Neural mechanisms of of selective visual attention

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Selective visual attention

It is among the most fundamental of cognitive functions, particularly in humans and other primates for whom vision is the dominant sense.

Selective visual attention describes the tendency of visual processing to be confined largely to stimuli that are relevant to behavior.

Owing to the extremely limited capacity of visual processing, and the high energy cost of neuronal activity, an animal must select the information that is most relevant at any point in time.

how do we select?

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Change blindness

Our capacity to process all the information available on the retina is extremely limited.

leaf disappearing

For example, in the change blindness (Simons & Levin, 1997), observers fail to notice large changes to visual scenes when the change coincides with a brief visual disturbance.

Although we experience a complete image of the visual world, our capacity to process all facets of available visual information is extremely limited.

These limitations are made compellingly evident in a number of perceptual demonstrations, such change blindness, the phenomenon in which observers fail to notice large changes to objects or scenes when the change coincides with a brief visual disruption (Simons & Levin, 1997).

Visual processing limitations are largely adaptive, given that what we tend to fully process (and perceive) only the information most relevant to our behavior.

Specifically, change blindness occurs when a scene and the same scene with a major change in it are presented for brief periods of time separated by a blank display.

The blank display inserted between the two scenes acts as a global visual transient (a distractor) that obscures the (the otherwise clearly notable, see next slide) localized transient in the scene that would normally capture our visual attention (as when an item suddenly appears, disappears, or moves).

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Biased competition model of selective visual attention

Limited capacity for processing information. At any given time, only a small amount of the information available on the retina can be processed and used in the control of behavior.

Selectivity, reflects the ability to filter out unwanted information (i.e., bottleneck).

At some point (or several points) between input and response, objects in the visual input compete for representation.

Attention biases competition towards information that is currently relevant to behavior.

Attended stimuli make demands on processing capacity, while unattended ones often do not.

Desimone & Duncan, Ann. Rev. Neurosci., 1995

Why the brain implements selective attention mechanisms?

allow entrance of the selected perceptual inputs into **working memory** and conscious perception;

move eyes (**gaze**) toward next target for preferential, foveal analysis;

direct actions, for instances reaching and grasping movements, at the selected object;

gate access of perceptual inputs to **memory** systems;

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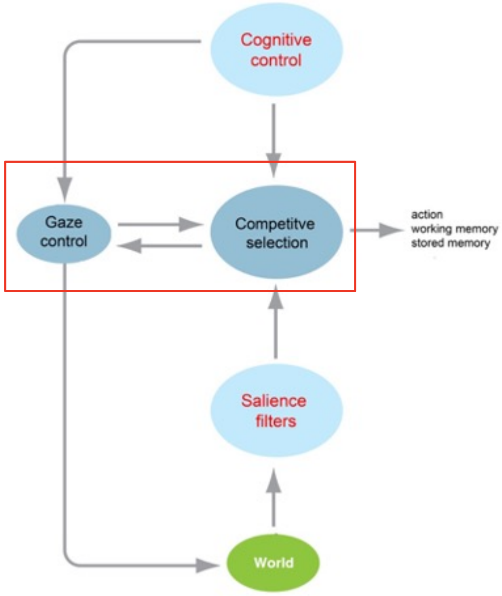
Working memory is a system that can temporarily store a limited amount of information that is currently used.
It facilitates planning, comprehension, reasoning, and problem-solving.

Functional components of selective visual attention



Salience filters: mechanisms that automatically enhance responses to stimuli that are infrequent in space or time, or are of innate or learned biological significance (i.e., food, predators, etc.);

Competitive selection: process that allows the neural representation (about the world, movements, memories, emotional state, etc.) with the highest signal strength for entry into working memory;

Cognitive control: process that regulates the relative signal strengths of the neural representations based on current goal

Varieties of visual selective attention

- top-down vs. bottom-up selective attention
- space-based vs. object-based selective attention
- covert vs. overt orienting of selective attention

Top-down visual attention

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voluntary

Top-down vs. bottom-up selective attention

Top-down or endogenous (voluntary) attention:

selective processing due to an endogenously generated signal (e.g., representation of a task rule, strategy, or motivational state). Top-down attention can be engaged to select one object (relevant to behavior) over another (e.g., attend to one location and ignore others, Posner, 1980), as well as to follow a particular instructional set or general rule (e.g., attend to and report the color of the presented word, Stroop, 1935).

Bottom-up or exogenous (automatic) attention:

selective processing that is generated externally by the physical properties of stimuli (e.g., brightness, color, shape, movement). Exogenous attention allows novel or salient information (e.g., a sudden change in luminance, Jonides & Yantis, 1988) to transiently interrupt goal-directed (voluntary) behavior.

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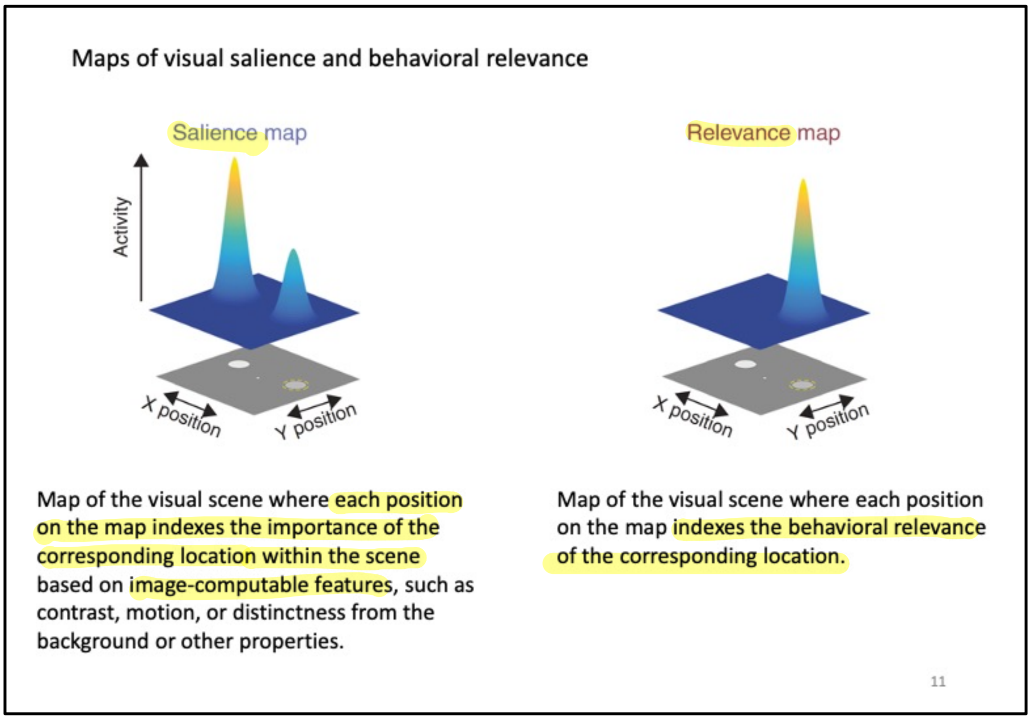


Salience map: In this example scene, in which two stimuli of differing contrast are presented and a participant is cued to attend to one (dashed yellow circle), a salience map would show higher activation at visual field positions corresponding to higher contrast, even if those elements of the scene are not relevant for behavior.

Relevance map: . In this example scene, the relevance map would only show activation at locations relevant to the behavior of the observer, independent of their visual salience. Visual locations corresponding to highly salient but irrelevant stimuli are not reflected in a pure relevance map.

In the brain, a cortical map of visual space can reflect a combination of both visual salience and behavioral relevance by virtue of its position within the visual processing hierarchy

Attentional template

Competitive selection can be influenced by cognitive processes, or TOP-DOWN mechanisms, through which task-relevant object are selected by attention.

According to psychologists Duncan and Humphreys (1989), the ATTENTIONAL TEMPLATE - a representation or description of the relevant object formed and held in the subject's working memory - can be used to give a COMPETITIVE ADVANTAGE to those objects in the visual scene that match that description.

