

RESPONSES OF CELLS IN THE SUPERIOR COLLICULUS DURING PERFORMANCE OF A SPATIAL ATTENTION TASK IN THE MACAQUE

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(With 15 figures)

ABSTRACT

Previous studies have reported that superficial layer cells in the superior colliculus (SC) give an enhanced response to a stimulus when it is the target for an eye movement. However, in a peripheral detection paradigm, no such enhancement was found when a stimulus was attended, in the absence of an eye movement. Inasmuch as behavioral studies have found attention deficits in the absence of eye movements following SC lesions or deactivation, we investigated this issue in a paradigm that is very sensitive to effects of attention. In a matching-to-sample paradigm, a sample stimulus was presented at one location followed by a brief test stimulus at that (relevant) location and a distracter at another (irrelevant) location. While maintaining fixation, the monkey indicated whether the sample and the test stimulus matched, ignoring the distracter. The relevant and irrelevant locations were switched from trial to trial. SC cells in the superficial layers tended to give enhanced responses when the attended test stimulus was inside the receptive field compared to when the (physically identical) distracter was inside the field. We found that responses to attended targets in the receptive field were larger than to physically identical, but ignored, distracter stimuli. These effects were found only in an "automatic" attentional cueing paradigm, in which a peripheral stimulus explicitly cued the animal as to the relevant location in the receptive field. No attentional effects were found in a "central" or "cognitive" cueing paradigm, in which the monkey had to learn the relevant location in a given block of trials. The larger responses to attended targets in the automatic cueing paradigm appeared to be due to a sustained elevation of cells' baseline activity when attention was directed to the receptive field, as well as a transient enhancement of the target response. Thus, responses of SC cells appear to be modulated by directed attention, even in absence of eye movements, probably reflecting the properties of cortical cells projecting to the SC.

Key words: Automatic attention, cognitive attention, single-units, awake-behaving monkey, discrimination task.

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RESUMO

Respostas de células no colículo superior durante o desempenho de uma tarefa de atenção espacial no macaco

Estudos prévios mostraram que células da camada superficial do colículo superior (SC) apresentam uma resposta aumentada a um estímulo visual quando ele é o alvo para um movimento ocular. Entretanto, esta amplificação da resposta não é observada quando o estímulo para o qual o animal presta atenção não é um alvo de um movimento ocular. No entanto, como estudos comportamentais após lesão ou desativação do CS mostraram déficit de atenção mesmo na ausência de movimento ocular, nós investigamos este assunto com um paradigma que é muito sensível aos efeitos da atenção. Num paradigma de pareamento de amostra, um estímulo amostra era apresentado em um local, sinalizando ao animal para prestar atenção naquele local. Após um intervalo esta amostra era seguida de um estímulo teste no mesmo local (relevante) e um estímulo-distração em uma outra localização (irrelevante). Enquanto o animal mantinha os olhos fixos em um alvo ele indicava se o estímulo teste era o mesmo da amostra, ignorando o estímulo-distração. Os locais relevantes e irrelevantes eram alternados de uma tentativa para outra. Células da camada superior do CS tenderam a dar respostas aumentadas quando o estímulo para o qual o animal estava prestando atenção estava dentro do campo receptor. Nós constatamos que as respostas ao estímulo em um local para o qual o animal estava prestando atenção eram maiores que quando o mesmo estímulo físico era apresentado no campo receptor, mas neste caso como um estímulo-distração, a ser ignorado. Esses efeitos foram constatados somente nos paradigmas de atenção automática, nos quais um estímulo periférico indica explicitamente ao animal a região relevante no campo visual. A potenciação causada pela atenção não foi observada nos paradigmas de pistas centrais ou cognitivas, nos quais o animal tinha que aprender em que local deveriam prestar atenção em cada bloco de tentativas. A maior resposta ao estímulo para o qual o animal presta atenção parece ser devida a uma elevação mantida da linha de base da atividade da célula quando a atenção é dirigida ao campo receptor, assim como a um aumento transiente da resposta ao alvo. Portanto, as respostas de células do CS parecem ser moduladas pela atenção espacial seletiva, mesmo na ausência de movimento ocular, provavelmente refletindo as propriedades das células corticais que se projetam para o colículo superior.

Palavras-chave: atenção automática, atenção cognitiva, unidades isoladas, macaco alerta operante, tarefa de discriminação.

INTRODUCTION

The superior colliculus (SC) of the macaque has long been known to play an important role in the generation of saccadic eye movements (Schiller *et al.*, 1971, 1980; Wurtz and Goldberg, 1972a,b). Cells in the intermediate and deep layers of the SC discharge before eye movements, and cells in the superficial layers give enhanced responses to visual stimuli that are the targets of eye movements (Mohler and Wurtz, 1976). This saccadic enhancement effect is thought to be generated in the intermediate layers and somehow propagated back to the superficial layers (Mohler and Wurtz, 1976). Lesions or chemical deactivation of the SC lead to a transient impairment in the

ability to move the eyes into the contralesional field, and micro-stimulation of the SC causes eye movement to the visuotopic locus of the stimulation site in the SC (Hikosaka and Wurtz, 1986; Munoz and Wurtz, 1993a,b and Ma *et al.*, 1991).

Recent lesion evidence has emerged, however, suggesting that the SC also contributes to spatial attention, in the absence of eye movements. This notion has been challenged, however, by single unit studies by Kertzman and Robinson (1988), who have studied units from the SC while monkeys were performing a task similar to the one used by Posner *et al.* (1980). These authors found no consistent or significant changes in the

response of cells to the target, depending on cue validity.

In contrast, behavioral data with lesions (Anderson and Symmes, 1969; Albano *et al.*, 1982) have shown that monkeys with complete SC lesions show neglect in the contralateral visual field not limited to eye movements. Albano *et al.* (1982) reported that the lesions of the SC impair a monkey's ability to detect the dimming of a peripheral stimulus. Similarly, Kertzman and Robinson (1988) find that unilateral chemical deactivation of the SC impairs a monkey's ability to switch attention into the contralesional field following an invalid attention cue in the opposite field. Rafal and Posner (1987) report a similar impairment in patients with supranuclear palsy, which is thought to affect the SC. They argue, that the SC is involved in the ability to "move" attention from one location to another. Finally, Desimone *et al.* (1989) find that focal deactivation of SC impairs a monkey's ability to discriminate a stimulus at the visuotopic locus of the deactivated zone if there is a distracter stimulus at another location in the visual field. They argue that, within the attention control system, each location in the visual field is in competition with every other location for attention. The SC forms one component of this control system, but it works in parallel with other structures. Dysfunction (through lesions or deactivation) of a portion of the visuotopic map in the SC throws the competition out of balance, giving an advantage to stimuli outside the dysfunctional zone (Desimone *et al.*, 1990). Thus, both the lesion and recording data suggest that the SC, particularly the superficial layers, does play some role in spatial attention in addition to its role in the generation of eye movements (cf. also Sprague, 1991).

The discrepancy in the amount of single unit data from the superior colliculus related to the initiation and control of eye movements (Wurtz and Goldberg, 1972; Schiller and Koerner, 1971; Wurtz, 1975; Schiller *et al.*, 1980; Sparks, 1986) and the sparse single unit data related to spatial attention led to a systematic study of cells in the superficial layers of the superior colliculus. A preliminary account of these data was presented elsewhere (Gattass and Desimone, 1991).

MATERIAL AND METHODS

Subjects

Two rhesus monkeys (*Macaca mulatta*) weighing 6-8 kg were used over a period of 18-25 months. All experimental protocols were conducted within NIH guidelines for animal research and were approved by the Institutional Animal Care and Use Committee (IACUC) at NIH.

Surgical procedures

Prior to the implantation of the recording chamber, the animals were placed in a plastic stereotaxic machine and scanned (Fig. 1) with Magnetic Resonance Imaging (MRI). A head-restraint post, recording chamber and scleral eye coil for monitoring eye position (Robinson, 1963) were implanted under aseptic conditions while the animal was anesthetized with sodium pentobarbital. Using the coordinates derived from the MRI images, the recording chamber was oriented in the Horsley-Clark stereotaxic plane and cemented on the skull above the superior colliculus. The animals received antibiotics and analgesics post-operatively.

Recordings

We mapped the superior colliculus in each animal prior to the beginning of the single unit study. Later, in each recording session we mapped a multiunit receptive field prior to the isolation of the single unit (see Fig 7 - bottom). The location of the multiunit receptive field were used to position the test stimuli and its companion distracter in a corresponding location in the other visual hemifield. Typically, two single units were isolated from the visually driven multiunit. These cells were studied under 24 different conditions containing foveal, extra-foveal and eye-movement tasks. We recorded from 832 cells in various depths in the superior colliculus. Some cells (268) did not give significant response in either the visual, oculomotor tasks and they were excluded from the sample. In addition, we arbitrarily divided the cells in two groups; one superficial and another intermediate with a cut off point at 900 μm from the collicular surface. The schematic diagram in Figure 2 shows that with this criteria most of the superficial cells were probably located in the *stratum opticum* (SO) or in the upper third of the *stratum griseum superficiale* (SGS). We report



Fig. 1 — Magnetic Resonance Imaging (MRI) at the level of the superior colliculus in Case 1. Scale bar = 5 mm.

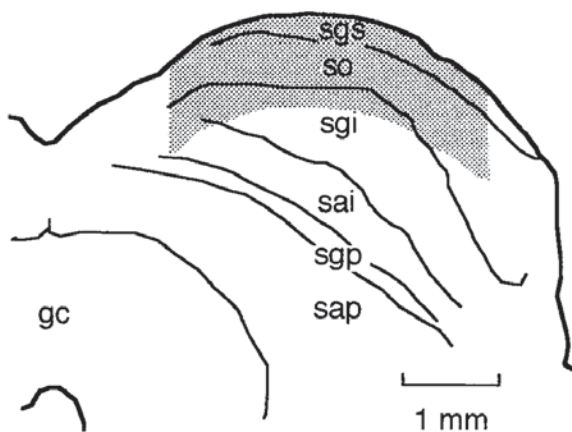


Fig. 2 — Schematic diagram of a Nissl stained coronal section of the superior colliculus at the level of the recording sites. Vertical bars delimit the range of recording sites locations included in this study. *sgs* = stratum griseum superficiale; *so* = stratum opticum; *sgi* = stratum griseum intermediale; *sai* = stratum album intermediale; *sgp* = stratum griseum profundum; and *sap* = stratum album profundum.

on spatial attention enhancement on a group of 493 cells from the superficial layers of the SC. The ratio of firing rate during sample presentation to the pre-trial activity was used to classify the cells either in excitatory or inhibitory ones.

