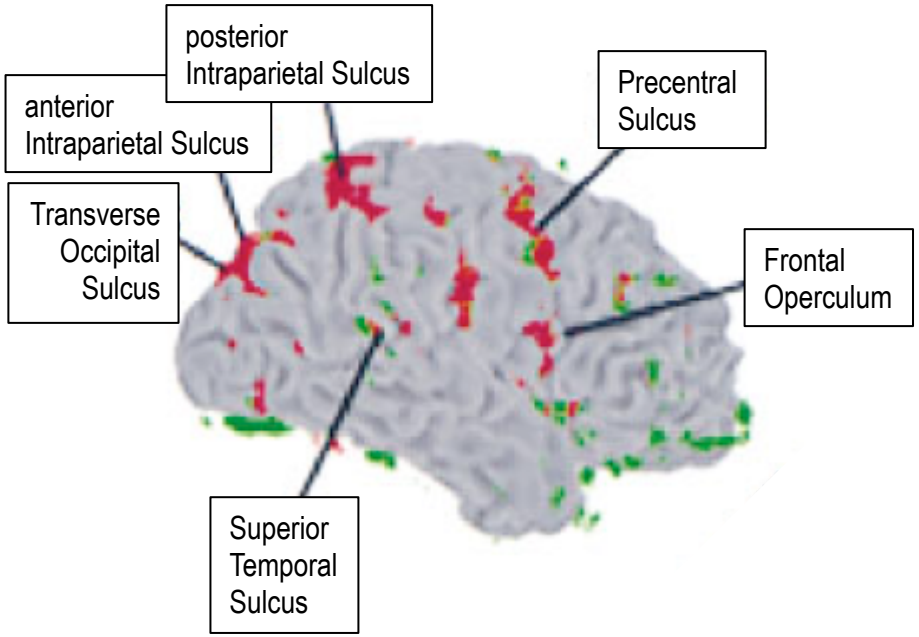
CONCLUSION:
"subjects cannot move their eyes to one location and attend to a different one".

RATIONALE:
The neuronal activity planning the saccade also determines the location of a covert focus of attention.

Corbetta *et al.* (1998) human fMRI reveals a common functional network for eye movements & shifting attention [REF 7]

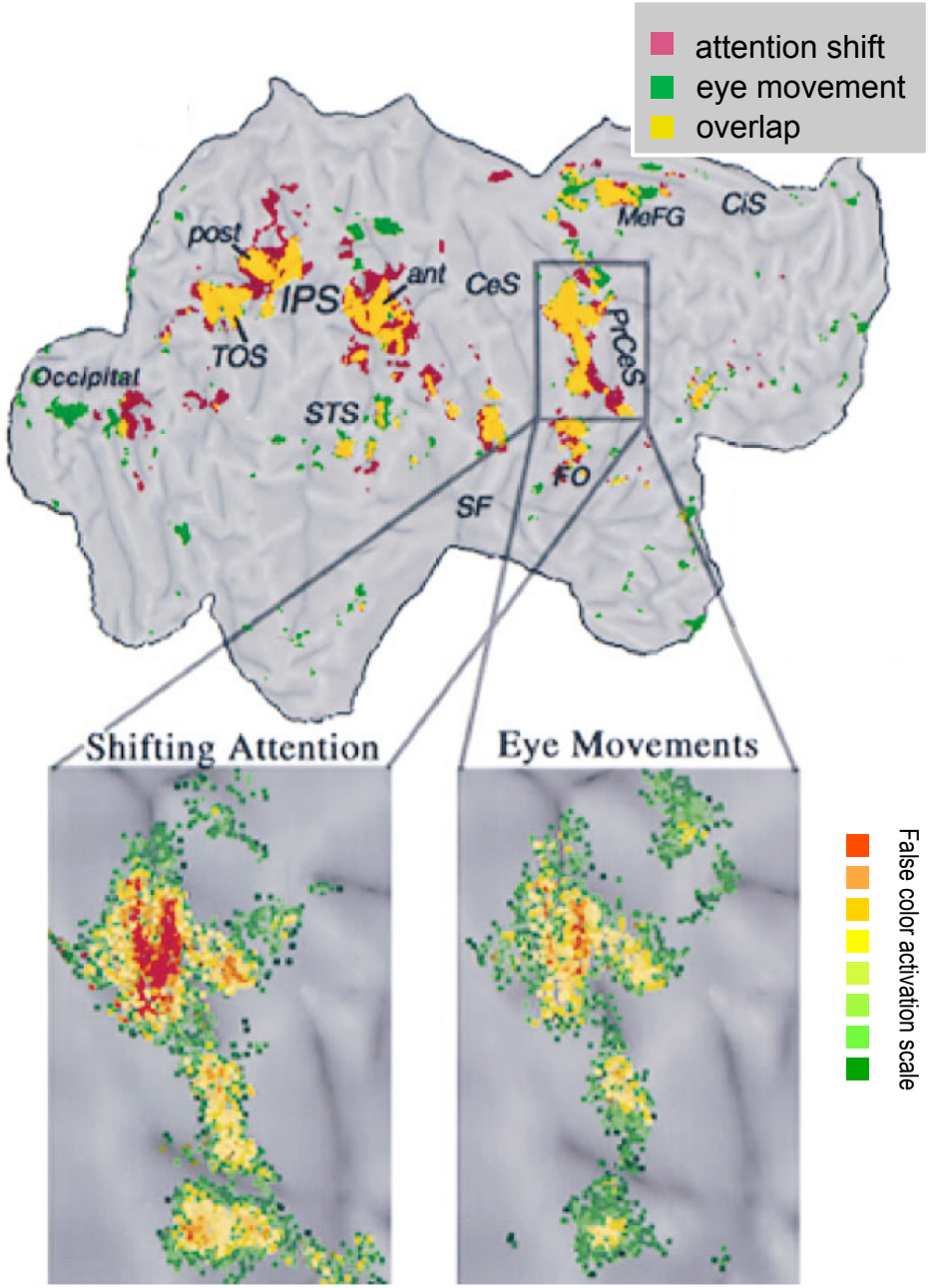
Evidence from:
1. Psychophysics (human)
2. Functional imaging (human)
3. Neurophysiology of FEF neurons (macaque)
4. Stimulation of FEF (macaque & human)

Data from right hemisphere of one subject



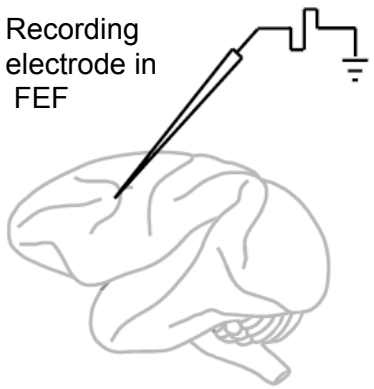
Attention shift task: to detect a series of stimuli along horizontal meridian whilst maintaining fixation (= covert attention);

Eye movement task: to detect the same sequence of stimuli, with eye movements now permitted (= overt attention).



Evidence from:
1. Psychophysics (human)
2. Functional imaging (human)
3. Neurophysiology of FEF neurons (macaque)
4. Stimulation of FEF (macaque & human)

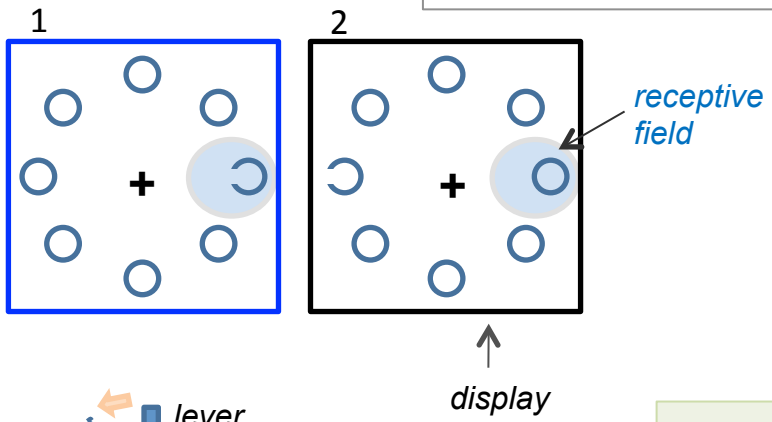
Thompson *et al.* (2005) "Neuronal Basis of Covert Spatial Attention in the Frontal Eye Field (FEF)" [REF 8]

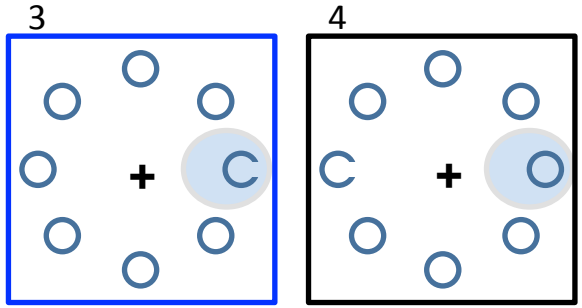


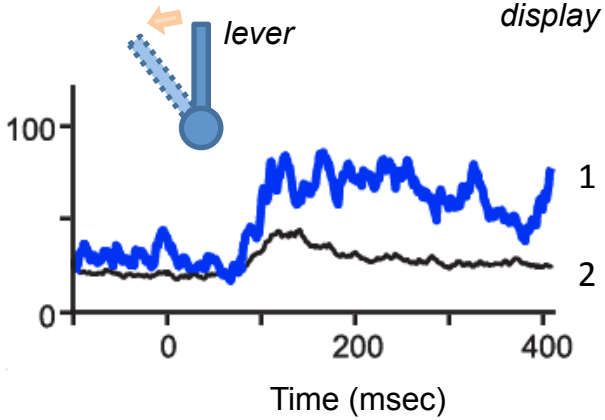
TASK:
1. Fixate central cross;
2. Locate C shape (but do not move eyes);
3. Keep fixating !
4. Pull lever right for C & left for Ↄ.

RESULT
A typical FEF neuron shows an enhanced response when the macaque is attending a target (C or Ↄ) located within its receptive field, *despite having no intention to move the eyes*.

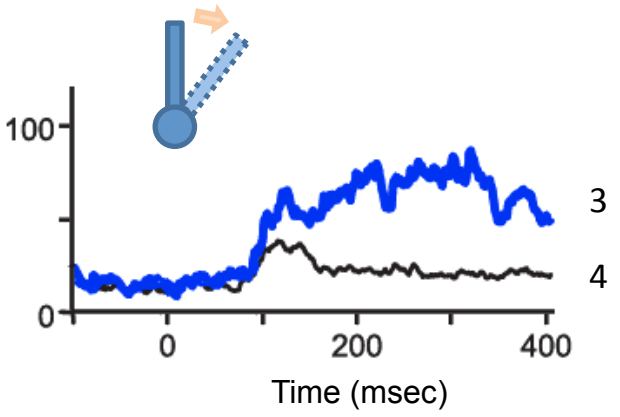
CONCLUSION
"We propose that spatially selective activity in FEF visually responsive neurons corresponds to the mental spotlight of attention…"







HOW THE NEURON WITH THE RECEPTIVE FIELD ILLUSTRATED RESPONDS IN TRIALS WITH 4 DIFFERENT DISPLAYS – (2 REQUIRING LEFT LEVER PULL & 2 RIGHT LEVER PULL)



Evidence from:
1. Psychophysics (human)
2. Functional imaging (human)
3. Neurophysiology of FEF neurons (macaque)
4. Stimulation of FEF (macaque & human)

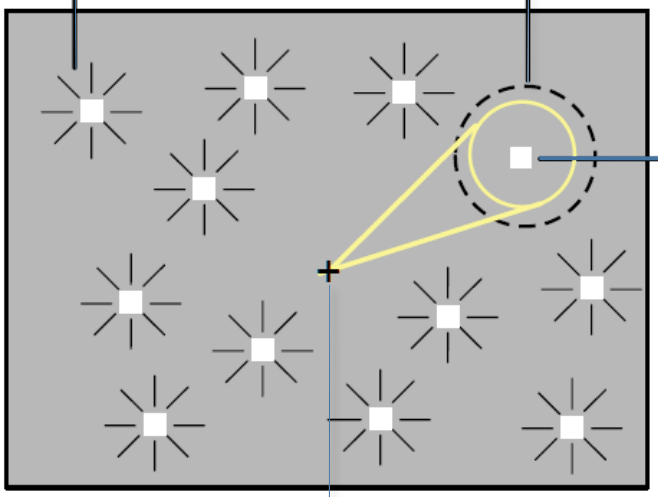
Moore & Fallah (2004) Effect of FEF microstimulation on visual attention [REF 9]

Superthreshold stimulation of FEF causes a saccade.

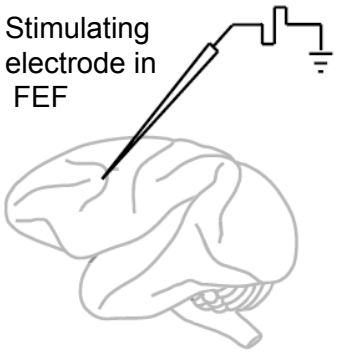
Subthreshold stimulation of FEF enhances detection of dimming (- i.e. enables successful detection of smaller intensity changes): appears to boost spatial attention at locus of movement field.

Distractor:
A flashing light jumping between multiple screen locations.

Movement field:
superthreshold stimulation of FEF elicits saccade to this location on screen.

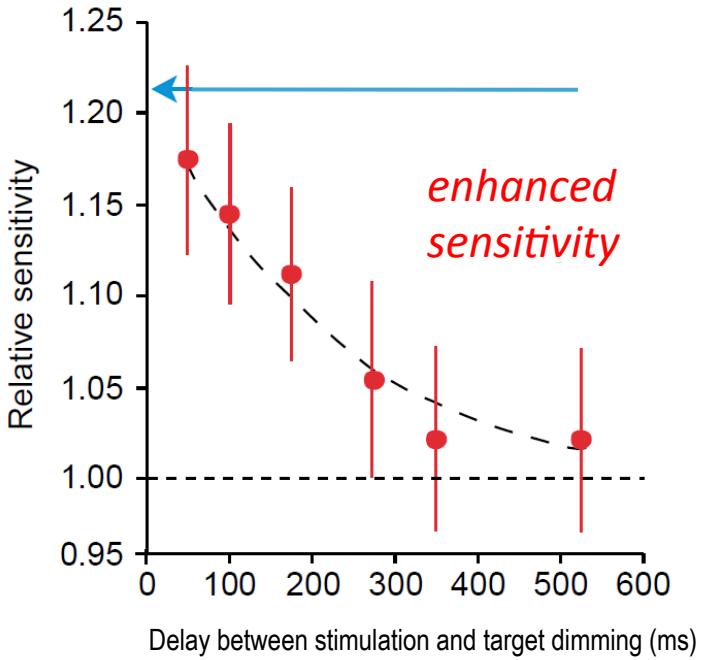


Target:
Is placed at location of movement field;
- task is to detect when target dims. Sensitivity measured by smallest detectable change in intensity.



