Cognitive Neuroscience
9/9/21

Attention

1. Phenomenology of visual spatial attention in humans

2. Impact of attention on sensory responses in visual cortex

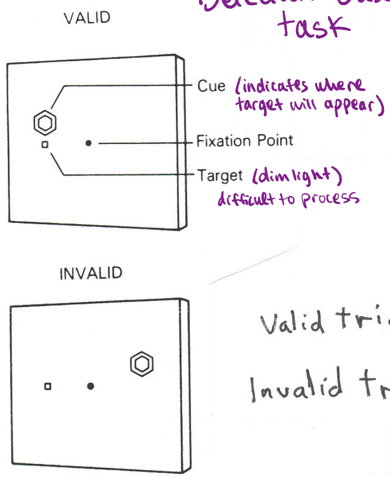
3. Control signals in frontal and parietal cortex: the ‘premotor’ theory of attention

(Executive control functions)

Everyone knows what attention is. It is the taking possession by 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, Principles of Psychology, 1890

Detection-based task

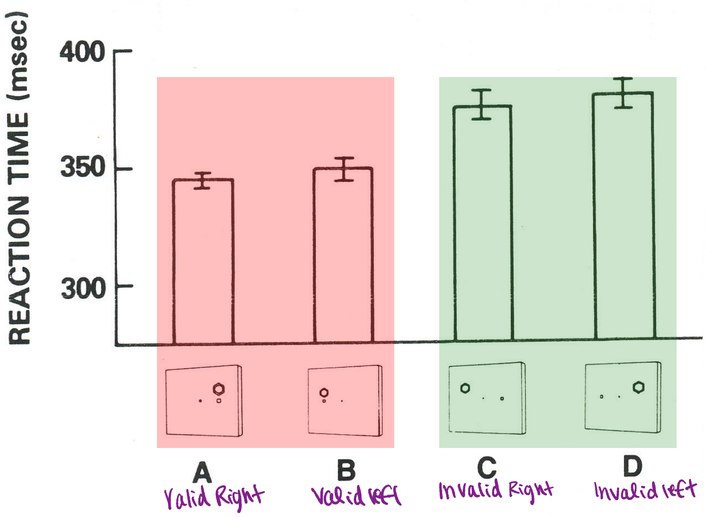


The Posner paradigm has been widely used for studies of covert orienting of attention.

Fig. 1. Cue and target configurations for experimental sessions. Each picture is a schematic representation of the tangent screen which the subjects faced. A central fixation point is turned on at the beginning and throughout each trial. Next a hexagonal stimulus (cue) is flashed for 75 ms followed after a variable interval by a small target light. Valid trials indicate that the cue and target are presented to the same visual hemifield. Invalid trials are those in which the cue and target are presented in opposite hemifields.

Valid trials: 70-85%

Invalid trials: 15-30%



Visual-visual interaction?

Fig. 2. Reaction times of normal subjects to valid, invalid, and diffuse cues. The vertical scale measures reaction times in msec for subjects to push a button in response to the onset of the target. At the bottom of each data column is a schematic representation of all of the stimulus conditions as seen by the subject. *A* is the validly cued target to the right visual field of the subject, *B* is a validly cued trial to the left visual field. These are followed by invalidly cued trials to the right (*C*) and left (*D*).

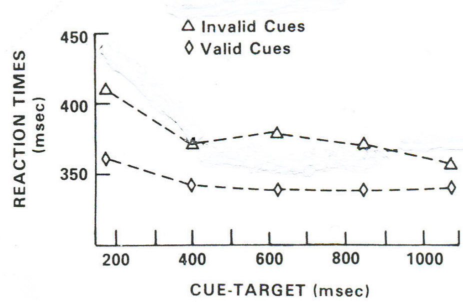


Fig. 3. Time course of validity effects for normal control subjects. The vertical axis indicates the reaction time in msec. The horizontal axis represents the time intervals between the onset of the cue and the onset of the target.

RT

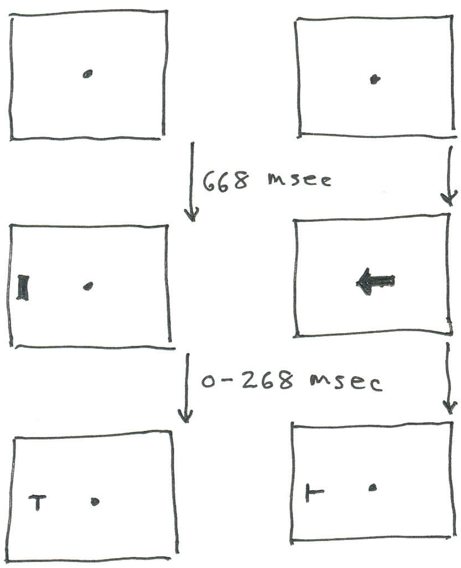
Invalid > Valid

Petersen et al.

Exp. Brain Res,

76: 267-280 (1989)

Conditions with **Peripheral** Cue | Conditions with **Central** Cue



Report orientation of the "T".

Cues were 100% valid. "T" and cue could be at 3:00, 6:00, 9:00 or 12:00.
"T" could have one of four orientations (T, ⊣, ⊥, ⊢).

Cheal & Lyon,
Quart. J. Exp. Psychol.
43A: 859-880 (1991)

Attention shifts more swiftly in response to a peripheral sudden-onset cue than in response to a central symbolic cue. There is much less improvement with practice for a peripheral sudden-onset cue than for a central symbolic cue. These observations suggest that sudden onset of a cue in the visual field periphery automatically captures attention.

Automatic (exogenous) ? | Voluntary (endogenous) ?

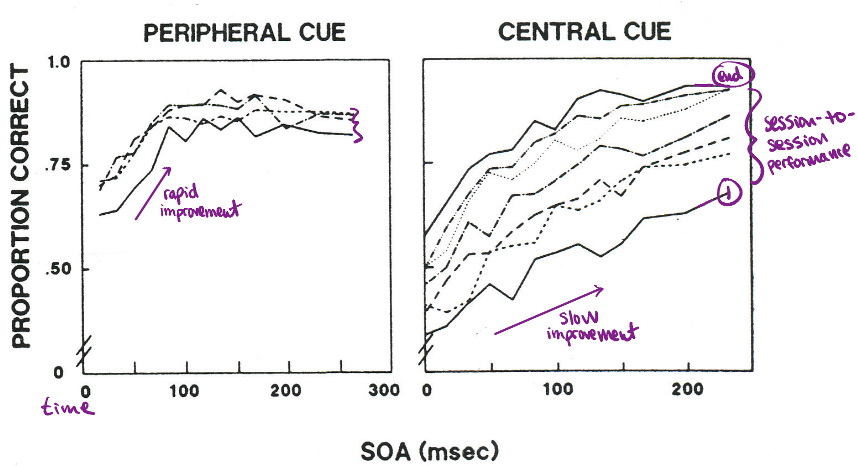


FIG. 5. Proportion correct as a function of cue–target SOA to show consistency of the shape of the curves with practice. Peripheral cue: four successive groups of 3000 trials for one observer in two-alternative, forced-choice discrimination of Ts in Experiment 1. Central cue: seven successive groups of trials (3744 trials for Groups 1–6, 2496 trials for Group 7) for one observer for the mean of three eccentricities in four-alternative, forced-choice discrimination of T-like characters in Experiment 8. Line styles for successive groups of trials are: 1: solid; 2: narrow dashes; 3: wide dashes; 4: dot-dash; 5: dots; 6: dot-dot-dash; 7: solid.