Behavioral Tasks

We studied the influence of spatial attention on the activity of single cells of the superficial layers of SC in awake monkeys performing extrafoveal spatial visual discrimination and eye movement tasks. Figure 3 illustrates the basic paradigm used in this study. The fundamental evaluation was made by comparing the responses of the cells to the same physical stimulus presented in the visual receptive field in different behavioral conditions. We compared the response in one trial in which the visual stimulus is an attended test stimuli with the response in another trial when the same stimulus is presented in the same location, as an ignored distracter. That is, we compared the response to the stimulus in the receptive field when

ATTENTIONAL ENHANCEMENT

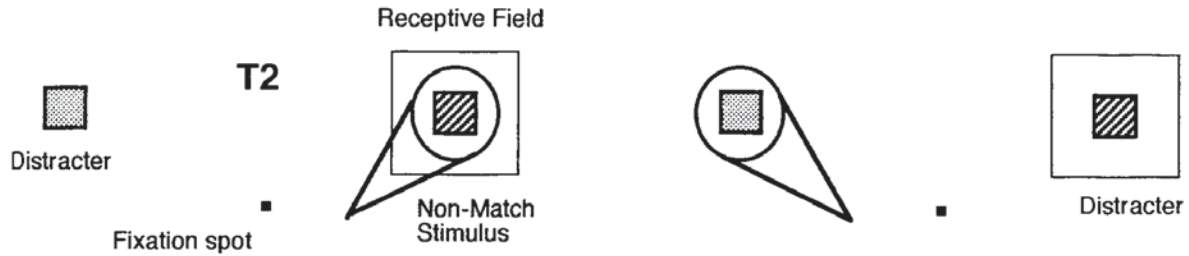


Fig. 3 — Attended versus unattended ratio. The relevant comparison refers to the responses of the cells to the same physical stimulus presented in the visual receptive field when the animal is paying attention to that location to the response of the stimulus in the same location when the animal is attending elsewhere.

DELAYED MATCH

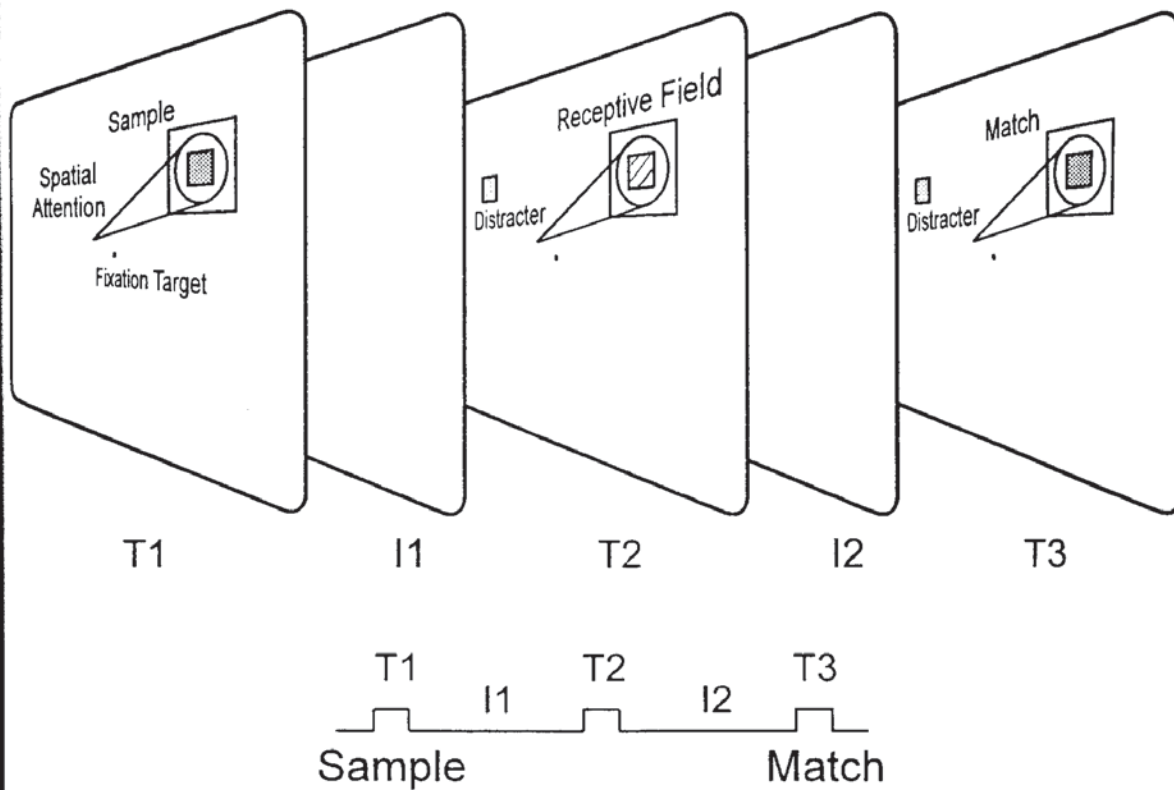


Fig. 4 — Schematic representation of the extra-foveal spatial attention discrimination task. Each plane represents a screen seen by the animal at a given time during a trial. The animal is rewarded when it releases the bar at the matching stimuli in the attended location.

the animal is paying attention to that location to the response of the stimulus in the same location when the animal is attending elsewhere.

The single unit analysis was followed by a population analysis based on the ratio of the response to the attended test stimulus to that of the distracter. This procedure was used to evaluate the strength of the attention signal in the population of collicular cells. That is, for each cell we calculated the firing rate of the cell from the stimulus onset to 180 ms for both conditions. The data from each cell was used to calculate ratio of the response to the attended to that of the unattended visual stimulus. The distribution of the ratios in the population of cells was then used to evaluate the bias of the population towards spatial attention. If there were no attention modulation we would observe a normal distribution of number of cells with different ratios centered at the no effect bin (black bar in Figs. 8-14). If the activity of the cells are modulated by spatial attention there would be a bias in the distribution with more cells with values bigger than 1.1 than those with values smaller than .91. Thus, the distribution will be asymmetric. We tested the asymmetry of the distribution with the Pearson chi-square test.

Attention Task with Distracter

The task used to manipulate the animal's attention was a modified version of delayed matching-to-sample (DMS). The stimuli were small colored bars, generally 0.8 by 0.8 degree, presented on a computer graphics display (Fig. 4). The background luminance of the display was 65 cd/m, and the stimulus luminance was 13,4 cd/m. The animal initiated a trial by grabbing a bar. After 200 ms, a small (0.2 degree) fixation stimulus appeared, which the animal was required to fixate. The fixation stimulus remained on for the remainder of the trial, and trials were aborted if the animal's gaze deviated from the fixation stimulus by more than 0.5 degree. At 30 ms after the animal achieved fixation, a single sample stimulus appeared at a peripheral location for 180 ms. Then, after a blank delay period of 200-300 ms, test stimuli appeared at two locations. The animal was supposed to attend to the test stimulus that appeared at the location of the sample, which we will term the "target", and to ignore the test stimulus at the other location, which we will term the "distracter". The target and distracter were on for

180 ms. On "match" trials, the target matched the location of the sample, and the animal was required to released the bar within 750 ms for orange juice reward, which terminated the trial. On "non-match" trials, the target did not match the sample, and the animal was required to continue holding the bar. On these trials, the non-matching target and the distracter were then followed by another blank delay period of 350-450 ms, followed by a third set of stimuli presented at the same two locations. In this case, the stimulus at the location of the previous sample was always a match, and thus served simply as a releasing stimulus for the animal's behavioral response, which was followed by juice reward. Incorrect trials were not rewarded and were typically followed by a 2 sec time-out period. Our primary interest was in the effects of attention at the time of target (and distracter) presentation, as this was the time at which the animal had to make its decision to release the bar immediately (match trials) or without its response until the releasing stimulus (non-match trials - Fig 5B). The sample stimulus served as an explicit spatial cue which indicated to the animal which of the subsequent two test stimuli it should attend to in order to perform the task. In addition to the explicit spatial cue in this design, there was also an implicit, non-spatial color cue for the attended spatial location. The distracter stimulus never matched the sample stimulus, and thus the animal had no reason to attend to it.

In the first part of this study we recorded single units while monkeys were performing discriminations tasks with unblocked trails. That is the location of the sample stimulus varied randomly from trial to trial. For a given trail, the animal could not predict where the sample stimulus would appear. Later, we presented the trials in blocks, with the sample at one location for 40-80 trials and at the other location for an equal number of trials, in alternation. Thus, after the first trial in a block, the animal could anticipate which location would contain the sample stimulus and the target for the remainder of the trials. One reason for using this blocked trial design was that Mohler and Wurtz (1976) reported that the saccadic enhancement of colliculus cells was much larger when trials using a particular location were run in blocks, so that the animal made eye movements to the same location for trial after trial.

One of the two locations tested in the visual field was always at the site of recording electrode in the SC, which was typically at 4-5 degree eccentricity in the upper or lower visual field. For most of the recordings, the other location was across the mid-line in a symmetrical position in the periphery. We also tested the animal with the attention at the fovea, with test stimuli at the site of recording electrode in the SC and a distracter across the mid-line in a symmetrical position (Fig. 5A).

Displaced Sample Task

To evaluate the strength of the attention bias in the population of cells, without the influence of sensory interactions induced by the sample stimuli in the receptive field, we studied a group of cell with sample stimuli in a displaced location. This sample would serve as an informative cue for the animal to pay attention at the test location (see insert in Fig. 11).