Macaque:
fixates central cross, but applies 'spotlight' of attention to the target.

Stimulation of FEF precedes target dimming



KEY:

Performance without distractors or stimulation

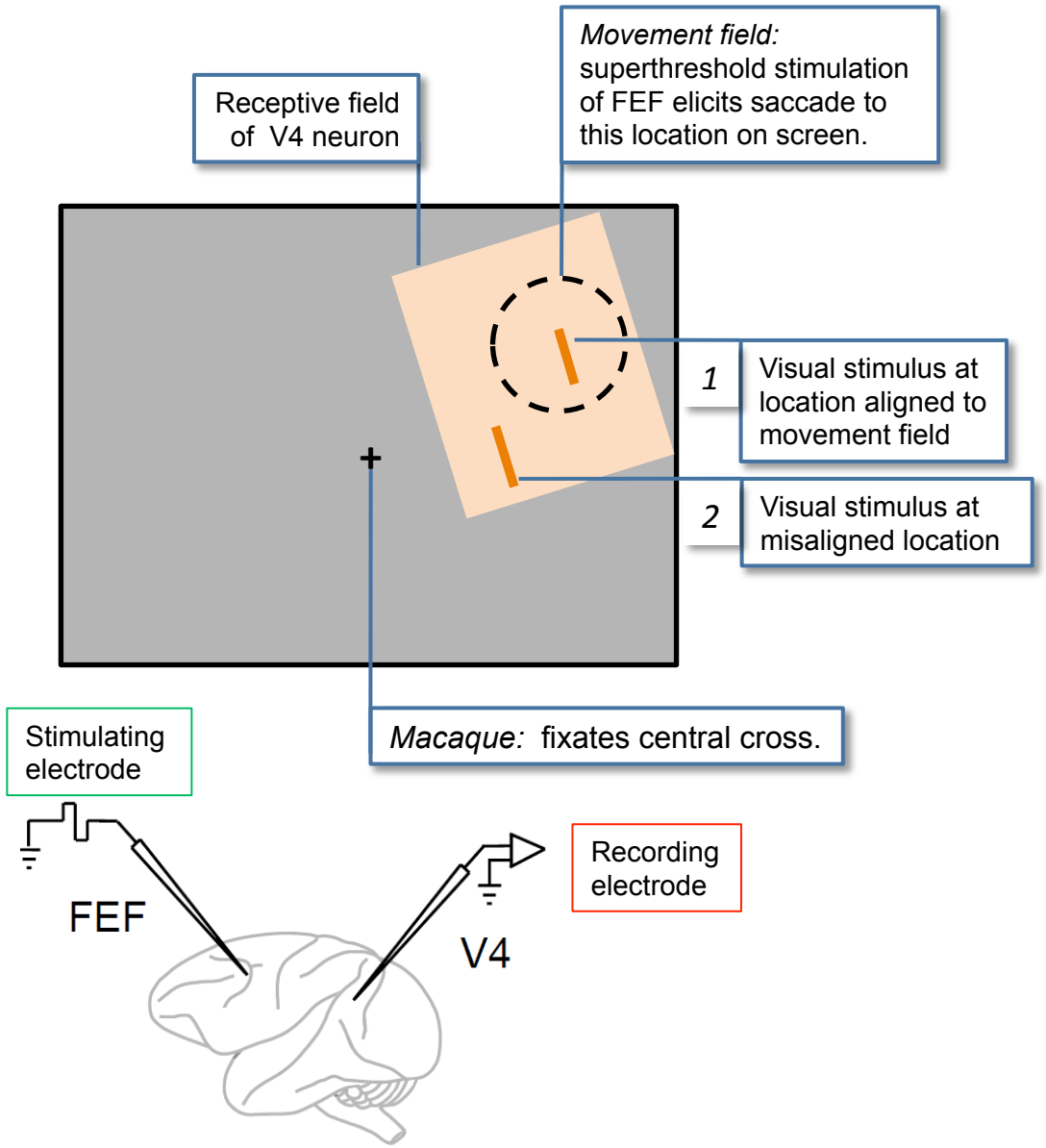
Performance with stimulation

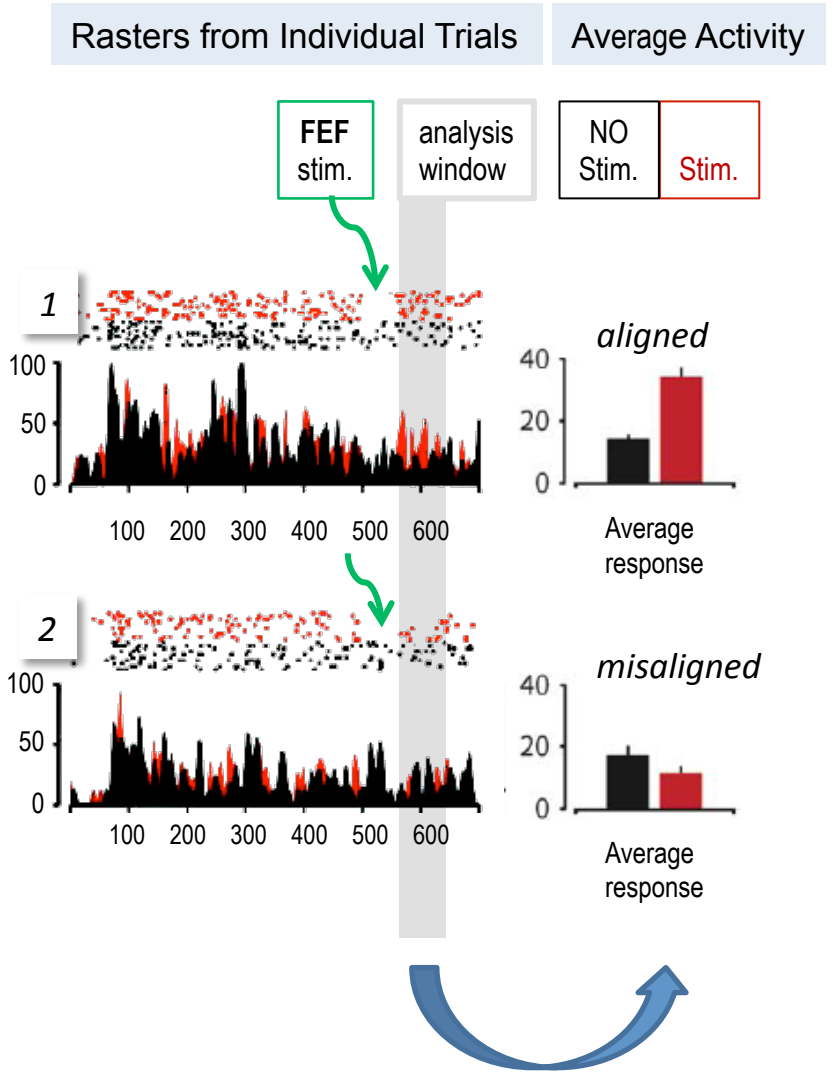
Performance without stimulation

Armstrong, Moore *et al.* (2006) Effect of FEF microstimulation on visual activity in area V4 [REF 10]

Evidence from:
1. Psychophysics (human)
2. Functional imaging (human)
3. Neurophysiology of FEF neurons (macaque)
4. Stimulation of FEF (macaque & human)

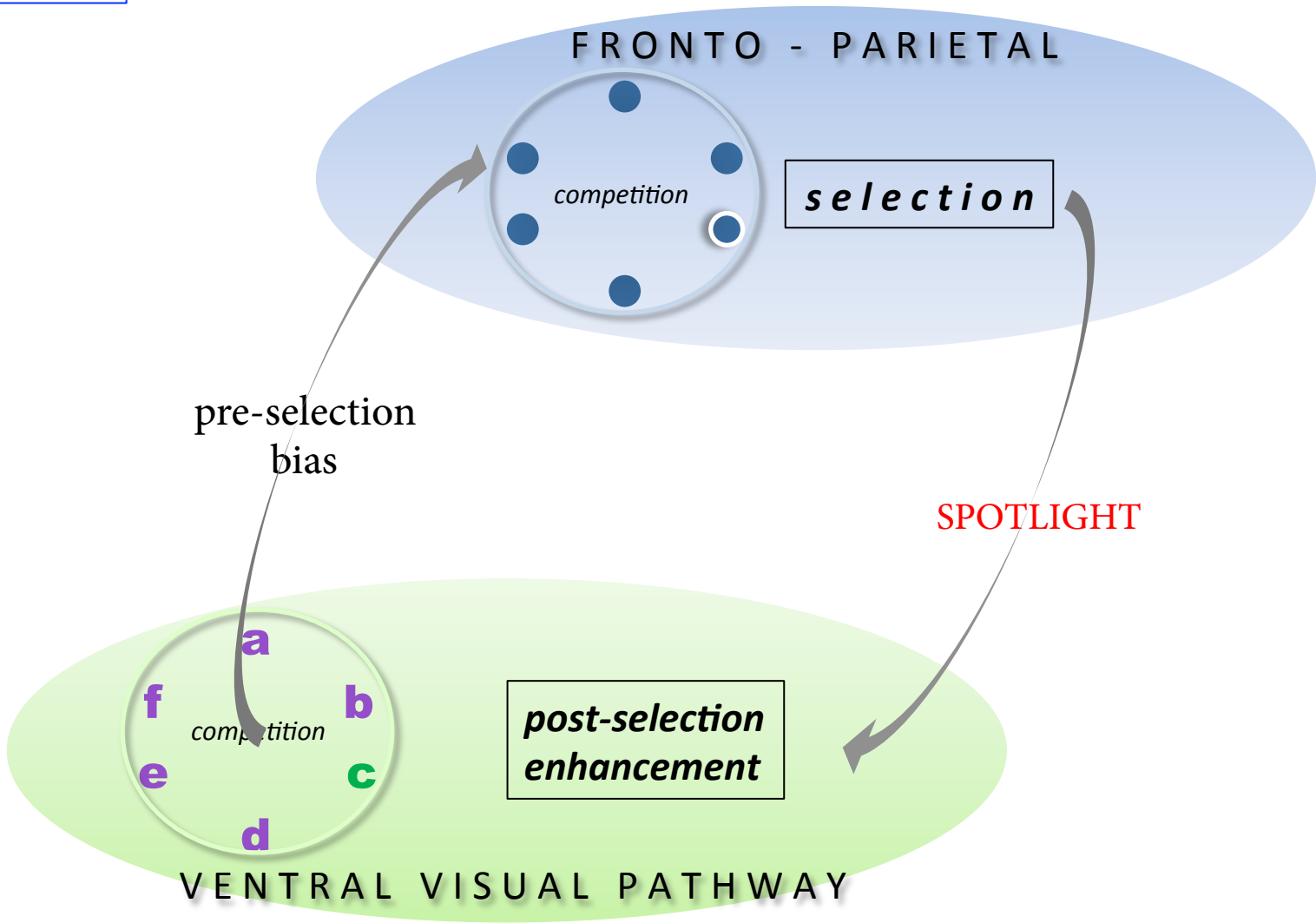
Subthreshold stimulation of FEF enhances response of V4 neuron to stimulus aligned with movement field of FEF neuron.





Neural interpretation of attention

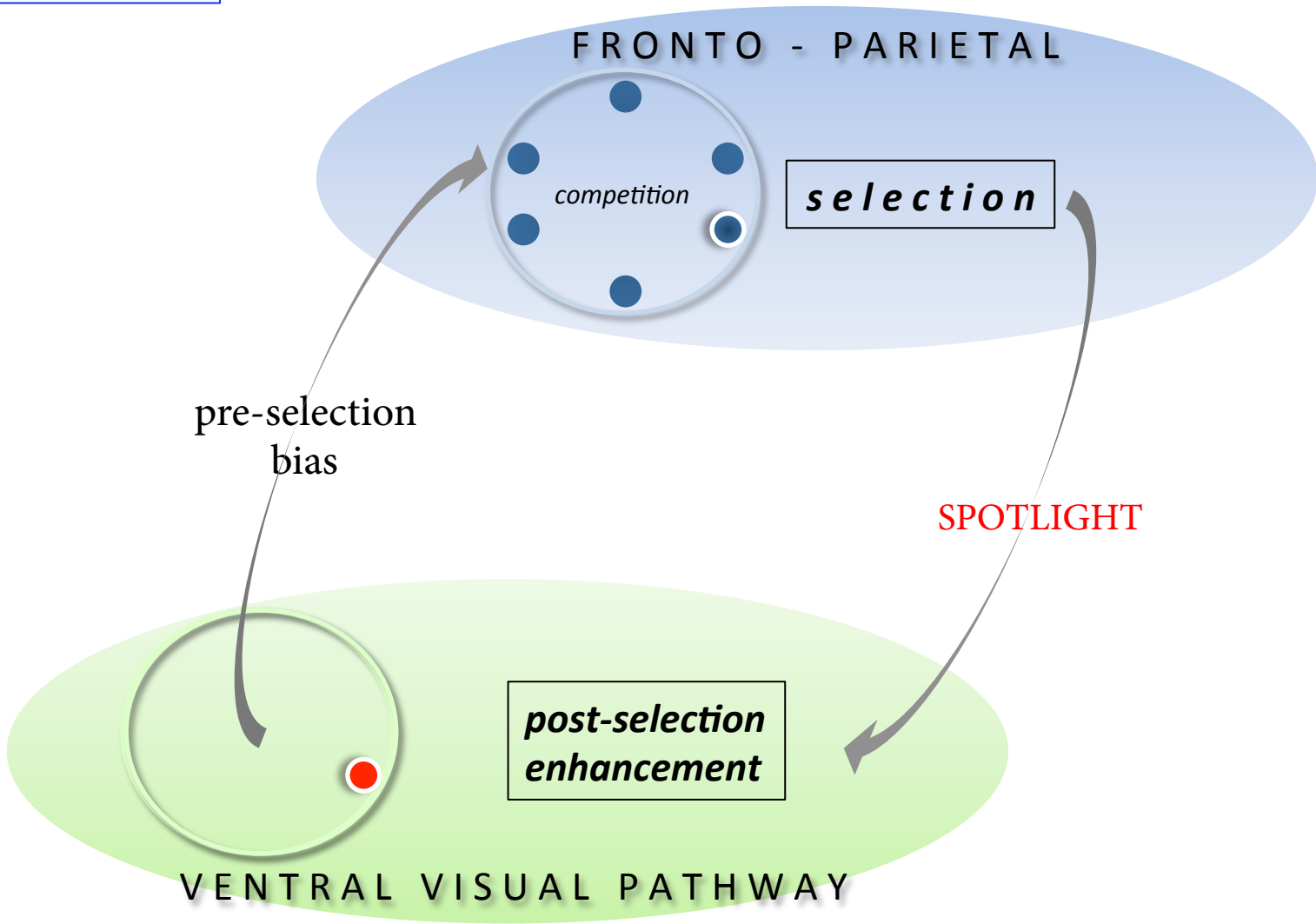
Spatial attention



A salient stimulus draws attention to itself;

