Neuronal Responses in Area 7a to Multiple-stimulus Displays: I. Neurons Encode the Location of the Salient Stimulus

Christos Constantinidis[1] and Michael A. Steinmetz

Zanvyl Krieger Mind/Brain Institute, Johns Hopkins University, 3400 N. Charles Street/Krieger Hall, Baltimore, MD 21218, USA
[1]Present address: Section of Neurobiology, Yale University School of Medicine, New Haven, CT 06510, USA

The primate posterior parietal cortex (PPC) plays an important role in representing and recalling spatial relationships and in the ability to orient visual attention. This is evidenced by the parietal activation observed in brain imaging experiments performed during visuospatial tasks, and by the contralateral neglect syndrome that often accompanies parietal lesions. Individual neurons in monkey parietal cortex respond vigorously to the appearance of single, behaviorally relevant stimuli, but little is known about how they respond to more complex visual displays. The current experiments addressed this issue by recording activity from single neurons in area 7a of the PPC in monkeys performing a spatial version of a match-to-sample task. The task required them to locate salient stimuli in multiple-stimulus displays and release a lever after a subsequent stimulus appeared at the same location. Neurons responded preferentially to the appearance of salient stimuli inside their receptive fields. The presence of multiple stimuli did not affect appreciably the spatial tuning of responses in the majority of neurons or the population code for the location of the salient stimulus. Responses to salient stimuli could be distinguished from background stimuli ~100 ms after the onset of the cue. These results suggest that area 7a neurons represent the location of the stimulus attracting the animal's attention and can provide the spatial information required for directing attention to a salient stimulus in a complex scene.

Introduction

The visual system is capable of processing only a small fraction of the information available in the field of view at any instant in time. Visual search and selective attention mechanisms allow the brain to focus resources sequentially on objects of interest. Although numerous models of selective attention have been proposed (Koch and Ullman, 1985; Olshausen *et al.*, 1993; Desimone and Duncan, 1995; Singer and Gray, 1995), the underlying neural mechanisms remain poorly understood. Early clinical data suggested that the association cortex of the parietal lobe is critical for visual attention. Parietal lobe lesions in humans, particularly those of the right hemisphere, result in difficulty to perceive stimuli that appear in the visual field contralateral to the lesion, despite an intact visual field and normal acuity. This syndrome is known as contralateral neglect (Critchley, 1966; Weinstein and Friedland, 1977). The acute symptoms of neglect typically subside with time and patients often recover their ability to detect stimuli in the contralateral field. What persists in some patients is the difficulty to detect a stimulus in the contralateral side when presented simultaneously with one in the unaffected visual field on the ipsilateral side, an effect known as extinction (Heilman, 1979; Posner *et al.*, 1984).

Brain imaging studies have confirmed the involvement of PPC in tasks that require visual–spatial processing, shifting of spatial attention, and spatial working memory. PPC is selectively activated in tasks that require either voluntary allocation of attention or detection of a target when subjects have no prior knowledge of its spatial location (Corbetta *et al.*, 1993, 1995; Nobre *et al.*, 1997; Kastner *et al.*, 1999). The two processes appear to be localized in discrete regions within the human PPC (Corbetta *et al.*, 2000).

The functional properties of neurons in PPC have been studied in neurophysiological experiments in monkeys performing a variety of visuospatial tasks. These studies demonstrate that responses to peripheral stimuli are enhanced when the animals are attentively fixating a central target and when the peripheral stimulus is to be the target of an impending saccade (Yin and Mountcastle, 1977; Robinson *et al.*, 1978; Bushnell *et al.*, 1981; Mountcastle *et al.*, 1981, 1987). Other experiments indicate that neuronal responsiveness is greatly diminished for stimuli repeatedly presented at an attended location or constantly present in the background (Steinmetz *et al.*, 1994; Robinson *et al.*, 1995; Steinmetz and Constantinidis, 1995; Gottlieb *et al.*, 1998). A subset of area 7a neurons continues to discharge long after the disappearance of a stimulus. This memory-related activity is independent of the animal's motor response in the task (Constantinidis and Steinmetz, 1996). These data suggest that the spatial location of novel and behaviorally relevant stimuli may be represented in the activity of neurons in PPC. Most studies of PPC, however, have employed single stimuli. Little is known about their responses to more complex multiple-stimulus displays.