Cognitive Attention Task

In this task, a block of 30 test trials is preceded by a set of 10 instruction trials that induce the animal to pay attention to a particular location in the visual field. In the instruction trials, a single sample stimulus is presented in the location where a single test stimuli will appear. These trials immediately cause the animal to engage his attention at that particular location. In the test trials, after the animal achieved fixation, a sample stimulus and a distracter appears at symmetrical peripheral location for 250 ms. Then, after a blank delay period of 200-300 ms, test stimuli and a distracter appear at two locations. The animal was supposed to attend to the test stimulus located at the learned location and to ignore the test stimulus at the other location (Fig. 5C).

Eye Movement Task

A group of 82 cells were studied with spatial discrimination and eye movement trials. In the spatial discrimination task the sample was presented extra-foveally, while in the simple eye movement task the sample was presented at the fovea. In the trials of the simple eye movement task a sample stimulus appears centered at the fovea and then with no delay the fixation spot and the test stimulus jump to the location of the receptive field and the animal is required to make an

eye movement to it. In this task the trial is aborted if the animal makes an eye movement prior to 100 ms (Fig. 5D). The eye position was recorded throughout the trial.

Location of the recording sites

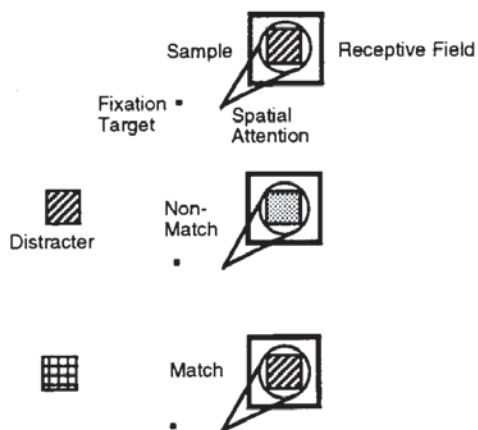
The location of the recording sites were determined by prior electrophysiological mapping (multiunit) of the SC (see insert in Fig. 7). MRI recordings were used to validate the reconstruction of penetration tracks. After the recording experiment these animals were used in another attention/SC-stimulation experiment. One animal is still alive and it has currently being used for electrophysiological recordings. After the stimulation experiment the cranial prosthesis of the second animal became loose and the animal was euthanised. An attempt was made to mark the location of the recording by injecting through the guide tube of the recording manipulator 0.3 μ l of 2% Fast Blue solution in saline. The animal was then deeply anesthetized with ketamine hydrochloride (25 mg/kg i.m.) and sodium pentobarbital (20-35 mg/kg i.v.). The chest was opened to expose the heart, the descending aorta was clamped and the monkey was perfused through the heart with cold buffered saline (NaCl .09%), followed by cold 4% paraformaldehyde. The brain was then removed from the skull, post-fixed for 24 hours in 4% paraformaldehyde /10% glycerol at 4°C. For the localization of the penetrations the brain was cut coronally in 40 μ m-thick sections on a sliding microtome. Stained (Nissl's method) and unstained sections were used to locate de recording sites. Very few tracers of the penetrations were found in the superior colliculus. The fluorescent tracer was found in the brachium of the SC in the pulvinar, above the foveal representation of the SC. The misplacement of the fluorescent tracer was attributed to the lack of stability of the cranial prosthesis in the recordings.

RESULTS

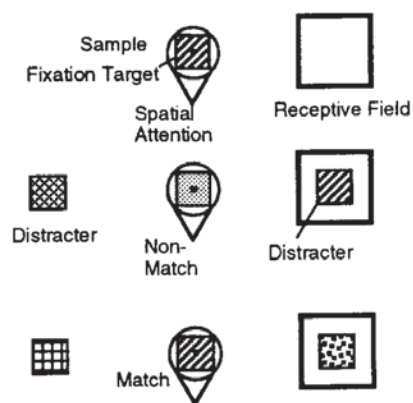
We recorded the activity of single cells in the superficial layers of the SC in monkeys performing a visual discrimination task in response to a target stimuli at one location in the visual field and a distracter stimuli presented at another location. We found that responses to attended targets in the receptive field were larger than to physically

Automatic Attention Tasks

A Extra-Foveal Attention with Peripheral Distracters

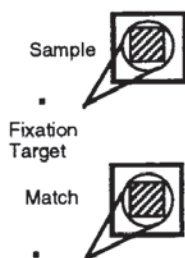


B Foveal Attention with Peripheral Distracters

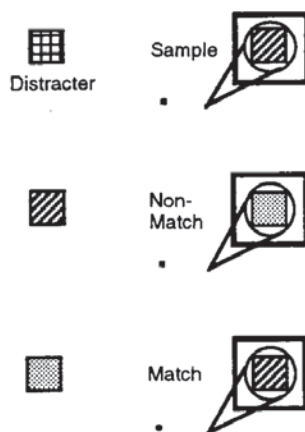


C Cognitive Spatial Attention Task

Learning trials



Test trials



D Eye Movement Task

Simple task

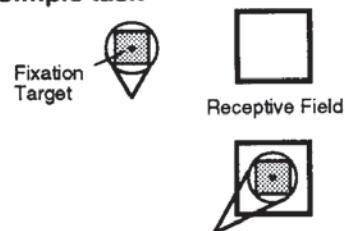


Fig. 5 — Schematic representation of spatial discrimination tasks (A, B and C) and eye movement task (D). A - Delayed matching to sample task with the sample stimulus cueing for location and color. The sample stimulus presentation ($T_1 = 180$ ms) is followed by 200-300 ms of blank screen and then a test stimulus is presented (T_2) for 180 ms in the presence of a distracter (see test). B - Foveal attention task. Sample and test stimuli are presented at the fovea, while a distracter is presented peripherally. C - Cognitive spatial attention tasks. While in the automatic task a single sample stimulus draws the attention to that location, in the cognitive task, previous instruction trials cue the animal to attend to a specific location. At the test trials a sample and a distracter appear at the same time (T_1) in different locations and the animal has to use the spatial information learned at the instruction trials to do the task. D - Eye movement task. The sample stimulus is presented at the fovea behind the fixation spot and then the stimulus and the fixation spot jump to the location of the receptive field. A small plus (+) represents the fixation spot, a large open square, the receptive field, and the small filled squares are visual stimuli. A cone or a drawing of a spot light represents the animal's focus of spatial visual attention.

identical, but ignored, distracter stimuli. The larger responses to attended targets appeared to be due to a sustained elevation of cells' baseline activity when attention was directed to the receptive field, as well as a transient enhancement of the target response. Thus, cells modulated by spatial attention showed an enhancement of its response to the visual stimuli. This enhancement is an additional increase in firing rate for excitatory cells or an additional decrease of firing rate for inhibitory cells.

Figure 6 shows the response of an excitatory cell that shows an attention enhancement. The response to the same sensory stimuli when this visual stimulus is an attended test stimuli is significantly higher than that when it is a distracter. The response to the attended test stimulus represented by the post-stimulus histograms is bigger

than that of the distracter. This effect is consistent in most correct trials as shown by the recording raster from individual trials. Figure 7 shows another example of enhanced response of a cell in the superficial layers of the SC with receptive field located slightly above the representation of the horizontal meridian at 3 degrees eccentricity from the fovea. The post stimulus histograms shown here indicate that the response of the cell to the same sensory stimulus flashed in its receptive field is bigger when it is an attended test stimuli than when it is a distracter. The visual response and the attention modulation from the cells in the superficial layers of the SC varied from cell to cell. In order to evaluate the influence of spatial visual attention in the entire population of cells we made no attempt to pre-select cells in the superfi-

ATTENTIONAL ENHANCEMENT

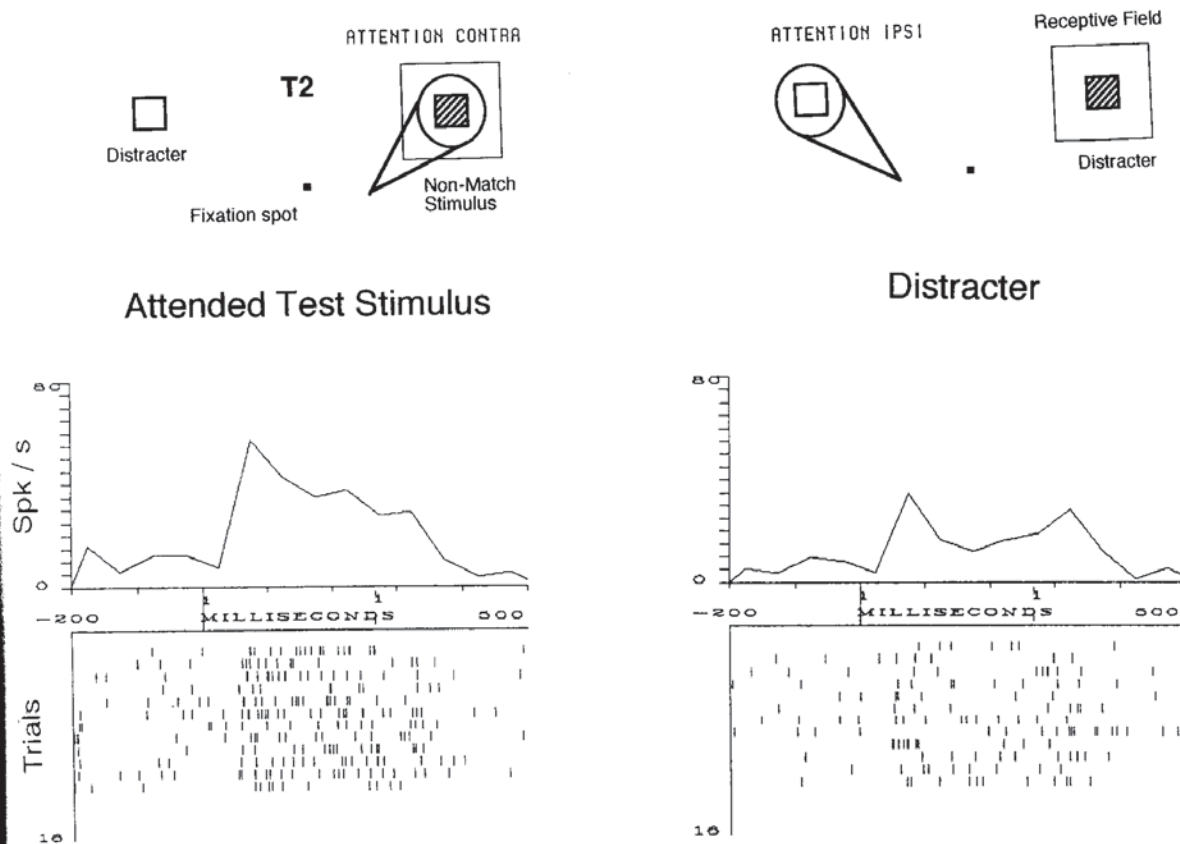


Fig. 6 — Post stimulus histogram and spike rasters of the response to the attended test stimulus and to the ignored distracter inside the receptive field. **Top:** Schematic representation of the stimuli and focus of attention at T2, during the presentation of the test stimuli. The magnitude of the response of the cell from the superficial layers of the SC to the same physical stimuli is bigger when the animal is attending to the location of the receptive field. (See also legend to Figure 4).