Neural interpretation of attention

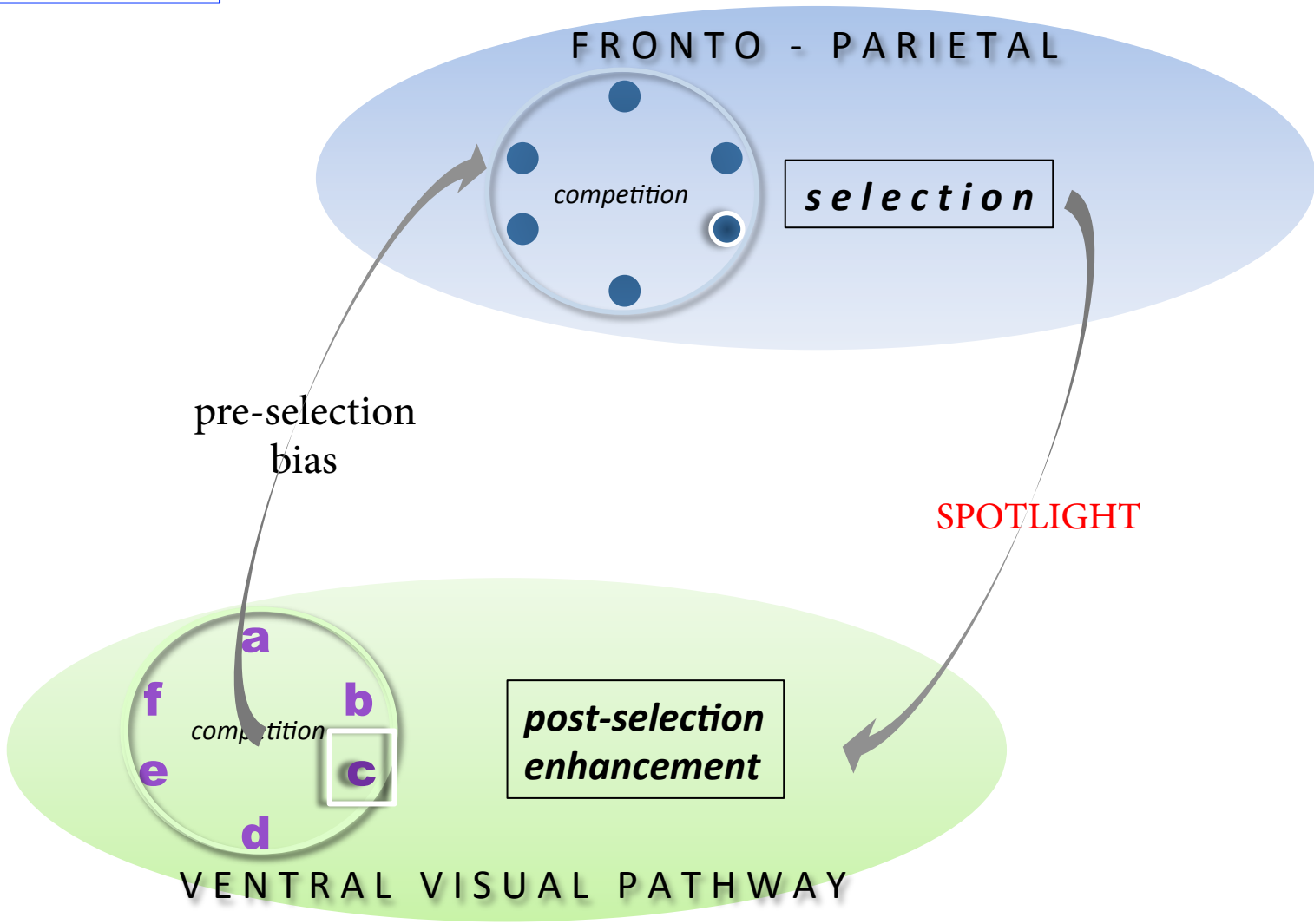
Spatial attention - cue



A transient cue draws attention to its location...

Neural interpretation of attention

Spatial attention - cue

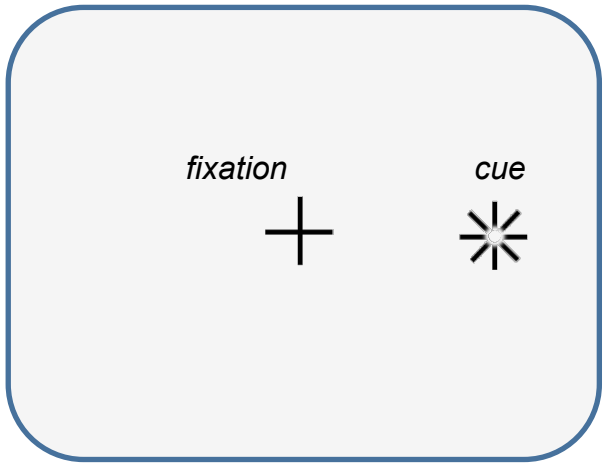


A transient cue draws attention to its location... and to a subsequent item at that location

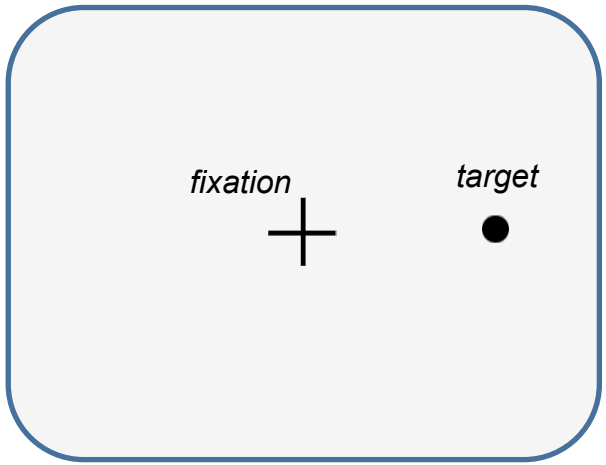
The Posner Task - a basic demonstration of spatial attention (in human or macaque) [REF 11]

Valid trial

SCREEN 1 - VALID CUE



SCREEN 2 - TARGET



Task:

1. Fixate;
2. Notice cue;
3. Maintain fixation;
4. Respond to appearance of target as quickly as possible.

Variables:

1. % valid & % invalid cues;
2. Cue-target interval (msec).

Result:

1. Reaction time (RT) is slower in trials with an invalid cue.
2. $RT_{invalid} - RT_{valid}$ measures the differential effect of spatial attention.
3. The cue may be invalid statistically (%valid = % invalid).

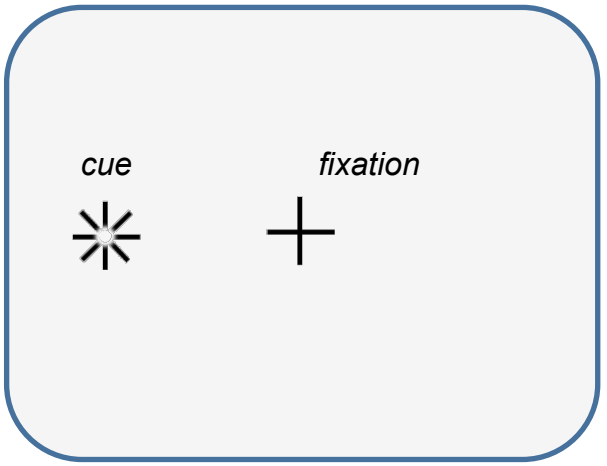
Conclusion:

1. It is possible to attend to a void location in space;
2. Such spatial attention heightens visibility and speeds reaction time; attending elsewhere slows reaction time.
3. Implies a 'reflexive' effect.

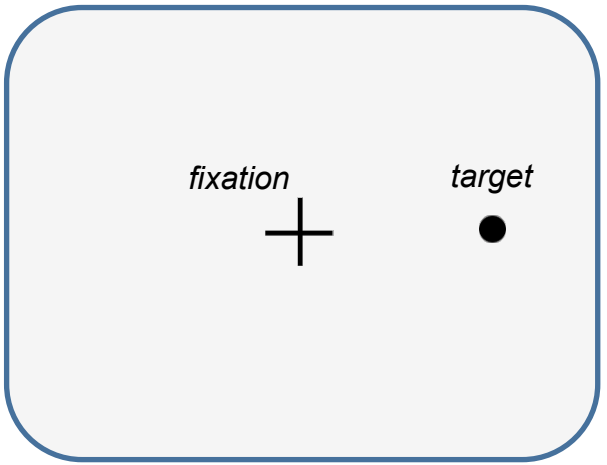
= 'exogenously' cued attention

Invalid trial

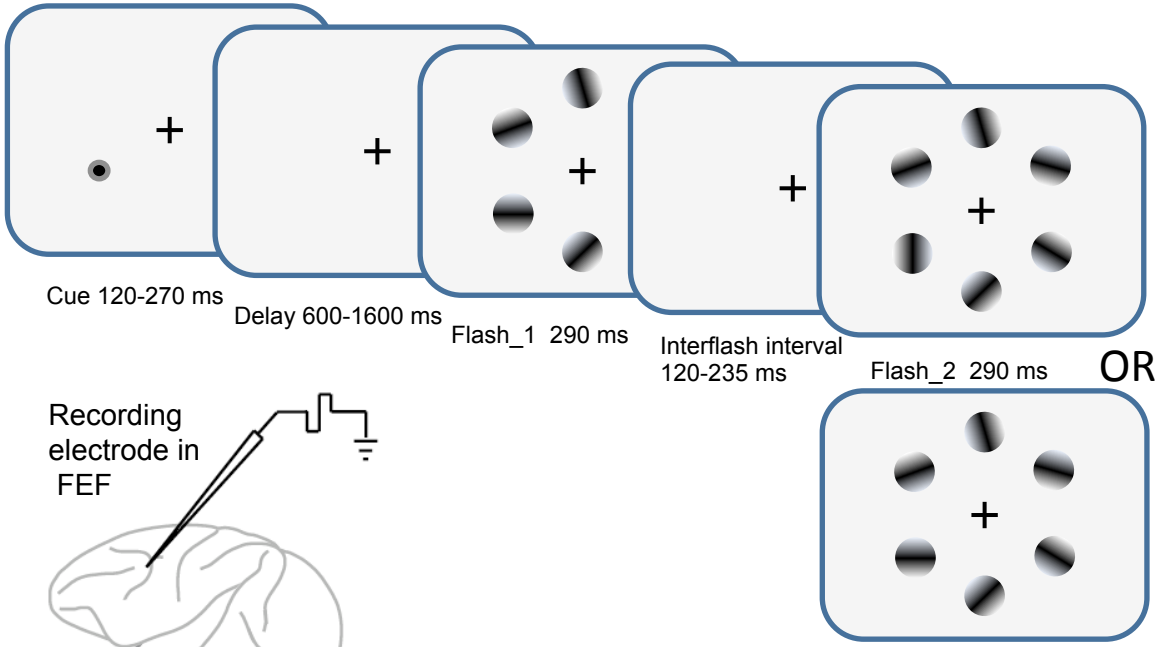
SCREEN 1 - INVALID CUE

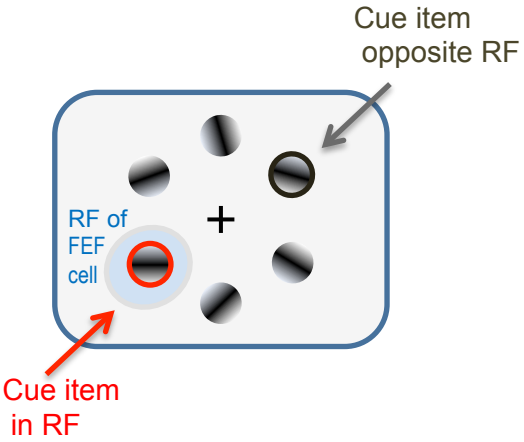


SCREEN 2 - TARGET



Armstrong *et al.* (2009)[REF 12] Cued spatial attention in FEF in a 'change-detection' task

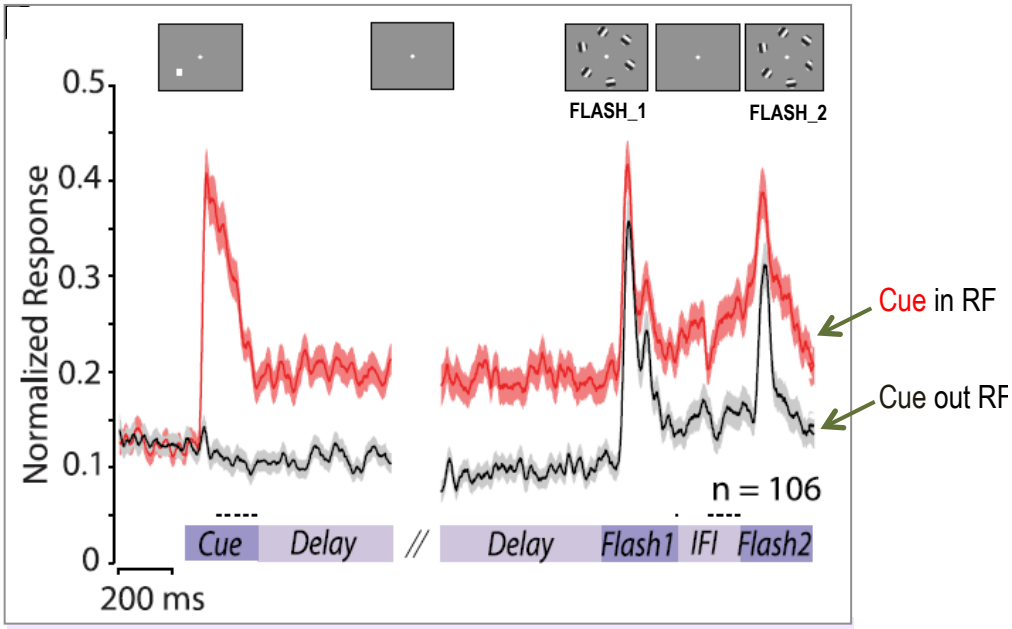




Task:
Detect change at cue location (on 50% of trials).
Respond using lever.