I want to eat a strawberry, I have a visual idea of the strawberry in the working memory $\Rightarrow$ competitive advantage

Duncan, Humphreys , Psychol. Rev., 1989

Depending on the task at hand, any kind of input - objects with a certain orientation or form or color, objects in a certain location or with a certain motion direction, etc. - can be behaviorally relevant. We distinguish object-based attention (i.e., selection is based on nonspatial features, such as orientation, form or color), and space-based attention (i.e., selection is based on spatial location or direction).

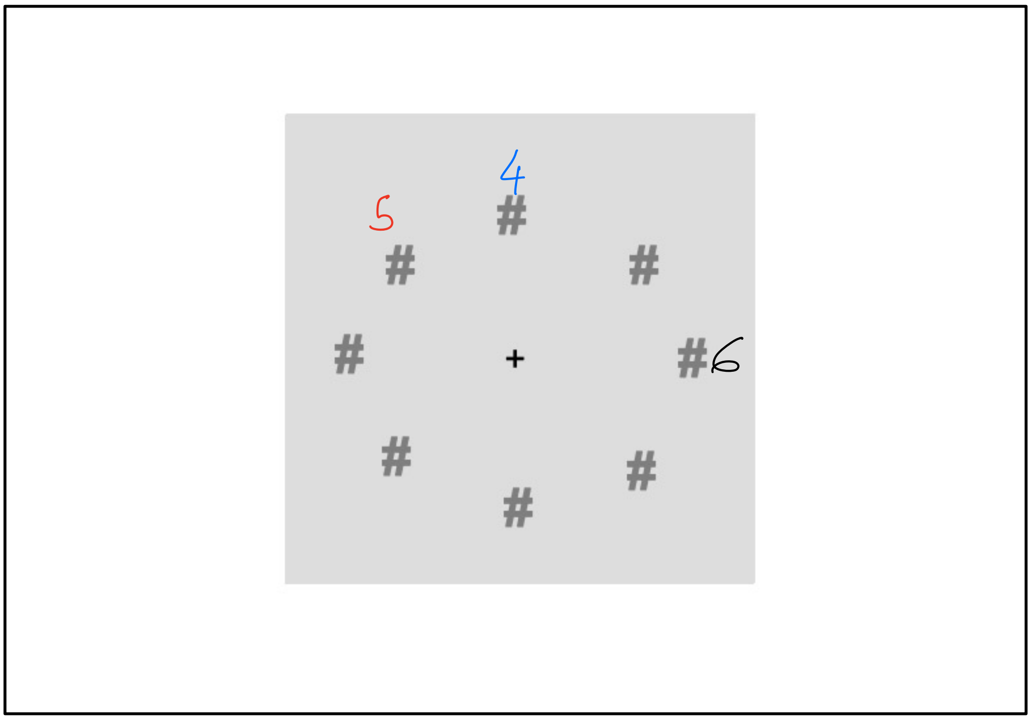
Some kind of short-term description of the information currently needed must be used to control competitive bias in the visual system, such that inputs matching that description are favored in the visual cortex.

Top-down attention: an example

For example, imagine that you are given the task of attending and reporting the identity of a red stimulus that will appear briefly in the visual field.

Following this instruction, a representation (attentional template) corresponding to the instruction that was given to you (i.e., pay attention to the red stimulus) is formed and maintained active in working memory.

This description serves to PRIME, through top-down mechanisms (feedback connections), the cortical areas that encode red color, such that the visual stimuli of this color will be processed more efficiently and with priority (competitive advantage) than stimuli of a different color.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Behavioral paradigms to study visual selective attention

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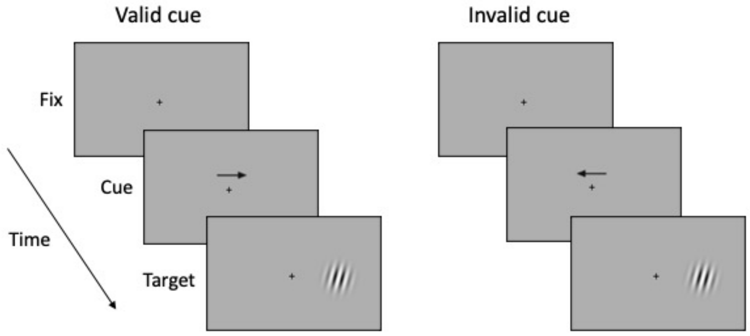

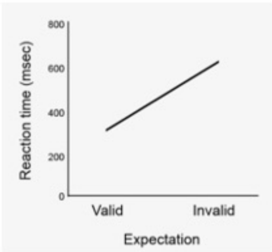

The cuing paradigm (Posner, 1980) is used to examine space-based attention

A participant fixates on the central cross of a screen. An arrow cue indicates where the target is more likely to appear. The cue is then followed by a target in either the correctly cued or the incorrectly cued location. Target detection is faster in the valid than in the invalid trials.

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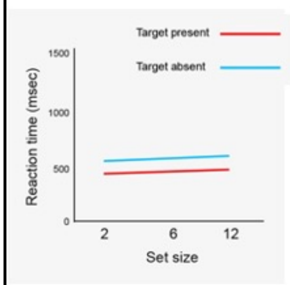
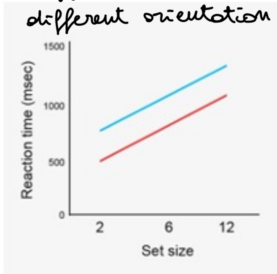
Feature (parallel) search

just one



Conjunction (serial) search

same target but distractors have different orientation



you need to look at the entire scene

The visual search paradigm is employed for studying the deployment of object-based attention.
The observer is presented with a display that can contain a target stimulus amongst a variable number of distractor stimuli.
The target is either present or absent, and the observers' task is to make a target-present vs. absent decision as rapidly and accurately as possible.

Efficiency of search decreases as the similarity between target and distractors increases, and increases as the similarity among distractors increases.

The most efficient searches are searches for a distinctive target amongst homogeneous distractors.

Treisman & Gelade, Cognit Psychol, 1980

Neural correlates of top-down attention

In neurophysiological studies, the basic observation is that selective visual attention increases visually driven firing rates of neurons encoding the attended stimulus;

This modulation is present as early as LGN and has been observed at nearly all levels along the ventral pathway of the visual system, including area V1, area V2, and area V4.

V1 is lower level

Nonetheless, there is also evidence to suggest that the magnitude of attentional enhancement increases as one ascends the visual hierarchy.

Analogous modulatory effects of attention have been demonstrated in visual areas of the dorsal stream, such as MT and MST.

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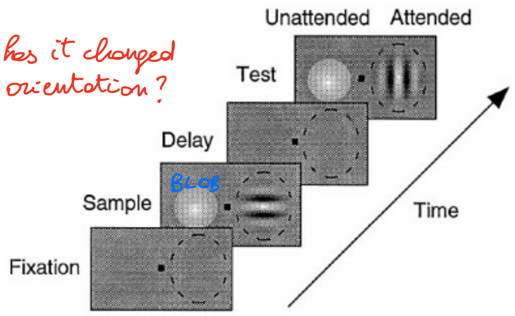


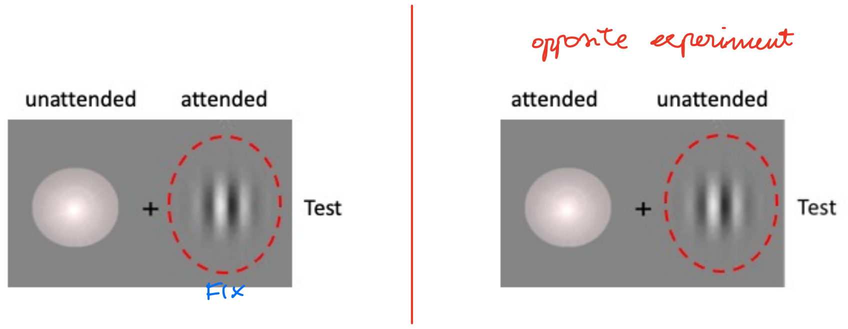
Orientation-tuning curves were constructed from neuronal responses in two behavioural states: attended vs. non attended.