ATTENTIONAL ENHANCEMENT

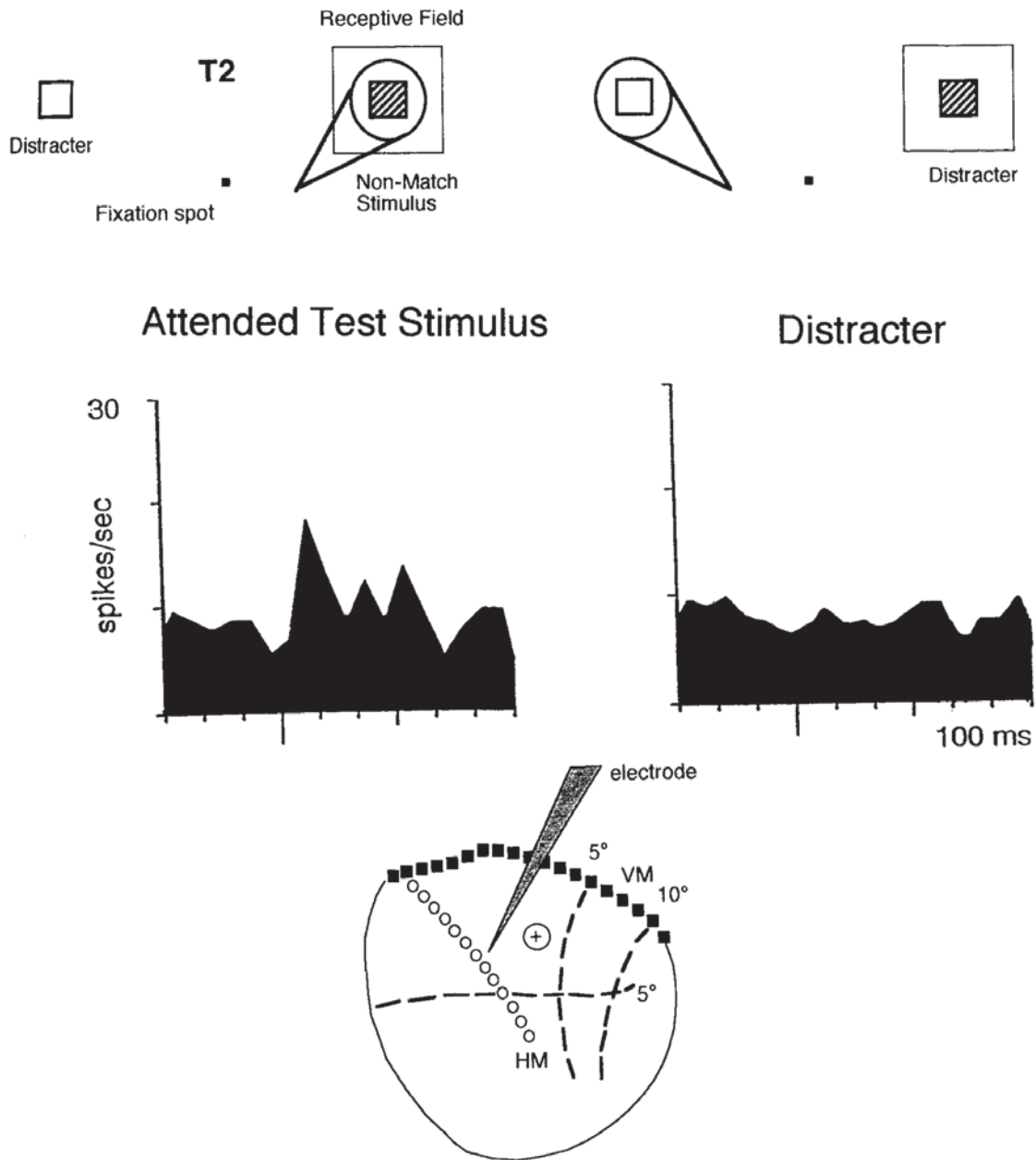


Fig. 7 — Post stimulus histogram of the single unit response to the attended test stimulus and to the ignored distracter inside the receptive field. **Bottom:** Location of the recording site (asterisk) in a reconstruction of the visual topography of the SC obtained previously with multiunit recordings. (See also legend to Figures 4 and 6).

cial layers. Thus, the sample of cells we have in different test paradigms has no bias.

We were interested in evaluating the strength of the attention signal in the population of collicular cells. Thus, the data from each cell was used to

calculate ratio of the response to the attended to that of the unattended visual stimulus. The index for inhibitory cells were the inverse of that for excitatory ones. The distribution of the ratios in the population of cells of the superficial layers was

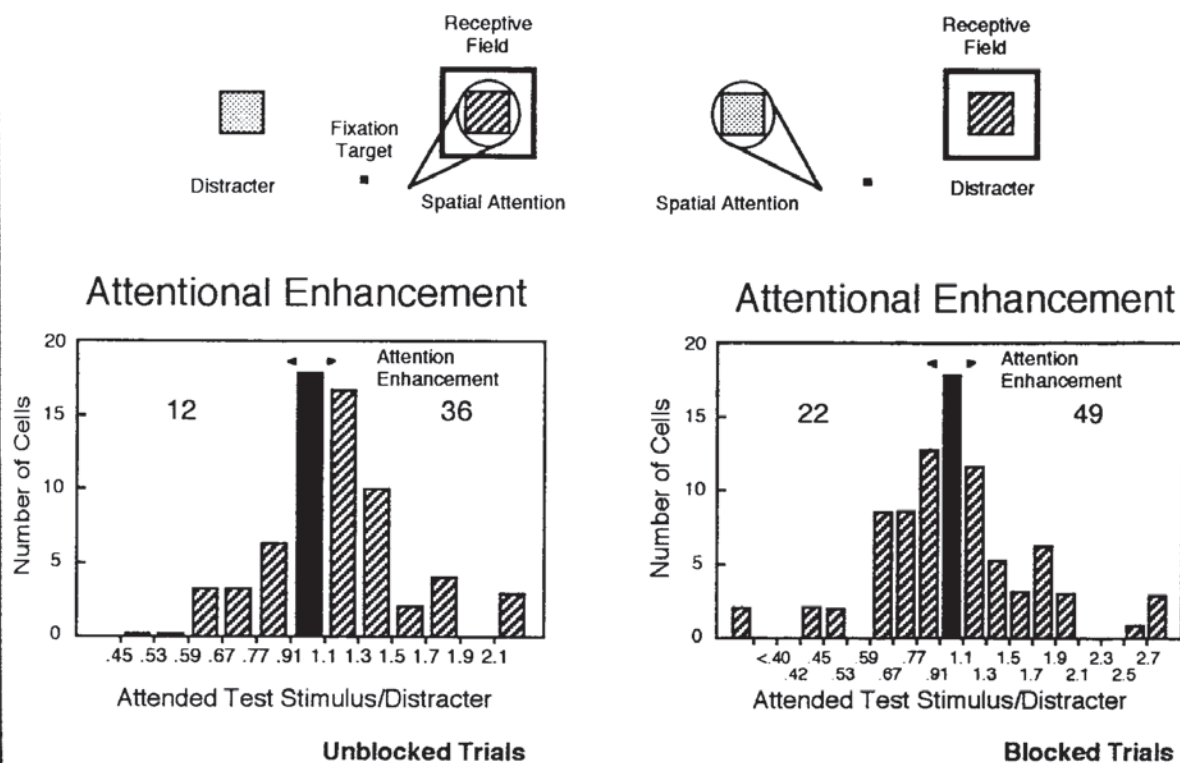


Fig. 8 — Distribution of the attention index from a population of 66 cells from the superficial layers of the SC studied with unblocked trials (*left*) and from a population of 88 cells studied with a blocked-trial paradigm (*right*). The number of cells with attention index higher than 1.1 is significantly higher than the number of cells with attention index smaller than 0.9 (attention bias) in both paradigms. (See also legend to Figure 4).

then used to evaluate the bias of the population towards spatial attention. Figure 8 - left shows the distribution of ratios for the phase of experiment with unblocked trials. The distribution of the indices for the cells of the superficial layers of the superior colliculus for the study with unblocked trials, shown in Figure 8-left, shows an asymmetric distribution with many more cells with indices larger than 1.1 than those with values smaller than 0.91., thus it shows a significant bias towards attention enhancement (Chi-square = 6.40; $p < 0.05$).

Wurtz and colleagues (Wurtz and Goldberg, 1972; Mohler and Wurtz, 1976) had shown that the saccadic enhancement effect in the superficial layers was most apparent with blocked trials. Thus, we repeated the same experiment with a blocked trial paradigm. That is, the test were made with the attended stimulus in the same location for a block of forty trials, before switching to the other location. Figure 8 - right shows the distribution of cells for the attended test stimuli versus distracter. The distribution of ratios of cells studied with blocked trials is similar to that of the un-

blocked trials (Chi-square = 5.29; $p < 0.05$). A bias of stronger responses both at the blocked and unblocked paradigms could be related to the enhancement of the response (potentiation) due to pure sensory interactions in the test condition, or it may be the result of the eye movement enhancement described by Mohler and Wurtz (1976). Since the test required the animal to maintain fixation, during the task the animal could be then programming an eye movement to the target, that he would do right after the reward.

