Everyday visual scenes contain a variety of stimuli that vary in their significance. The companion paper demonstrates that neurons in the posterior parietal cortex (PPC) are capable of encoding the spatial locations of the salient stimulus in multiple stimulus scenes. The present experiment sought to address how neuronal responses to stimuli appearing in the receptive field are modulated after attention has been drawn to one of multiple stimuli in a visual scene. We recorded from area 7a of the PPC in monkeys trained to do a spatial version of a match-to-sample task. The results show that neuronal responses are greatly suppressed when stimuli appear at previously attended locations. No reduction in responsiveness is observed for locations where stimuli had previously appeared but did not draw attention. These results support the hypothesis that area 7a has a role in redirecting attention to stimuli appearing at novel, unattended locations.

Introduction

Psychophysical studies in humans have demonstrated that validly cueing attention decreases the reaction time required to detect a stimulus presented at the cued location (Posner, 1980; Posner et al., 1980). A number of experiments in monkeys have addressed the effects of spatial attention and reveal a modulation of neuronal responses depending on whether attention has been directed inside or out of the receptive field. Experiments in the ventral visual stream (V4, IT) reveal enhanced responses to the stimulus appearing at a previously cued location (Moran and Desimone, 1985; Luck et al., 1997; McAdams and Maunsell, 1999; Reynolds et al., 1999). Some experiments in the dorsal visual stream (MT, MST, LIP) suggest that responses are also enhanced for attended stimuli (Bushnell et al., 1981; Treue and Maunsell, 1996). However several studies in posterior parietal cortex (PPC) showed that when attention has been already drawn at a location in space, subsequent appearance of a stimulus at the same location elicits a diminished response (Steinmetz et al., 1994; Robinson et al., 1995; Steinmetz and Constantinidis, 1995; Powell and Goldberg, 2000). These results led to the hypothesis that PPC has a role in redirecting visual attention.

The latter experiments were performed using a single stimulus as a cue to draw attention. The reduced responsiveness could therefore be the result of passive stimulus repetition within the receptive field, rather than the effect of directing attention. To address this issue we recorded activity from area 7a of the PPC, while animals viewed multiple stimulus displays. Animals were trained in a spatial version of a match-to-sample task requiring them to locate salient stimuli and release a behavioral lever when a subsequent stimulus appeared at the same location. We examined responses to single stimulus displays following arrays of stimuli. The results show that after the presentation of a multi-stimulus display, neuronal responses were only decreased at the location of the stimulus that attracted attention. These results are consistent with the hypothesis that area 7a provides a signal to redirect attention to a salient stimulus, when it appears at a previously unattended location.

Materials and Methods

Two male monkeys (Macaca mulatta) weighing ~5 kg were studied in this experiment. The surgical and recording procedures employed in these experiments were identical to those described in the companion paper.

Task and Stimuli

The animals were trained in a spatial version of a delayed match-to-sample task, using salient stimuli differing in color (Fig. 1). The cue consisted of either single or multiple-stimulus displays. The cue was followed by non-match and match displays that always consisted of a single stimulus. A stimulus constituted a match if it appeared at the same location as the salient stimulus in the cue display. Trials with cues of green or red color, consisting of a single stimulus or an array and followed by zero, one or two non-match stimuli were all randomly interleaved.

Data Analysis

We compared responses to match and non-match stimuli by first subtracting spontaneous activity from each and then computing the ratio Match/Non-match response. A value of 1 suggests equal responsiveness to match and non-match stimuli. A value of 0 is indicative of complete suppression of match responses to the level of spontaneous activity. Negative values suggest inhibition of match responses below the background activation levels. We compared responses to non-match and match stimuli appearing at the same spatial location, immediately after the presentation of the cue with no other intervening nonmatch stimuli. This is the case for the non-match stimuli in Figure 1A and the match stimuli in Figure 1B.

Responses to match stimuli after single and array cues were compared by computing the contrast ratio (S - A)/(S + A). S represents the response to a match stimulus following presentation of a single cue (Fig. 1B, left), and A represents response to a match stimulus following an array cue (Fig. 1B, right). The same procedure was performed for non-match stimuli appearing after single-stimulus and array cues (Fig. 1A). Comparisons always involved match or non-match stimuli appearing at the same location. Additionally, non-match responses following single and array cues (Fig. 1A) were only compared if they followed cue presentations at the same location.

Results

Database

We recorded 321 visually responsive neurons from two rhesus monkeys. We defined visually responsive neurons as those having a statistically significant increase in activity in response to stimulus presentation at any test location (ANOVA, P < 0.05). We based our analysis on 202 neurons tested with color stimuli that responded differentially to single stimuli appearing at the nine grid locations (one-way ANOVA, P < 0.05).
Match and Non-match Responses Following Multiple Stimuli

Responses to match stimuli were significantly suppressed compared to responses to non-match stimuli appearing at the same locations. This was true whether the cue consisted of a single stimulus or an array of stimuli. An example of this effect is shown in Figure 2. This area 7a neuron responded strongly to a non-match stimulus appearing inside its receptive field (Fig. 2A, right histograms). The responses to the identical stimulus in the same location were greatly suppressed when it appeared as a match stimulus that followed cue presentation at the same location (Fig. 2B). The magnitude of the response to the non-match and match stimuli did not depend on whether the cue was a single stimulus or array (upper and lower panel in Fig. 2A, B). The trials used to construct these histograms were all randomly interleaved during the experiment.