The study examined how attention affected the orientation tuning of neurons in V1 and extrastriate area V4.

Monkeys performed a delayed match-to-sample task in which oriented stimuli were presented in the RF (dotted circle) of the neuron.
On some trials the animals were instructed to pay attention to those stimuli, and on other trials they were instructed to pay attention to other stimuli outside the RF.

Gaussian were fit to neuronal responses to twelve different orientations for each behavioral state.

McAdams & Maunsell, J. Neurosci., 1999



Monkeys were instructed either to pay attention to oriented Gabor inside the RF, or to pay attention to other stimuli (a colored Gaussian blob) outside the RF.

space-based → animal pays attention to the right or left

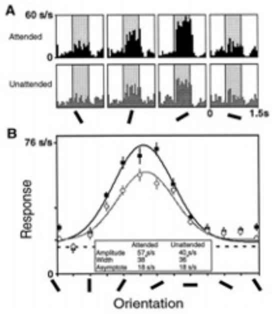
McAdams & Maunsell, J. Neurosci., 1999

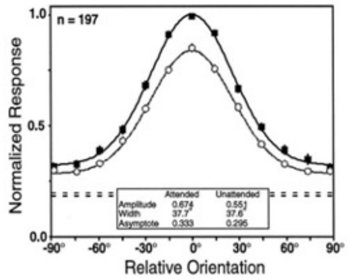
The animals were trained to perform a delayed match-to-sample task in which oriented gratings (12 different orientations) were presented in the receptive field of the neuron being recorded.

On some trials the animals were instructed to pay attention to those stimuli, and on other trials they were instructed to pay attention to other stimuli outside the receptive field.

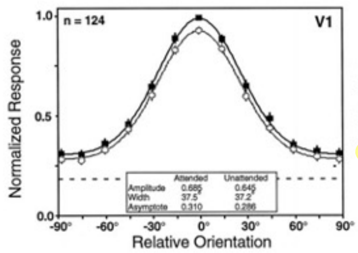
In this way, orientation-tuning curves could be constructed from neuronal responses collected in two behavioral states: one in which those oriented stimuli were attended by the animal and one in which those oriented stimuli were not attended by the animal.

We want to see if attention changes something





Population-tuning curves for V4 neurons for the attended (black solid squares) and unattended (white open circles) task modes. The overall increase in response amplitude in V4 was 31%.



Population-tuning curves for V1 neurons for the attended (black solid squares) and unattended (white open circles) task modes. The overall increase in response amplitude in V1 was 6%.

Results showed attentional modulation of the amplitude of orientation-tuning curves in both areas V4 and V1 (smaller effects), but there was little evidence for change in the width of tuning.

The principal action of attention appeared to be a multiplicative scaling of responses.

McAdams & Maunsell, J. Neurosci., 1999

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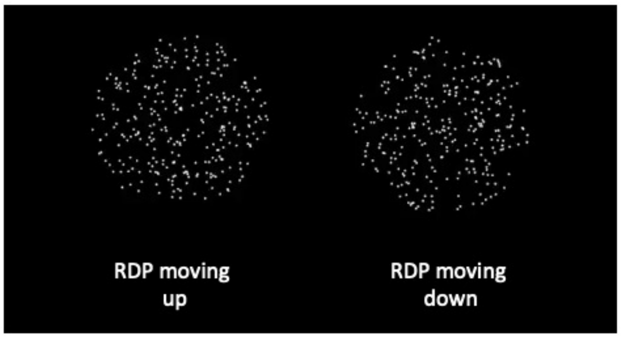
top-down attention

Selective visual attention can be directed toward a specific region of space (i.e., space-based attention), but also be guided by feature information indicating some non-spatial properties of the target, such as color, shape, direction of motion, etc (i.e., object-based attention).

Middle temporal (MT) area is crucial for the perception of visual motion.
MT neurons show direction tuning curves (bell-shaped response profiles) depending on the direction of motion of the stimulus (random dot pattern, RDP).



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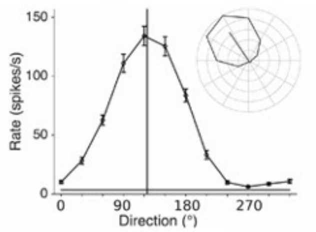
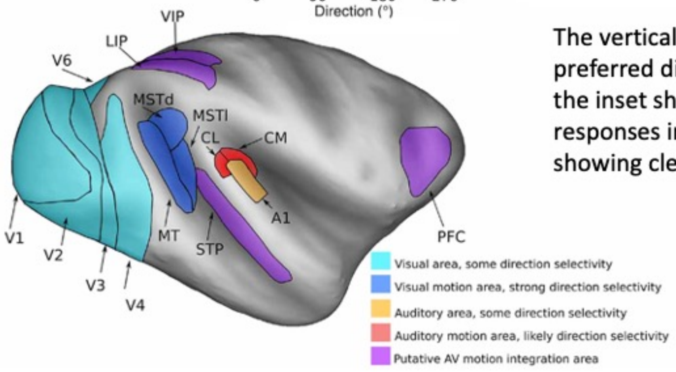
Treue & Martınez-Trujillo, Nature, 1999

Spatial attention modulates the responses of neurons selective to direction of motion in area MT and MST.



A typical visual direction tuning curve from a neuron in the monkey visual cortex (area MT) in response to a moving dot stimulus.

The vertical line indicates the preferred direction of motion, and the inset shows the mean spiking responses in polar plot form, showing clear direction selectivity.



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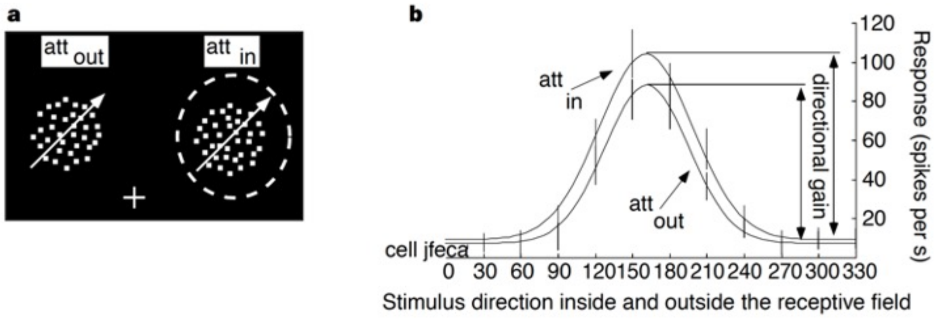
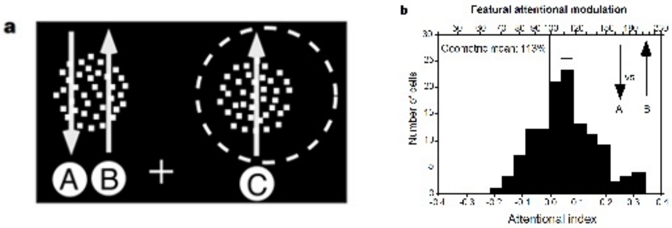


Experiment 1: Effect of spatial attention

a, One RDP was presented inside the RF (dashed circle) while the other was presented in the opposite hemifield. In a given trial, both RDPs moved in the same of 12 possible directions.

b, The upper curve shows the response when the monkey was attending to the stimulus inside the receptive field (marked att in), and the lower curve plots the responses when the monkey was attending to the stimulus outside the receptive field (marked att out).
These tuning curves show an increase in directional gain in the attended condition.