Rafal and Posner (1987) have shown that patients with mid-brain lesions involving the superior colliculus are impaired in their ability to move the attention and they lack the inhibition of return. These patients have difficulty to move their eyes and they also have difficulty to move their attention covertly. Previously, Posner and Cohen (1984) have shown that an unexpected peripheral visual stimulus can produce two opposite effect on attention. These effect appear sequentially first as a facilitation and then as an inhibition. Facilitation was present if a target was presented 150 ms or

less from the onset of the non informative cue. If the target was presented 300 ms or more from the onset of the non-informative cue this effect was replaced by inhibition. Early facilitation has been considered to be related to an automatic and covert orienting of attention, while late inhibition (inhibition of return) can be related to an opposite process reflecting a reduced tendency to attend to a previously attended location. Thus, their study of manual reaction time showed that with short intervals between valid cue and visual target there is facilitation while with long intervals there is inhibition.

To test the influence of delay between sample and test stimuli we studied 75 cells with intervals of 100, 250 and 650 ms between sample and test stimuli. An unexpected and rather clear effect was observed in these experiment. Figure 9 shows no attention enhancement with short 100 ms interval, and a clear enhancement with 250 ms interval (Chi-square = 10.79; $p < 0.05$), which decays slightly with 650 ms interval (Chi-square = 2.42; $p < 0.05$).

In the paradigm we used to evaluate the modulation of attention on the activity of the cells, shown in Figures 4 and 5, the attended target is always the second stimulus in the receptive field while the distracter is the first stimulus that is presented in that trial, at that location. It is therefore possible that the existence of a previous sample would enhance the response to the non-match stimulus. This pure sensory potentiation would explain the attention enhancement results. In order to directly test this hypothesis we first studied the distribution of ratios to the location of the receptive field versus the location of the distracter in trials where attention was directed to the fovea. Figure 10 shows that the asymmetry of the ratios favoring the location of the receptive field disappears and that the response to the stimulus in the receptive field was slightly better if during the sample presentation there was no distracter in the receptive field. Thus, suggesting either an inhibition when attention was directed to the fovea or sensory habituation due to the presentation of a distracter in the receptive field prior to the test stimuli. We also compared in Figure 11 - left the response to the sample to that of the non-match stimulus. If there was sensory potentiation due to a stimulus in the receptive field prior to the test

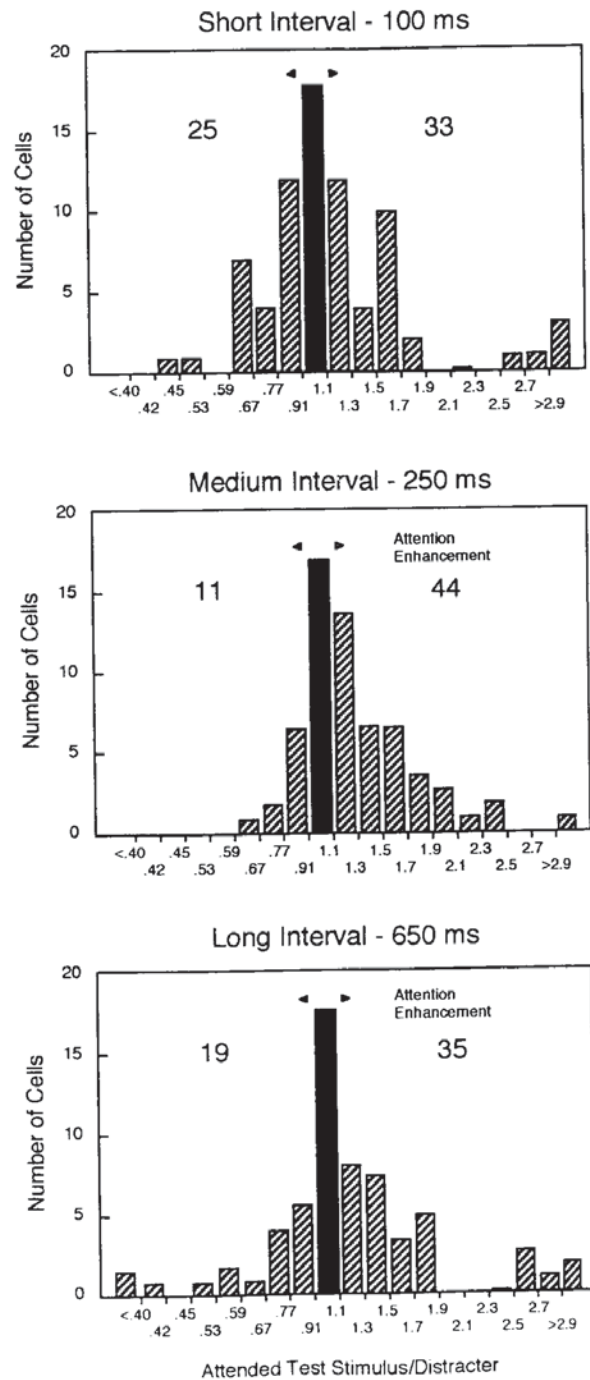


Fig. 9 — Distribution of the attention index from a population of 75 cells studied with different delays between the sample and test stimuli. Attention bias is significant in trials with delays of 250 ms [44/11] and trials with longer delays [35/19]. There are no bias [33/25] with short (100 ms) delays. (See also legend to Figure 4).

stimuli the sample response would be smaller and distribution would show smaller ratios. However the data shown in Figure 11 - left, do not support

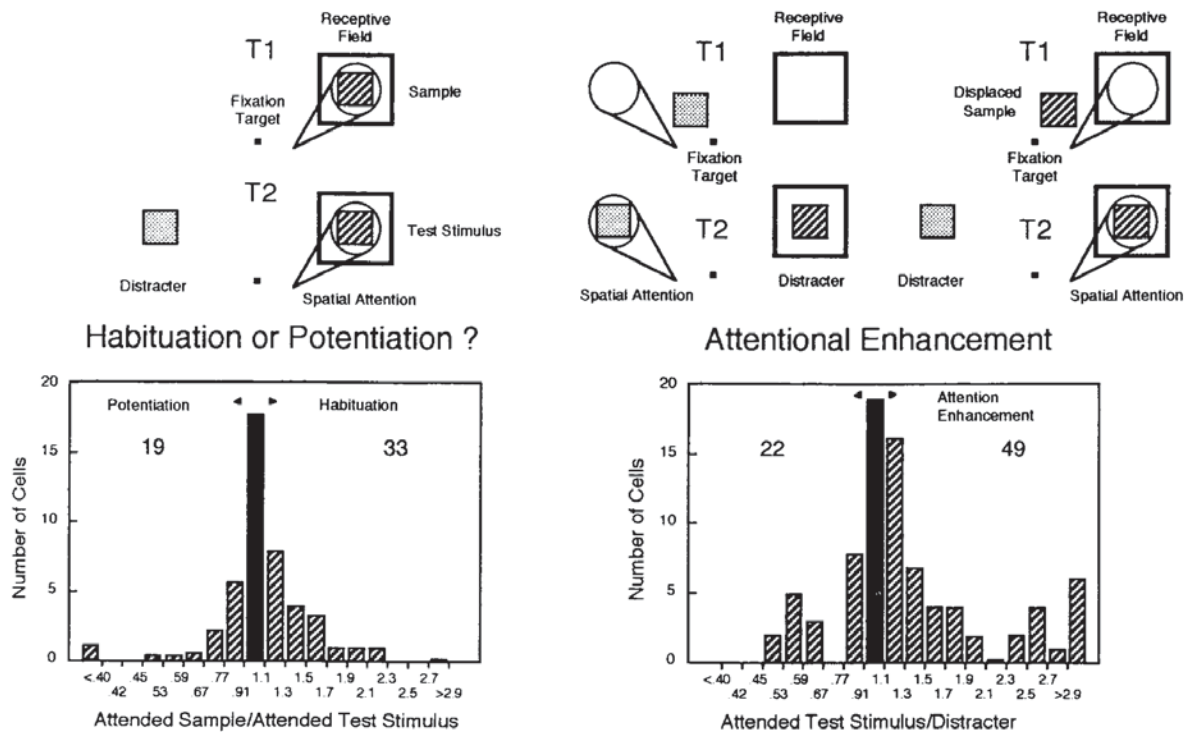


Fig. 10 — Distribution of the sensory potentiation and sensory habituation (*right*) indices and attention enhancement (*left*) index from a population of 88 cells. The top drawings represent the relevant comparisons in different conditions. The ratio of firing rates during sample presentation to that during attended test stimulus is a measure of sensory potentiation or habituation. The ratio of attended versus unattended test stimuli in trials with displaced sample is a measure of pure attention enhancement, without any interference of sensory interaction (See also legend to Fig. 4).

this hypothesis but, on the contrary, it indicates a certain degree of habituation. The habituation was not strong or statistically significant, but the shape of the distribution did change slightly. Habituation in single cells of the superior colliculus has been described by Rizzolati and collaborators (1974), and if there is habituation it is working against the attention modulation observed in the population. In order to rule out the sensory interaction we use a delayed task in which the sample stimulus was presented outside the receptive field in a displaced position. The result of this evaluation in the 122 cells is shown in Figure 11 - right. In these trials the sample was presented close to the fovea, at the right or the left signal that the test stimuli would appear at the usual extrafoveal location on the side cued by the sample. The asymmetry in the distribution, favoring the attention enhancement, was statistically significant (Chi-square = 5.29; $p < 0.05$), and it was comparable to the ones shown in Figure 8.

During the extrafoveal discrimination task we recorded the eye movements during and after

each trial and there is no tendency for the first saccade to go to the target. Typically, immediately after the reward, the monkey breaks fixation and moves its eyes to unpredictable locations. Thus, the notion that the enhancement was related to the programming an eye movement to the receptive field did not found support in the eye position data. However, in order to directly test the effect of programming an eye movement while maintaining fixation we included eye movement tasks in the session early in the study. The result with unblocked trials already had shown a discrete eye movement enhancement. The new eye movement task was carried out with blocked trials to see if the bias for eye movement enhancement would dominate in the population of cells, since Mohler and Wurtz (1976) had described that the eye movement enhancement builds up in subsequent blocked trials.

