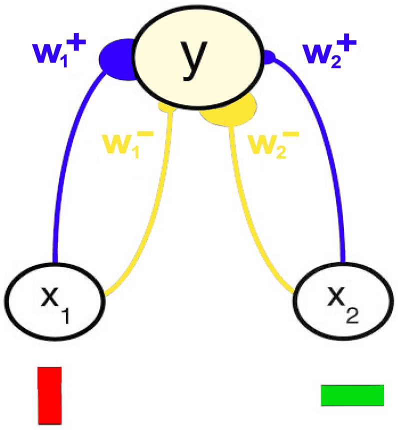

$$E = a_1 x_1 w_1^+ + a_2 x_2 w_2^+ \quad (1)$$

$$I = a_1 x_1 w_1^- + a_2 x_2 w_2^- \quad (2)$$

$$\frac{dy}{dt} = (B-y)\,E - y\,I - D\,y \quad (3)$$

$$\lim_{t \to \infty} y = \frac{B\,E}{E+I+D} \quad (4)$$

To simulate the results of Moran & Desimone (1985) and Reynolds et al. (1999), a simple feedforward competitive neural network has been used, defined by 4 equations below.
Attention (a) is assumed to increase the strength of synapses between the population activated by the attended stimulus (e.g., in V1 or V2) and the output cell (e.g., V4).
Increasing the strength of the signal from the attended stimulus population causes it to have a greater influence on the total excitation and inhibition.
Consequently, the response of the cell is driven toward the response that would be elicited if the attended stimulus were presented alone.
Equations 1 and 2 describe the total excitatory (E) and inhibitory (I) inputs to the cell.
Equation 3 describes how the firing rate of the output neuron (y) changes over time. This equation was originally introduced by Grossberg (1973) to avoid neurons saturating their responses to strong inputs (e.g., high-contrast stimuli), while remaining sensitive to weak inputs.
The first term [(B - y)E] governs excitatory input. B is the maximum response of the cell, therefore, (B - y) is always positive. The second term (-yI) governs inhibitory input. The third term (-Dy) is a passive decay term.
Equation 4 describes equilibrium response of the output neuron.

Reynolds et al., J. Neurosci., 1999

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Selective attention improves performance primarily by reducing interneuronal correlations

The responses of sensory neurons are variable, and laboratory studies typically deal with this variability by averaging responses to many stimulus presentations.

In the real world, however, people and animals must respond to individual stimulus events, and the brain is thought to compensate for neuronal variability by encoding sensory information in the responses of large populations of neurons.

Thus, it is crucial to understand the way information is encoded in populations of neurons.

1) If the noise in individual neurons is independent, averaging the responses of many neurons will lead to a very accurate estimate of the mean, no matter how noisy the individual neurons are.

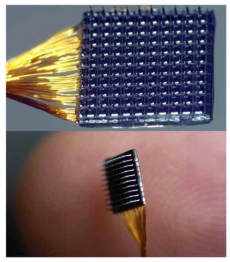
2) If, however, there are positive correlations in the trial-to-trial fluctuations of the responses of pairs of neurons, then the shared (or correlated) variability can never be averaged out, leading to a more variable (and less accurate) estimate of the mean activity in the population.

Cohen & Maunsell, Nature Neurosci., 2009

40

Cohen and Maunsell (2009) investigated the effect of attention on correlated variability by recording from populations of neurons in V4 using chronically implanted 6x8 arrays of microelectrode in two rhesus monkeys.
The distance between adjacent electrodes was 400 µm.

Each monkey had two arrays, which allowed to monitor populations of neurons in both hemispheres simultaneously.



They recorded from 376 single units and 2,746 multiunit clusters, (including 66,578 simultaneously recorded pairs in the same hemisphere and 59,990 pairs in opposite hemispheres) in 41 recording days.

For each pair of simultaneously recorded neurons and each attentional condition, the correlation coefficient between spike count responses during the 200 ms interval preceding the orientation change was calculated.
This estimate, termed noise correlation, measures the correlation between neuron pairs in trial-to-trial fluctuations in responses.

