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CONTRIBUTIONS OF THE PULVINAR TO VISUAL SPATIAL ATTENTION

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Abstract—Neurons in a subdivision of the pulvinar resemble those in parietal cortex: many respond to visual stimuli, some of these have a spatial selection mechanism, and some have signals about the occurrence of eye movements. These properties suggest a role in visual spatial attention. Injection of GABA-related drugs into this part of the pulvinar alters animals' performance on an attentional task. These data support our hypothesis that the pulvinar contributes to visual spatial attention.

INTRODUCTION

THE PULVINAR nuclei form the largest mass in the primate thalamus and have evolved proportionately with the occipital, temporal, and frontal association cortices [3]. The association cortices and pulvinar nuclei have developed phylogenetically along with an animal's ability to perform complex integrative functions. Because the pulvinar is richly interconnected with the association cortex, it is reasonable to assume that this complex of nuclei may deal with higher level integrative and associative functions [2, 7]. Visual spatial attention can be included in a list of the many higher level functions that are well developed in primates and may well have regions of association cortex and the thalamus involved in its neutral control.

Visual spatial attention is viewed here as a selection process; the active enhancement of processing in one area of the visual field at the expense of other areas of visual space. In addition, we use the term attention for processes that can be shown to be independent of any particular movement. Although shifts of visual attention are most often coupled with saccadic eye movements, they are not obligatorily linked to them. Primates have the ability to attend to images in their peripheral visual fields so that the direction of attention is not always the same as the direction of gaze [7, 8, 9, 11].

The work reported here is an attempt to delineate an attentional role for a part of the pulvinar. A subregion of the pulvinar has neurons with physiological properties that make them good candidates for mediating spatial attentional processes, and injection of transmitter-related drugs into the subregion containing these neurons specifically changes an animal's performance on an attentional task.

METHODS

Detailed descriptions of many of our experimental techniques have been published in previous reports [6, 7, 11]. After initial training, animals were surgically implanted with a scleral search coil for measuring eye movements, a

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cylinder for recording from neurons in the pulvinar, and bolts for head restraint. The subnuclei of the pulvinar were localized by physiological mapping of the superior colliculus, lateral geniculate nucleus, and retinotopically organized regions of the pulvinar.

For recording the properties of single neurons from the pulvinar, rhesus monkeys were trained to perform several behavioral tasks. In the basic task, the animals learned to fixate on a spot of light that would dim as the signal for a bar response. Monkeys were rewarded with a drop of water for correct responses. While the animals maintained fixation, other lights were flashed onto the tangent screen in order to determine the visual characteristics of pulvinar cells. To test the effects of different behavioral conditions on visual activity, we compared responses to identical stimuli presented during this basic fixation task, presented as targets for saccadic eye movements, or presented as detection targets when the animals were not allowed to move their eyes.

Experiments were controlled with an on-line digital computer, and spike data were analyzed on-line as raster dot displays and histograms. Eye movements were recorded using the scleral search coil technique and were processed on-line by the computer. Most other data were stored for additional off-line analysis. The sites of interesting cells were marked with small lesions for subsequent reconstruction from histological sections.

For studies of the effects of transmitter-related drugs on attentional behavior, monkeys were taught to fixate a spot of light and press a bar when a peripheral target appeared on the tangent screen to the left or right of fixation (Fig. 1). Reaction times were measured in all conditions. Eye position was monitored by the computer to guarantee that fixation was maintained throughout each trial. After animals learned this basic task, the paradigm was modified so that other lights (considered as cues) preceded the onset of the target lights. Cues were 5° hexagons flashed near the target locations (Fig. 1). The sequence of events was (1) appearance of the fixation point, (2) fixation by the monkey, (3) the brief flash (75 msec) of the cue, (4) appearance of the target spot, (5) bar response by the monkey, and (6) delivery of a water reward. The animals' only task was to fixate and respond rapidly to the onset of the target by depressing the bar.

Following training, a cannula was implanted over the region of thalamus of interest, and transmitter-related drugs could then be introduced into the pulvinar through the cannula by pressure injection. We used muscimol, a GABA-agonist, and bicuculline, a GABA-antagonist. Injections were 1–5 micrograms in 1.0–1.5 microliter volumes. After several test sessions, animals were perfused and the injection sites were localized by histological reconstruction.