The task of directing attention to one of multiple stimuli without prior knowledge of the target location has been shown to activate PPC in human imaging studies (Corbetta *et al.*, 1995). The ability to perform such tasks is severely compromised by parietal lesions (Posner *et al.*, 1984). Understanding the neuronal operation performed in these conditions is important for elucidating the function of PPC in selective attention. Previous studies have shown that neurons in the frontal eye fields respond selectively to the presentation of visually salient saccade targets in multiple-stimulus displays (Schall and Hanes, 1993; Schall *et al.*, 1995). The current experiments were designed to determine if neurons in area 7a of the parietal cortex were capable of encoding the location of salient stimuli in multiple-stimulus displays independent of eye movements.

We sought to test how PPC responds to displays of multiple stimuli, one of which is known to attract the animal's attention. Our hypothesis is that the activity of posterior parietal neurons selectively represents the spatial location of the stimulus that attracts attention. This signal could serve to guide visual attention, focus neural processing on the salient stimulus, or to register the stimulus in working memory. We recorded single-unit activity from neurons in area 7a of the PPC of monkeys. Neurons in this area have large receptive fields that are well suited for integrating across a wide expanse of the visual field in order to locate salient stimuli in complex displays. We used visual displays containing either single stimuli or arrays of stimuli where one differed in color from the others. Monkeys were

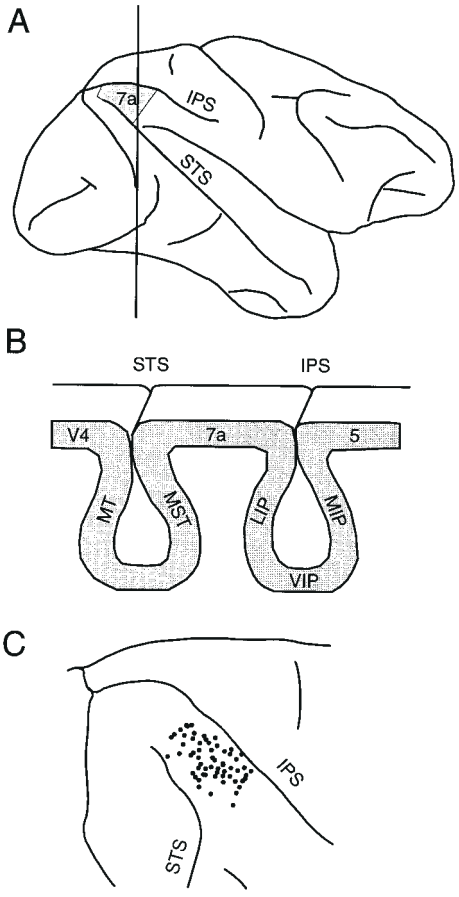

Figure 1. Recordings were made in area 7a of the posterior parietal cortex, bounded by the intraparietal and superior temporal sulci. (*A*) Lateral view of the macaque brain. (*B*) Cross-section through the posterior parietal cortex at the level indicated by the vertical line in (*A*). (*C*) Anatomical reconstruction of recording sites where we encountered task-responsive units. Posterior parietal cortex is shown in dorsal view. IPS, intraparietal sulcus; LIP, lateral intraparietal area; MIP, medial intraparietal area; MST, medial superior temporal area; MT, medial temporal area; STS, superior temporal sulcus; VIP, ventral intraparietal area.

trained in a spatial version of a match-to-sample task that required them to detect the salient stimulus in the display and release a lever after the disappearance of a subsequent stimulus at the same location. Eye movements were prohibited by requiring continuous fixation of a central target light. Our results indicate that area 7a neurons respond more strongly to salient than to background stimuli appearing inside their receptive fields. The population activity in these neurons revealed a representation of the spatial location of the salient stimulus in the multiple-stimulus display. The loss of such a signal could account for the neglect and extinction phenomena following parietal lesions.