Treue & Martınez-Trujillo, Nature, 1999



On the X axis, binning is according to the attentional index (in Fig.b,: (Att in B - Att in A)/(Att in B + Att in A);

Experiment 2: Effect of non-spatial, featural attention

a, The stimulus inside the receptive field always moved in the cell's preferred direction (for instance, upward pointing arrow); the stimulus outside moved in either the same (B) or the opposite direction (A).

b, Histogram comparing responses of 131 cells to the stimulus inside the RF when attention was on the preferred (B) or anti-preferred (A) direction outside the receptive field. The histogram is shifted to the right (mean shift 13%) indicating an increased response when the stimulus moved in the cell's preferred direction.

Treue & Martınez-Trujillo, Nature, 1999

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Experiment 2. Psychophysical studies suggest that attention can also be selectively allocated to stimuli that match a particular feature, for example color, orientation, motion direction, etc. To test for such effects of non-spatial, feature-based attention, Treue & Martınez Trujillo (1999) introduced a variation into Experiment 1.
While the stimulus inside the receptive field now always moved in a given neuron's preferred direction, the other stimulus moved in either the same (as in the previous experiment 1) or the opposite direction.

This allowed the attended direction to be switched without changing the attended location and without changing the stimulus inside the receptive field.

Authors compared the neural responses (to the stimulus C inside the RF) when attention was directed to the stimulus outside the receptive field, moving either in the preferred (stimulus A) or anti-preferred (Stimulus B) direction.

Attentional Index = 0 indicates that neuronal responses to stimulus C inside the RF do not vary depending on the direction of the attended stimulus outside the RF;
Attentional Index > 1 indicates that neuronal responses to stimulus C inside the RF are larger when attending to the preferred direction stimulus outside the RF.

Attending to the preferred motion outside the receptive field increased the response by, on average, about 13% above the response evoked when attending a null direction stimulus outside the receptive field.

Attending to a given direction enhances the responses of neurons whose preferred direction aligns with the attended direction and reduces the responses of those neurons preferring the opposite direction.

These findings shows that spatial and feature-based attention represent separate (and summable) processes that have a multiplicative effect on the responses of neurons.

Treue & Martınez-Trujillo, Nature, 1999

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These results demonstrate a physiological correlate of non-spatial, feature-based attention by showing neuronal response modulations in the absence of spatial shifts of attention.

Thus, attending to a given direction enhances the responses of neurons whose preferred direction aligns with the attended direction and reduces the responses of those neurons preferring the opposite direction.

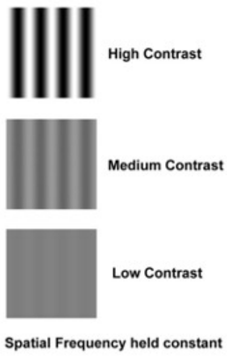
These findings shows that spatial and feature-based attention represent separate (and summable) processes that have a multiplicative effect on the responses of neurons.

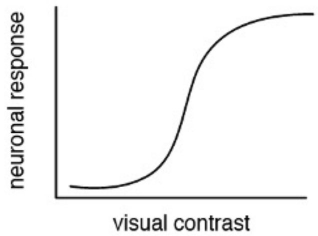
Such attentional modulations resemble changes to a neuron’s sensory gain and thus can be mimicked by sensory effects, such as reducing the luminance contrast of a stimulus, which similarly does not change the tuning width of direction-selective neurons, suggesting that response modulation based on attentional and sensory aspects employ common mechanisms.

Neuron response modulations are not only obtained by manipulating the behavioural relevance (i.e., top-down attention) of stimuli.

In the visual system, a non attentional, enhancement effect can be achieved by changing stimulus contrast (i.e., bot intensity bottom-up effect).

Visual neurons typically produce increasing responses as a function of stimulus contrast , up to a plateau, and the contrast-response function (CRF) takes the form of an H-ratio function (similar to a sigmoid).

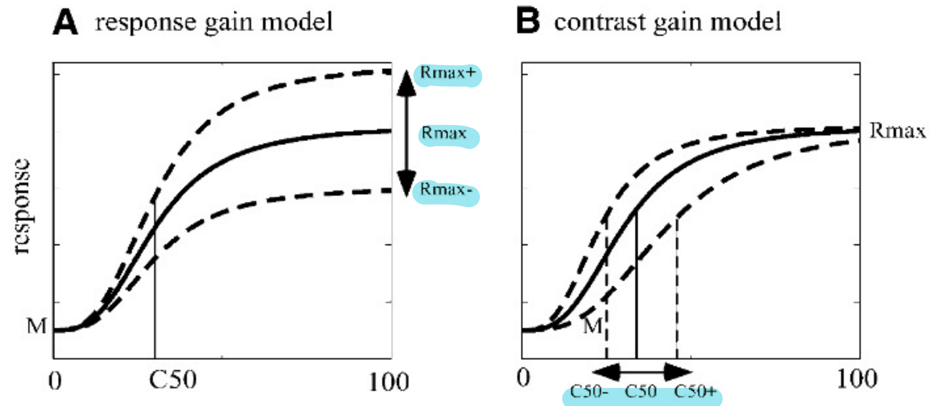




Two alternatives hypotheses to explain the effect of attention on the neuron response to a stimulus inside its RF:

Hypothesis 1
Response gain model: attention has a multiplicative effect on the neuronal response. The response is multiplied by a constant factor, and the effect of attention is maximum for the highest stimulus contrasts. The result is that the CRF function (sigmoid curve) moves upward.

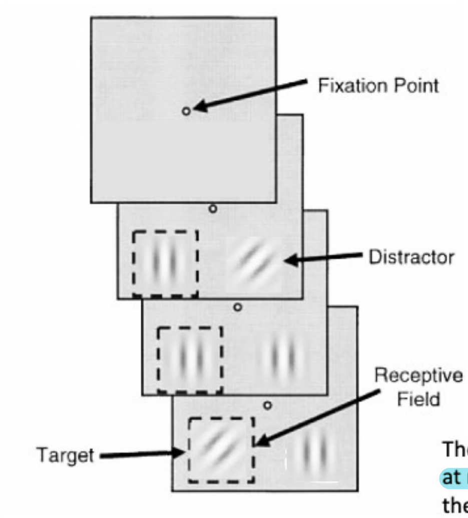
Hypothesis 2
Contrast (sensitivity) gain model: attention increases sensitivity to contrast. The effect of attention is maximum in the area of the curve where the neuronal response is most dynamic (steep). The result is that the sigmoid curve shifts to the left.



$$\text{response} = \frac{\text{Rmax} * C^n}{C^n + C50^n} + M$$

Martinez-Trujillo & Treu, Neuron, 02

Attention increases sensitivity of V4 neurons



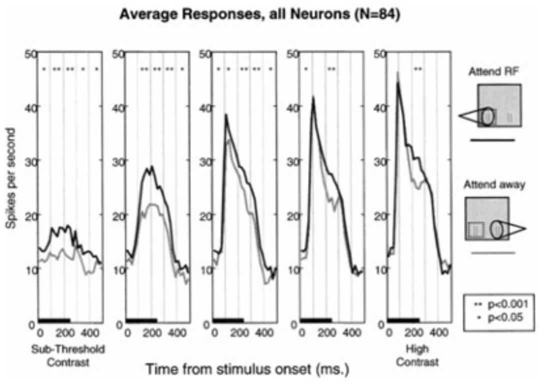
After the fixation point appears in the center, two stimuli (sinusoidal luminance gratings) were presented on the screen, one inside the RF, and one outside the RF.

In separate blocks, the animal paid attention to the stimulus inside the RF (attend RF) or outside the RF (attend away).

It was therefore possible to compare the neuronal responses to identical stimuli, when the monkey either attended to them or else attended to the stimuli appearing in the opposite hemifield.

The luminance contrast of each stimulus was selected at random from a set of five contrasts that spanned the dynamic range of each neuron's CRF, and thus the effects of attention could at each point along the CRF.

Reynolds et al., J. Neurosci, 2000



Response (in spikes per second) over time from the onset of the stimulus (in milliseconds) at a particular contrast, averaged across the entire population of neurons.

Attention caused largest increases in firing rate to stimuli that were near the contrast–response threshold (second panel from left). Here, attention caused a 24% increase in the average firing rate.