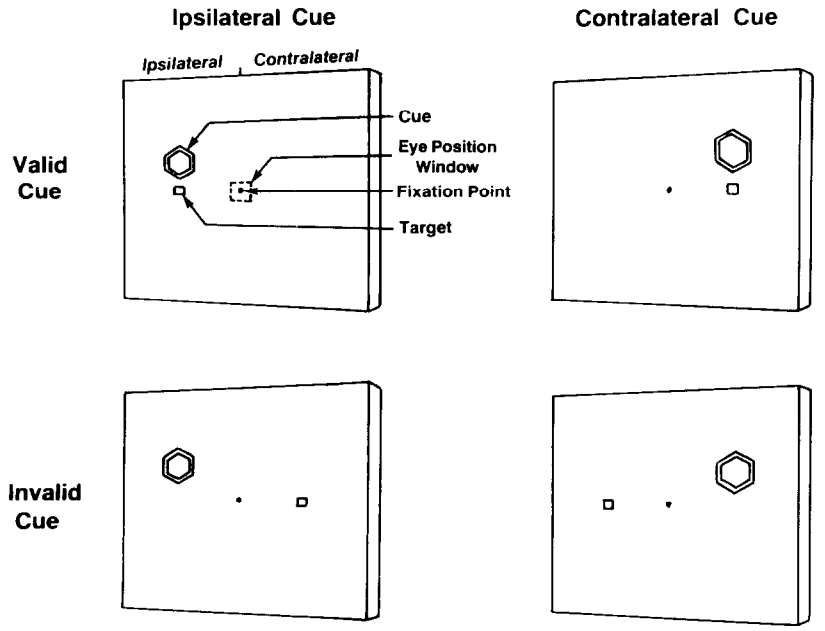

FIG. 1. Cue and target conditions for assessment of injection into the pulvinar. Illustrated are four schematic views of the monkey's tangent screen. Each shows the location of the fixation point, computer-generated eye position control, cue, and target. Valid cues are on the same side as the subsequent target; invalid on the opposite. Ipsilateral and contralateral refer to the side of the drug injection.

RESULTS

Neuron recording

The pulvinar nuclei consist of several subdivisions that can be characterized on anatomical and physiological grounds. On the basis of physiological mapping experiments, there are at least three distinctive regions located in the anterior portion of the lateral and inferior pulvinar nuclei [1, 7]. The first two regions (PI and PL) are retinotopically organized and are located in the cytoarchitectonically-defined inferior and lateral pulvinar. The third has a poor, if any, retinotopic organization and is confined to a part of the lateral pulvinar not taken up by the mapped area. We have termed this latter region Pdm, because it is located in the dorsomedial part of the lateral pulvinar; it is this subnucleus (Pdm) that will be the focus of this paper. Neurons in this area have three characteristics which relate them to visual spatial attention: they are visually responsive, these responses can be selectively modified by attentional behavior, and they have a signal related to saccadic eye movements that could indicate the beginning of a new period of attentional scanning. These properties are quite similar to neuronal properties of area 7 [7, 11], a region long thought to contribute to attention [4, 7, 9, 11].

Visual properties. About 60% of the cells in Pdm discharge to the onset of visual stimuli presented during periods of fixation. Most cells respond to stationary as well as moving stimuli. The visual receptive fields are large and have sizes comparable to those of cortical area 7, with which this region is interconnected [2, 7]. Figure 2 illustrates the outlines of visual receptive fields from samples of neurons recorded in cortical area 7 and from Pdm. These visual receptive fields are quite large when compared to those in the geniculostriate system or those in the adjacent parts of the anterior pulvinar. The majority of Pdm cells respond well to all directions of stimulus movement and few have simple directional selectivity. As in cells recorded from area 7, Pdm cells are not generally selective for stimulus