Materials and Methods

Two male rhesus monkeys (*Macaca mulatta*) weighing ~5 kg were studied in this experiment. Single-unit recordings were performed in area 7a of the PPC (Fig. 1). All animal care and experimental procedures were in compliance with National Institutes of Health and Johns Hopkins University guidelines.

Behavioral Task

The animals were trained on a spatial version of a delayed match-to-sample task (Fig. 2). Monkeys sat on a dimly illuminated room with their heads fixed and viewed a computer monitor that stood 45 cm away. They pulled and held back a lever at the onset of a 0.5° target light and maintained eye position throughout the trial within a ±1° window surrounding the fixation target. An eye movement beyond the allowed window resulted in immediate termination of the trial and a brief warning tone. The trials consisted of a series of stimulus presentations separated by delay periods during which only the fixation target was present on the screen. The duration of stimulus presentation and delay periods was typically 500 ms. The animals were required to attend the location of the salient stimulus in the first presentation (cue) and to release the lever when a subsequent presentation contained a stimulus at the previously cued location (match). The monkeys were trained to delay their behavioral responses until the disappearance of the match stimulus in order to separate neuronal activity evoked by the visual stimuli from potential influences of hand and eye movements associated with the end of the trial. They were required to respond within 500 ms after the offset of the match stimulus in order to prevent them from performing the task by timing.

The cue and match stimuli were separated in time by zero, one or two presentations in which a salient stimulus appeared at uncued locations (non-match). Each stimulus presentation consisted of either single stimuli or 3 × 3 grids of stimuli in which one stimulus (salient) differed in color from the eight others (distractors).

Visual Stimuli

The animals were tested with 4° red or green squares as salient stimuli, appearing either alone or in a field of distractors of the opposite color (Fig. 2). Salient stimuli and distractors were presented on a computer monitor and were adjusted for equal luminance (measured by a Pritchard PR-1980 photometer). Cue presentations consisted of either single stimuli or multiple-stimulus arrays. Multiple-stimulus arrays always consisted of nine stimuli, centered on fixation with individual stimuli spaced 25° apart. These eccentricities are larger than those typically used in human psychophysical experiments, but enabled us to study 7a neurons, the majority of which have peripheral receptive fields extending well beyond 5–10°. Single stimuli of either color were used as non-match and match stimuli.

Each neuron was tested with trials using either single or array cues of red or green color appearing at each of the nine locations. Trials were also included in which only the fixation point was present. The monkey was rewarded on these trials for releasing the key in response to a slight dimming of the fixation point. These trials provided behavioral relevance to the fixation point and focused the animal's attention to the fixation point prior to the appearance of any stimuli. All types of trials were randomly interleaved.

Some neurons were tested with stimulus arrays consisting of nine stimuli of the same color and no salient stimulus (no-cue trials). No-cue presentations were always followed by a single stimulus in the same format as the other the match-to-sample trials. The monkey initially withheld the behavioral lever until the end of the presentation and was not rewarded. The animal eventually realized that only one stimulus followed the cue in trials with no salient stimulus and released the lever in time to receive a reward. Animals were not trained with no-cue trials prior to recording session. These trials represented less than 0.5% of the total number of trials used during recording in order to avoid adverse influences on the behavioral strategy of the monkey in the match-to-sample task. Only those trials with eye movements or early key releases were excluded from the analysis of the no-cue trials.

Training

The monkeys were first trained to fixate and pull back a lever upon the appearance of a 0.5° target on the screen. They received a liquid reward if they maintained fixation and released the lever when the fixation target dimmed. Eye position was monitored with a scleral eye coil. A simple form of the match-to-sample task was introduced after the monkey was able to maintain fixation for periods of 4–5 s. Two peripheral stimuli appeared in sequence at the same location (a cue and a match) and the monkey was rewarded for maintaining fixation and releasing the lever within a 500 ms window after the disappearance of the match stimulus. Non-match stimuli were then added and then trials with 0–2 non-match stimuli were randomly interleaved so that the monkey could not perform the task by timing. Training then advanced to the use of multiple-stimulus