In the new eye movement task, the stimulus jumped from the fovea to the receptive field, and the animal was required to make an eye movement to it. Figure 12 access the contribution of eye

Foveal Task

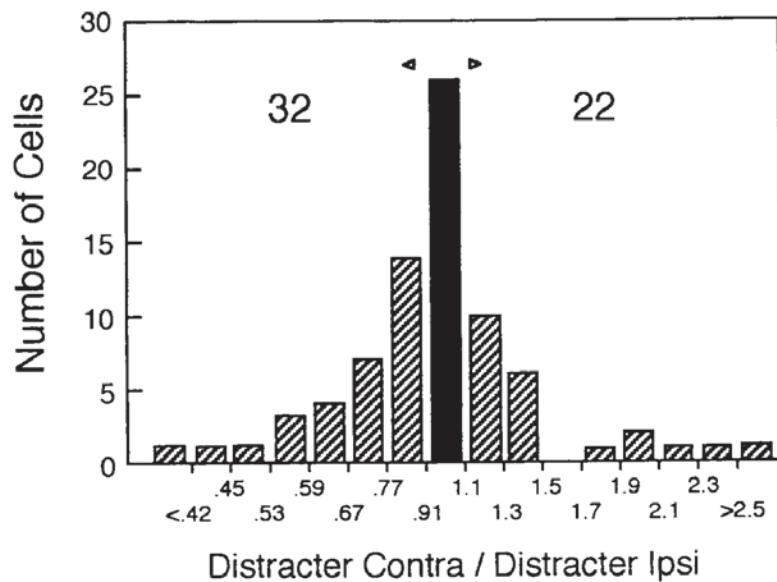
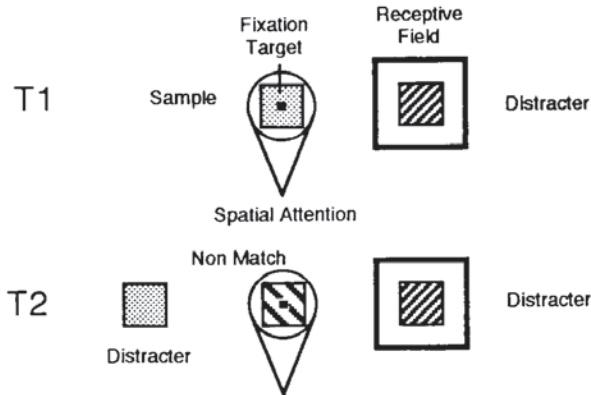


Fig. 11 — Distribution of indices from a population of 80 cells from the superficial layers of the SC when attention is on the fovea. (See also legends to Figs. 4 and 11).

movement programming and spatial attention enhancement. Figure 12 - left shows the distribution of cells for ratios to the response to the eye movement target to that to the ignored distracter. The distribution shows a significant bias (Chi-square = 6.02; $p < 0.05$), but due to the nature of this task it would be better interpreted as the ratio of response with eye movement plus attention versus no eye movement plus no attention.

In order to evaluate the contribution of the eye movement enhancement separately from that

of the attention enhancement we studied the distribution of cells with ratios to the response to the eye movement target versus that to the attended sample. The result is shown in Figure 12 - right. The bias in the distribution shows that the attention enhancement is stronger in the population of cells studied. This was actually the most puzzling result of this entire study. We don't know how to explain why we didn't see more eye movement enhancement, as previous described. It is possible that different mechanisms are related to different

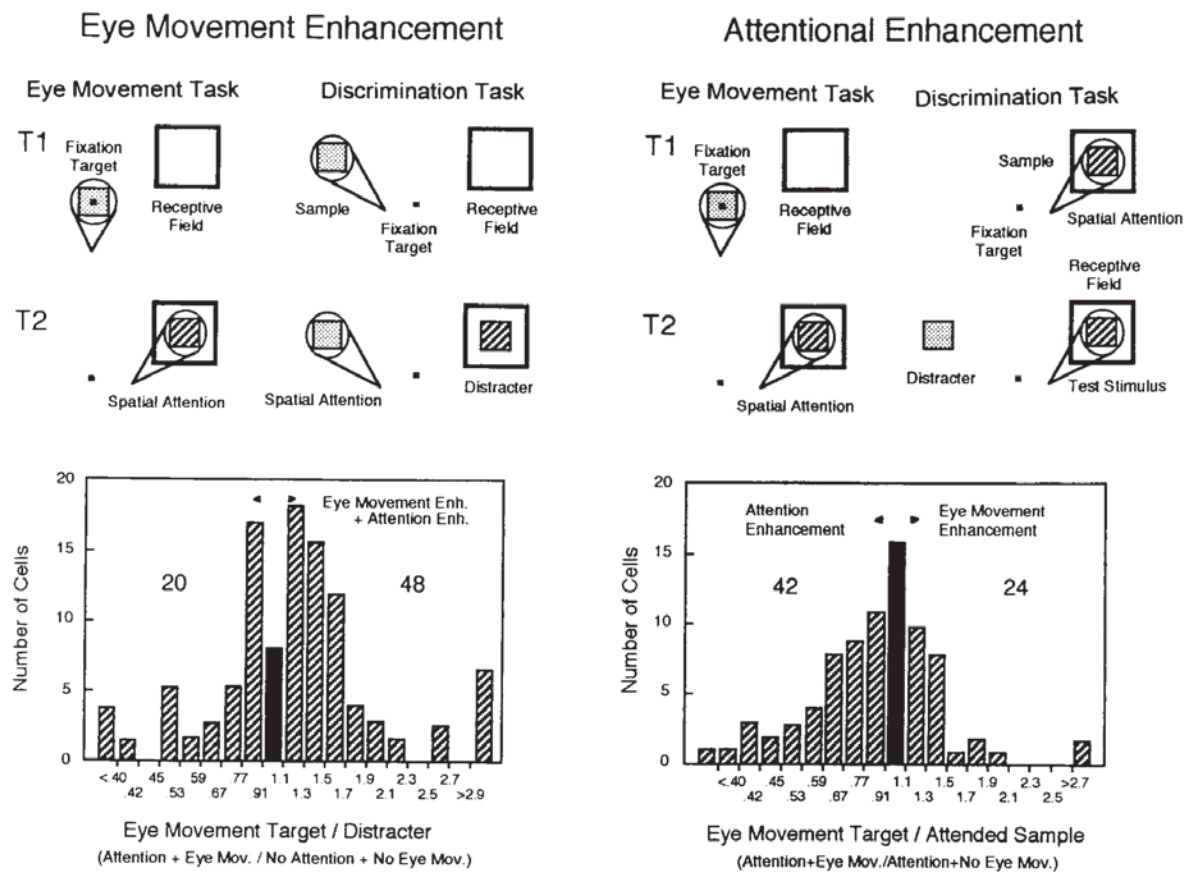


Fig. 12 — Distribution of indices for eye movement enhancement and attention from a population of 82 cells from the superficial layers of the SC. The distribution of ratios of firing rates to the response of a stimulus when it is a target for an eye movement to that when the stimulus is a distracter is a measure of the combined effect of eye movement enhancement and attention (*left*). The distribution of ratios of firing rates to the response of a stimulus when it is a target for an eye movement to that when the stimulus is an attended stimulus compares the effect of eye movement enhancement versus attention enhancement (*right*). (See also legends to Figs. 4 and 11).

types of tasks, namely detection of dimming versus extrafoveal discrimination of color.

The analysis of the asymmetry of the population indices are consistent with sensory habituation and spatial attention enhancement in the superficial layers of the SC. Figure 13 shows these effects at the cellular level in a more complete set of single unit data. At the left we show histograms with the response to the sample summed from all conditions (A); the response to the attended test stimulus in the receptive field (B); the response to the distracter in the receptive field (C), and to an eye movement target in the receptive field (D). In Figure 13E we show post-stimulus histograms and spike rasters for one condition with the same sensory stimuli. This cell has good visual response and the analysis of the histograms at the cellular level illustrate properties of the population. For

example, sensory habituation and spatial attention enhancement are can be directly evaluated in Figure 13. The response to the sample is bigger than that of the test stimulus (sensory habituation) and the response to the attended test stimuli is bigger than that of the distracter (attention enhancement).

Desimone and Moran (1985) studied the visual properties of single units in area V4 and they have suggested that this area plays a role in spatial visual filtering mechanisms important for figure to ground segregation. They have used a cognitive attention task to study the competition of an attended stimuli and of an ignored distracter inside the receptive field. In this task, previous instruction trials cues the animal to attend to a specific location, while in the test trials no location cue is given to the animal. Inasmuch as a sample and a distracter appears at the same time in different lo-