This experiment demonstrates (a) exogenous control by a spatial cue; (b) endogenous control by a spatial cue; and (c) endogenous control by a central cue.

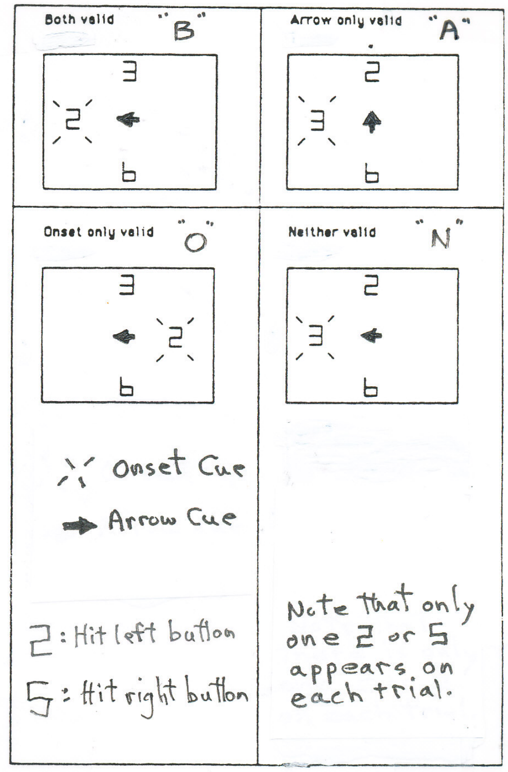
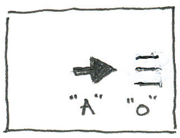


Figure 2. stimulus patterns used in Experiments 1 and 2. Only the target "2" is used in these examples, although "5" was used as a target equally often in all conditions.

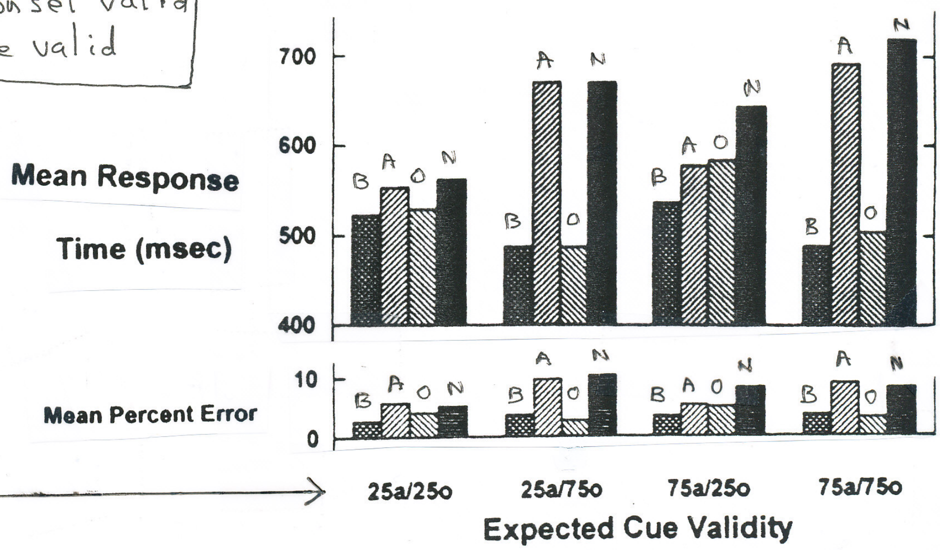
① Types of cue:



(both occur on every trial)

② Condition on this particular trial:

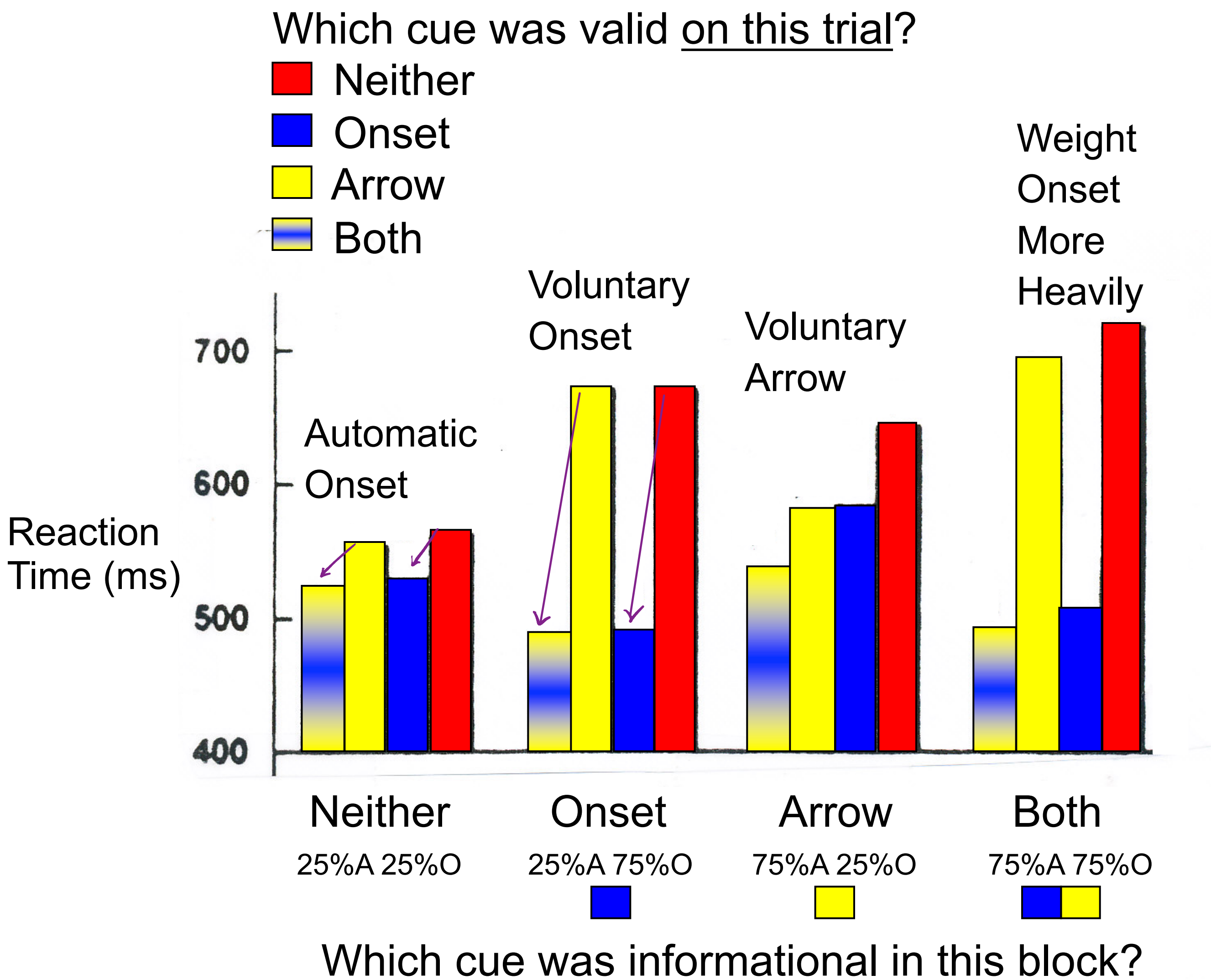
"B" = both cues valid
"A" = arrow only valid
"O" = peripheral onset valid
"N" = neither cue valid