As stimulus contrast increased, the effects of attention on the neuronal response decreased.

The results support the hypothesis that attention causes an increase in V4 neurons' sensitivity but without a substantial increase in the response to high-contrast stimuli. This increase in sensitivity is reflected in a leftward shift in the CRF.

The largest changes in firing rate with attention were observed for stimuli that were within the dynamic range of the CRF.

Reynolds et al., J. Neurosci, 2000

Attention alters visual cortical receptive fields

Vision is limited by many factors including the visual system's spatial resolution (or acuity), the ability to discriminate two nearby points in space.

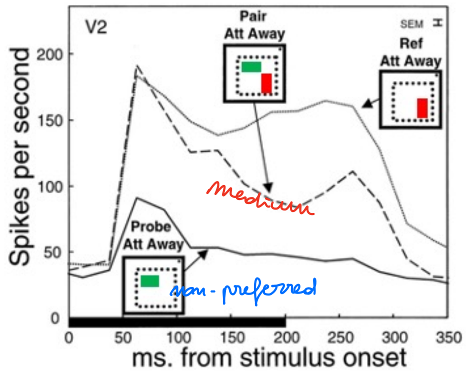
This shift in spatial attention results in enhanced visual processing, including enhanced spatial resolution, contrast sensitivity, and speed of information processing, at the attended location.

The idea that attention operates by changing the spatial selectivity of single neurons was first suggested by Moran and Desimone (1985).

They recorded from single neurons in monkey visual area V4 while the monkey attended to one of two stimuli presented inside the neuron's classical RF.

One of the two stimuli elicited a strong response from the neuron when presented alone (effective stimulus), whereas the other stimulus elicited a weak response when presented alone (non-effective stimulus).

Moran & Desimone, Science, 1985



When presented simultaneously without attention on either stimulus, the neuron's response approximately corresponded to the average of the response to either stimulus by itself.

When attention was allocated to one of the two stimuli, the neuron's response was primarily determined by the attended stimulus, meaning that its firing rate was enhanced when the preferred stimulus was attended but reduced when the non-preferred stimulus was attended.

The neuron's response was thus biased in favor of the attended stimulus, whereas the influence of the unattended stimulus on the response was attenuated, as if the neuron's RF had contracted around the attended stimulus, so that the unattended stimulus now would fall outside this area.

Reynolds et al., J. Neurosci., 1985

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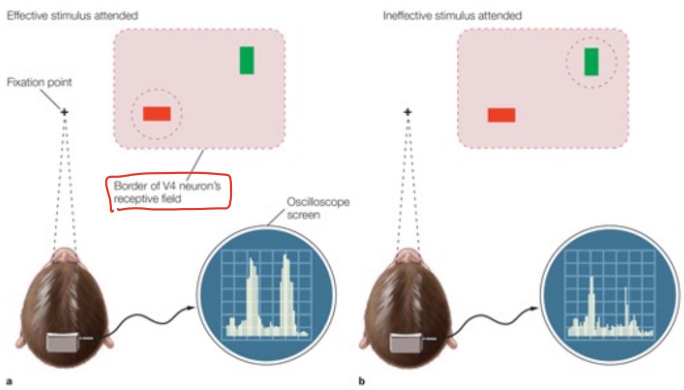
Moran & Desimone, Science, 1985



The areas circled by dashed lines indicate the attended locations for each trial.
A red bar is an effective stimulus, and a green bar is an ineffective stimulus for this V4 neuron.
The neuronal firing rates are shown to the right of each monkey head.
The first burst of activity is to the cue, and the second burst in each image is to the target array.

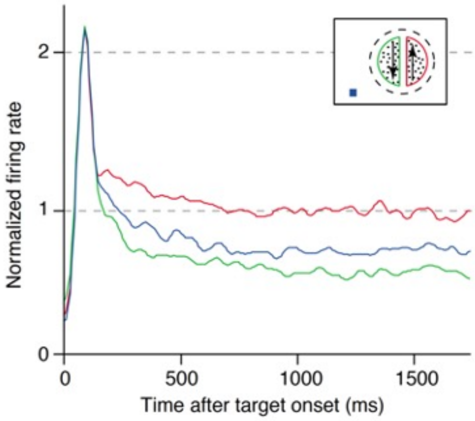
Moran & Desimone, Science, 1985

The curves indicate the firing rate averaged across 64 cells from the middle-temporal area (MT) and the medial superior temporal area (MST).

Two half-circle shaped random dot patterns were presented inside the RF, one moving in the preferred direction and the other in the anti-preferred direction of the neuron.

The x-axis plots the time (in ms) from the onset of the stimuli.

The animal was instructed before every trial to direct its attention the preferred direction stimulus inside the RF (red line), toward the anti-preferred direction stimulus inside the RF (green line), or to a square on top of the fixation cross (blue line) outside the RF.



Note that attentional modulation sets in later than the sensory response.

This could be caused by response saturation in the onset response or could be be a reflection of a genuine delay between the two effects.

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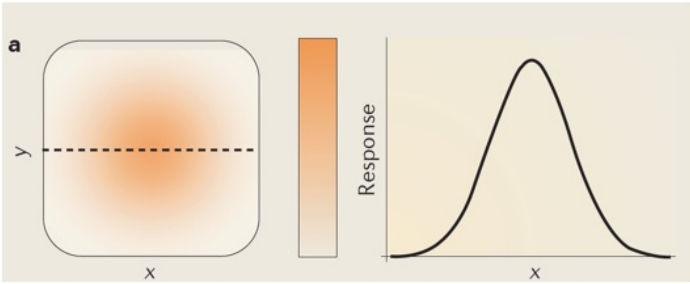
Treue and Maunsell, Nature 1996



A given stimulus typically elicits the strongest response from the centre of the RF, with the response gradually declining as the stimulus is presented further away from the centre of the RF.

Thus, the RF can be well described by a two-dimensional Gaussian distribution.

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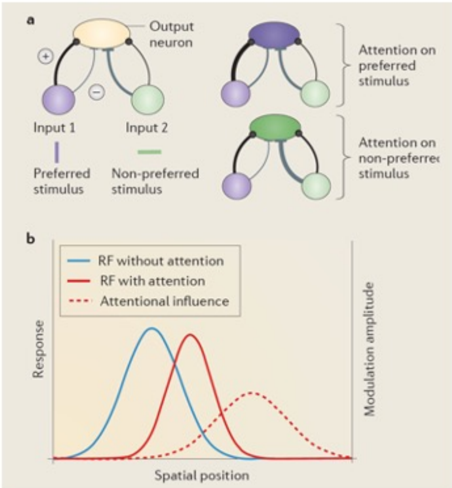
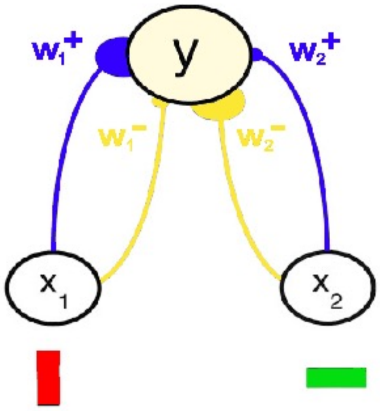
Mechanisms of attention effects on receptive fields



a) Two input populations of neurons project to the neuron of interest (output neuron). The input population responding to the stimulus preferred by the output neuron (purple) has predominantly. excitatory connections (thick black line), whereas the one responding to the non-preferred stimulus has predominantly inhibitory connections (thick grey line) to the output neuron. Attention strengthens the connections from the input population that responds to the attended stimulus, so that the response of the output neuron is dominated by the attended stimulus.

b) Attention changes the gain of inputs to the RF. The strength of the attentional influence (red dashed line) follows a Gaussian distribution, with the strongest modulation at the attentional focus and weaker modulation elsewhere. Multiplicative interaction of the baseline RF (blue solid line) and the attentional influence (red dashed line) results in a Gaussian RF profile (red solid line) that is narrower and shifted towards the attentional focus.



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

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

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

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

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

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.