These effects were consistent across the population of neurons. Sixty-seven neurons were tested with match and non-match stimuli inside their receptive field, following single and array cues. The average response to a match was 29% of a non-match response at the same location (71% suppression). For 35 neurons (52%) responses to a match were significantly reduced compared to responses to a non-match stimulus at the same location. Only two neurons displayed significantly higher responses to a match stimulus (two-tailed t-test, \( P \leq 0.05 \)). Approximately equal reduction in responsiveness was observed for match stimuli following a single cue or an array. The median values of match responses after single and multiple stimulus cues were 36% and 27% of non-match responses respectively. The distribution of match relative to non-match responses for all neurons tested is shown in Figure 3. A neuron-by-neuron comparison of the response to matches following a single and array cues is shown in Figure 4A. Each data point represents the responses of a single neuron to matches of the same color and appearing at the same location. Points falling on the diagonal indicate equal suppression of match responses. We computed the contrast ratio \((S - A)/(S + A)\) for match responses following the two types of cue displays (see Materials and Methods). The average value was 0.06, suggesting that responses to a match stimulus following an array were approximately equally suppressed as match responses following a single-stimulus cue.

This suppressive effect of the match was largely independent of the ability of the neuron to represent the location of the salient stimulus in the array. A regression analysis between the correlation coefficient for single and array responses (shown in Fig. 8 of the companion paper) and the match/non-match ratio, showed no significant dependence (\( P > 0.4 \)).

Responses to non-match stimuli following array cues were not significantly different from responses following single cues, for the majority of the neurons. Two hundred and two neurons were tested with non-match stimuli of the same color and at the same...
location, following single and array cues. We computed the contrast ratio \((S - A)/(S + A)\) for the non-match responses following each type of cue display (see Materials and Methods). The average value was 0.03, suggesting approximately equal non-match responses following each type of display. Results from all neurons tested are shown in Figure 4B. Most of the responses fall near the diagonal, indicating equal responsiveness following single cues and arrays. Only 10% (21/202) of the neurons had significantly higher non-match responses following a single cue and 9% (18/202) following an array cue (two-tailed \(t\)-test, \(P < 0.05\)).

Taken together, these data demonstrate that responses are suppressed following cue stimuli but not distractors at the same location. These results argue that the decreased responsiveness to a match stimulus is an effect of the focus of attention, rather than passive repetition of a match stimulus inside the receptive field. It is still possible, however, that a habituation effect reduces match responses only if a previous stimulus elicits a strong response from the neuron. A distractor appearing inside the receptive field but failing to elicit a strong response may not be sufficient to elicit this suppression effect. To account for this possibility, we examined responses to match stimuli that appeared after an intervening, non-match stimulus, which did not elicit a response. An example is shown in Figure 5. This neuron responded well to a non-match stimulus appearing inside the receptive field (Fig. 5A), but not to the same stimulus appearing as match in the receptive field (Fig. 5B). Responses to match stimuli appearing inside the receptive field immediately after the cue or after an intervening stimulus are shown in Figure 4C for 32 neurons tested with match stimuli of the same color, appearing at the same location. In each case, the response was almost identical, suggesting that the decreased responsiveness to stimuli appearing at the cued location is not simply an effect of habituation due to the preceding response.

Discussion
Our results indicate that responses of neurons in area 7a are suppressed for stimuli appearing inside the locus of attention. This reduction in responsiveness does not depend on whether a single stimulus or a salient stimulus among distractors served to direct attention. Conversely, responses were not suppressed by the prior presentation of background stimuli that did not summon attention.

Pop-out Effect
Multiple stimulus displays like the ones we used in our experiments have been extensively studied in the human psychophysical literature. Human observers are able to detect a target that differs from its background in one stimulus modality such as color, orientation or binocular disparity in one step, without having to search through each item of the display (Treisman and Gelade, 1980; Bergen and Julesz, 1983; Nakayama and Silverman, 1986). Such stimuli are said to ‘pop-out’ and they can capture attention even when a subject is not searching for the particular target \textit{per se} (Egeth and Yantis, 1997). On the contrary, target stimuli defined by a conjunction of features, such as color and...
shape, require a serial search of the display and the time required for their detection increases as function of the number of elements in the display. When subjects are not allowed sufficient time to scan the display, they often report illusory conjunctions, e.g. a red circle and a green square may be perceived as a red square and a green circle (Treisman and Schmidt, 1982). There is not a strict dichotomy between search for a single feature and that for a feature conjunction. Human subjects can detect target stimuli defined by a conjunction of features in parallel, provided they are sufficiently different from the distractors (Duncan and Humphreys, 1989).