→ attended and unattended stimuli

Cohen & Maunsell, Nature Neurosci., 2009

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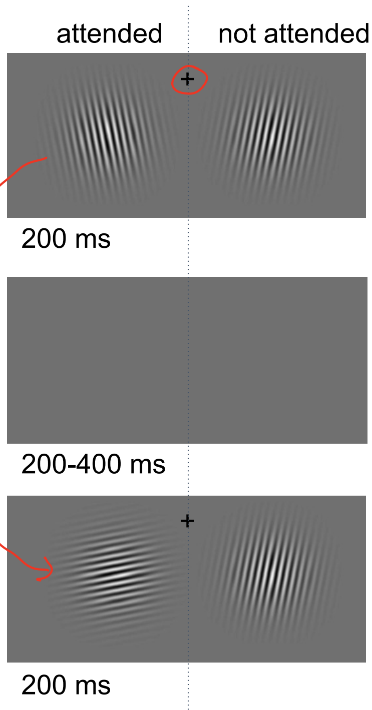
experiment mode



Orientation change–detection task:

two Gabor stimuli flashed on (200 ms) and off and the monkey's task was to detect a change in the orientation of either stimulus.

Attention was manipulated in blocks by cueing the monkey as to which stimulus (left or right) was more likely to change (cue valid on 80% of trials).

The monkey was rewarded for making a saccade toward the stimulus that changed, even on the unattended side.

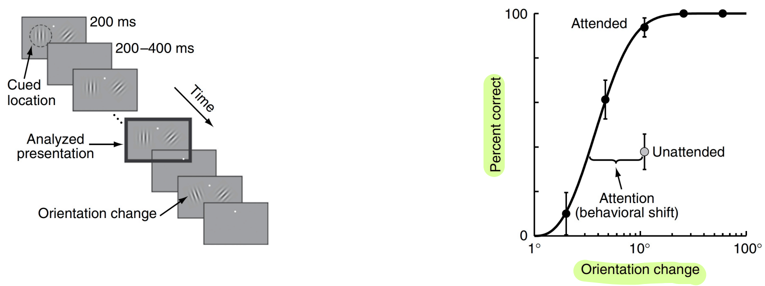
measures sensitivity of the animal

Cohen & Maunsell, Nature Neurosci., 2009

42 can change slightly or more

when attended, the guess is more accurate

otherwise it must be a pretty strong change



Psychometric performance from a typical example experiment.

The percent correct as a function of orientation change in degrees for trials in which the change occurred at the attended (black points) or unattended (gray point) location is shown.

Unattended changes occurred only at the middle difficulty level (11°). Attentional improvement in behavior was quantified as the lateral shift between the percent correct on unattended trials and the fitted psychometric curve for attended trials.

attention → better and faster response

Cohen & Maunsell, Nature Neurosci., 2009

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The results showed that:

Attention increased V4 neuron firing rates, as indicated by the difference between the mean firing rates on trials in which the attended stimulus was inside of or outside of the neuron's RF (see a);

Attention reduced the trial-to-trial variability of individual neurons, as indicated by a drop in the Fano factor, the ratio of the variance of the firing rates to the mean (see b);

Attention decreased noise correlation, that is the correlation between the variability or fluctuation of the responses of pairs of neurons, in each trial. It represents how much variability (or noise) is shared by a group of neurons.

For pairs of neurons in the same hemisphere, correlation was lower when the stimulus in the neurons' RF was attended (black line) than when it was unattended (gray line). Pairs of neurons in opposite hemispheres (dashed lines) had correlations that were close to zero (see c).

Noise correlation was highest for neurons with similar tuning (positive signal correlation) and lowest for neurons with opposite tuning (negative signal correlation). However, the effect of attention on noise correlation did not depend on the degree of tuning similarity (signal correlation) between cells (see d).