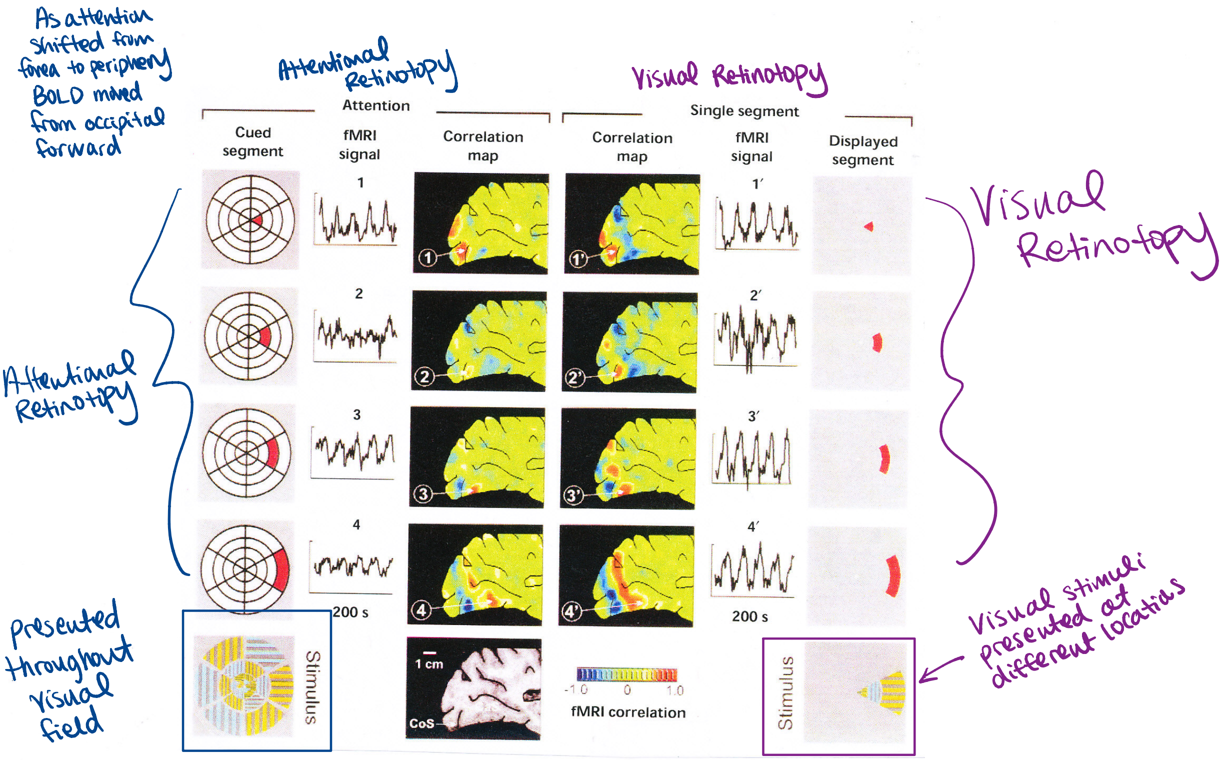
③ Percentage of Cue validity within a given block of trials

Figure 4. Mean response time plotted against the expected cue validity for each of four groups of subjects (e.g., 25a/25o = Group 1, for which 25% of the arrow cues and 25% of the abrupt onsets were likely to indicate targets). The data are plotted separately within each group for respective (left-to-right columns) trials on which both cues indicated the target position, only the arrow cue was valid, only the onset cue was valid, or neither cue was valid.

J.F. Juola et al.
Perception & Psychophysics
57: 333-342 (1995)

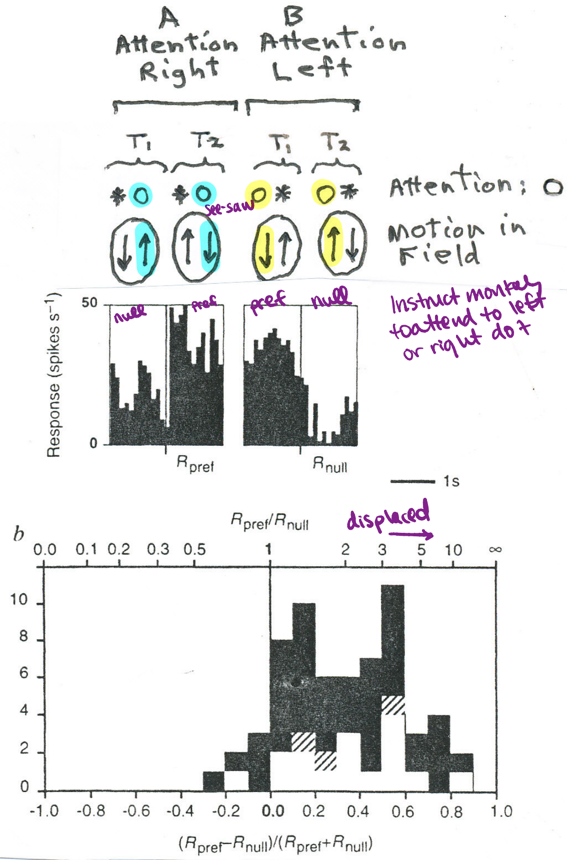


Which cue was valid on this trial?
Neither
Onset
Arrow
Both
Automatic Onset
Voluntary Onset
Voluntary Arrow
Weight Onset More Heavily
Reaction Time (ms)
700
600
500
400
Neither
25%A 25%O
Onset
25%A 75%O
Arrow
75%A 25%O
Both
75%A 75%O
Which cue was informational in this block?



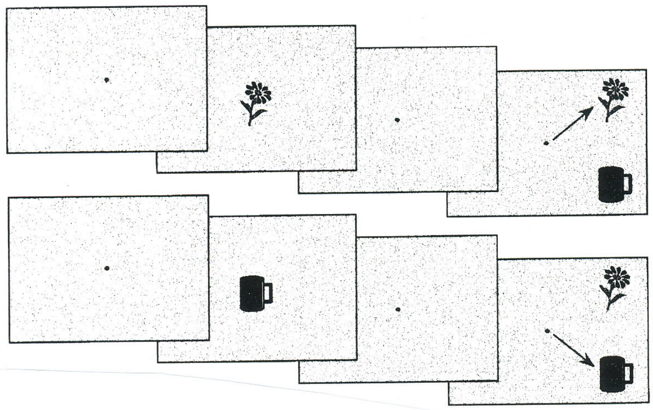
Brefczynski & DeYoe
Nature Neuroscience
2: 370 (1999)

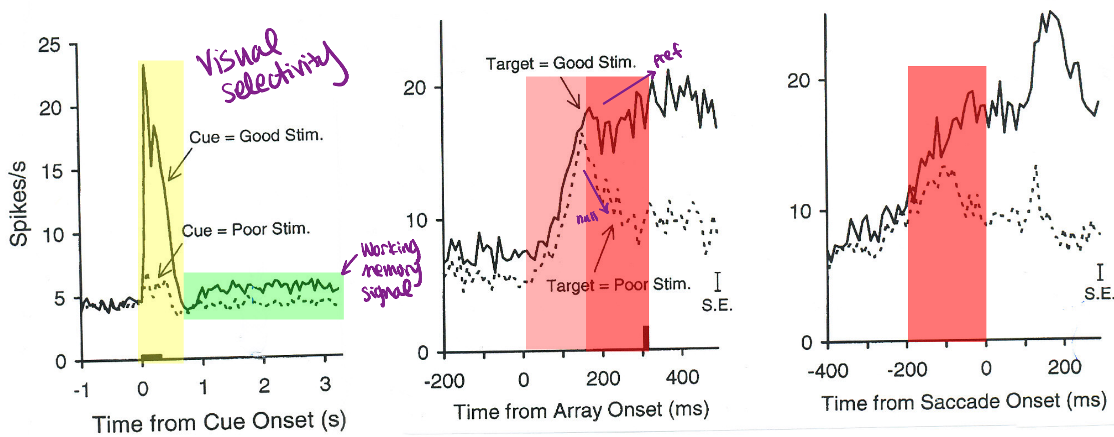
Human primary visual cortex contains a map of the contralateral visual hemifield. As a "single segment" compact visual stimulus is moved from the center (1′) to the periphery (4′) of the visual field, BOLD activation measured with fMRI migrates forward from the occipital pole. When, in the presence of a complex whole-field display, subjects are instructed to attend to one segment of the display ("cued segment") BOLD activation reflects its location. As the attended segment moves from center (1) to periphery (4), BOLD activation migrates forward from the occipital pole.