Observe:
Cued FEF neurons retain elevated activity throughout each trial.

Conclude:
Persistent activity in FEF corresponds to spatial attention, acting to select the task-relevant stimulus on appearance.

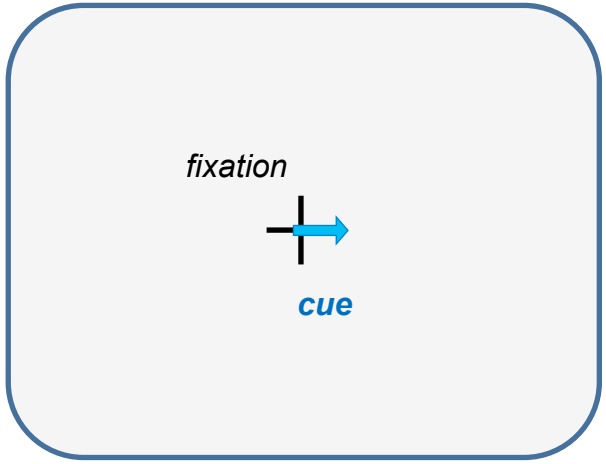


Comparison of average neural activity in the two cue conditions

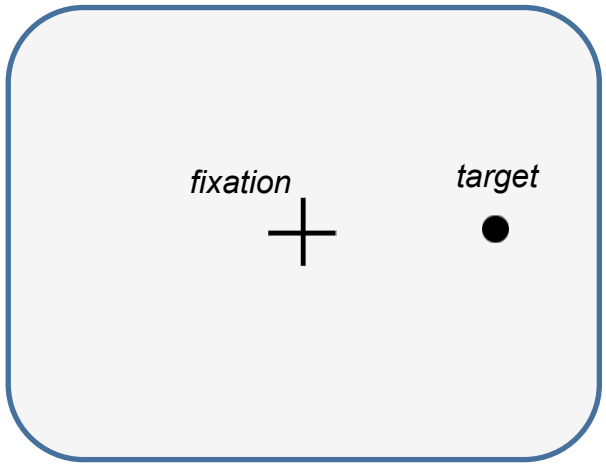
The Posner Task - a basic demonstration of spatial attention (in human or macaque) [REF 11]

Valid trial

SCREEN 1 – VALID ***SYMBOLIC*** *CUE*



SCREEN 2 - TARGET



Task:

1. Fixate;
2. Notice cue;
3. Maintain fixation;
4. Respond to appearance of target as quickly as possible.

Variables:

1. % valid & % invalid cues;
2. Cue-target interval (msec).

Result:

1. Reaction time (RT) is slower in trials with an invalid cue.
2. $RT_{invalid} - RT_{valid}$ measures the differential effect of spatial attention.
3. Cue must be valid statistically (% valid >> % invalid).

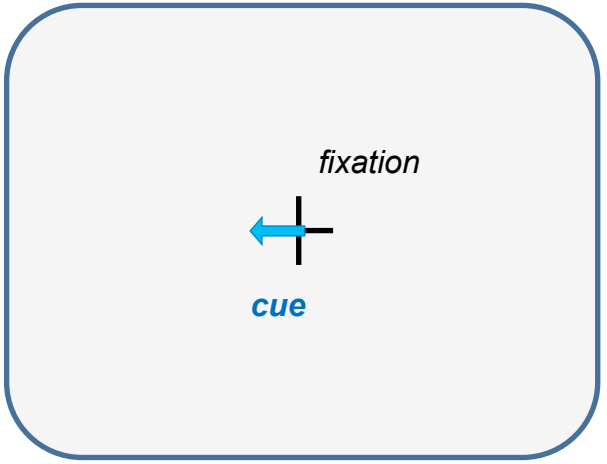
Conclusion:

1. It is possible to attend to a void location in space;
2. Such spatial attention heightens visibility and speeds reaction time; attending elsewhere slows reaction time.
3. Implies a 'cognitive' effect.

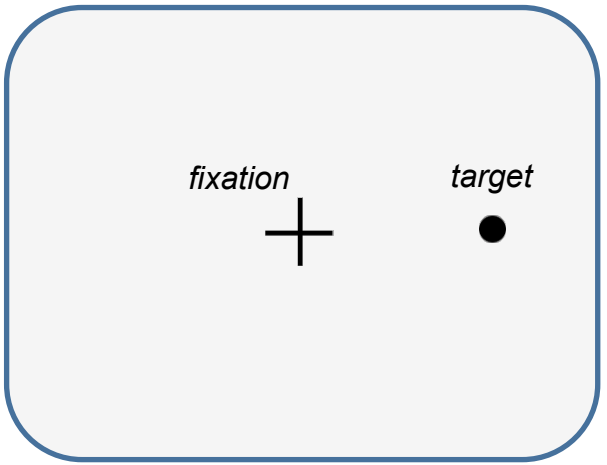
= 'endogenously' cued attention

Invalid trial

SCREEN 1 – INVALID ***SYMBOLIC*** *CUE*

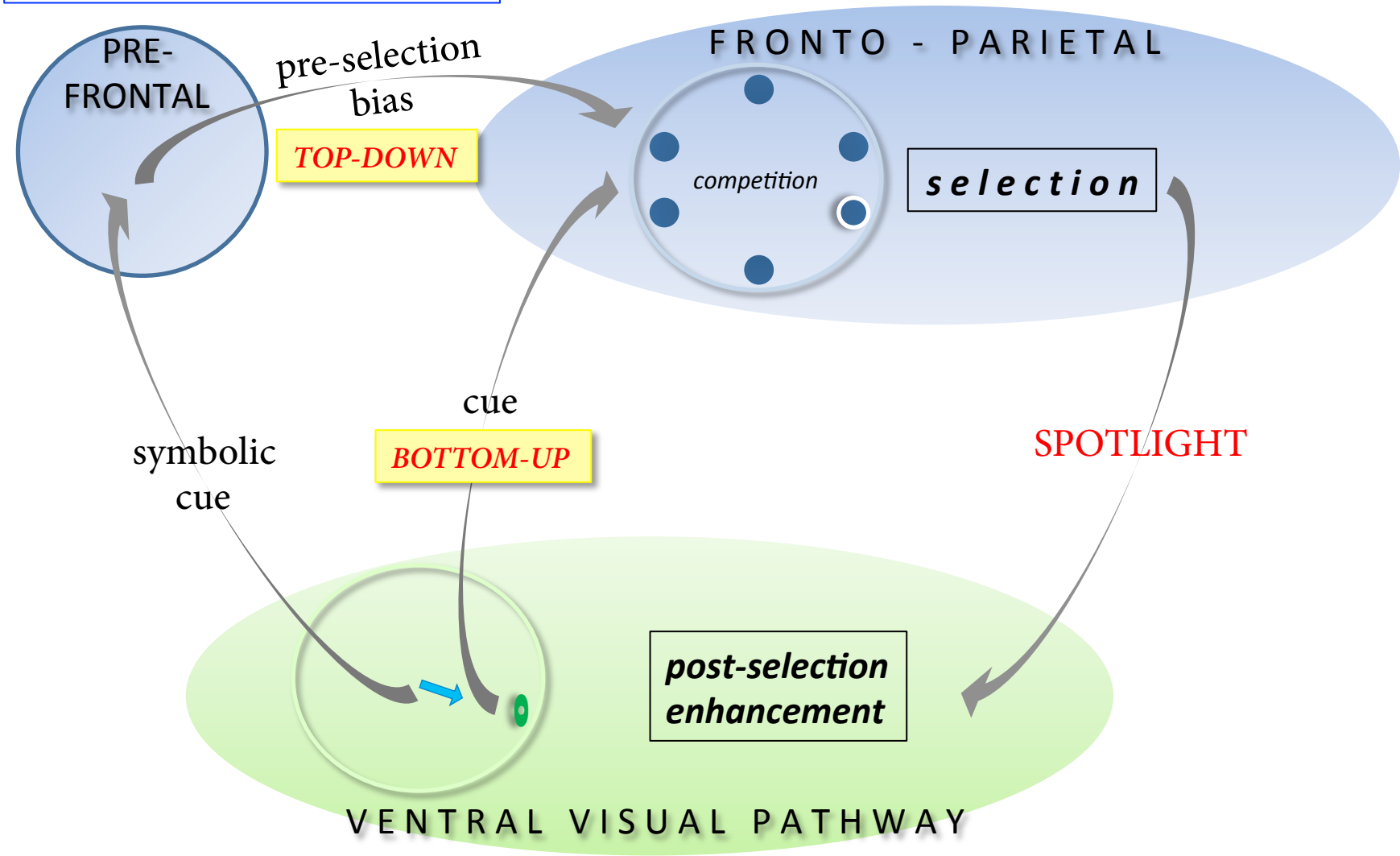


SCREEN 2 - TARGET

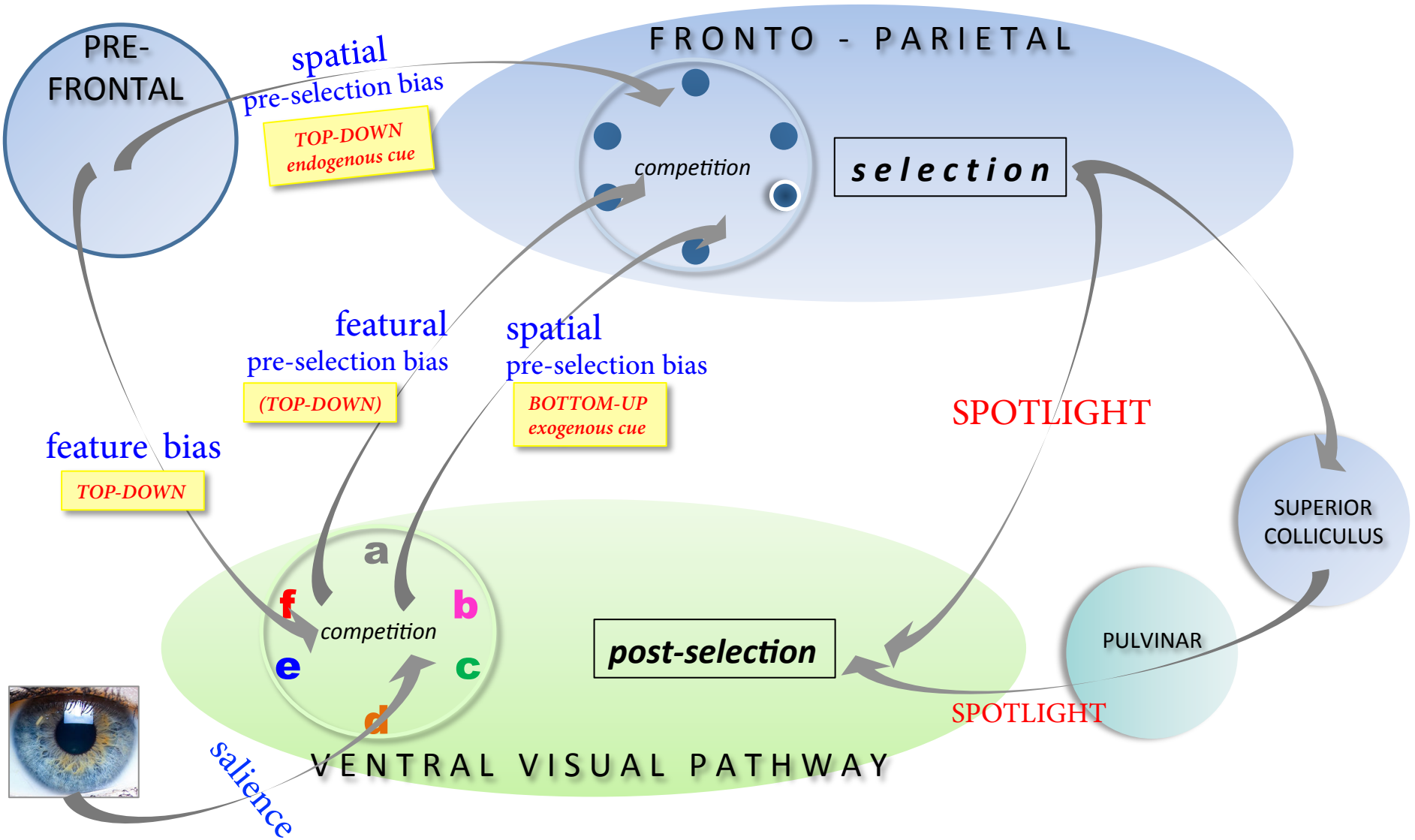


Neural interpretation of attention

'spatial attention' - summary



Neural interpretation of attention: *triple pre-selective 'radar'*



What is the effect of attentional selection ?