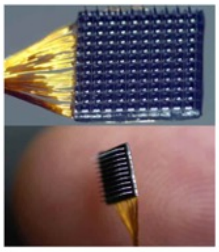
Thus, it is crucial to understand the way information is encoded in populations of neurons.

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

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.

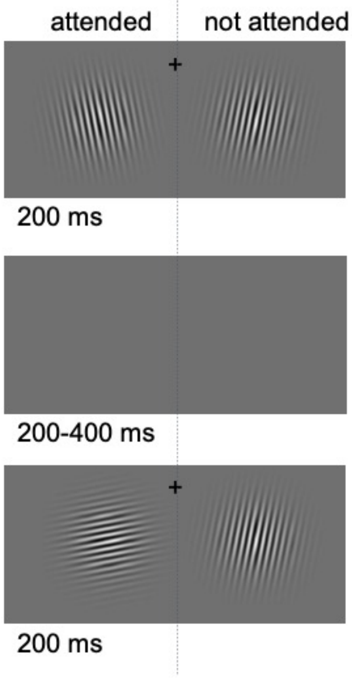


Each monkey had two arrays, which allowed to monitor populations of neurons in both hemispheres simultaneously.

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.

Cohen & Maunsell, Nature Neurosci., 2009



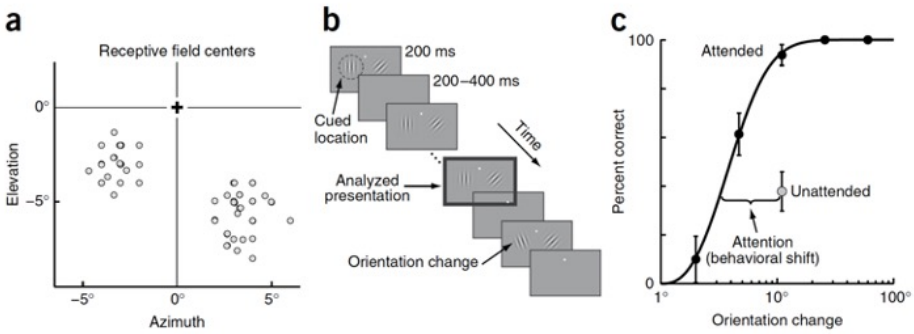
Orientation change–detection task:

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 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.

Cohen & Maunsell, Nature Neurosci., 2009



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.

Cohen & Maunsell, Nature Neurosci., 2009

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);

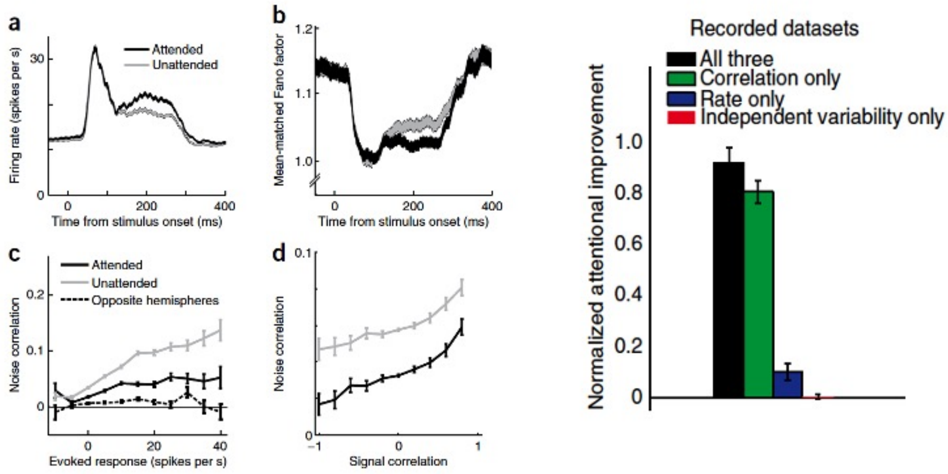
Attention reduced the trial-to-trial variability of individual neurons, as indicated by a drop in the Fano factor, the ratio of the variance of the firing rates to the mean (see b);

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



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

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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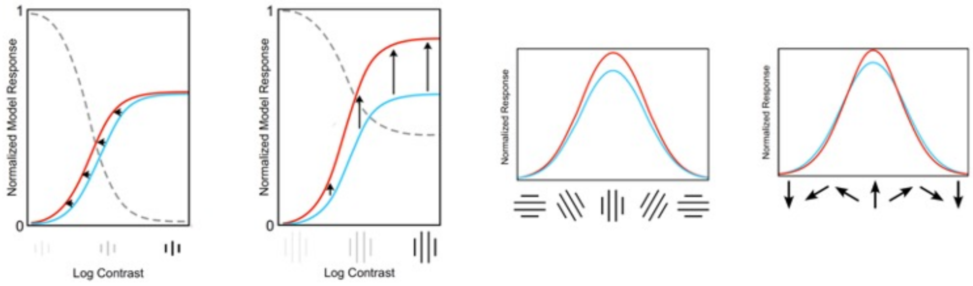
Attentional modulations



Contrast gain

Response gain

Multiplicative scaling

Multiplicative sharpening

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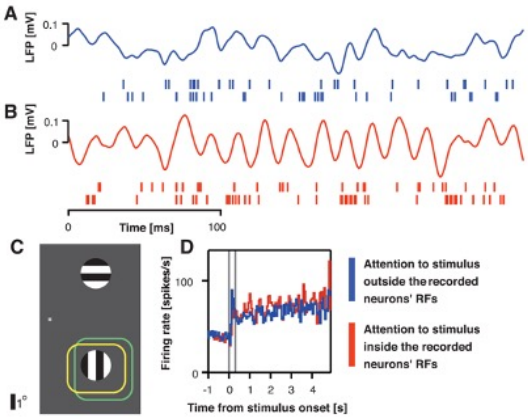
Selective visual attention modulates oscillatory neuronal synchronization

In addition to increasing the information available in the neuron firing rate , attention can potentially enhance signal efficacy via synchrony among neurons encoding the attended stimulus.

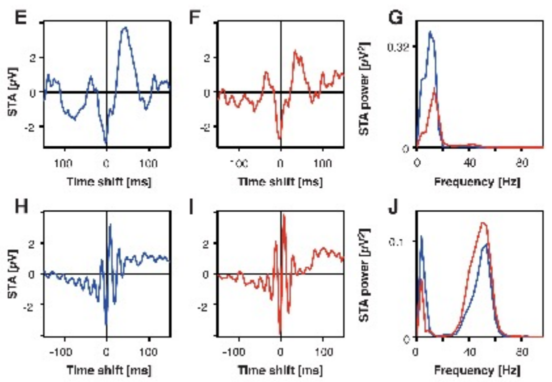


Spikes from small clusters of neurons (multi-unit activity) and local field potentials (LFPs) simultaneously from multiple V4 sites with overlapping receptive fields (RFs) (Fig. A, B)

Neurons in cortical area V4 were recorded while monkeys attended to behaviorally relevant stimuli and ignored distracters.

The response histograms (Fig.D) show stimulus-evoked responses but no clear effect of attention, either during the pre-stimulus delay or during the stimulus period

Fries et al., Science, 2001



The spike-triggered average of the LFP (termed STA) was used to assess the strength of postsynaptic activity at one cortical site caused by spiking at another location.

Delay-period STAs for attention outside the RF (E) and into the RF (F) and the respective power spectra (G). Stimulus-period STAs for attention outside the RF (H) and into the RF (I) and the respective power spectra (J).

During the stimulus period, there were two distinct bands in the power spectrum of the STAs (Fig. 1J), one below 10 Hz and another at 35 to 60 Hz.

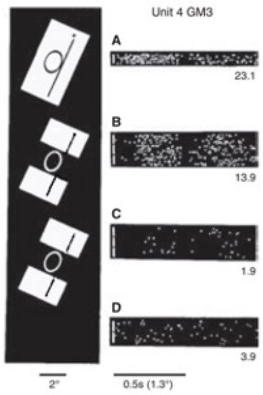
With attention, the reduction in low-frequency synchronization was maintained and, conversely, gamma-frequency synchronization was increased.