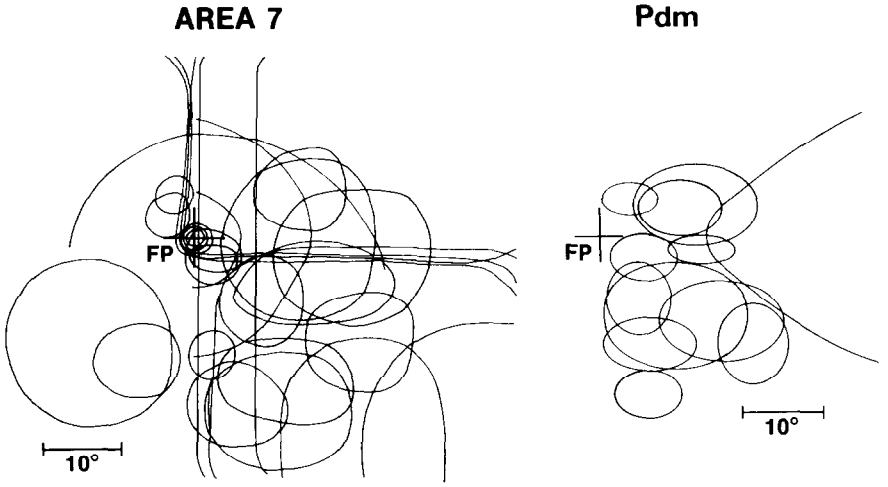

FIG. 2. Outlines of visual receptive fields for populations of cells in cortical area 7 and pulvinar region Pdm. Each outline represents the area of visual space in which lights would change the discharge patterns of a cell. All visual receptive fields are drawn as if the cells were recorded from the left side of the brain and the animals were fixating the cross marked FP. (Data on the left reproduced with permission from ROBINSON *et al.* [10]; on the right, unpublished observations from Petersen, Robinson and Keys).

orientation, length, or width. Few neurons in either area have antagonistic surrounds or internal inhibition. The mean latencies in both area 7 and Pdm for visual responses are long (86 msec mean) and varied. The response latencies differ from those of the adjacent regions of the anterior pulvinar.

In sum, the selectivity of the responses of cells in Pdm is very crude when compared to that in the geniculostriate system and those in the retinotopically mapped regions of the pulvinar [7]. These cells are not well organized for discriminating the fine features of visual stimuli. Nonetheless, they do respond to the presence of light in restricted portions of the visual environment.

Behavioral modulation related to spatial attention. Visual stimulation occurs under many different behavioral conditions. In order to determine how cells in Pdm relate to visual behavior, it is important to know their responses in different contexts. Neurons in Pdm respond more strongly to stimuli that are targets or cues for active behavior than to those which are not associated with such behavior [7]. For example, about 40% of these cells respond more intensely to a light flashed in their visual receptive field when that light is the target for a saccadic eye movement than when the identical image is flashed during continued fixation. Compare Fig. 3(A) and (B). When the cells were tested for eye movement relations, this change in response was shown not to be due to frank eye movement activity.

If the process we have found in Pdm is related to spatial attention, then it should be dissociable from the actual movement of the eyes themselves. The test of this issue is having the monkeys respond to the dimming of a peripheral visual stimulus but constraining it from making eye movements to the light. Since the animals perform this task reliably, we conclude that they are attending to the peripheral target. As shown in Fig. 3(C), cells in Pdm also show enhancement without an eye movement; thus the enhancement effect is independent of an actual eye movement and is probably related to the shift of attention common to both the saccadic eye movement and peripheral detection tasks.

It is possible that this change in activity is due to a general arousal necessitated by task difficulty, or some other reason. To function in an attentional system, the process that causes the enhancement must be part of a selective process; the behavioral modulation of Pdm neurons shows spatial selectivity as documented by a control experiment (Fig. 3(A), (C), and (D)). Here, two stimuli are flashed onto the tangent screen, one inside of the visual receptive field and one outside of it. On one block of trials, the monkey responds with a bar release to a light flashed inside of the visual receptive field when it dims. There is an enhanced response (Fig. 3(C)) compared to the response during standard fixation (Fig. 3(A)). On another block of trials, the monkey responds to the dimming of a target outside of the visual receptive field, and there is no enhanced response (Fig. 3(D)). Such experiments exclude the possibility that non-selective factors such as arousal, task difficulty, or the offset of the fixation point could account for the effect. This experiment documents the spatially selective nature of the enhancement effect and excludes non-specific influences as the cause of the modulations. Enhancement with spatial selectivity and eye movement independence has been found only here in Pdm and in area 7 [5, 7, 12].