NEURALLY:

- Enhanced activity of neurons representing selected item;
- Object attention
  (Enhancement spreads to representations of all the features of the attended object);
- Enhanced network synchronisation of neural representation;

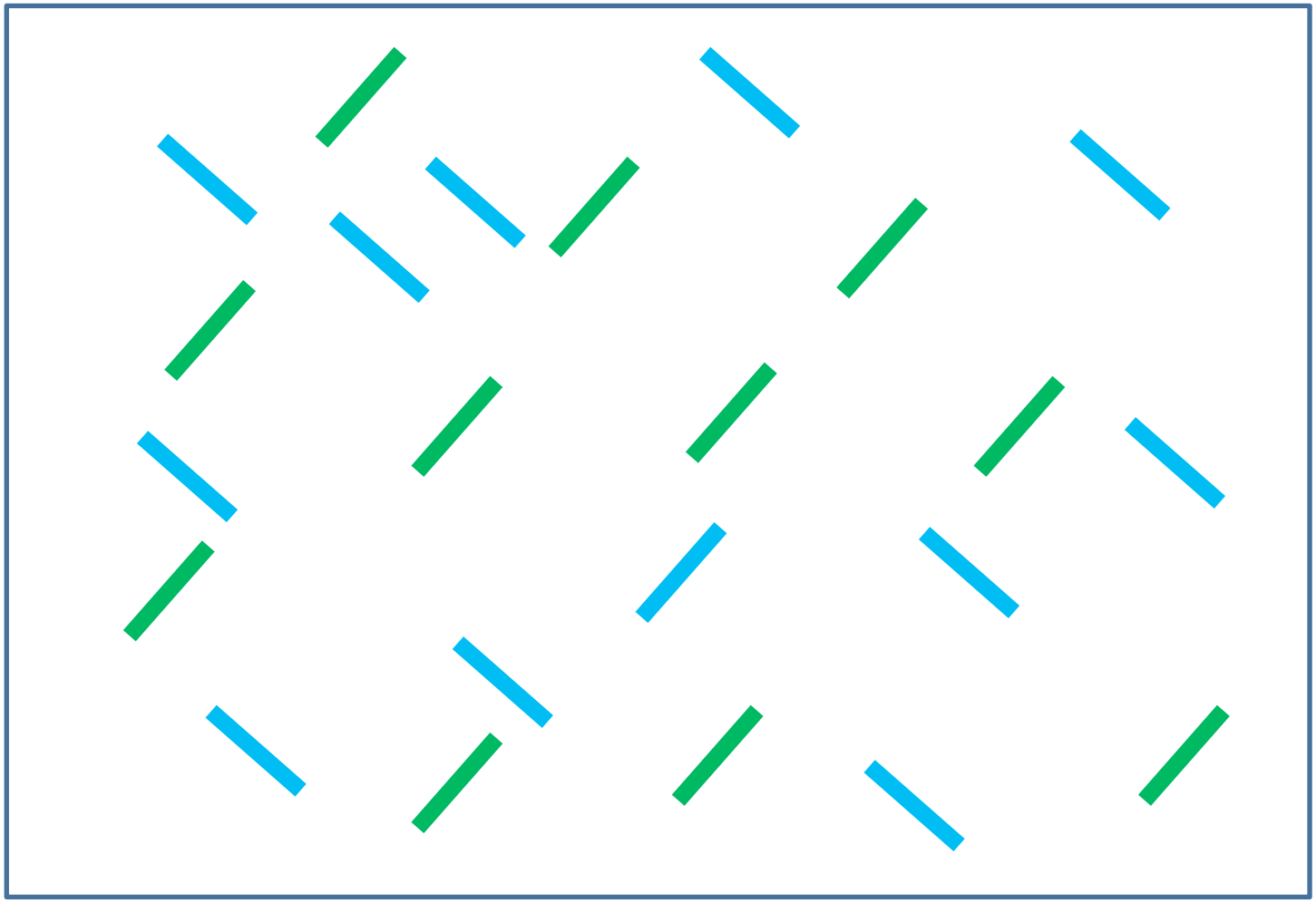
PERCEPTUALLY:

- Noticing items in a scene; the capacity to report what has been seen.
  (e.g. as demonstrated by 'change blindness' & 'inattentive blindness')
- Binding.

Change Blindness: Demonstration

Casual viewing provides the ‘gist’ of a scene;
- attention is required to appreciate details.

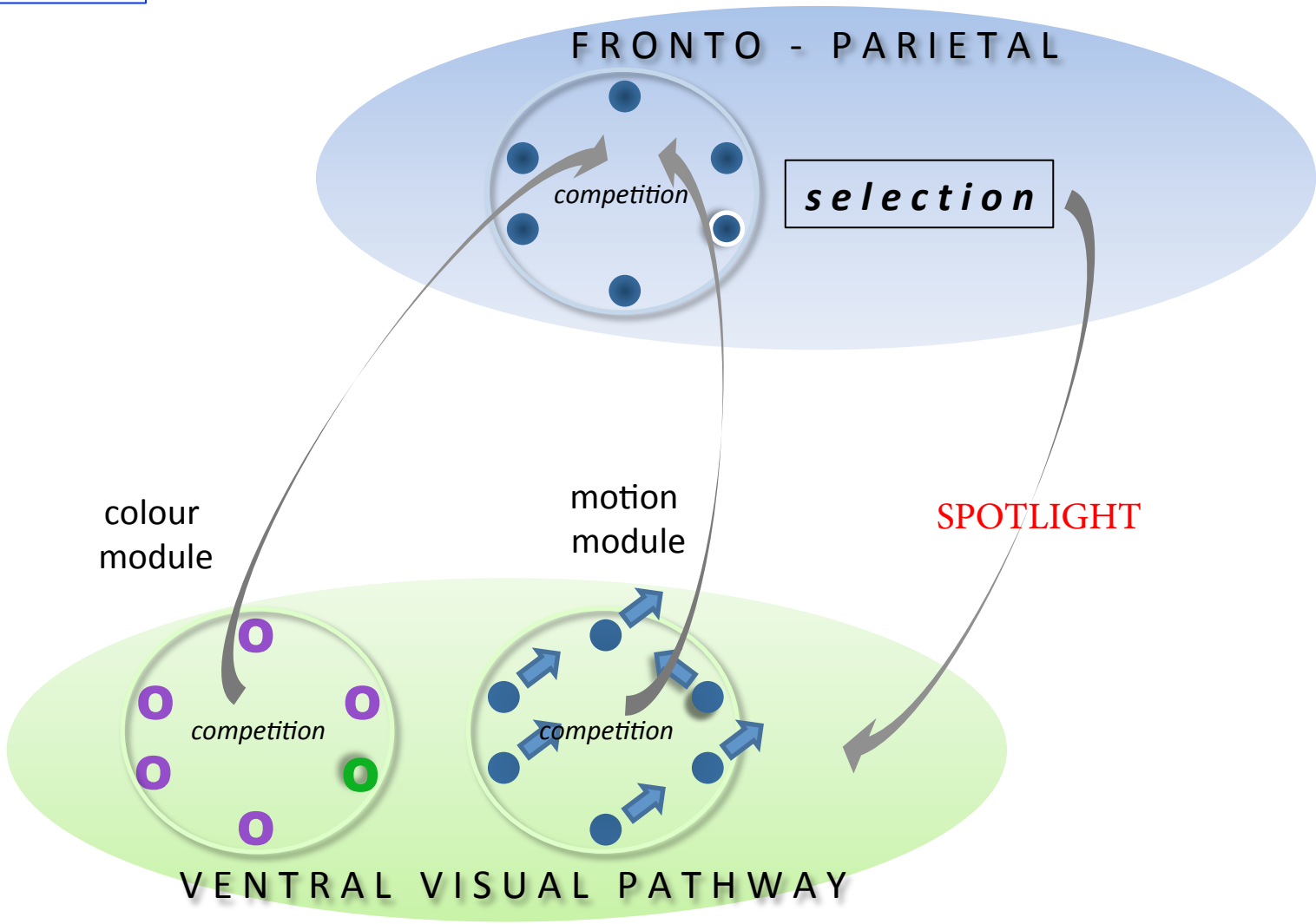
Conjunction search task



Here, the odd-one-out item is defined by a unique combination of features. It does not pop-out perceptually, but can only be found by scrutinising each item in turn (known as a 'serial search'). This implies that attention is necessary for 'binding', i.e. for awareness of what features are combined in each item individually.

Neural interpretation of attention

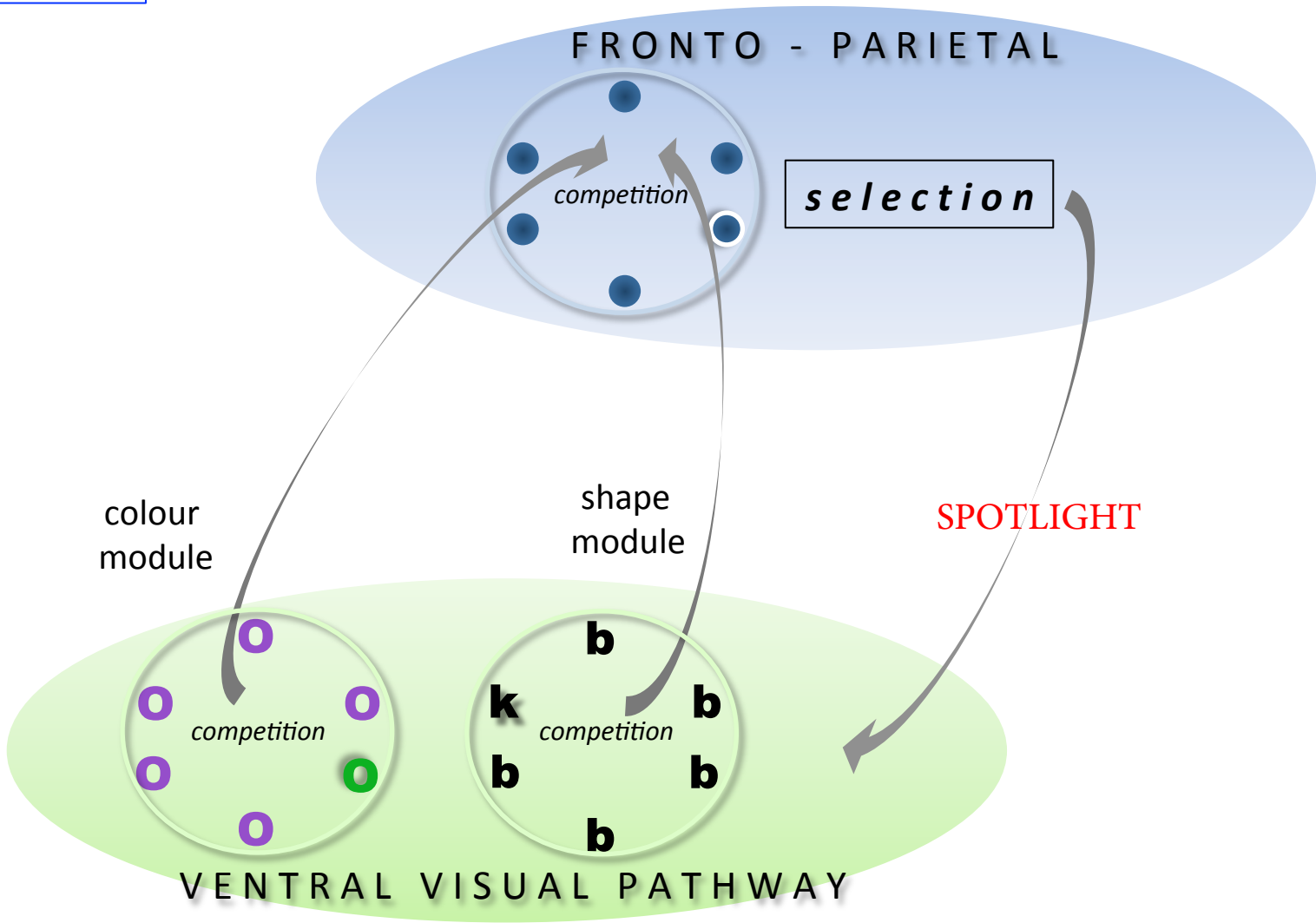
'Object' attention



The salient item(s) in each feature map/module may not be concordant; *e.g. colour v. motion.*

Neural interpretation of attention

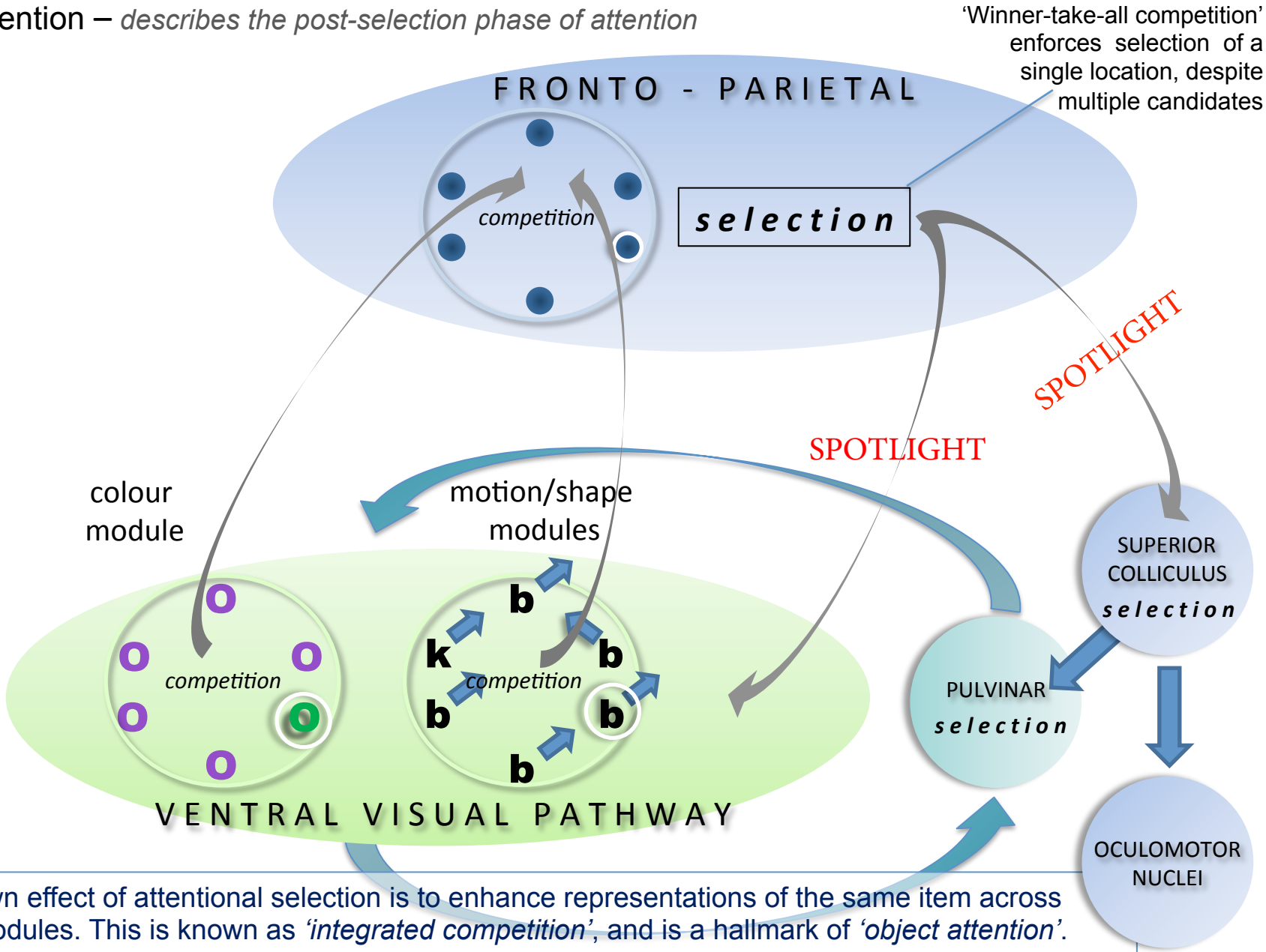
'Object' attention



The salient item(s) in each feature map/module may not be concordant; *e.g. colour v. shape.*