Cohen & Maunsell, Nature Neurosci., 2009

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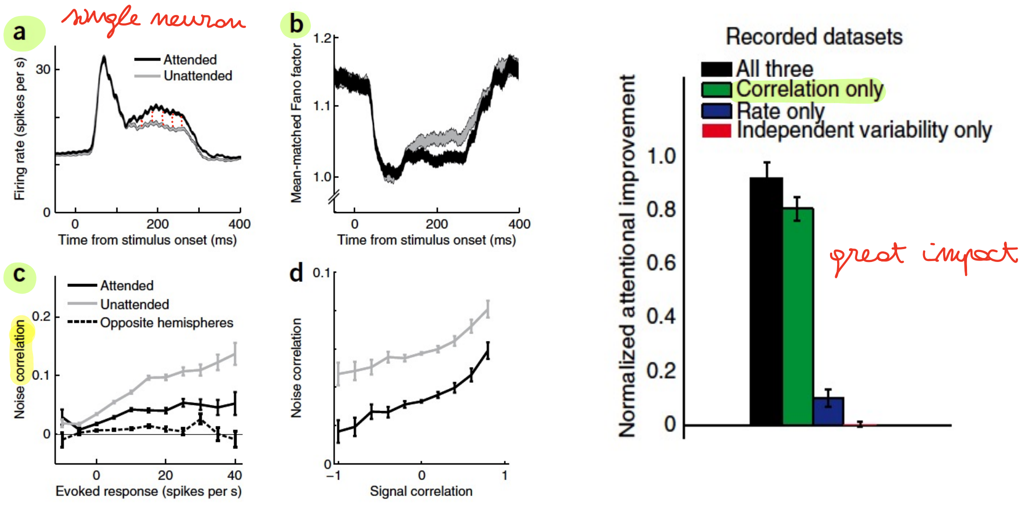
→ attention brings less variable responses

$\sigma \downarrow$ Fano $\downarrow$

$\text{Fano} = \frac{\sigma}{\mu}$

single neuron



less correlation with attention

great impact

What is the relative importance of increasing single neuron discharge (blue), reducing individual variability (red) and reducing correlated noise (green) in increasing the sensitivity of the neuronal population in the attended vs unattended condition?
Cohen and Maunsell find that the main role played by attention is to reduce correlated variability.

Cohen & Maunsell, Nature Neurosci., 2009

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Cohen et al., (2009) found that attention improves neural and behavioral performance primarily by changing noise correlations.

Noise correlations in cortex are thought to arise primarily from common, noisy inputs.

A decrease in correlation combined with an increase in firing rates is consistent with a decrease in the strength of an effectively inhibitory input that is common across the population.

One possibility is that attention results in a decrease in the weights or activity of inputs that cause divisive normalization, a mechanism that normalizes responses to many stimuli in a receptive field and has recently been proposed to underlie selective visual attention (Reynolds & Heeger, 2009).

Cohen & Maunsell, Nature Neurosci., 2009

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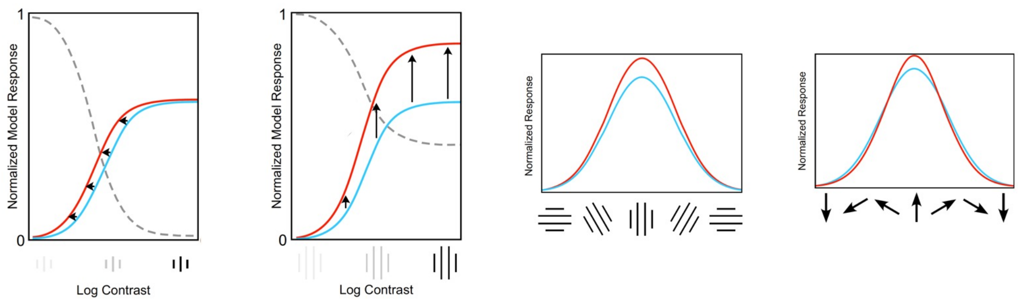
Attentional modulations