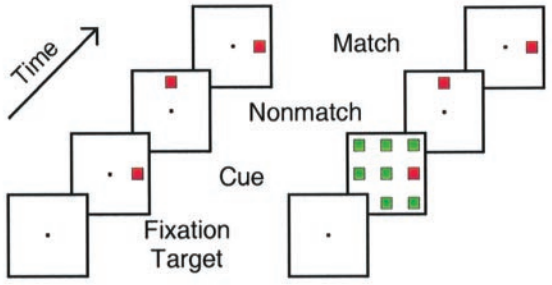

Figure 2

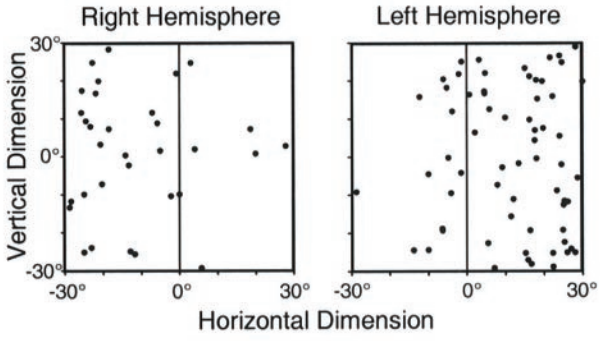

Figure 3

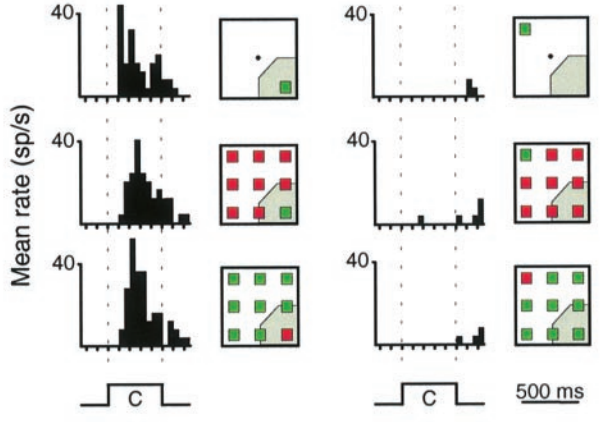

Figure 4

arrays as cues. Distractors were initially introduced as smaller and dimmer stimuli and the monkeys learned to ignore them. The distractors became progressively larger and brighter so that the monkeys would distinguish salient stimuli from distractors based on their color alone. Monkeys were trained with sets of trials that included both green and red salient stimuli, so that they would not develop a bias for one of the two colors or be able to predict the color of the salient stimulus in a set. Experiments began when the animals were able to perform the task with an error rate less than 15% (excluding eye movement errors). The most common errors during recording sessions were breaks in fixation due to blinks.

Surgical Procedures

Monkeys were implanted with a standard head holding device after an initial period of acclimation to the laboratory surroundings and training on the fixation task. A second surgery was performed to implant a scleral eye coil a few weeks later (Fuchs and Robinson, 1966). Neural recordings were accomplished via a 1 cm diameter craniotomy placed after the animal had achieved criterion performance in the task. The craniotomy was covered with a plastic cap that was removed before each recording session. All surgical procedures were performed under sterile conditions using general anesthesia. Prophylactic antibiotic and analgesic drugs were administered after each surgery.

Figure 2. Behavioral task. Trials consisted of a series of visual presentations separated by delay periods with only the fixation target present. Successive time frames represent the sequence of stimulus presentations (delay periods are not shown). The duration of stimulus and delay periods was typically 500ms. Trials in which the match immediately followed the cue were randomly interleaved with those in which the cue and match were separated in time by one or two presentations of a stimulus at an uncued location (non-match). Cue presentations consisted of red or green squares either alone (left) or in a field of distractors of the opposite color (right). Arrays were centered on the fixation point with elements spaced 25° apart. Trials with presentations using single or multiple stimuli of either color were randomly interleaved so that the monkey could not predict the color or location of the salient stimulus.

Figure 3. Points represent the preferred locations of neurons recorded in the left and right hemispheres. Preferred locations were determined by fitting a two-dimensional Gaussian to neuronal responses for single stimuli at each of the nine locations.