Eye movement signal. Another subset of cells in Pdm discharges in association with saccadic eye movements. This burst of activity is closely time-locked to the eye movement. These cells generally discharge during and after the eye movement. They become active with visually guided eye movements in the light, visually guided eye movements in the dark, eye movements made spontaneously in total darkness, and nystagmus-like eye movements in the dark. This signal is independent of beginning eye position; it seems to loosely code the

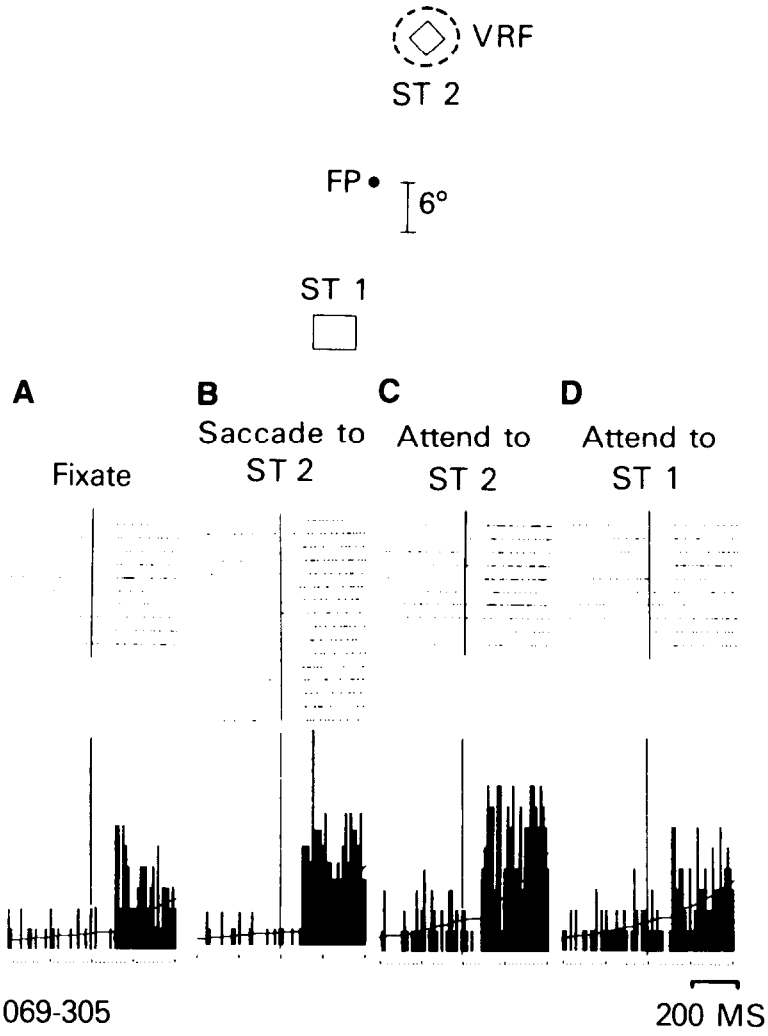

FIG. 3. Spatial selectivity and eye movement independence of enhancement in Pdm. Data in A show the response of the cell to two stimuli flashed on the tangent screen, one in the visual receptive field (ST2, VRF) and one outside (ST1). The monkey maintained fixation throughout these trials. When the animal made a saccadic eye movement to the stimulus in the receptive field (B) there was an enhanced response. When the animal attended to the light inside of the visual receptive field, there was an enhancement of the response (C). When the animal attended to the light outside of the visual receptive field, there was no enhanced response (D). These data show that the effect is present with active use of the light in a particular region of space; it can be produced with either attentive or saccadic use of the light. (Modified and reproduced with permission from PETERSEN *et al.* [7]).

direction and amplitude of the eye movement. We conclude from these observations that this activity is not related to visual factors or the behavioral influences of the trained task. These cells signal that an eye movement has just occurred, but the signals do not encode much information about the specific metrics of the eye movement. Such a signal could indicate the beginning of a period of fixation and that an attentional scan should start.

Influences of pharmacological manipulation on attentional behavior

Because the physiological data just presented suggest that the area Pdm is likely to be involved in visual spatial attention, we wished to directly assess the contribution of this region to attentional behavior. POSNER *et al.* [8, 9] have found in humans that reaction times can be influenced by visual cues, and these reaction time changes have been attributed to attentional processes. We found that monkeys are similarly influenced. Reaction times to peripheral visual targets are fastest if the location of the target is correctly indicated by an antecedent visual stimulus (Fig. 1, valid cue). Slower reaction times are observed when the target location is incorrectly indicated by a visual stimulus (Fig. 1, invalid cue). Monkeys trained on this task show similar changes in reaction times. Since the visual stimulation from the target is constant, and the motor response is identical in all conditions, the factors that alter the reaction times do not have simple sensory or motor explanations. The hypothesis is that a localized cue shifts attention to its locus, and this shift speeds responses to lights at that location and slows responses to lights at other locations. If Pdm participates in visual spatial attention, as our electrophysiological data suggest, then an alteration of the function of Pdm