Neural interpretation of attention

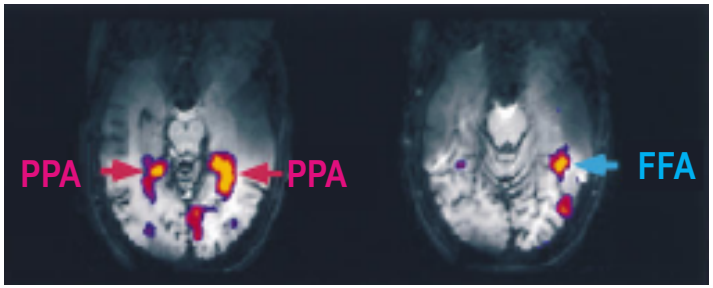
'Object' attention – *describes the post-selection phase of attention*



The top-down effect of attentional selection is to enhance representations of the same item across all maps/modules. This is known as *'integrated competition'*, and is a hallmark of *'object attention'*. The relevant neural circuitry may include interactions with pulvinar, as well as frontoparietal cortex.

O'Craven *et al.* (1999) Human fMRI evidence for objects as the 'unit' of attention [REF 13]

face *or* house moves ⟷



PARAHIPPOCAMPAL PLACE AREA

FUSIFORM FACE AREA

Stimulus:
Static face & moving house; OR static house & moving face. A series of different examples is presented.

Task:
Attend house; or face; or motion: report 'repeats' within the attended category.

Observe:
(i) Face activates FFA; house activates PPA; motion activates V5. Each of these areas shows enhancement when its corresponding feature is attended.
But more importantly...
(ii) If attending house or face - relative activation of V5 depends on whether the attended face/house is moving or static;
(iii) If attending motion – relative activation of FFA & PPA depends on which is moving.

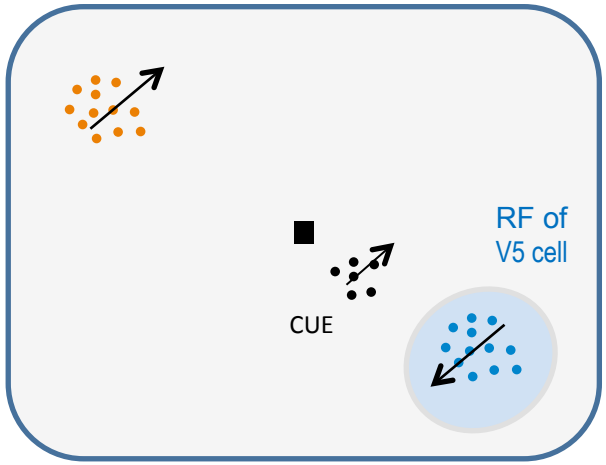
Conclusion:
In all conditions tested, attentional enhancement spreads to the task-irrelevant feature of the attended component of the image.

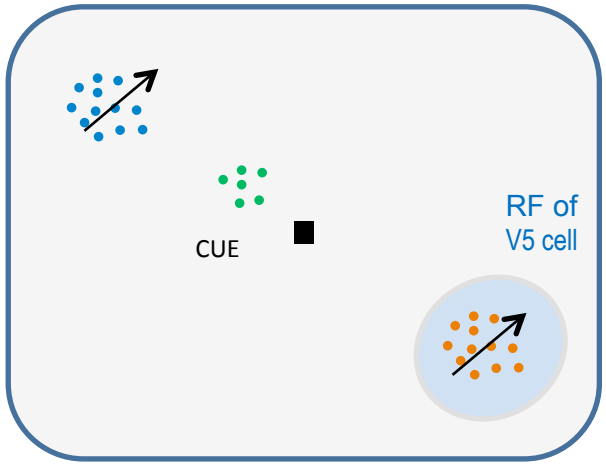
Interpretation:
The object becomes the 'unit' of selection, irrespective of whether attention has been directed to it because of a particular feature, or because of its location. The representations of all features of that object are enhanced within their respective feature-specific areas of cortex.

'Object-attention' describes the post-selection phase of attention.

Evidence for object attention: single unit physiology

Katzner *et al.* (2009) Transfer of feature enhancement in single neuron activity (area V5) [REF 15]





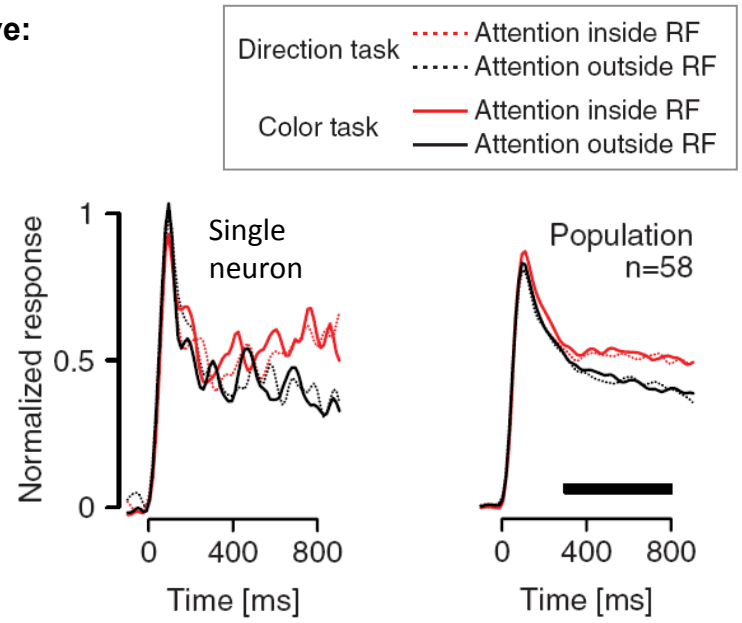
Task:

1. Fixate centre;
2. Cue instructs both location (top-left or lower-right) and feature dimension (i.e. motion or colour) to be attended;
3. Detect change in direction or change in colour, at top-left or lower-right location, as cued;
4. Hence, there are 4 variants of the task.

Stimuli:

1. Restricted to 2 colours & 2 directions of motion;
2. Always use preferred direction for stimulus within V5 test RF;
3. The outside RF stimulus may match in colour and/or direction, or neither.

Observe:



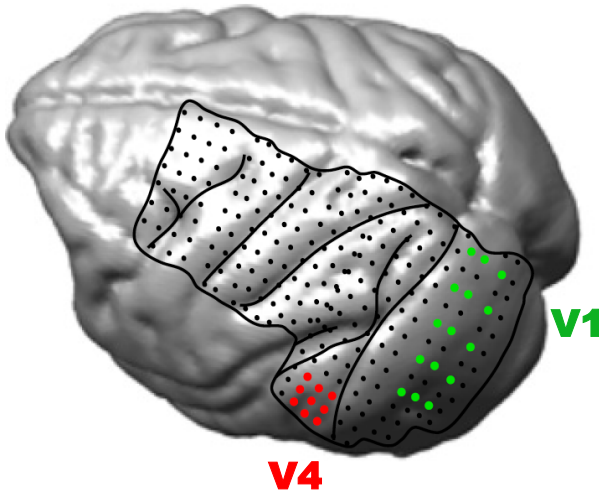
Conclusion:

1. Attentional enhancement is identical for motion- or colour-focussed attention;
2. The result is consistent with the concept of ***object attention.***

Bosman *et al.* (20012) The effect of attention: synchronisation between V1 and V4 [REF 16]

Task:

1. Fixate small grey square;
2. A change in colour of the fixation square is the cue to attend the grating of matching colour;
3. Maintain fixation whilst waiting to detect a change in the cued grating;
4. Respond manually when cued grating changes.

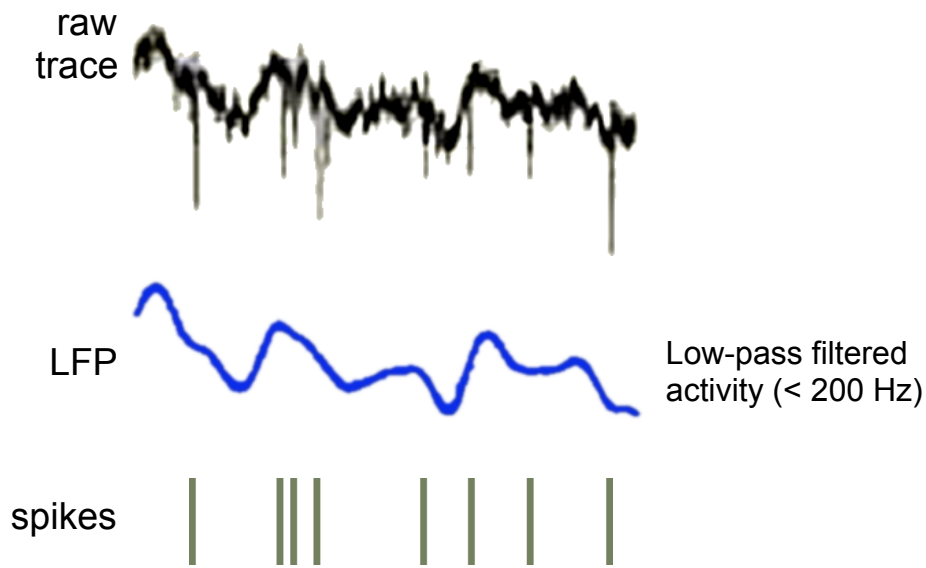


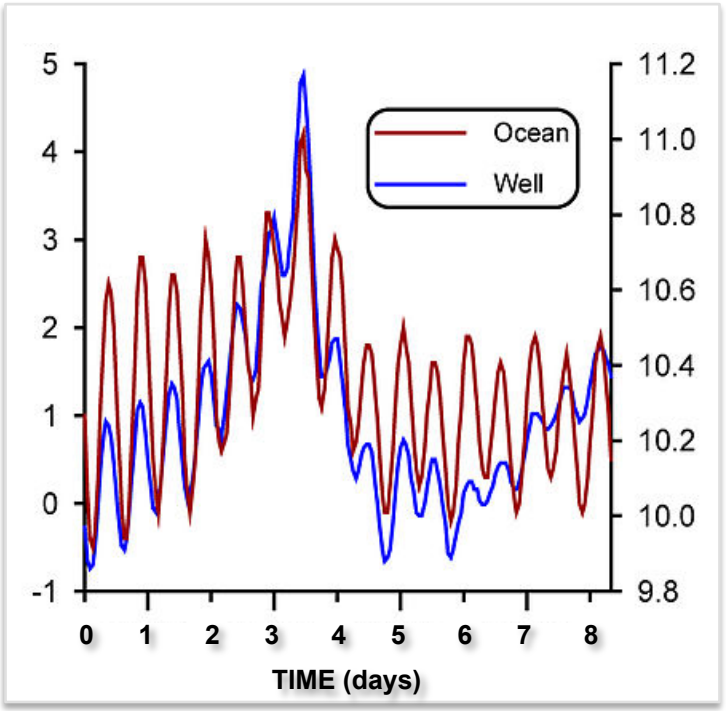
ECoG (electrocorticogram electrode array):
- a subdurally implanted grid of surface contact electrodes – records LFP

LFP = local field potential

Local Field Potential (LFP): the sum of all low frequency non-spiking synaptic activity & dendritic membrane potential changes, within a radius of 200-400 um of electrode tip.