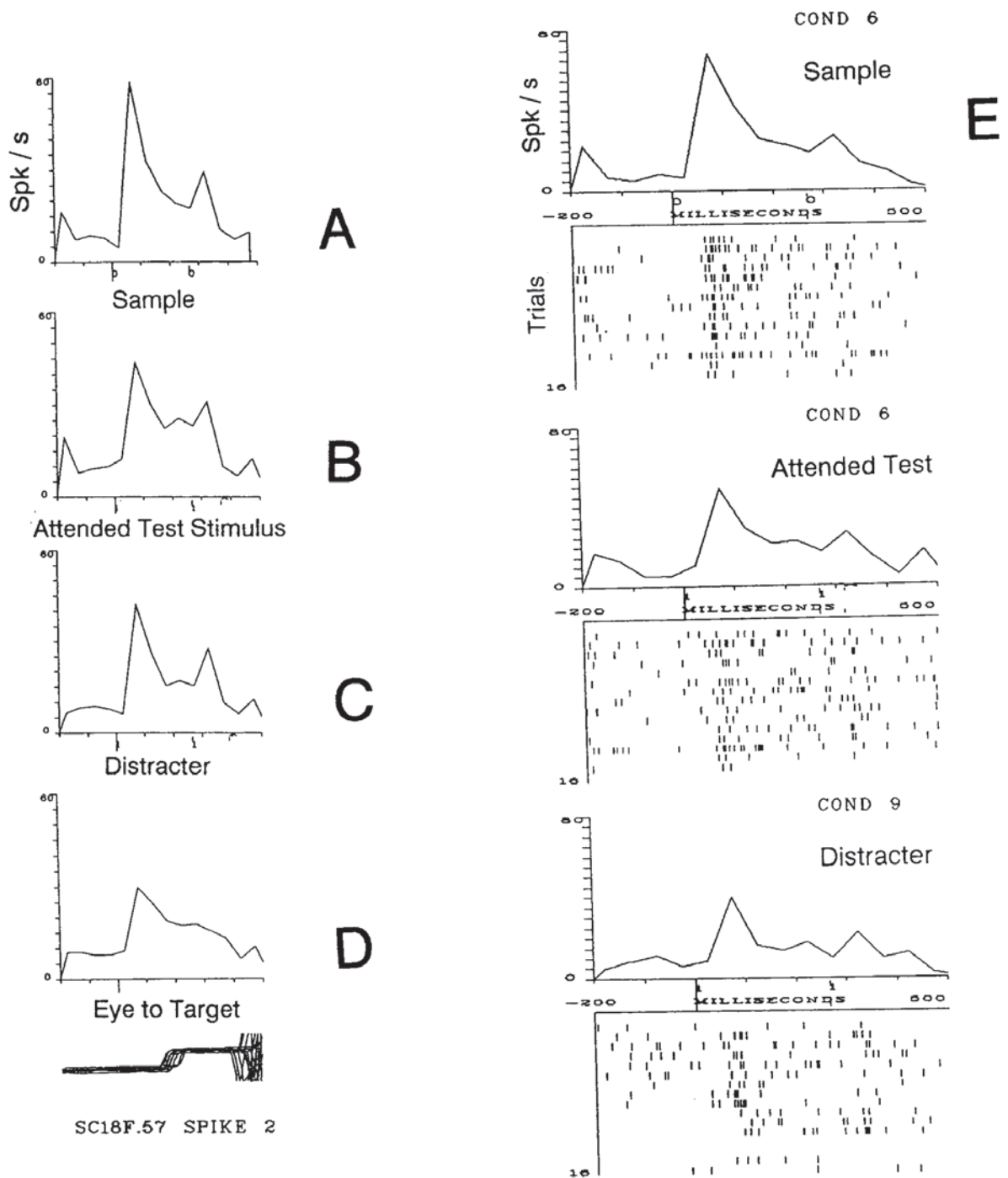


Fig. 13 — Post stimulus histogram (PSH) of the response to the sample, to the attended test stimulus, to the ignored distracter inside the receptive field while the animal maintains fixation on a small visual target and to the same stimulus when it is a target for a eye movement. A-D: PSH from all conditions with stimuli of different colors. E: PSH and spike raster averaged from one condition. Lower left: Superimposed eye movement tracers (See also legend to Figures 4 and 6).

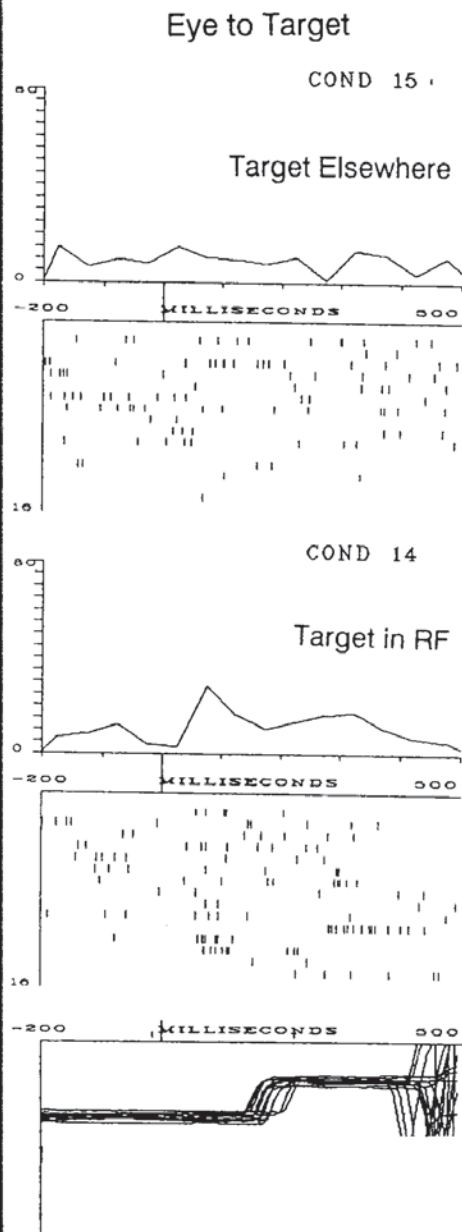


Fig. 13 (Cont.)

cations in the beginning of the trial and the animal has to use the spatial information learned at the instruction trials to do the task. We studied single units in the superficial layers of the SC using the same paradigm used by Moran and Desimone (1985). Figure 14 shows the distribution of the attended versus unattended index from a population of 102 cells in two animals. No attention bias was observed in the response of the SC cells with this paradigm (Chi-square = 0.06 ; $p=0.81$).

Cell firing and attention

The effect observed here on the cell activity was a combination of a sustained elevation of cells' baseline activity when attention was directed to the receptive field, as well as a transient enhancement of the target response. We averaged separately all excitatory and all inhibitory cells to access the influence of attention on baseline firing rate and on transient excitatory or inhibitory responses. A sustained elevation of 10-15% of the baseline activity of the cells and a transient enhancement of 15-30% was obtained in the population of excitatory cells. The effect on inhibitory cells was smaller (5-10%) on the baseline activity, but comparable to that of the excitatory cells on the transient enhancement. The combined effect on the baseline and on the attended response to the target is in average comparable to the sensory habituation caused by the previous sample. The transient effect on the cellular activity of excitatory cell is opposite to the one of inhibitory cells. In a group of cells (about 12% of the population) the response to the visual stimuli was clear and a clear transient enhancement was observed in these cells. In this population the average firing rates to the attended test stimulus was up to 40% bigger than that for distracter. A bias of similar magnitude was observed for a selected population of inhibitory cells. In another group of cells (about 36% of the population) the response to the visual stimuli was only significant in the attended condition. The visual response to the distracter was very poor (Fig. 7). For these cells spatial visual attention was necessary for the cell to respond to the stationary colored stimuli.

In summary, the data presented here supports the existence of modulation by automatic spatial visual attention and not by cognitive attention on the response of cells of the superficial layers of the superior colliculus.

DISCUSSION

Spatial visual attention enables us to emphasize information from important (attended) locations in the visual field over less important (unattended) ones. In man spatial attention enhances both the processing of visual information as well as the oculomotor programming. Attention is an universal process. It is involved in simple visual functions, such as in a simple detection

Cognitive Task

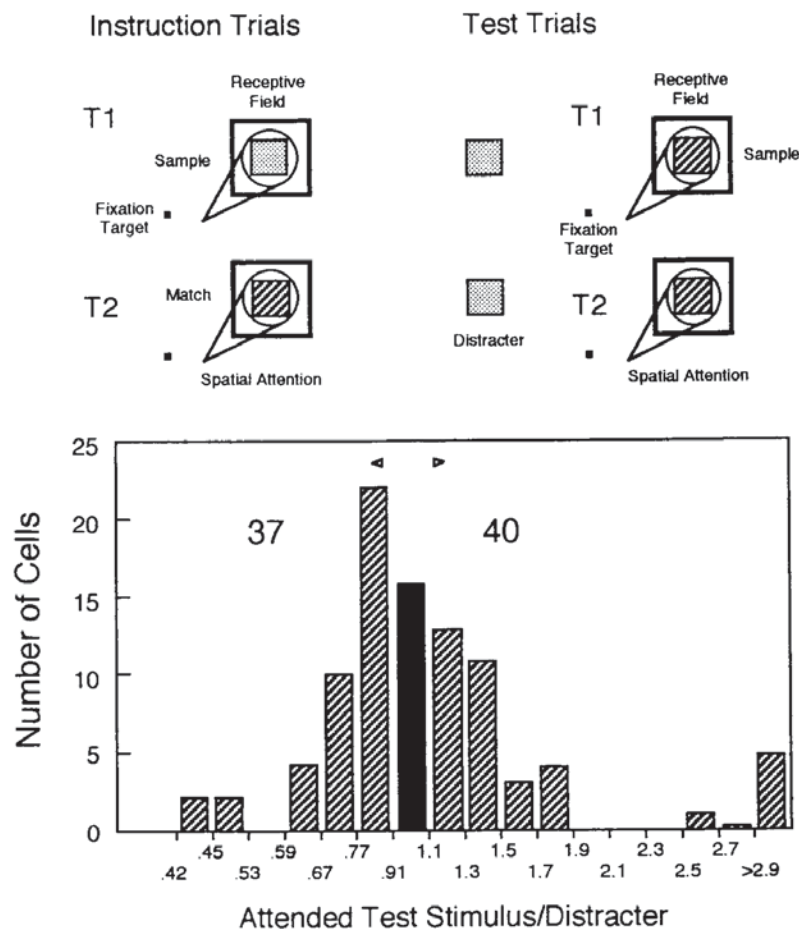


Fig. 14 — Distribution of the cognitive attention index from a population of 102 cells from the superficial layers of the SC. The top drawings represent instructional trials (*left*) and test trials (*right*). The attended versus unattended ratio was determined in test trials (See also legend to Fig. 4).

paradigm as well in complex functions such as reading (Posner, 1978; Posner, 1980; Posner, 1981; Posner and Cohen, 1984; Posner and Petersen, 1990). At the cellular level, robust attention effects are seen in areas of the cerebral cortex both from the ventral (Moran and Desimone, 1985) and dorsal (Treue and Maunsell, 1996) pathways of visual information processing. In monkeys, several recent studies have shown modulation of spatial visual attention in the activity of cells in the prestriate cortex. Visual properties of units of area V4 have suggested that this area plays a role in spatial visual filtering mechanisms important for figure to ground segregation (Desimone and Moran, 1985; Moran and Desi-

mone, 1985; Spitzer *et al.*, 1988). Similar effects of attentions have been reported in areas MT and MST (Treue and Maunsell, 1996). Recent behavioral studies have shown the competitive nature of this cognitive spatial visual attention mechanism (de Weerd *et al.*, 1996) in areas V4 and TEO. The inferotemporal cortex and area V4 areas involved with spatial visual attention receive projection from the SC via pulvinar (Desimone *et al.*, 1989; Desimone *et al.*, 1990).