Figure 4. PST histograms depict responses of one area 7a neuron for each of the six cue presentations shown in the frames to the right of each group (ordinate values in impulses/s; bin size = 50 ms). The shaded area represents the neuron's approximate receptive field. Strong responses were observed to salient stimuli presented inside of the receptive field either alone (top left) or with distractors (middle and bottom left). Weak responses were observed when the salient stimuli appeared outside the receptive field (right panels), even when distractors appeared inside the receptive field (middle and bottom right).

Electrophysiological Recordings

Extracellular recordings from isolated single neurons were performed using multiple-electrode arrays (Mountcastle *et al.*, 1991). Microelectrodes consisted of quartz glass filaments with metal cores of tungsten–platinum alloy. Simultaneous recordings from up to seven electrodes were possible. The system allowed for the precise placement of electrodes in coordinates relative to the center of the recording chamber. Voltage readings from the electrodes were displayed on oscilloscopes and action potentials of single neurons were isolated using differential amplitude discriminators. The times of occurrence of these action potentials were stored digitally with a resolution of 100 µs. The onset and offset of visual stimuli, the pulling and release of the behavioral lever, and eye position readings from the scleral coils were also recorded and stored.

Anatomical Localization

Stereotaxic coordinates were used to position the recording chamber over area 7a. A mark was placed on the skull at –10 mm to the intra-aural line and 10 mm lateral to the midline. The craniotomy was drilled perpendicular to the cortical surface and centered on this location. Recordings were restricted to the crown regions of the gyrus and electrodes were not advanced more than 2–2.5 mm from the top of the cortex (Fig. 1*A*). Marker pins were inserted at the center of the craniotomy and the brain was photographed and sectioned after the completion of the experiment. Recorded neurons were localized in the cortex based on the coordinates of each penetration relative to those of the marker pins.

Fluorescent dyes were used to mark and identify the tracks left by the electrodes during the last day of recordings in each hemisphere of one monkey (DiCarlo *et al.*, 1996). Seven electrodes, arranged in a straight line and spaced 1 mm apart from each other, were coated with fluorescent dyes and inserted into the brain. Serial brain sections were digitized and a three-dimensional model of the parietal lobe was reconstructed. The dye marks were visualized with a fluorescence microscope. Electrode coordinates were used to localize all penetration sites on the cortical surface relative to the dye-marked electrode tracks (Fig. 1*C*). Less than 3%

(9/321) of the visually responsive neurons were recorded near the lateral bank of the intraparietal sulcus corresponding to lateral intraparietal area (LIP) (Andersen *et al.*, 1985). Although LIP is distinguished by a thick myelination of the underlying white matter, we were unable to determine a sharp border between it and area 7a. The neurons recorded near this border did not differ significantly in any of their physiological properties of the rest of the population and were included in subsequent analysis.

Analysis of the Influence of Distractors

Neuronal responses to multiple stimuli were studied by comparing the discharge rates evoked by a single stimulus appearing at each grid location to those evoked by arrays with the salient stimulus at matching locations. The responses during the cue presentation only were analyzed for this paper. Analyses of match and non-match responses will be presented in the companion paper. Average discharge rates were measured in an interval equal to the duration of the cue presentation (typically 500 ms). Neurons were included in this analysis if they satisfied three criteria: (i) they responded to at least one visual stimulus with a discharge rate significantly above baseline (*t*-test, $P < 0.05$), (ii) they were studied with single and array stimuli with a salient stimulus appearing at each of the nine grid locations, and (iii) their responses were significantly different for single stimuli appearing at the nine grid locations (one-way ANOVA, $P < 0.05$). The latter criterion was used to remove neurons with responses that were not spatially tuned or were highly variable from subsequent analysis.

A one-way ANOVA was used to compare responses to arrays of stimuli with the salient stimulus appearing at each of the nine grid locations. The null hypothesis was that the neuron could not discriminate between a salient stimulus and a distractor and responded equally well when either one fell inside its receptive field. The effect of distractors on a neuron's spatial tuning was quantified by computing the correlation coefficient between the neuron's responses to the single stimulus presented at the nine grid locations and to responses when the same stimulus appeared among distractors.