Contrast gain

Response gain

Multiplicative scaling

Multiplicative sharpening

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Bottom-up visual attention

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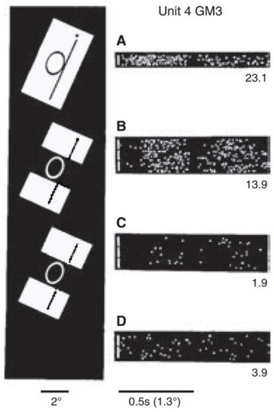
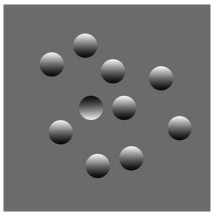
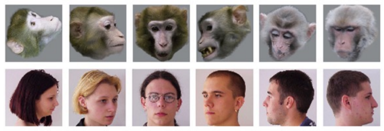
Neurons at the earliest stages of visual processing are tuned to simple visual features such as luminance and color contrast, edge orientation, direction of motion, or stereo disparity.

Processing becomes increasingly more specialized with the progression from low-level to high level visual areas, such that higher-level visual areas include neurons that respond only to terminations, corners or junctions, shape-from-shading cues, illusory contours, or views of specific real-world objects.







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A model for the control of bottom-up attention

salience filter → movement
brightness
new objects → danger

Early visual features are computed pre-attentively in a massively parallel manner across the entire visual field.

Early stages of visual processing decompose the incoming visual input through an ensemble of feature-selective filtering processes.

Although attention does not seem to be mandatory for early vision, it can vigorously modulate, in a top-down manner, early visual processing (see top-down control).

It has been hypothesized (Itti & Koch, 2001) that the various feature maps feed into a unique 'saliency' or 'master' map, a 2D map whose activity topographically represents visual saliency, irrespective of the feature dimension that makes the location salient.

This bias attention to focus onto the most salient location

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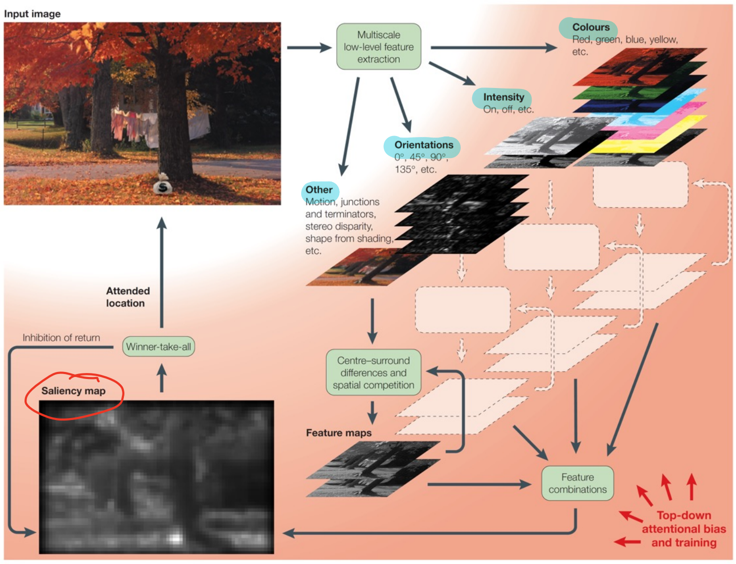
A saliency map can provide an efficient control strategy for the deployment of attention on the basis of bottom-up cues.



multiple // maps

for maps

not required attention but it can enhance the efficiency

single master map that recaps

Itti & Koch, Nat Rev Neurosci, 2001

51

saliency doesn't depend on the actual reason (e.g. colour) but it knows just if it's salient

Visual targets composed of features that are dissimilar from surrounding distracters are more salient and more easily located during search tasks.

These "popout" stimuli are believed to draw attention in a bottom-up manner, with search being driven largely via "parallel" or "preattentive" processing .