Monkeys can similarly perform visual search based on a single feature or a conjunction (Bichot and Schall, 1999). Our current results suggest that the neuronal effects of attention in PPC were almost identical when attention is guided by a single stimulus or a pop-out element (Fig. 4). Responses to a stimulus appearing at the cued location were equally suppressed when the cue appeared alone or as a pop-out stimulus. No such suppression was observed when a stimulus appeared at the location of a distractor that presumably failed to attract attention.

**Match Suppression is a Dynamic Effect of Attention**

Several lines of evidence suggest that the suppressive effect depends on the animal's locus of attention rather than repeated appearance of a stimulus inside the receptive field. Stimuli appearing as non-matches following presentation of an array as cue are not suppressed, even though they appear at the location of a distractor stimulus in the array. Furthermore, suppression is not dependent on a strong response from the stimulus preceding the match presentation. In fact responses to a match delivered immediately after the cue or after an intervening stimulus were virtually identical for our sample of neurons (Fig. 4C).

A previous study in our laboratory using exclusively single stimuli but testing a much larger sample of neurons showed equal ratios of suppression for match responses appearing after zero, one or two intervening non-match stimuli, whether or not...
the latter elicited a response (Steinmetz and Constantinidis, 1995). This result suggested that responses continue to be suppressed at the cued location for at least 2–3 s (the onset asynchrony between cue and match appearing after two intervening non-matches). It must be emphasized that our behavioral task introduced no uncertainty about the location of the target stimulus and allowed the animals to focus their attention accordingly on each trial, which could account for such a prolonged effect. Trials with the cue appearing at the same location were sometimes delivered in blocks in that experiment, enabling the animals to predict the cue location. If the suppression to the match was due to a passive, habituation phenomenon, responses to successive cue and match presentations would be expected to diminish progressively as they always appeared at the same location. An intertrial interval of −2.5 s intervened between the match stimulus and the cue presentation of the following trial, in the range of the stimulus onset asynchronies over which we observed reduced match responses. Contrary to this prediction, we observed that the responses to the cue diminished after the first presentation but the same was not true for the match (Fig. 6). What differed for the cue and match presentations was that the animal was uncertain about where the cue was going to appear when a block of trials was initiated, but no such uncertainty existed about the location of the match in each trial. The critical factor that predicted the reduced responsiveness to a stimulus was the ability to securely orient attention, rather than a prior appearance of a stimulus at the same location.

Our results are in agreement with recordings from area LIP, which show similar decrement of neuronal responses when a stimulus appears at an already attended location, even when a stimulus outside the receptive field served to summon attention to that location (Robinson et al., 1995; Powell and Goldberg, 2000). Taken together, these results indicate that suppression after repeated stimulation is not a passive effect that can be sustained for several seconds, but in each case correlates with the allocation of attention.

Attention is not the only factor that can modulate the responses of neurons in the PP cortex. A recent study made use of a color stimulus inside the receptive field to signal whether a monkey should execute a saccade or a reach movement towards the target (Snyder et al., 1998). In some trials, a stimulus reappeared at the receptive field and instructed the animal to execute its original plan, or to switch between a saccade and reach movement. If the first stimulus instructed a saccade, reduced responses were observed in area LIP for the second appearance of the stimulus. This is similar to our own results. However, a modest increase in response was observed if the first stimulus instructed a reach movement and the second a saccade. The effect was more pronounced in the cortical area the authors call the ‘parietal reach region’ (Snyder et al., 1997), which roughly corresponds to area MIP (Felleman and Van Essen, 1991). The finding suggests that the location of attention is not the only factor modulating the responses of posterior parietal neurons and that the type of motor response may also be a factor. This may be particularly true for area LIP where a much larger percentage of neurons display peri-saccadic activity than area 7a and also for areas specialized for reach movements.

Role of Posterior Parietal Cortex in Reorienting Attention

The selective representation of a salient stimulus in a multiple stimulus display and the lack of responsiveness at a cued location suggest that PPC may provide a spatial signal to reorient attention when stimuli appear at unattended locations. One of the most dramatic demonstrations of an attentional deficit following posterior parietal lesions is the increase in reaction time for detecting a stimulus in the affected hemisphere, after (invalidly) cueing the opposite field (Posner et al., 1984). Posterior parietal lesions, however, at least after their acute phase, do not impair patients greatly in detecting a stimulus when validly cued in either hemisphere. These results led Posner and colleagues to propose that PPC is responsible for disengaging attention, but not for orienting it to a new location. The latter function was attributed to the superior colliculus. This idea was widely disseminated (Posner et al., 1988; Posner and Petersen, 1990) but has been hard to reconcile with the physiological properties of neurons in PPC (Andersen et al., 1997; Colby and Goldberg, 1999). Our results provide insight that could account for this discrepancy. Neurons in PPC may provide a spatial signal to orient visual attention only when it has already been engaged at another location. In our behavioral paradigm, this would correspond to a spatial signal for the position of a non-match stimulus after the cue. When attention has not been engaged, however, a spatial signal from the PPC may not be critical for perceiving or further processing a newly appearing stimulus. Indeed posterior parietal neurons respond weakly to stimuli appearing when the animal is not in a state of attentive fixation (Mountcastle et al., 1981; Mountcastle et al., 1987).

Notes

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