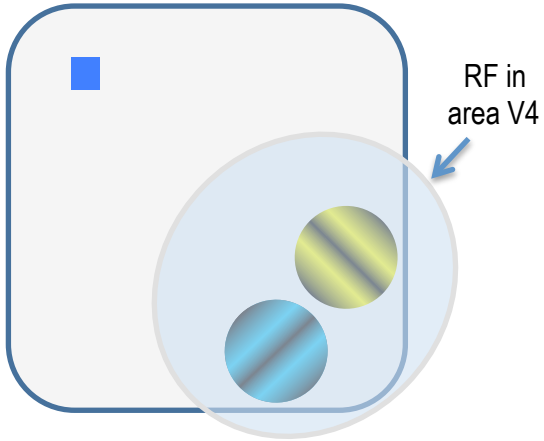
LFP magnitude is a measure of synchronisation of local activity

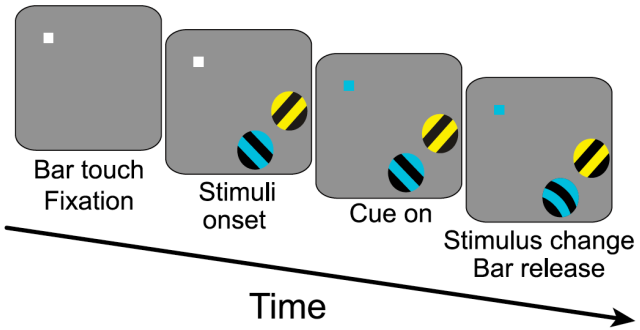


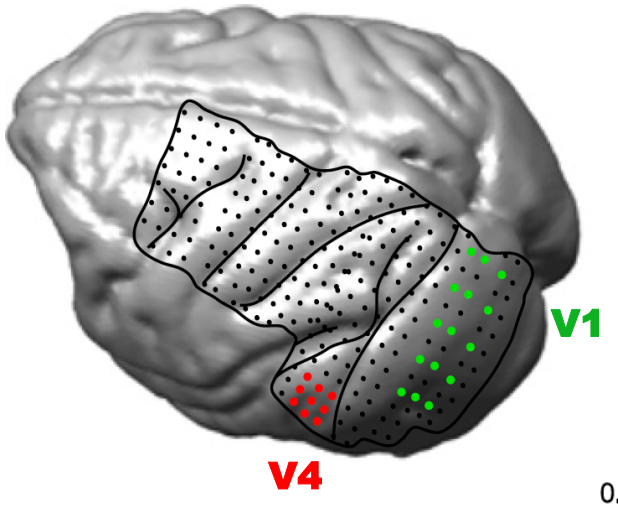


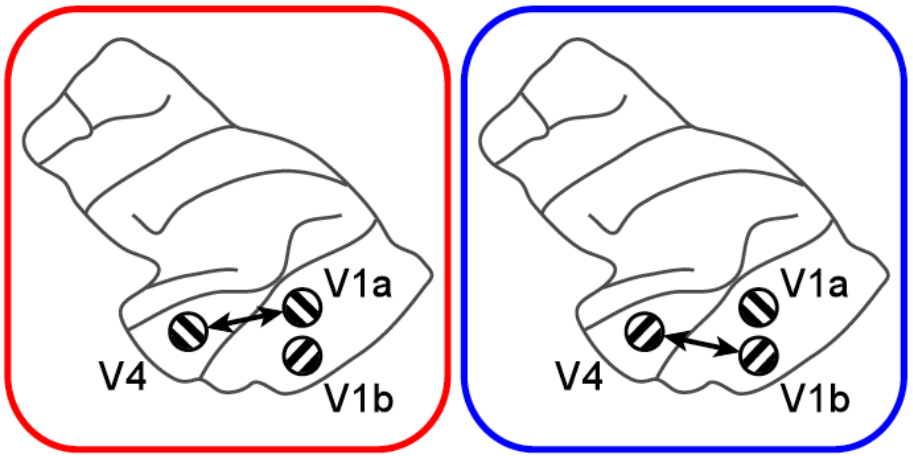
'Coherence' is a frequency-dependent measure of the consistency of phase relationships between the LFPs recorded at two separate sites.

Bosman *et al.* (20012) The effect of attention: synchronisation between V1 and V4 [REF 16]

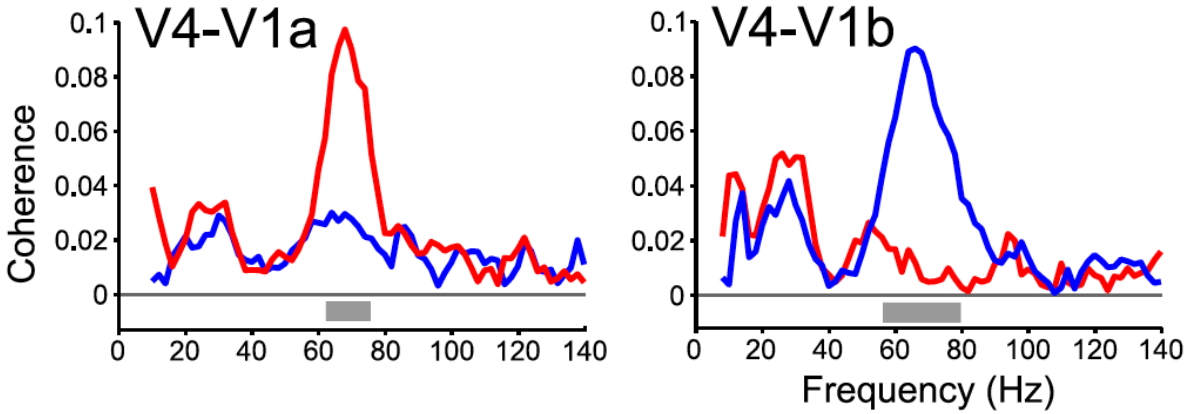




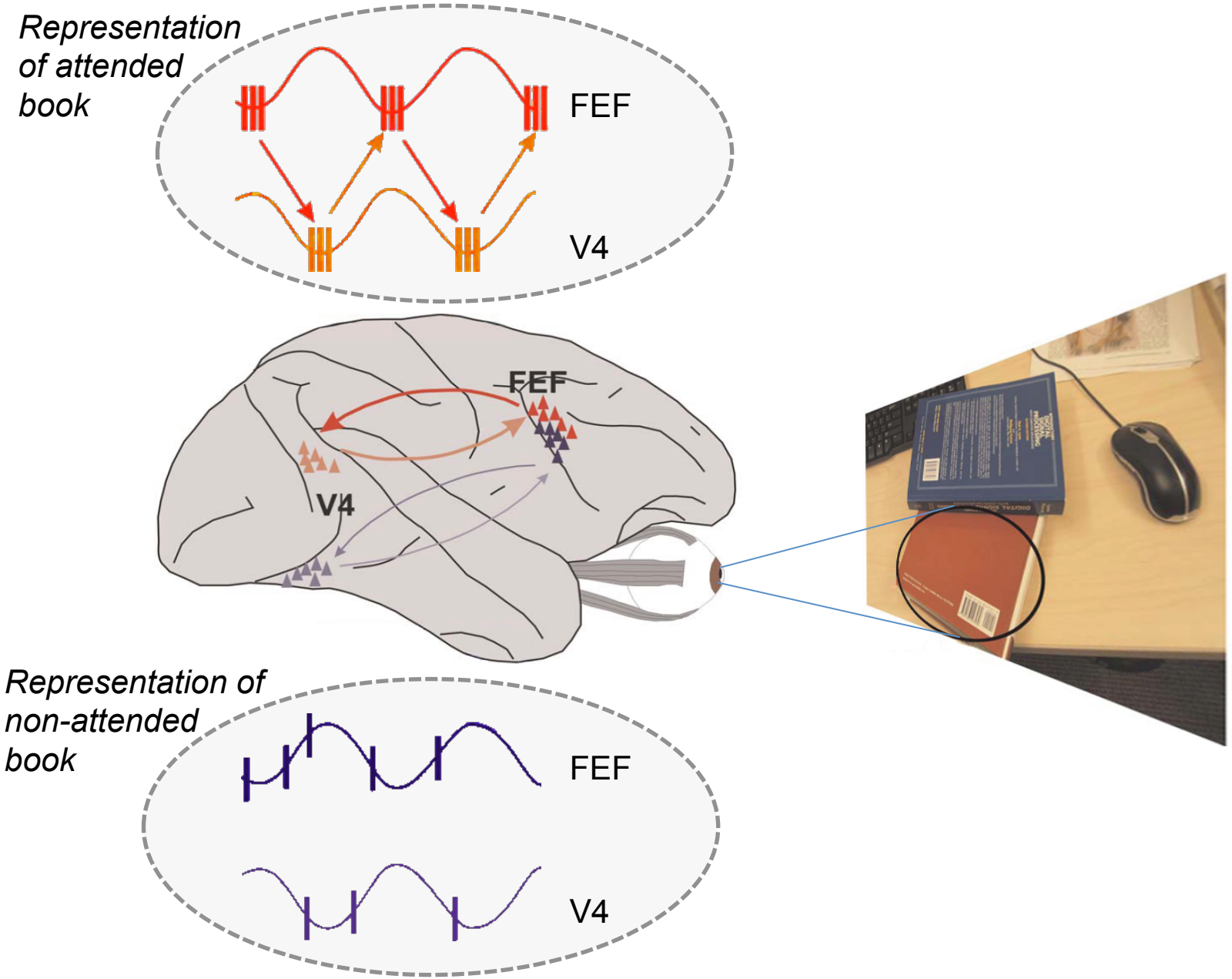




ECoG ('electrocorticogram' electrode array):
- a subdurally implanted grid of surface contact electrodes – records LFP



Gregoriou *et al.* (2009) The effect of attention: synchronisation between FEF and V4 [REF 17]



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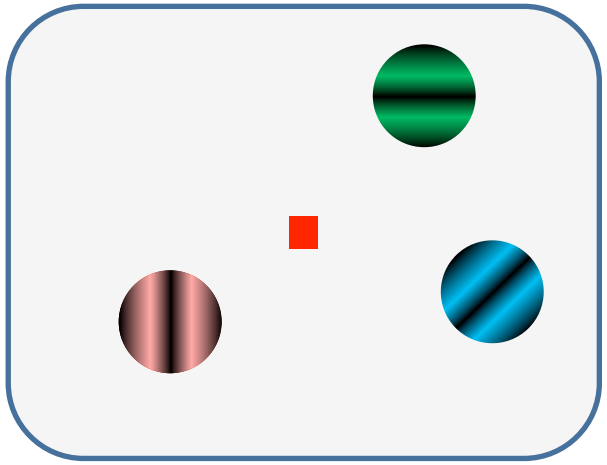
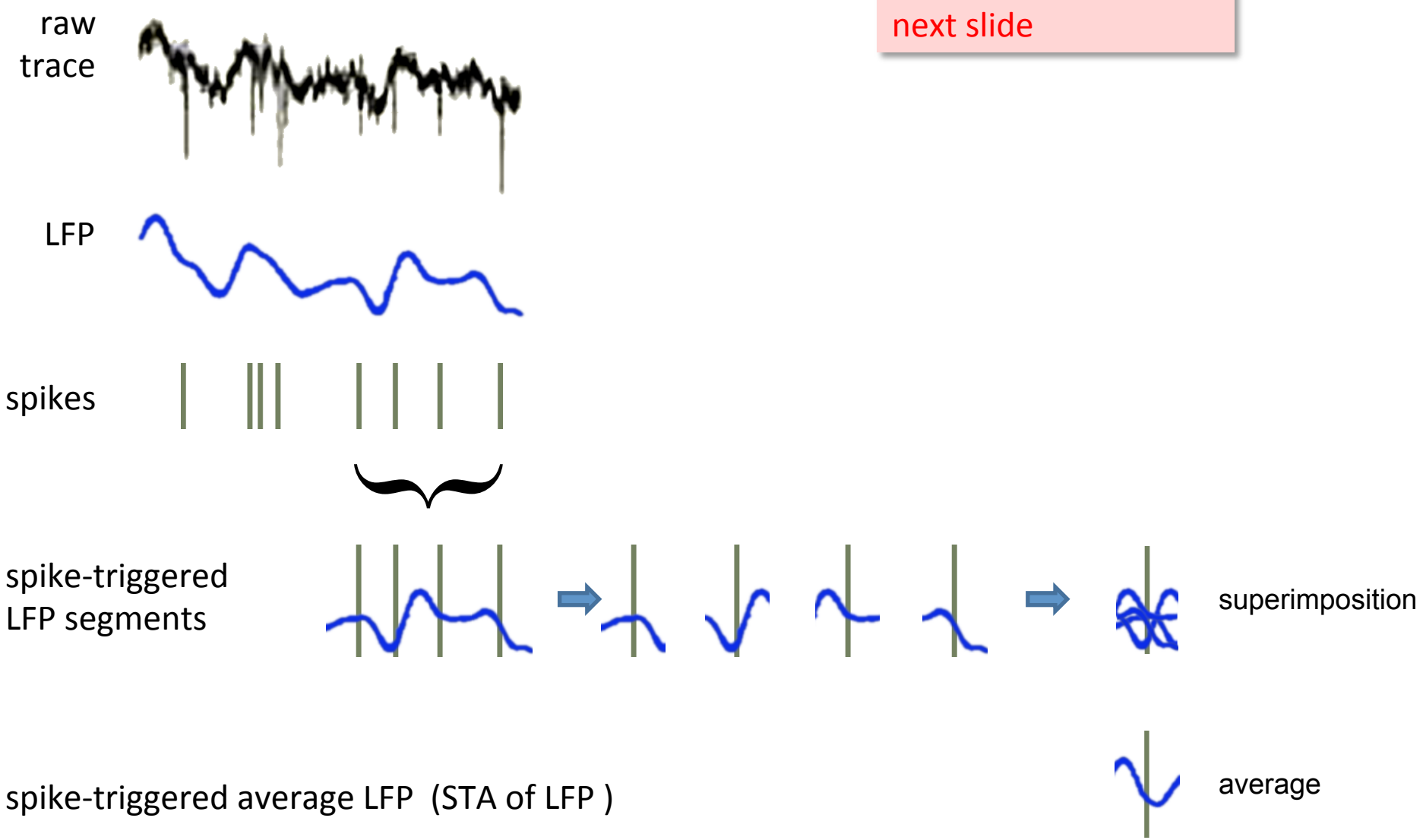


Task:

1. Fixate centre square;
2. A change in colour of the fixation square is the cue to attend the grating of matching colour;
3. Keep fixating whilst waiting to detect a colour change in the cued grating;
4. Respond manually when cued grating changes colour.