Record in Area MT from a neuron selective (in this example) for downward motion while two dots are moving back and forth out of phase (whenever one dot is moving up, the other is moving down) in its receptive field. The monkey is instructed on interleaved trials to attend either to the left or to the right dot. Whichever dot the monkey is paying attention to, the neuron fires when that dot is moving downward: time 2 (T_2) in case A and time 1 (T_1) in case B.

Treue & Maunsell, Nature 382: 539-541 (1996)





Bob Desimone and his colleagues have shown that population activity in inferotemporal cortex is high when the monkey attends to (and selects as an eye-movement target) the neuron's preferred image and low when he attends to the nonpreferred image.

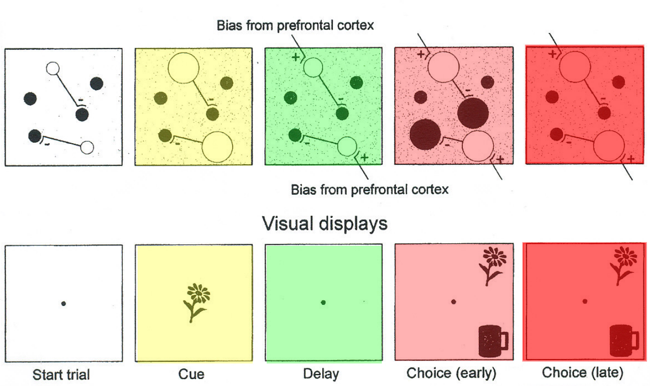


FIG. 22. Schematic representation of the search task with 2-stimulus arrays confined to the contralateral hemifield, and of the pattern of activity in a representative population of inferior temporal (IT) neurons. *Bottom diagrams* illustrate the visual displays during the relevant portions of the task. Each dot in the *top diagrams* represents an individual neuron, and the size of the dot indicates relative firing rate. A specific cue (here exemplified by the flower) activates the subpopulation of IT cells tuned to any of the various features of the cue. During the delay period, this subpopulation maintains a higher level of sustained activation, relative to other cells that are tuned to the properties of the distracter. When the search array is 1st presented, both the target and the nontarget initially activate neurons for which they represent effective sensory stimuli. Later, cells tuned to the properties of the target stimulus remain active, whereas cells tuned to the properties of the distracter are suppressed. This late divergence in activation may depend on competitive interactions within IT cortex, here schematically depicted by inhibition of cells tuned to the distracter (cup) by cells tuned to the target (flower). We hypothesize that the competitive interactions are biased by top-down feedback projections from prefrontal cortex. In a given trial these projections give a competitive advantage (positive bias) to cells in IT coding the cue-target stimulus in that trial, at the expenses of cells coding the distracter.

They have put forward a model based on "biased competition" to explain this effect.

Chelazzi et al.
J. Neurophysiol. 80: 2918-2940 (1998)

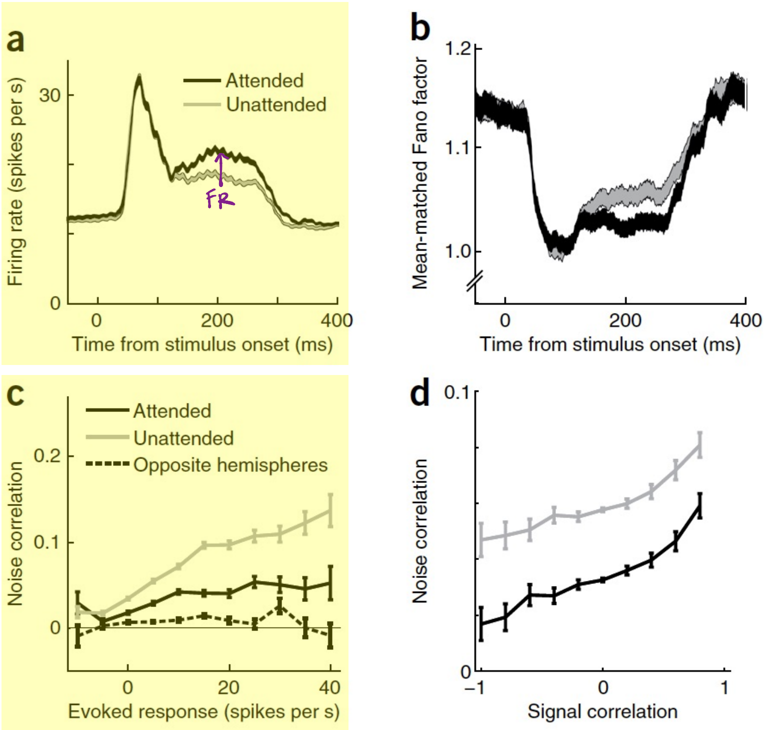


Figure 2 Attentional modulation of firing rate, Fano factor and noise correlation. (**a**) Attention increased firing rates. A peristimulus time histogram of firing rates for all 3,498 single neurons and multiunit clusters on trials in which the stimulus in the same hemifield as the neuron's receptive field was attended (black line) or unattended (gray line) is shown. Line width represents the s.e.m. Ripples reflect the 85-Hz frame rate of the video display. (**b**) Attention decreased mean-matched Fano factor. Plotting conventions are as described in **a**. (**c**) Attention decreased noise correlation. Spike count noise correlation (for responses over the period from 60 to 260 m following stimulus onset) is plotted as a function of the mean stimulus modulation for the pair of neurons (firing rate during the stimulus–firing rate during the interstimulus blank period). For pairs of neurons in the same hemisphere, correlation was lower when the stimulus in the neurons' receptive field 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. Error bars represent s.e.m. (**d**) Raw nois correlation, but not attentional modulation, depended on signal correlation. Mean noise correlation is plotted as a function of signal correlation, which can be thought of as the similarity in spatial and feature tuning of the two neurons (see Online Methods). As has been previously reported, noise correlation increases with signal correlation. However, the difference in correlation between the attended (black line) and unattended (gray line) conditions did not depend on signal correlation. Error bars represent s.e.m.

Marlene Cohen and colleagues have described another effect of attention on neuronal visual responses in area V4: a reduction in noise correlation. Even when a stimulus is identical from trial to trial, a V4 neuron responds to the stimulus with a strength that varies across trials in a seemingly stochastic (or noisy) fashion. In pairs of simultaneously recorded neurons, the cross-trial variations tend to be positively correlated. Attention reduces this effect. The reduction of noise correlation can be thought of as arising from lowered susceptibility of the two neurons to noisy common inputs.