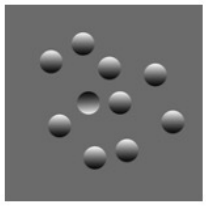
Fries et al., Science, 2001

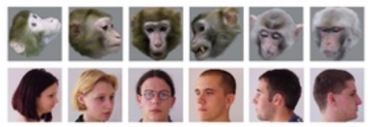
Bottom-up visual attention

Neurons at the earliest stages of visual processing are tuned to simple visual features such as luminance and color contrast, edge orientation, direction and velocity 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

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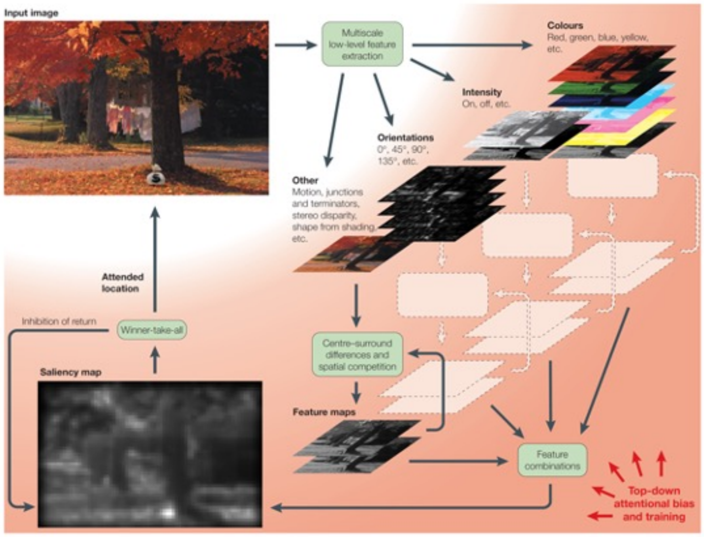
A saliency map can provide an efficient control strategy for the deployment of attention on the basis of bottom-up cues.

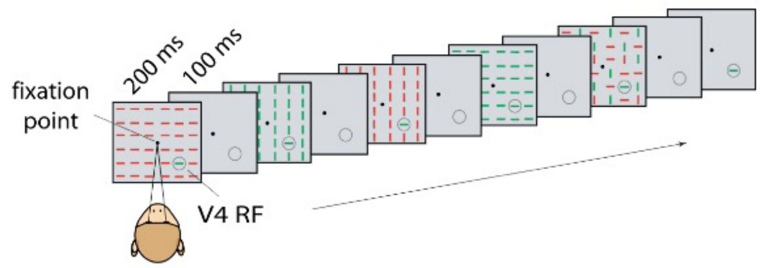


Itti & Koch, Nat Rev Neurosci, 2001

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

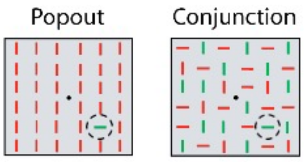
These “popout” stimuli are believed to draw attention in a bottom-up manner, with search being driven largely via “parallel” or “preattentive” processing .

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.

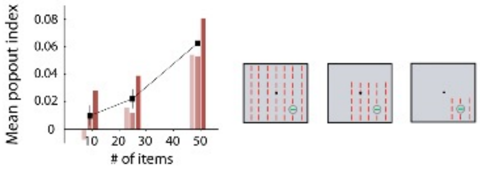


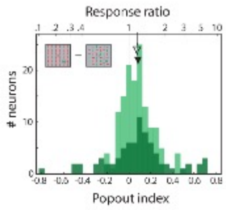
To study the impact of bottom-up (stimulus-driven) effects of salience on area V4 responses, visual stimuli were presented during a fixation task.

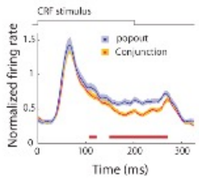
In this task, 300 ms following fixation, a series of five stimulus arrays plus the singleton were presented inside the neuron's RF for 200 ms each, with 100 ms in between presentations.
The array stimuli were behaviorally irrelevant; in no condition was the monkey rewarded for responding in any way to 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.



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.







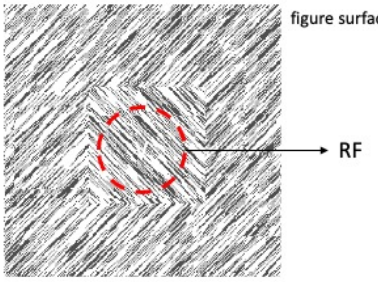
The magnitude of the popout modulation increased with the number of array items and the number of features that define the popout stimulus
Response difference (popout-conjunction) histograms for 82 neurons for stimulus arrays that varied in size (49 items, i.e., 48 surrounding items and 1 RF stimulus; 25 items; 9 items), or in which feature distinguished the RF stimulus from the non-RF items (color, orientation, or both).

Left, Distribution of Popout Index (response-popout/response-conjunction) for a population of 137 neurons (light green) and for a subpopulation of 76 neurons in which surround responses were subtracted (dark green).

Right, 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.

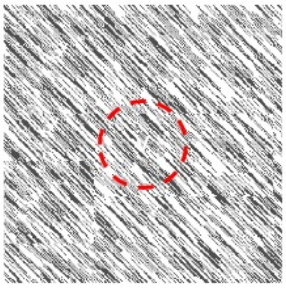
Burrows et al., J. Neurosci, 2006

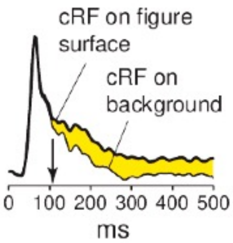
Neural correlates of bottom-up attention



A square patch was made to perceptually pop out as a circumscribed figure by virtue of differences between the orientation of the texture elements within that patch and the surround.

V1 neurons gave significantly higher responses when the RF covers the figure surface compared to the background surface at 100 ms, even though the stimulus within the RF is identical in both situations.

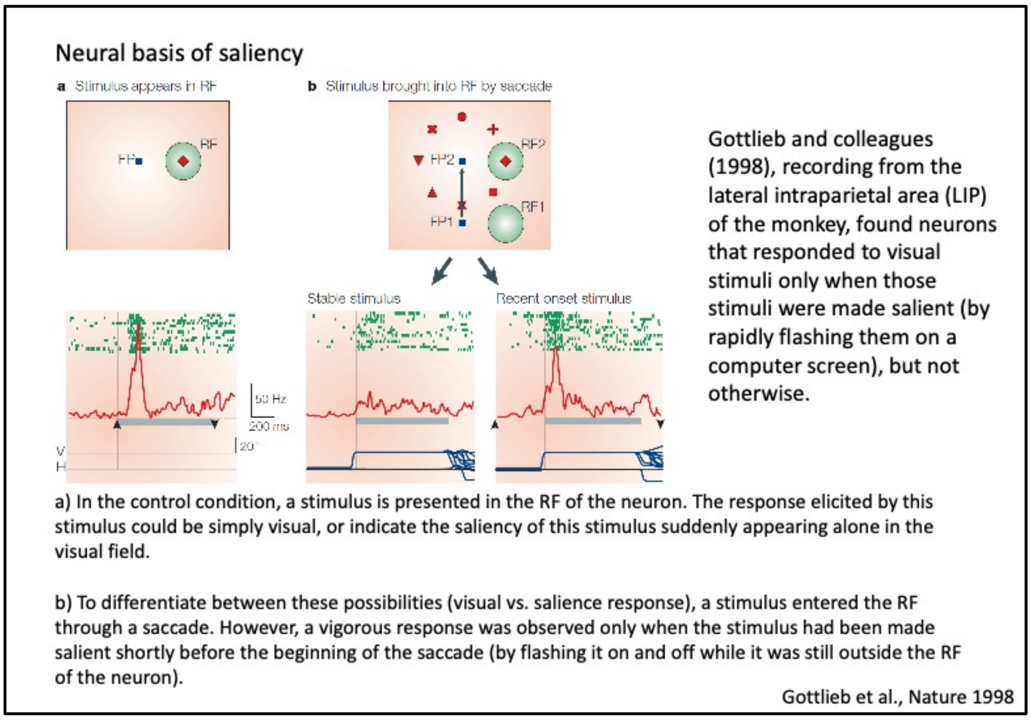




This response enhancement is delayed relative to the initial visual response to the onset of the search display, suggesting that it is mediated by recurrent feedback connections.