Single unit versus population analyses

Recording from single neurons has been considered an important tool for understanding the neural mechanisms of perception (Barlow *et al.*,

1967; Barlow, 1986). In this study we found about 15% of cells with clear visual responses and these responses were enhanced when attention was focused at the receptive field location. The majority of cells showed poor visual response, nonetheless these responses were enhanced by spatial visual attention. The paradigm used to isolate the cells was not dependent on good visual responses, thus the sample of single unit recorded from was completely unbiased. The only condition to study the unit was a good signal to noise ratio (good isolation) and that the recording site where located within the first 950 μ m of the surface in the superficial layers of the superior colliculus. The majority of the cells of the superficial layers of the SC of monkeys performing test requiring maintained fixation gave poor responses to the unattended distracter flashed on the receptive field. The strength of these responses contrast with the brisk responses recorded in SC in anesthetized monkeys. We attribute the weak strength of these responses to the use of static (not moving) presentation of colored 0.7 degree squares, and the use of a test requiring the suppression of saccadic eye movement inasmuch as the animals are required to hold fixation at a visual target through-

out the trial. The population analyses showed statistically significant asymmetric distribution for all the relevant tests of automatic attention. This strong effect observed in the population analysis contrasts with the small number (15%) of cells with good visual response and clear attention enhancement.

Effect of stimulation of the SC

The result with single units gains support on previous data on the effect of stimulation of the superior colliculus (Gattass and Desimone, 1992). Electrical stimulation at the site of the irrelevant distracter in the SC causes it to gain control over attention, causing impaired performance of the task at the relevant location. Stimulation at unattended sites without a distracter stimulus cause little or no impairment in performance. The effect of stimulation decays with successive stimulation. The animals learn to ignore the stimulation unless the parameters of the task are varied. Stimulation of the foveal representation in the SC disrupts or delays a saccadic eye movement when the target is located in the ipsilateral visual field. Thus, stimulation of the foveal region of SC impairs ipsiversive saccades, as reported by Munoz and Wurtz (1993b). This result of inhibition on the ocular-

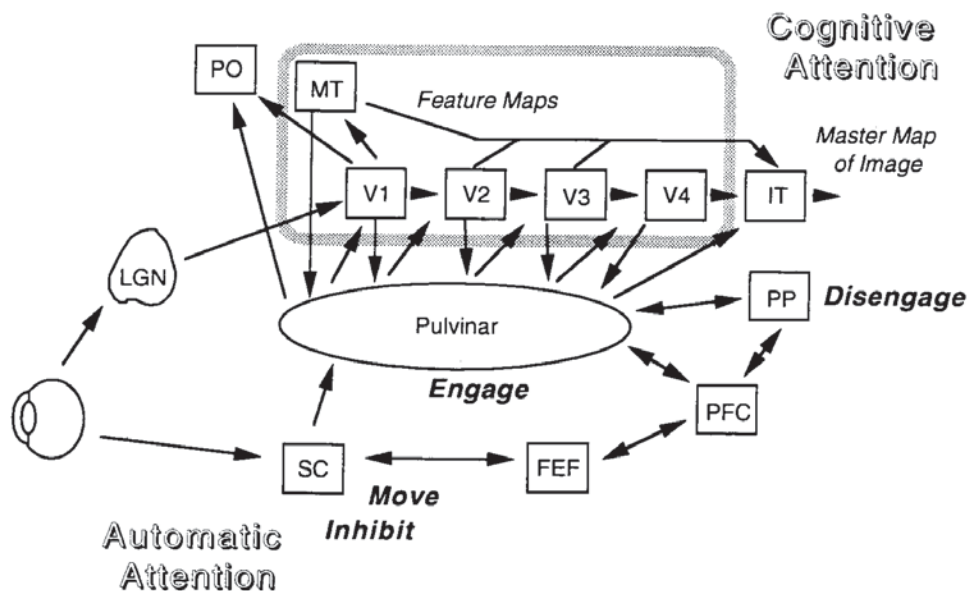


Fig. 15 — Schematic diagram of neuroanatomical circuit underlying automatic and cognitive attention. An attempt was made to correlate the anatomical structures to the basic mechanisms of disengage, move, engage and inhibit of the focus of attention proposed by Posner and Petersen (1990) and the feature and master maps proposed by Treisman (1988). V1, V2, V3, V4, PO and MT are cortical visual areas; LGN, lateral geniculate nucleus; FEF, frontal eye field; PFC, pre-frontal cortex; PP, posterior parietal; SC, superior colliculus.

motor control parallels the inhibition at the cells of the superficial layers of the superior colliculus when the animal attend to the fovea (Fig. 10). These data is consistent with the competition model of attention control. Stimulation of the SC tips the balance of the competition to the stimulus at the site of stimulation (Gattass and Desimone, 1992). Thus, the SC makes contributions jointly to both oculomotor control and automatic spatial attention.

Models of Spatial Visual Attention

Rafal and Posner (1987) using a very simple attention task in patients with cortical (parietal) and subcortical (pulvinar and superior colliculus) lesions have proposed a model for the Posterior Attention System which deals with spatial visual attention (Posner and Petersen, 1990). For these authors, attention is a continuous process with four operational steps: Disengage, Move, Engage and Inhibit (Fig. 15). Patients with lesions in the parietal cortex show a primary deficit in the disengage operation of spatial visual attention. These patients are unable to move their attention to the direction contralateral to the lesion (bad visual hemifield). Midbrain lesions involving the superior colliculus impair the ability to move the attention and the patients lack the inhibition of return. These patients have difficulty to move their eyes and they also have difficulty to move their attention covertly. In patients with pulvinar lesions one sees a deficit in the ability hold attention to the target stimulus when competing information is present in the visual field. Monkeys and patients with lesions in the pulvinar seem to have a great deal of difficulty in filtering out or ignoring irrelevant stimuli that occur at a location other than the one to which they are attending (Desimone *et al.* 1990; Petersen *et al.*, 1985; Robinson and Morris 1987). In this sense these animals and patients are more distractible, that is they have difficulty in the process of engaging their attention.

Posner's simple task for attention can be described as follows: The patient faces a computer screen and is instructed to press a key, as fast as possible, using his right (dominant) hand. A center cross and two peripheral squares are presented at the screen and the patient is instructed to maintain fixation at the center cross. The trial begins when one of the peripheral squares (cue) brightens and draws the patient attention to a peripheral loca-

tion. On valid trials, the target stimulus is projected at that location, inside the bright square. Since attention is already there, the reaction times are fast, the detection thresholds are low and the electrical activity recorded from the scalp at the occipital pole is enhanced. If the cue is presented in one side and the target in another, the trial is considered invalid. In these trials the reaction time are long, the detection thresholds are high and the electrical encephalic activity reduced. Attention is first disengaged of the incorrect location and then moved to the target location. Once the attention is back from the cued location, this previously attended location is now disfavored by the attention system and the animal respond more slowly at that location than to any other location in the visual field. This tendency to make slower responses to the previously attended location is called inhibition of return. This inhibition is not present in patients with midbrain lesions. From the perceptual point of view, when the eyes are fixed, attention can be summoned to another location other than fixation and the information at that location will then be enhanced. From the oculomotor perspective, attention at that location can help to determine where to move the eyes and in the normal behavior, in many cases, the eye will actually move to that location. When the eyes move to another location the previously attended location is processed less efficiently than other locations. Following the eye movement, novel locations which have not been attended to in the last few seconds are favored over previously attended locations. Posner's model of attention assumes that attention precedes the eye movement. In this respect this model is different from the one proposed by Goldberg and Wurtz (1972) in which signal programming the eye movement, coming from the deep layers of the superior colliculus propagates upwards to the superficial layers and engages spatial visual attention. The projection of the superior colliculus to the cortex, via the pulvinar nucleus, contributes to the visual and attentional properties of cortical visual areas (Gross 1991; Treue and Maunsell, 1996). The study with awake behaving monkey allow us to reveal cellular mechanisms underlying cognitive processes. The scope and specificity of these experiments are very narrow in the sense that different tasks may involve different cognitive mechanisms. Posner

experiments uses a non-informative cue, a flashing square not related to the probability of appearance of the test stimulus at that location. This paradigm is different from the ones used in this study. In the automatic task the sample always cues the animal to attend to its location on trial by trial basis, whereas in the cognitive task the location cued by the instruction trials has to be stored in memory to be used during the block of test trials. In addition, Posner's task is a detection paradigm with no memory mechanism involved, while in these experiments we used a discrimination paradigm with short term and long term working memory involvement's. The memory involvement may be the responsible for the elevation of background activity in the inter stimulus interval, as it was shown in the cortex (Miller and Desimone, 1991). In addition, psychophysical experiments by Treisman and her colleagues (Treisman and Souther, 1985; Treisman, 1986, 1988) have accumulated evidence in favor of pop up model for spatial attention. In this model, the sensory information present in the visual maps of the extrastriate areas (feature maps) are spatially enhanced by an intrinsic, local mechanism at the level of the early visual areas. The information converge to a focus onto a master map of the image enhancing the activity at that point or filtering out the non-focus area. The result of this process may be equivalent to the mechanisms proposed by Desimone and Moran (1985) upon which competing processes within extrastriate areas, such as V4, would favor processing of receptive field in a specific location of the visual field allowing the information in this region to prevail over the noise. Figure 15 shows a summary diagram with the areas underlying visual attention. It is based on the assumption that the attentional process is composed by a series of mechanisms which involves different cortical areas and subcortical structures. The visual topography of the cortical areas (Gattass and Gross, 1981; Gattass *et al.*, 1981; Gattass *et al.*, 1985; Gattass *et al.*, 1988; Gattass *et al.*, 1987; Rosa *et al.*, 1988; Fiorani *et al.*, 1989; Neuenschwander *et al.*, 1994) and of the pulvinar (Allman *et al.*, 1972; Gattass *et al.*, 1978a,b; 1979; Bender, 1981) and superior colliculus provide the topographical framework for spatial visual attention. This scheme incorporates the distinction of at least two attentional mechanisms: one *automatic*,

mediated by the superior colliculus and another *central* or *cognitive* one, not related to the superior colliculus, but rather to visual area V4.

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