In comparison, targets made up of a unique conjunction of (non-target) features are more difficult to locate and require longer search times for increasing numbers of distracters.

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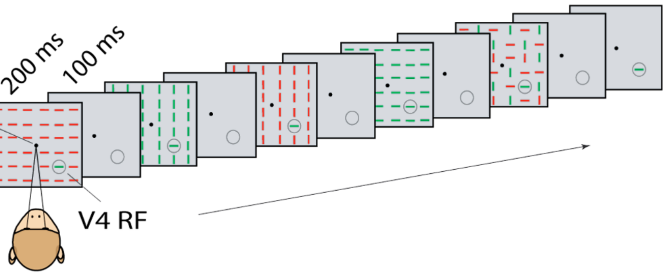

To study the impact of bottom-up (stimulus-driven) effects of salience on area V4 responses, visual stimuli were presented during a fixation task.

In this task, 300 ms following fixation, a series of five stimulus arrays plus the singleton were presented inside the neuron's RF for 200 ms each, with 100 ms in between presentations. The array stimuli were behaviorally irrelevant; in no condition was the monkey rewarded for responding in any way to the stimulus inside the RF or the surrounding items.
Thus, there was no goal-driven basis for the animal to attend to the RF stimulus or any other stimulus in the display.

53

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shares features with distractors

not salient

Popout and conjuction target stimuli

In the left display, attention is automatically drawn to the odd item (i.e., it "pops out"), whereas in the right display it must be located via serial search.

Popout targets are composed of features that differ from the features of surrounding distracters, while conjunction targets are composed of a unique combination of features that are present in the surrounding distracters.

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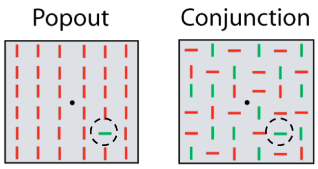
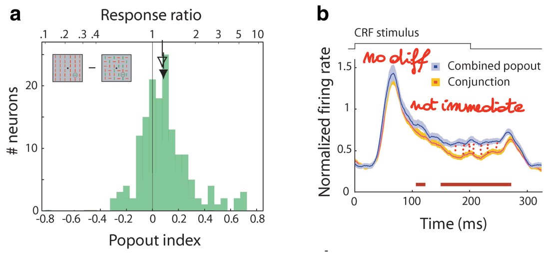


V4 neurons exhibit enhanced responses to pop-out stimuli (i.e., stimuli that differ from uniform surrounding items), relative to stimuli composed of a conjunction of surrounding features, placed inside the RF (dotted circle in the figure on the left) of a neuron.



bottom-up attention

a, Distribution of Popout Index (response-popout/response-conjunction) for a population of 137 neurons.

b, Mean normalized response of the V4 population to the popout (blue) and conjunction (red) arrays. Red lines indicate the time bins with a statistically significant separation of the popout and conjunction responses.

Burrows et al., J. Neurosci, 2006

55

Causal control of visual attention

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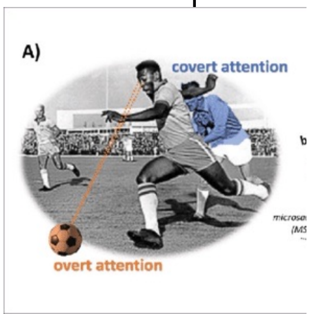
Overt vs. covert attention

Gaze direction and the attention focus are often spatially aligned (i.e., overt attention).

Nonetheless, it is also possible to attend to objects of interest in the visual scene without shifting our gaze (i.e., covert attention).

Covert attention is the form of spatial attention most often studied in vision neuroscience.



covert attention

dissociation

overt attention

aligned with gaze

it's impossible to move the eyes without moving attention

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Relationship between saccade preparation and spatial attention

Ferrier (1886) found that removal of the Frontal Eye Field (FEF) in one hemisphere can impair gaze shifts and spatial attention toward the contralesional (opposite) hemifield. He hypothesized that the "power of attention is intimately related to volitional movements of the head and eyes"

In the 1980s, Rizzolatti et al., proposed a premotor theory of attention, according to which the same neural mechanisms are involved in directing spatial attention and saccade programming.