Extracting a spike-triggered average of the local field potential (STA of LFP)

This is relevant to understanding the next slide



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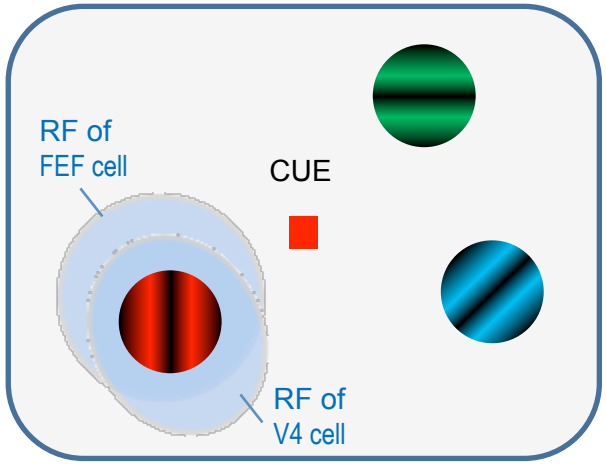
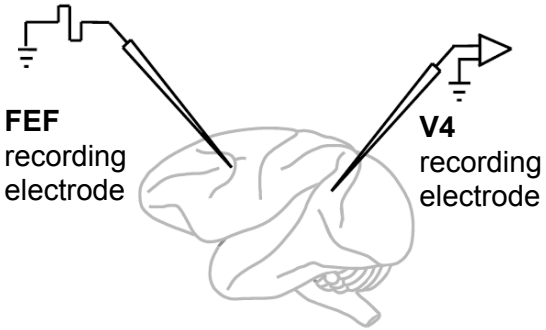
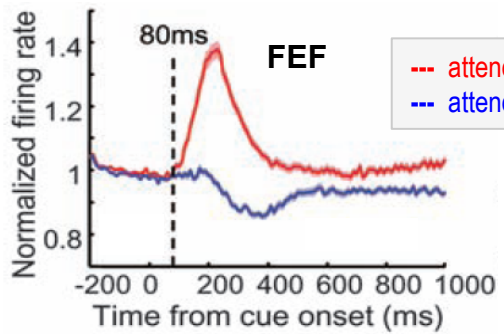
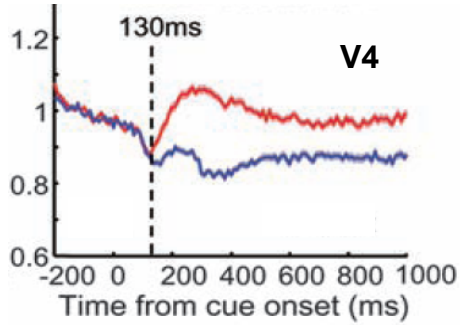


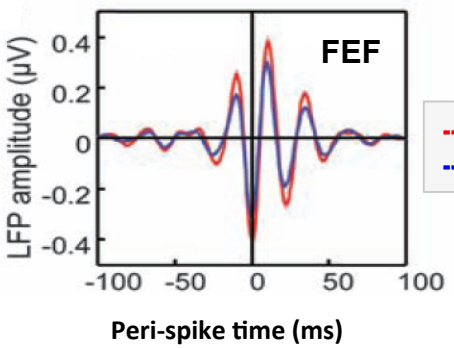


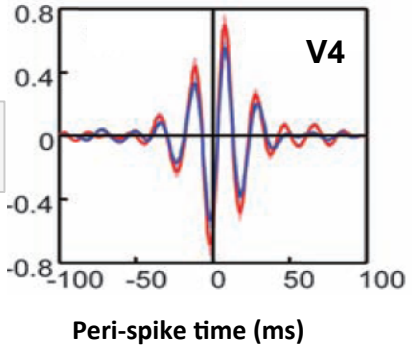
1. Enhanced activity (shown here by average activity of all recorded neurons)



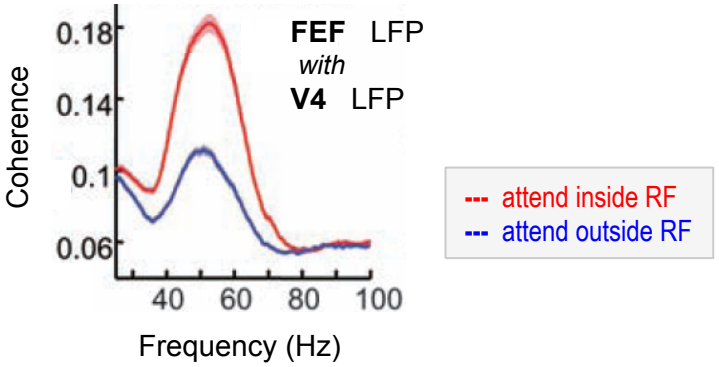


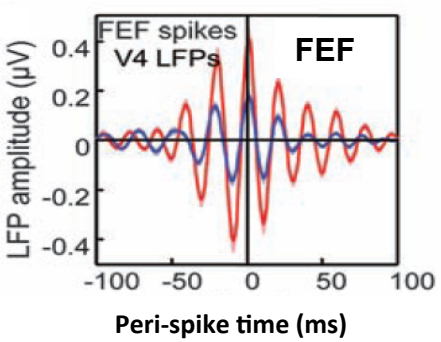
2. Enhanced local synchronisation (shown here as STA of LFP)
[= spike triggered average of local field potential]

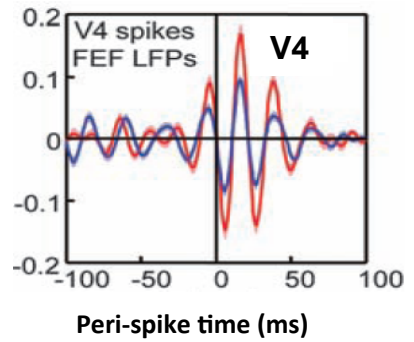




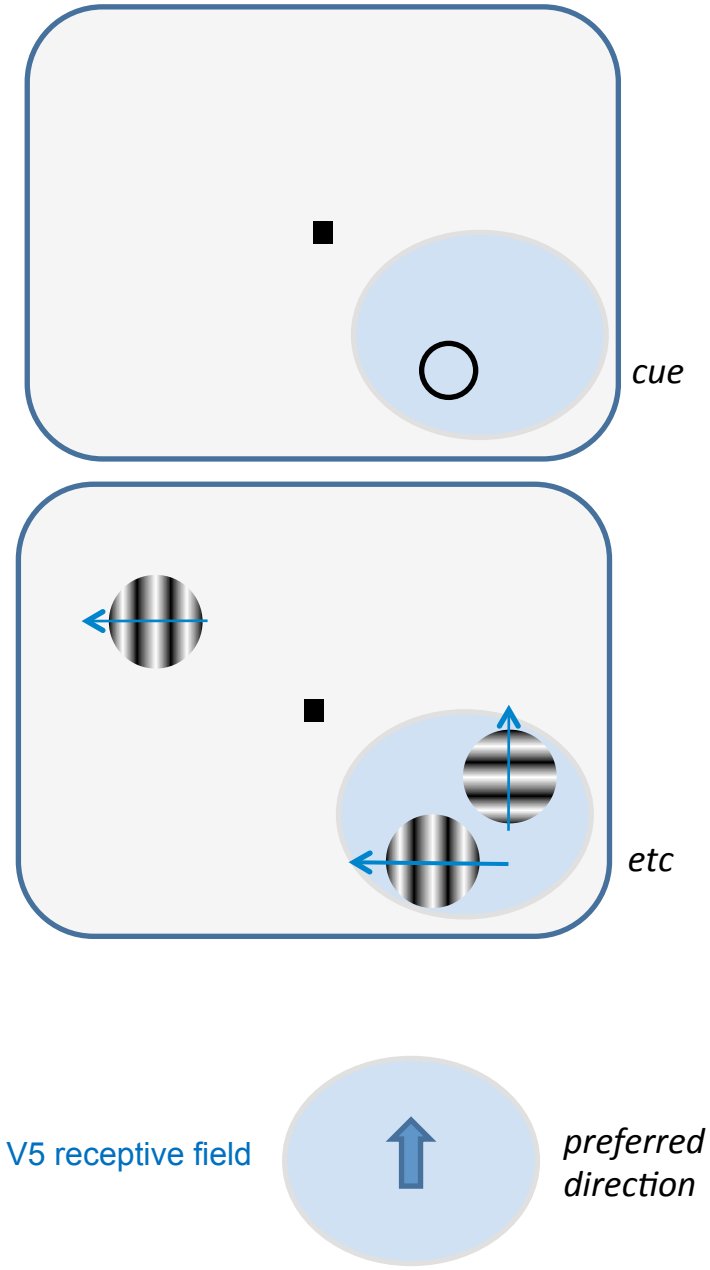
3. Enhanced inter-area synchronisation (1) LFP-LFP coherence; (2) 'crossed' STA of LFP (spikes of one area with LFP of the other)







Lee & Maunsell (2010) Effect of two stimuli within receptive field (area V5) [REF 19]

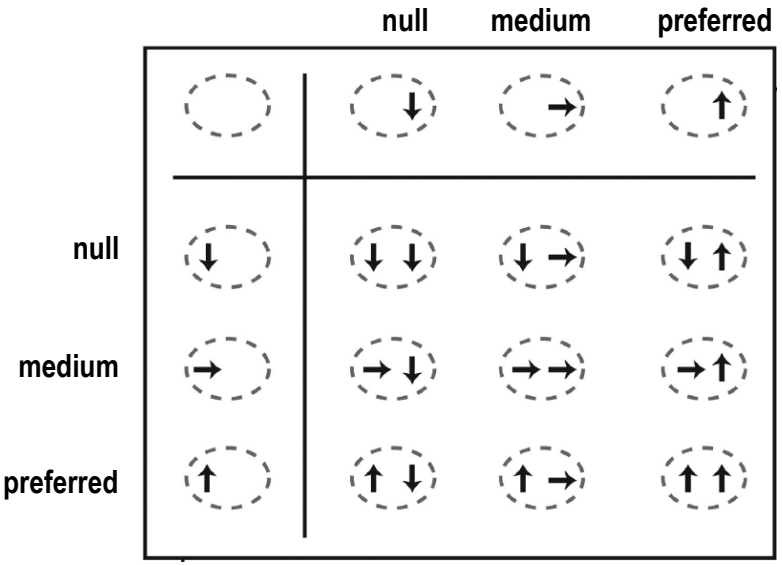


Task:

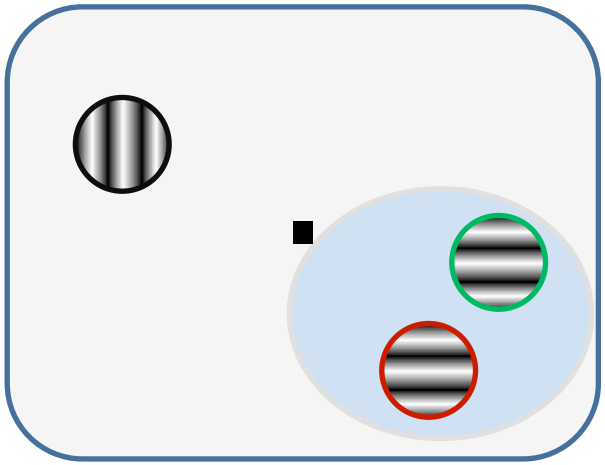
1. Fixate centre;
2. Cue instructs which stimulus to attend;
3. Keep fixating centre!
4. Report change in speed at cued location.

Experimental Design:

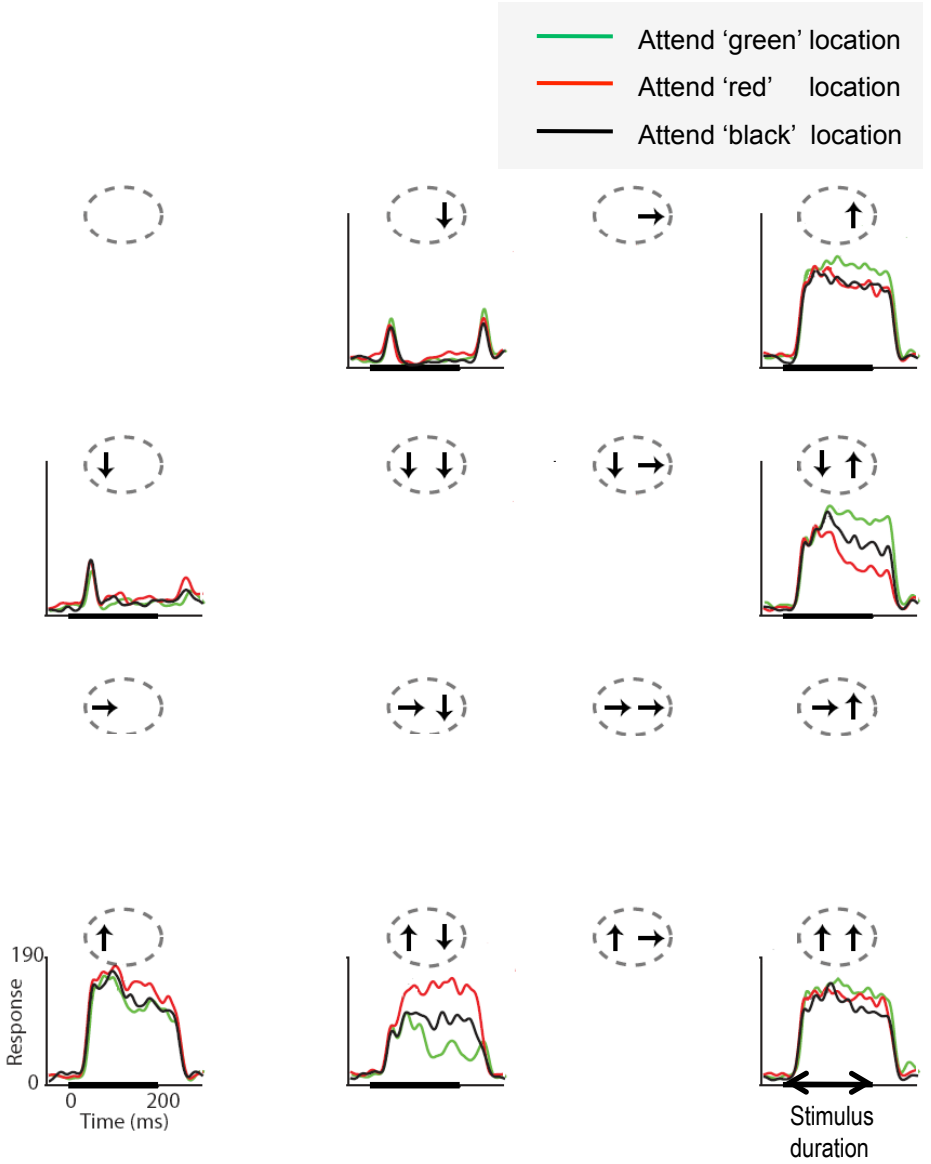
5. A sequence of gratings, with different directions of motion, is presented at each of 3 locations; 2 locations are inside RF and the 3rd is diagonally opposite.
6. At each location, 1 in 4 trials has no grating; hence, in a minority of trials, only one grating is presented within the RF.
7. The macaque may be cued to attend to either location inside RF, or to the 3rd location outside the RF.
8. The trial terminates when a target grating is presented at the cued location with a higher speed, that the macaque notices and responds by breaking fixation and making an eye movement to its location.



Lee & Maunsell (2010) Effect of two stimuli within receptive field (area V5) [REF 19]



V5 receptive field



Observe:

1. When attention is directed outside of RF, response to dual stimuli (one preferred, one null) within RF is intermediate between between responses to single preferred and single null stimuli.
2. Attention directed to preferred component of dual stimuli enhances this response; attention directed to null component diminishes it.

Conclusion:

3. This observation supports the rationale of the 'Biased Competition' account of attention.

Only showing responses to selected stimulus combinations, for clarity