Noise correlation:
across trials w/ indentical conditions, is the variation in trials b/t 2 neurons identical?

Cohen and Maunsell, Nat. Neurosci. 12: 1594-1600 (2009).

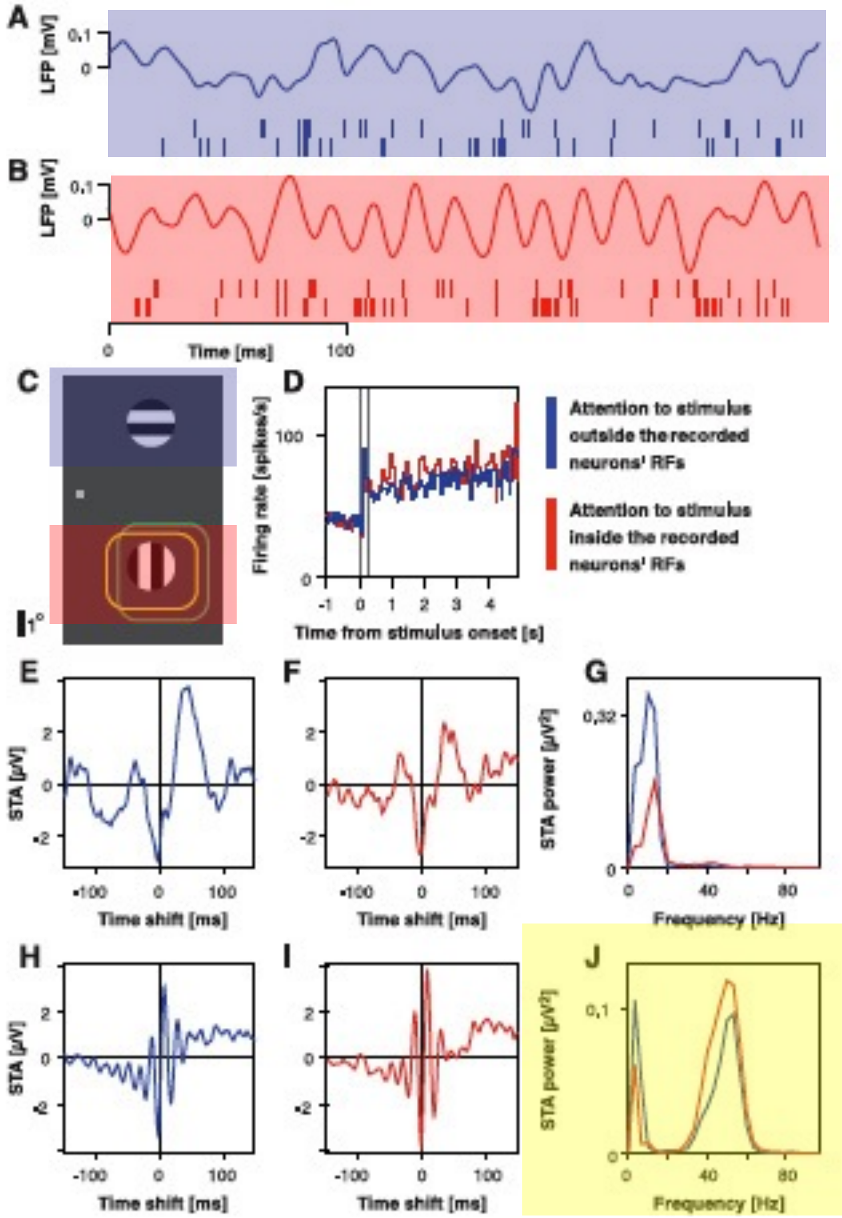


Fig. 1. Attentional modulation of oscillatory synchronization between spikes and LFP from two separate electrodes. Raw stimulus–driven LFP and multi-unit activity with attention outside the RF (**A**) and into the RF (**B**). (**C**) RFs (not visible to monkey; green: spike recording site, yellow: LFP recording site); fixation point and grating stimuli are to scale. The RFs for both recording sites were determined from the multi-unit activity and included only one of the two stimuli. In separate trials, this stimulus was either attended or ignored. Data are from 300 correct trials per attention condition. (**D**) Firing-rate histograms. Vertical lines indicate stimulus onset and 300 ms after stimulus onset. Delay period was the 1-s interval before stimulus onset, and stimulus period was from 300 ms after stimulus onset until one of the stimuli changed its color. 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**).

In crowded visual scenes, attention is needed to select relevant stimuli. To study the underlying mechanisms, we recorded neurons in cortical area V4 while macaque monkeys attended to behaviorally relevant stimuli and ignored distracters. Neurons activated by the attended stimulus showed increased gamma-frequency (35 to 90 hertz) synchronization but reduced low-frequency (<17 hertz) synchronization compared with neurons at nearby V4 sites activated by distracters. Because postsynaptic integration times are short, these localized changes in synchronization may serve to amplify behaviorally relevant signals in the cortex.

Fries, Reynolds, Rorie and Desimone, Science 291: 1560 (2001)