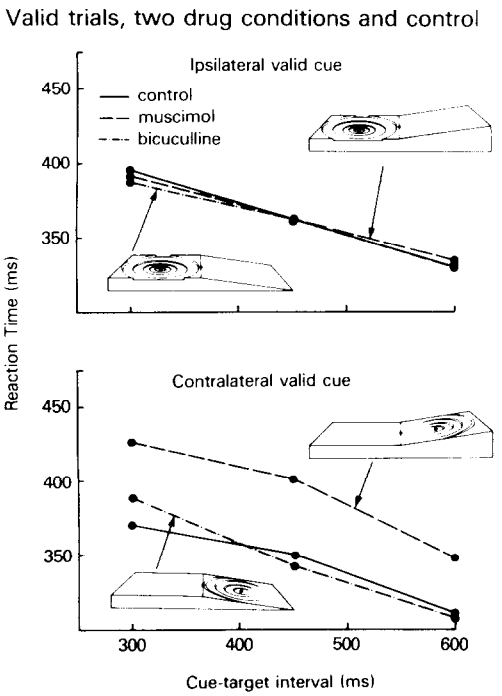

FIG. 4. Effects of GABA-related drugs on validly cued trials. The two cartoons within each graph represent views of a tangent screen. The sculptured pit indicates the location of the cue; the spot represents the location of the target. The spot on the central vertical line depicts the fixation point. Elevations on the right side of the screen suggest the impeding effect of muscimol on shifts of attention in that direction; depressions on the right side refer to the facilitatory effect of bicuculline on the shift of attention in that direction. As illustrated by the data on the top of the figure, neither drug changes reaction times when the cue and target are both presented in the visual field ipsilateral to the injected thalamus. Data on the bottom show the effects of the drugs when the cue and target are presented to the visual field contralateral to the injected thalamus. When muscimol is injected the reaction times are slowed; bicuculline has a small speeding in this stimulus condition (unpublished observations, Petersen, Robinson and Morris).

by changes in its pharmacological state should be associated with changes in attentional performance. Injections of GABA-related drugs do indeed change performance on this cued-visual attention task.

When cue and target are presented in the visual field ipsilateral to the injection of bicuculline or muscimol into the pulvinar, there is little change in the reaction times to the target (Fig. 4, top). This suggests that any influences of the drugs are relatively confined to the contralateral visual field. When the cue and target are presented in the field contralateral to an injection of muscimol into Pdm there is a slowing of the reaction times (Fig. 4, bottom). This suggests that increases in GABA-related inhibition could lead to a slowing of the shift of attention in the contralateral direction. Bicuculline injections do lead to a small speeding in reaction times when the cue and target are in the contralateral visual field. Since reaction times are already quite fast in this condition, the expected speeding caused by the lowered GABA effectiveness is more difficult to detect.

More compelling observations can be made when cues and targets are in opposite visual fields (invalid cues). When the cue is presented in the visual field ipsilateral to the injections and the target in the field contralateral, there is a significant slowing of reaction times after muscimol injections (Fig. 5, top). This suggests again that the increased GABA-related inhibition impedes the shift of attention toward the contralateral visual field. Under the same stimulus conditions, bicuculline injections are associated with faster reaction times (Fig. 5,