Later studies demonstrated that visual detection and discrimination are facilitated at the endpoints of saccades.

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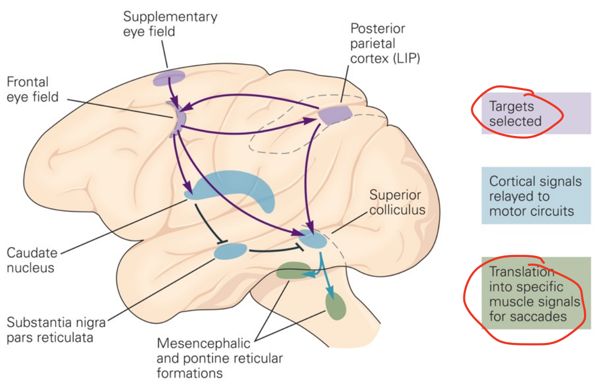
The Frontal Eye Field (FEF) in the prefrontal cortex



FEF neurons receive projections from most visual areas and project to both the brainstem saccade generator and the SC, which is a midbrain structure with a known involvement in saccade production.

However, the FEF also sends feedback projections to much of the visual cortex, suggesting a pathway by which saccade related signals can influence visual processing.

forward and back communication

The visual responses of some classes of FEF neurons (visual and visuo-movement) are enhanced when the RF stimulus is used as a saccade target compared to when no saccade is made to the stimulus.

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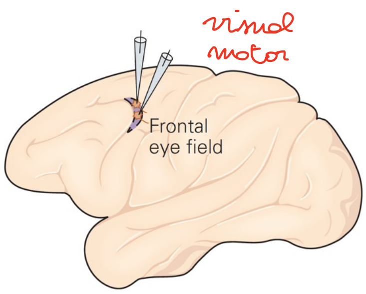

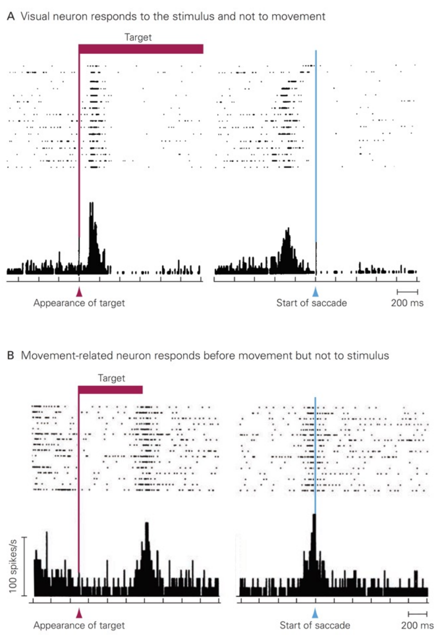

Visual and movement-related neurons in the frontal eye field (Bruce & Goldberg, J. Neurophysiol, 1985)

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The primate frontal eye field (FEF)

slow preparation
very fast movement

The FEF plays a well established role in the generation of saccades.

Single-unit recordings have shown that many neurons in the FEF are active around the time of saccades of specific magnitude and direction and that a topographic representation of saccade vectors exists across the FEF.

Electrical microstimulation of sites in the FEF can produce saccades of a particular vector.

Ablating the FEF causes pronounced deficits in generating eye movements to visual targets.

In humans, functional MRI studies have shown activity in the FEF is correlated with visually guided saccade generation, and transcranial magnetic stimulation (TMS) of the FEF has been shown to disrupt saccade generation.

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Visual activity in a number of brain regions is enhanced immediately before an animal targets a RF stimulus with a saccadic eye movement. preparation

Presaccadic visual enhancement was first observed among neurons of the superior colliculus (Goldberg & Wurtz (1972), but later studies demonstrated the effect in the FEF, parietal cortex and several extra striate visual areas.