Premotor Theory of Attention

836 Colloquium Paper: Corbetta Proc. Natl. Acad. Sci. USA 95 (1998)

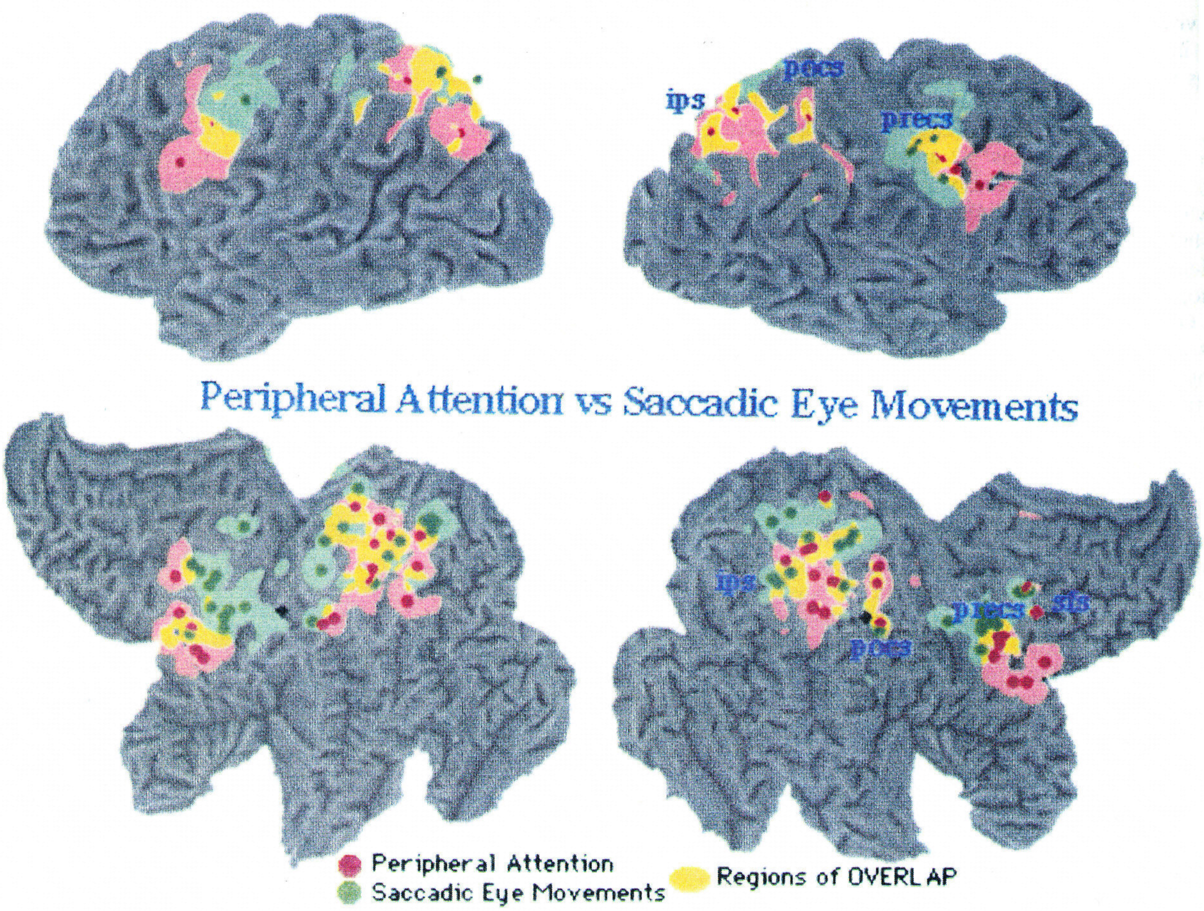
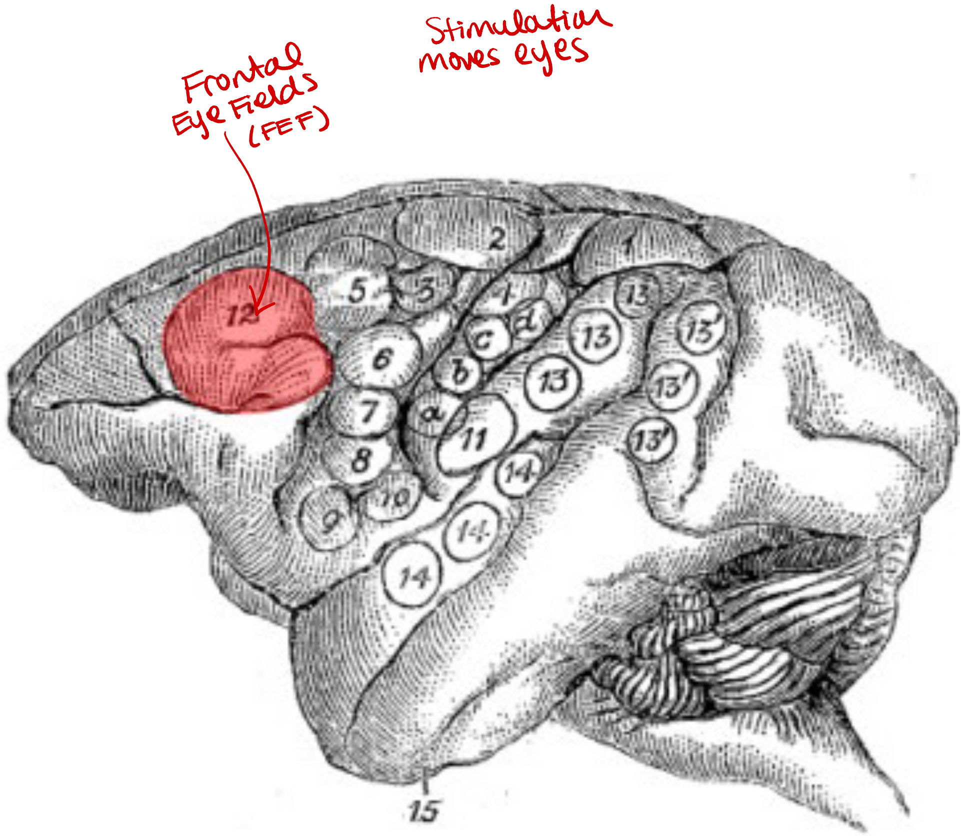


FIG. 5. Visible Man Brain as in Fig. 2. Foci for attention from Fig. 2 (red) and eye movement from Fig. 4 (green). Areas of overlap are in yellow

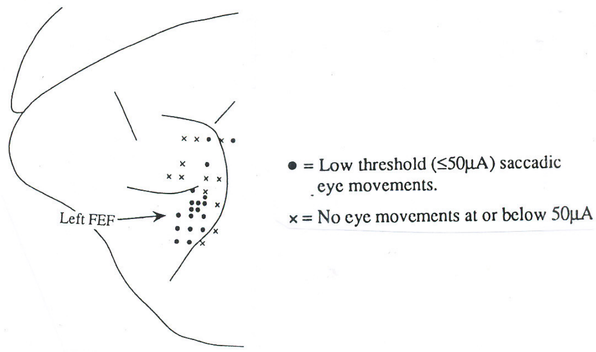
Preparing to move eyes → prep for visual processing

In human fMRI studies, frontal and parietal areas active in conjunction with covert peripheral attention largely overlap areas active in conjunction with saccadic eye movements.

Marked overlap b/t cortex
eye movement & covert attention



Ferrier 1875



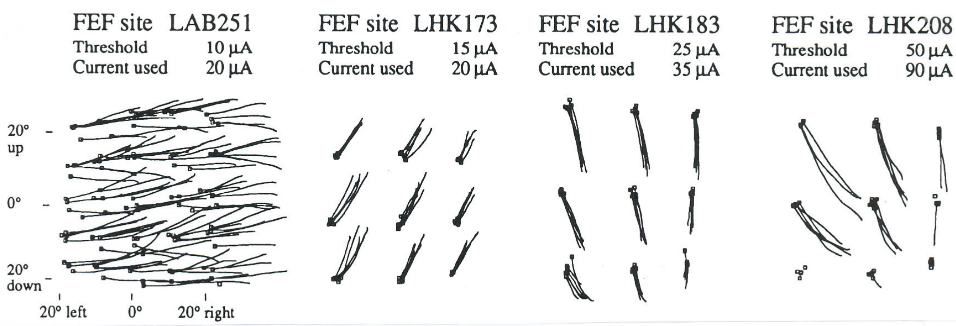
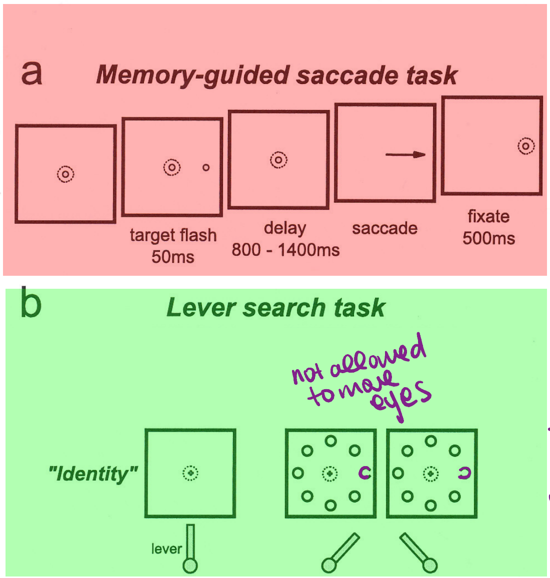


FIG. 4. Elicited saccades from 4 frontal eye field (FEF) sites. *Top*: 2-dimensional plots of elicited saccades from different orbital positions. Squares: eye positions at time of stimulation. Squares without saccade trajectory lines: trials where saccades were not elicited. Threshold was defined as the current necessary to elicited saccades during central fixation in half of the stimulation trials. The current used to elicit saccades in the orbital position tests was ~10–20 µA above threshold.