The mere organization of visual elements into perceptual object may capture attention automatically.

Lamme et al., J. Neurosci, 1995



Effect of a recent onset stimulus on the responses of one LIP neuron.

a) Neuron response when a diamond-shaped visual stimulus was flashed for 1 s at the right while the monkey maintained central fixation. The approximate location of the neuron's receptive field (RF) is indicated by the shaded green area.

a) Responses during the stable-array task. Top, illustration of the visual display at the time of the saccade from FP1 to FP2 (arrow). Eight symbols arranged in a circular array remained stably on the screen throughout collection of these data. During presaccadic fixation (at FP1) the neuron’s receptive field lay at position RF1, entirely outside the array. The saccade brought the receptive field to position RF2 The neuron had minimal responses in the stable-stimulus condition when all eight symbols remained stably on the screen. It responded strongly in the recent-onset condition when seven stimuli were stable but the diamond was turned on and off on each trial. Its firing rate in a 200-ms interval beginning at the end of the saccade was 21 +/-11 Hz (mean and sd) in the stable-stimulus condition and 53 +/-23 Hz in the recent-onset condition.

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

overt attention

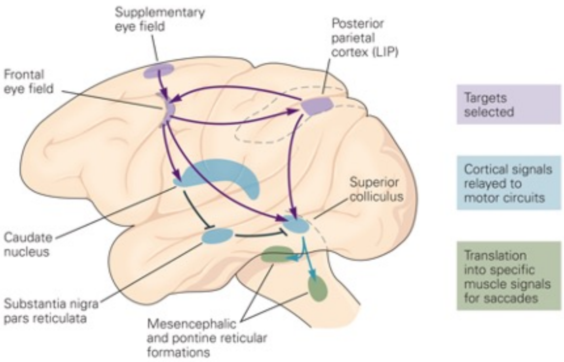
Relationship between saccade preparation and spatial attention

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.

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.

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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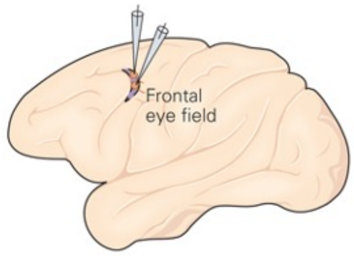
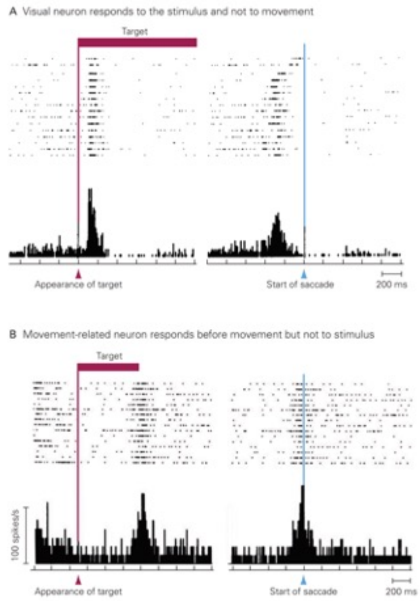


Visual and movement-related neurons in the frontal eye field (Bruce & Goldberg, J. Neurophysiol, 1985)



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

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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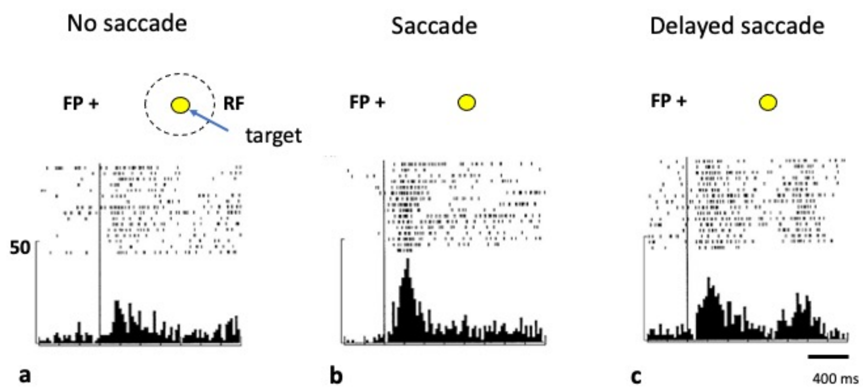
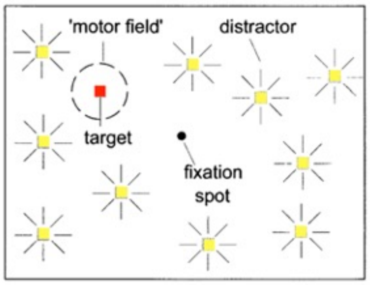
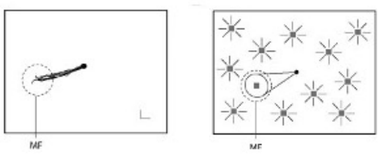


Presaccadic visual enhancement

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.

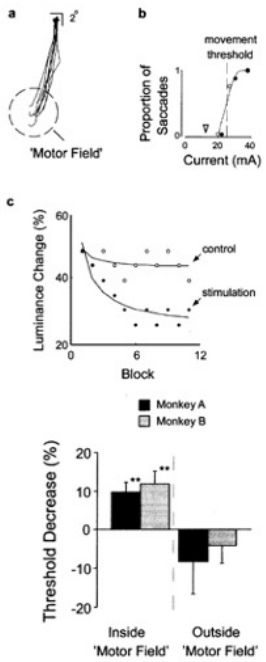
Moore & Fallah (2001) were the first to examine the effect of intracortical microstimulation on visual attention.

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



(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.

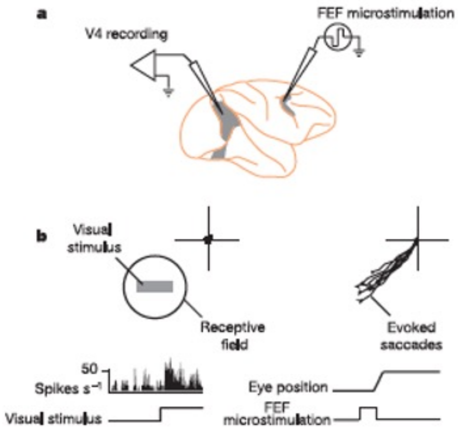
The subthreshold stimulation of the FEF immediately before (approximately 100ms) the appearance of the target significantly improved the animal's performance in detecting the luminance change (sensitivity).

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

Moore & Fallah, PNAS, 2001

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).

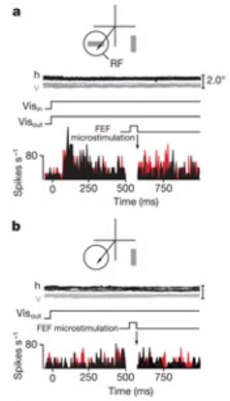


The enhancement effect was significantly increased by the presence of distracting stimuli (attentional competition).

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

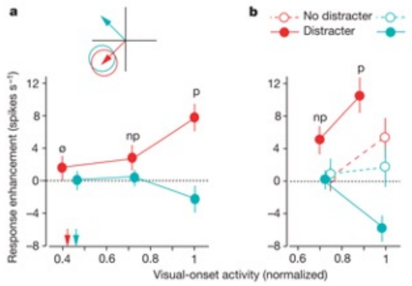
The results suggest that the gain of visual signals is modified according to the strength of spatially corresponding eye movement commands

Moore & Armstrong, Nature 2003



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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