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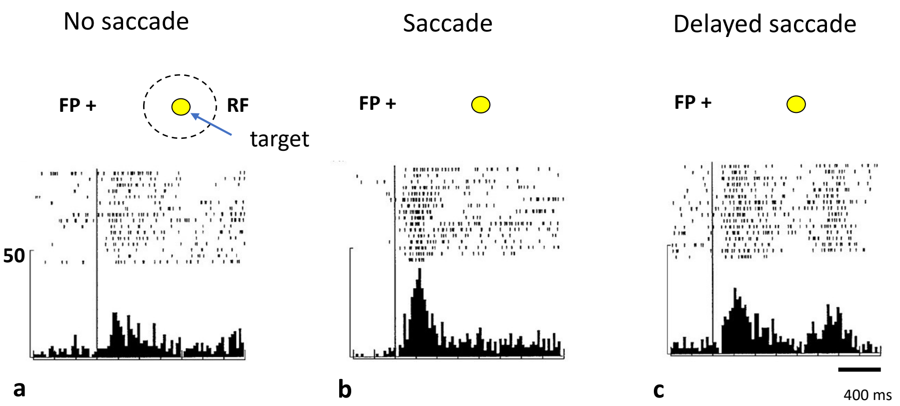
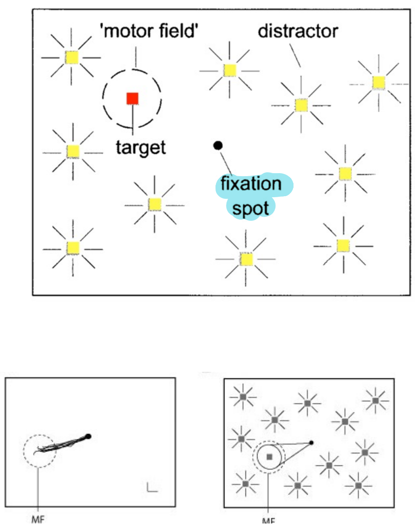
FP is more important



Presaccadic visual enhancement

The neuronal responses to a target visual stimulus presented inside the receptive field (RF, dashed line) were enhanced when the animal prepared a saccade Inside the receptive field (b, c), as compared to when the animal maintained fixation (e.g., to FP, as in a).



Control of eye movements and spatial attention

Several studies have employed electrical microstimulation to investigate the role of gaze-control structures in the deployment of spatial attention.

Moore & Fallah (2001) were the first to examine the effect of intracortical microstimulation on visual attention.

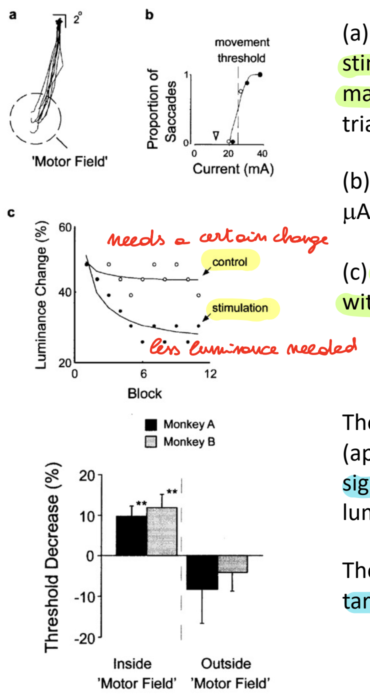
The monkey was trained to fixate on the central fixation spot and attend to a peripheral target that could transiently dim at a random time during the trial.

While the monkey awaited the dimming, visual distractors were randomly flashed throughout the display to further require the monkey to attend only to the target stimulus.

The dotted circle marked ‘’motor field’’ signifies the location to which the eyes move during supra-threshold stimulation.