Russo & Bruce
J. Neurophysiol.
69: 800 (1993)

Electrical microstimulation of the monkey frontal eye field (FEF) elicits a saccadic eye movement. The direction and amplitude of the saccade tend to be constant at a given site regardless of the eye's starting point. At a site where neurons have visual receptive fields 10° to the right of fixation and fire during spontaneous 10° rightward saccades, microstimulation would commonly elicit 10° rightward saccades.



Covert allocation to target w/ no eye movement

Figure 1. The tasks. ***a***, The memory-guided saccade task. After the monkey fixated on a central spot, a peripheral stimulus identical to the fixation spot was flashed for 50 ms at one of six or eight locations. After a delay, the fixation spot was removed, and the monkey was instructed to make a saccade to the remembered target location. ***b***, The manual lever search task. After the monkey grasped a lever in the vertical position, a small fixation cross appeared. After the monkey fixated on the central cross, a search array appeared in which one of the stimuli was different. In the location search ("Location"), the monkey was rewarded for turning the lever in the same direction as a different-colored stimulus in relation to the fixation cross. In the identity search ("Identity"), the monkey was rewarded for turning the lever in the same direction as the gap in the C stimulus.

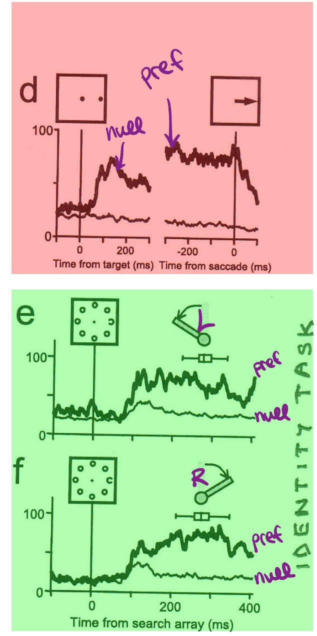


Figure 3. Representative examples of two visually responsive FEF neurons. ***a–c***, The activity of a visuomovement neuron recorded during the memory-guided saccade task aligned on both target onset and saccade initiation (***a***) and the two complements of the location search task in which the target was red and the distractors were green (***b***) or in which the target was green and distractors were red (***c***). The monkey was rewarded for maintaining fixation on the central cross and indicating the location of the singleton target with a lever turn. ***d–f***, The activity of a visual neuron recorded during the memory-guided saccade task aligned on both target onset and saccade initiation (***d***) and the identity search task in which the monkey was rewarded for indicating the direction of the C target among O distractors as pointing left (***e***) or right (***f***). For all plots, the activity on trials in which the target landed in the receptive field of the neurons (thick line) is plotted with the activity on trials in which no stimulus (***a***, ***d***, thin line) or in which distractors (***b***, ***c***, ***e***, ***f***, thin line) landed in the receptive field of the neurons. The box-whisker plot in each search panel indicates the median, quartiles, and range of lever turn reaction times. Diagrams showing the correct direction of the lever turn when the target was in the receptive field of the neurons are above each box-whisker plot.

Thompson et al.
J. Neurosci. 25: 9479 (2005)

Neurons in the monkey frontal eye field (FEF) not only carry visual, delay-period and motor signals during the MGS task (Fig. 1a & Fig. 3a, d) but also fire when the monkey is simply covertly attending to a stimulus in the response field (Fig. 1b & Fig. 3b-c, e-f).

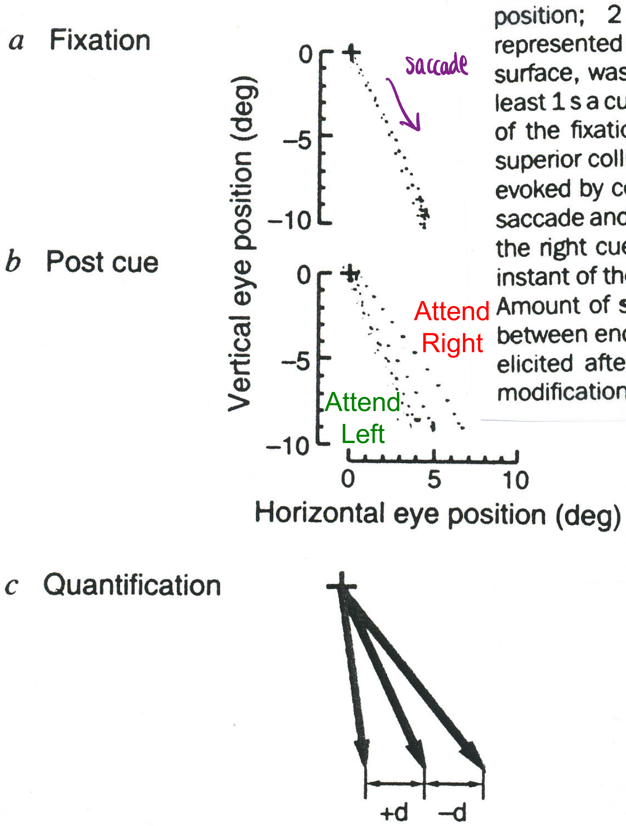
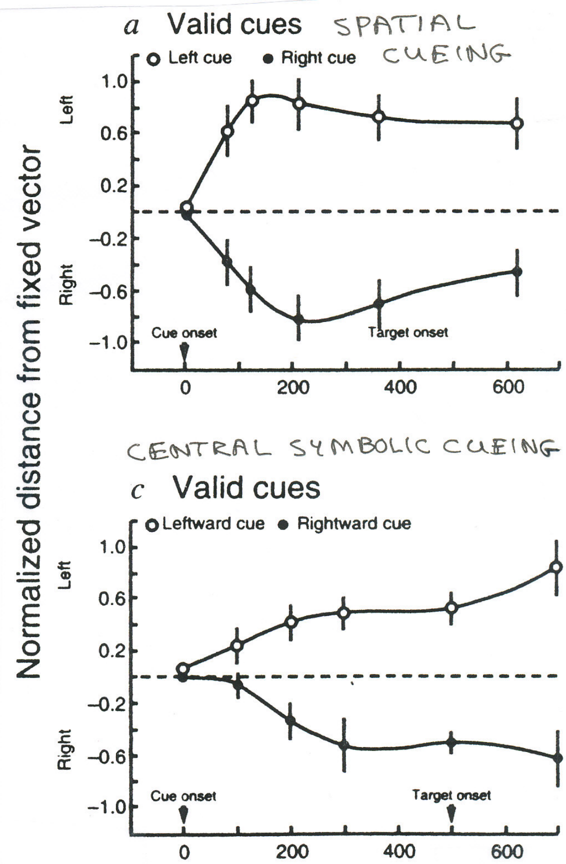


FIG. 1 *a*, Three fixed-vector saccades evoked during periods of fixation. *b*, Modified saccades after the cue onset. *X–Y* plots of the monkey's eye position; 2 ms between dots. Monkey fixated a central stimulus represented by +. The site of a burst cell, 1.7 mm from the collicular surface, was stimulated. In *b*, after the monkey maintained fixation for at least 1 s a cue appeared indicating the target location (12° to the left or right of the fixation point). At various random times after the cue onset, the superior colliculus was stimulated (five trials). The direction of the saccade evoked by collicular stimulation was different from that of the fixed vector saccade and shifted toward the cued location. Red traces were evoked after the right cue, blue were after the left cue, and black were evoked at the instant of the cue onset. *c*, Scheme showing how we analysed these data. Amount of shift of the evoked saccade was calculated as a distance (*d*) between end points of the averaged fixed-vector saccade and the saccade elicited after the cue onset. Positive values were arbitrarily assigned to modifications to the left.