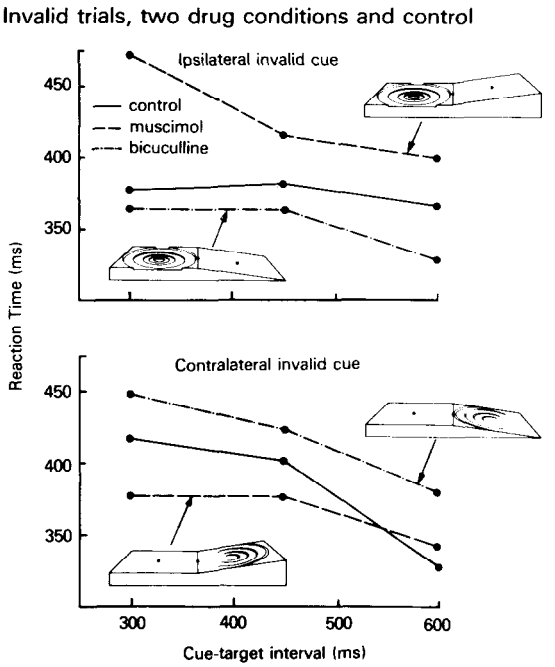

FIG. 5. Effects of GABA-related drugs on invalidly cued trials. The format and cartoons are the same as in Fig. 4. When the cue is flashed in the visual field ipsilateral to the injected pulvinar and the target contralateral, muscimol is associated with slowed reaction times and bicuculline with speeded reaction times. The opposite effects are seen when the cue is flashed in the visual field contralateral to the injected pulvinar and the target ipsilateral. Here, bicuculline is associated with slowed reaction times and muscimol with speeded responding (unpublished observations, Petersen, Robinson, and Morris).

top). These data suggest that the decreased GABA effectiveness facilitates the shift of attention to the contralateral visual field.

Up to this point, all of these results could be attributed to general slowing of reactions to stimuli on the contralateral side following muscimol injection and opposite effects for bicuculline. However, when only the cue is flashed into the visual field contralateral to the injected pulvinar and the target is flashed to the ipsilateral field, the effects of the drugs are the opposite (Fig. 5, bottom). Under these conditions, bicuculline is associated with a slowing of reaction times. Conversely, injections of muscimol lead to a speeding of reaction times. Again, the decreased GABA effectiveness caused by bicuculline injection can most easily be associated with a facilitated shift of attention; this added to the shift of attention caused by the cue results in extremely slow reaction times. Muscimol injection fights against the shift of attention into the contralateral field and allows faster reaction times than control. The effects of either of the drugs seems most closely related to the effectiveness of the cue. Since the cue is the attention-controlling element of this task, we can conclude that manipulation of Pdm affects spatial attentional behavior.

DISCUSSION

The studies reported here show several physiological properties of neurons in the Pdm area of the pulvinar that suggest that they function in visual spatial attention. These neurons are responsive to visual stimuli. Although the information is crude, it can indicate the onset of targets. Many of these same neurons have a selection process; they respond more vigorously to stimuli that are the targets for behavior in spatially distinct zones of visual space than to identical images that are not the targets of such behavior. The effect which causes this augmentation of responding is independent of eye movement just as the psychological phenomenon of attention is separable from movement [8]. Finally, some neurons in Pdm discharge during and after saccadic eye movements. Such cells may indicate to the attentional mechanisms that a gaze shift has just occurred thereby initiating a new attentional scan of the visual world. These neuronal properties could provide mechanisms useful to a system involved in visual spatial attention.

The neural activity that we have sampled correlates with parts of the animal's behavior that we attribute to spatial attention; to determine if the activity in this part of the brain is indeed related to spatial attention, we utilized a direct behavioral measure. We employed a different attentional task, one developed by POSNER [8] for use with humans. This task has the same attributes as the tests that we used to establish the attributes of the behavioral modulation that were found in Pdm neurons: (1) spatial selectivity of effect (different reaction times to spatially valid vs invalid cues), and (2) movement independence (different reaction times even though eyes were not allowed to move and identical bar release was used in all conditions). We were able to alter attentional performance by altering the functioning of this part of the brain. When we micro-injected a drug which increases inhibition (muscimol), the animals performed as if they had difficulty shifting their attention to the contralateral visual field. A drug that had the opposite pharmacological effect (bicuculline), had the opposite behavioral effect; decreases in GABA effectiveness were associated with facilitated shifting of attention to the contralateral visual field. The results of these experiments are not readily interpreted as alterations in sensory processing or motor responding. They are explained most parsimoniously by proposing that the drugs influence an attentional system directly. As

such these data support our hypothesis that area Pdm is indeed related to visual spatial attention.

We feel that these results are interesting on two levels. First, we were able to move from the correlative result of physiological recordings to a behavioral result in a similar setting and draw the same conclusion from each result. The results lend confirmation to each other and are more satisfying than either would have been individually. Second, we are excited that we were able to bring neurobiological tools to bear on a particular psychological process that is an internal covert process not readily observable in terms of everyday behavior. We were able to measure the effects of this covert process on neurons, and the effects of altering the functioning of a discrete set of neurons on this covert process.

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