Moore & Fallah, PNAS, 2001

greater sensitivity



(a) Individual saccade vectors obtained with suprathreshold stimulation at an FEF site, illustrating how the motor field was mapped. Vector traces show eight saccades evoked in eight trials at a current of 38 µA.

(b) The open arrowhead indicates the subthreshold current (13 µA) used during the spatial attention task.

(c) Luminance change detection (% contrast) obtained with and without microstimulation.

The subthreshold stimulation of the FEF immediately before (approximately 100ms) the appearance of the target significantly improved the animal's performance in detecting the luminance change (sensitivity).

The improvement in performance was observed only if the target appears in the motor field

Moore & Fallah, PNAS, 2001

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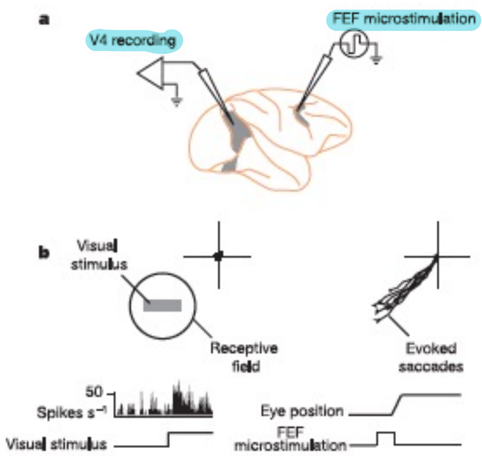
In a subsequent study Moore et al. (2003) examined the functional interaction between saccadic preparation and visual cortical processing, by microstimulating sites in FEF and measuring its effect on the activity of neurons in extrastriate visual cortex (area V4).

Visual responses in area V4 could be enhanced after a brief subthreshold stimulation of retinotopically corresponding sites in FEF sites (a particular FEF site, in which the end point of the evoked-saccade vector could fall within the RF of V4 neurons).



The enhancement effect was significantly increased by the presence of distracting stimuli (attentional competition).

Furthermore, stimulation of FEF sites with motor field not corresponding to the RF location of V4 neurons suppressed V4 responses.

The results suggest that the gain of visual signals is modified according to the strength of spatially corresponding eye movement commands

Moore & Armstrong, Nature 2003

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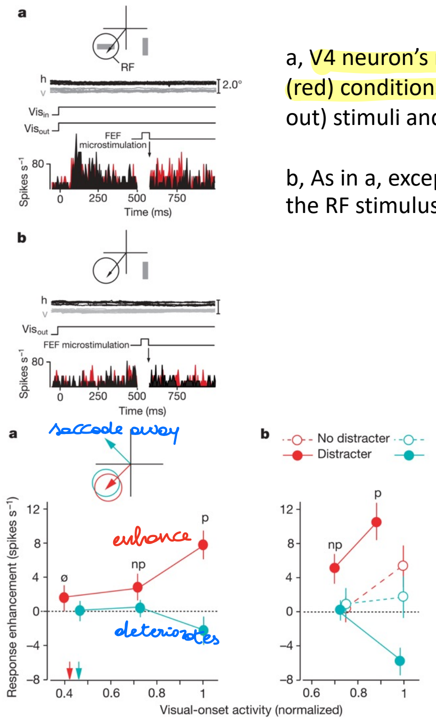

a, V4 neuron's mean response during control (black) and stimulation (red) conditions. Shown after the onset of RF (Vis in) and non-RF (Vis out) stimuli and after a 50-ms subthreshold (20 µA) stimulation.

b, As in a, except that histograms show the neuron's response when the RF stimulus was not presented.

a, The mean response difference between stimulation and control conditions (stimulation - control) when the evoked saccades (arrows) shifted the monkey's gaze to a point within (red) or outside (blue) the RF (circles) of the recorded V4 neuron. 0 (no stimulus), np (a non-preferred stimulus) or p (a preferred stimulus) in the RF.

b, conditions with and without a non-RF stimulus (distracter) are shown separately.

Moore & Armstrong, Nature 2003

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subthresholding can change the behaviour

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