A clever demonstration that when monkeys shift attention covertly they also program eye movements to the attended locations. Eye movements elicited by collicular electrical stimulation are deflected left or right when the monkey attends left or right.



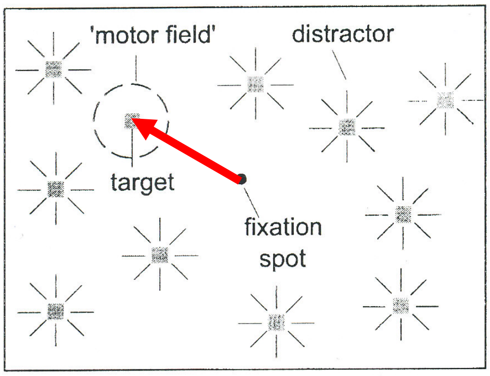
SC → map of eye movements

FIG. 3 Effects of peripheral cueing (*a*) and symbolic cueing (*c*) on the shift of the evoked saccade during a hand-response task. The format of the figure is as Fig. 2. The data in *a* and *b* represent the average of 8 different collicular sites.

Kustov & Robinson
Nature 384: 74–77 (1996)

eye movement plan w/out moving eyes

a



Delivered electrical Stimulation while RF was over target

↓ strength of stimulation (excitation not saccade)

b

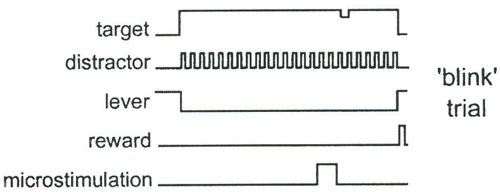
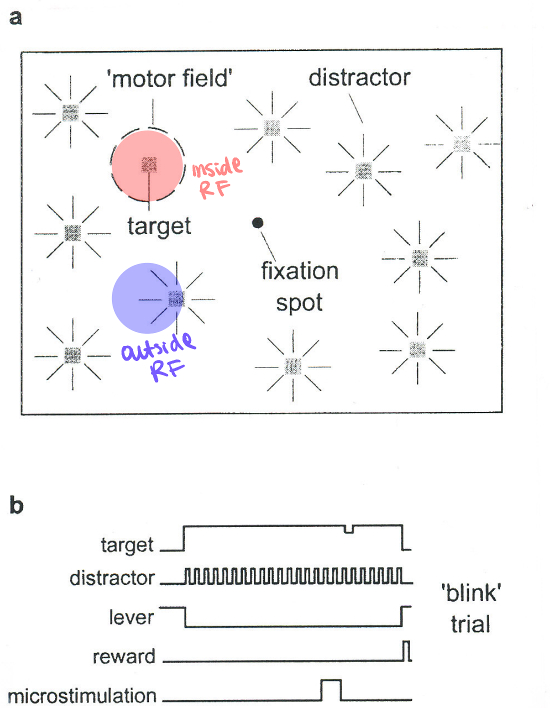


Fig. 1. Schematic depiction of the spatial attention paradigm used to measure the effects of microstimulation. (*a*) Illustration of the visual display viewed by the monkey. The monkey was trained to fixate on the central fixation spot and attend to a peripheral target that could transiently dim at a random time during the trial. While the monkey awaited the blink event, 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 suprathreshold stimulation. (*b*) The temporal sequence of events during a typical microstimulation trial. The monkey attains fixation, depresses the lever to start the trial, and then releases the lever if and when the target dims. Throughout each trial, a distractor is flashed at random locations at a fixed rate (32 Hz). The top set of traces marked 'blink' trial shows the sequence of events in a trial in which the target transiently dims (32–48 ms) at a random time (500–1,300 ms) and the monkey is rewarded for releasing the lever within 600–800 ms. Note than in this trial a 100-ms (subthreshold) stimulation train immediately precedes the blink event. The interval between the onset of the 100-ms stimulation train and the onset of the blink event, which varied from 50 to 175 ms, was defined as the stimulation onset asynchrony.

Moore & Fallah (PNAS 98:1273 (2001)) electrically stimulated the monkey frontal eye field (FEF) at currents so low that they did not elicit eye movements. Attention still shifted in the direction the eyes would have moved, as reflected by a decrease in brightness threshold for detection of a small spot flashed in a field of distractors. FEF thus appears to control attention.



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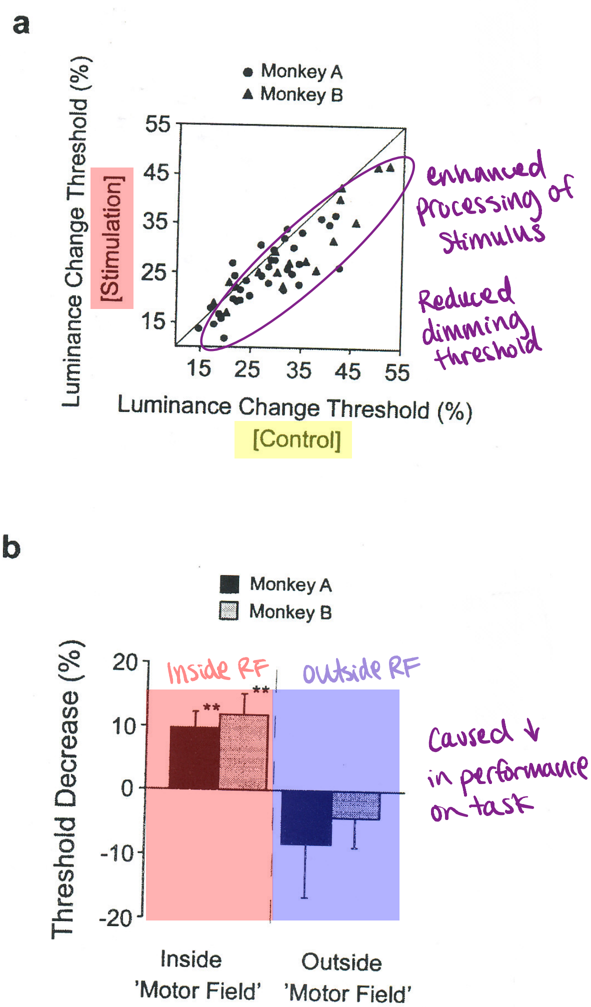

Fig. 3. Effect of microstimulation on psychophysical thresholds in two monkeys performing the spatial attention task. (*a*) Comparison of the distribution of luminance change thresholds obtained with and without stimulation when the attention task was performed inside of the MF. The vast majority of threshold points fall below the line of unity, illustrating the tendency of thresholds to be lower with stimulation. (*b*) Average decrease in psychophysical thresholds obtained when the attention task was performed inside or outside the MF in each monkey. The reduction in threshold signifies the difference in target luminance change required for equal performance on stimulation and control trials, expressed as a percentage of the control contrast threshold [(1 − [$contrast_{stim.}/contrast_{control}$]) × 100]. Positive values denote decreases in threshold with stimulation, whereas negative values denote increases. Targets positioned outside of the MF were on average 17° from the MF, but within the same hemifield. Double asterisks (**) denote a significance of $P < 0.001$.

Moore & Fallah (PNAS 98:1273 (2001)) electrically stimulated the monkey frontal eye field (FEF) at currents so low that they did not elicit eye movements. Attention still shifted in the direction the eyes would have moved, as reflected by a decrease in brightness threshold for detection of a small spot flashed in a field of distractors. FEF thus appears to control attention.

FEF IS controlled in processing of attention