Population Analysis

A population model was constructed by combining the responses of all neurons to a particular stimulus. The responses of each neuron to single stimuli presented at the nine locations were initially fitted to a two-dimensional Gaussian. A preferred location for each neuron was assigned as the coordinates of the function's peak value. The mean square error and correlation coefficient between the experimental data and the fitting function were computed for each neuron. Neurons with correlation coefficients >0.85 and mean square errors <0.075 were included in the model.

A population response to a single stimulus at a particular location was constructed by plotting a family of vectors on an x–y plane. Each neuron was represented by a vector. The amplitude of each vector was proportional to the neuron's actual response to the stimulus. The x–y coordinates of each vector corresponded to the neuron's preferred location. The vectorial representations were convolved with a two-dimensional Gaussian to produce a smoothed function of the population response to a particular stimulus presentation.

Two-dimensional Gaussian functions with standard deviations that were equal in both dimensions were calculated at each point x, y as follows:

$$g(x,y) = \frac{1}{2\pi\sigma^2}\exp-\left(\frac{x^2+y^2}{2\sigma^2}\right) \quad (1)$$

The population response of N neurons to presentation of a single stimulus was estimated for each point as:

$$P(x,y) = \sum_{i=1}^{N} r(X_i,Y_i)\cdot g(X_i - x, Y_i - y) \quad (2)$$

The variable r denotes the actual response of neuron i to the stimulus. The neuron's preferred location is represented as (X_i,Y_i). Our database contained a larger sample of neurons recorded from the left hemisphere, resulting in an over-representation of the right visual space (Fig. 3). This problem was corrected by mirroring the responses of all neurons across the vertical meridian. We repeated the vector analysis to estimate the population response to stimuli presented for each of the nine grid locations for single stimulus presentations and again for salient stimuli among distractors.

Receiver Operating Characteristic Analysis

The ability of area 7a neurons to discriminate between a salient stimulus and a distractor in a multiple-stimulus array was assessed by plotting a Receiver Operating Characteristic (ROC) curve. The ROC analysis compares two response rate distributions and estimates the probability that an ideal observer can discriminate correctly between the two stimuli that generated the two distributions. The method does not depend on assumptions about the variance or shape of the two distributions.

Each point in the ROC curve represents the probability that a stimulus will be correctly classified as salient and the probability that it will be falsely classified as salient, for one criterion response level. If, for example, an ideal observer used a response level of 10 impulses/s as a criterion to classify a stimulus as salient and the neuronal response to the true salient stimulus exceeded this response criterion 75% of the time, then the rate of hits would be 75%. If the response to a distractor exceeded the 10 impulses/s criterion 25% of the times, the rate of false-positives would be 25%. The ROC curve is constructed by plotting the rate of hits (ordinate) as a function of the rate of false-positives (abscissa) for a range of criterion levels. The set of criterion levels for each neuron was defined by the union of the set of response rates to the salient stimulus and the set of response rates to the distractor; it ranged from zero to the maximum response rate of each neuron. The curve constructed based on these criterion levels fully describes the ROC; any additional criteria would produce data points falling on the plotted curve. If the salient stimulus and distractor distributions were identical, the hit rate and false rate would be the same for all criterion response level and all the points in the ROC curve would fall on the diagonal. The area under the ROC curve thus represents the probability of correctly discriminating the salient stimulus based on discharge rate alone (Tolhurst *et al.*, 1983).

Time Course

The time course of neuronal responses to arrays of stimuli was examined by constructing population peristimulus time histograms (PSTHs). The receptive field of each neuron was determined from the responses to single stimuli. We compared the response at the location that elicited the best single-stimulus response to that at the location outside of the receptive field that elicited the worst single-stimulus response (usually diametrically opposed to the best location). Responses from single trials were converted to spike density functions by convolving each spike with a Gaussian pulse of 10 ms standard deviation (Richmond *et al.*, 1987; Schall and Hanes, 1993). The discharge rate of each neuron was then calculated in 10 ms bins, aligned on stimulus onset. Responses from all neurons were averaged together to produce a population PSTH.

Results

Database

We recorded activity from 321 visually responsive neurons in two rhesus monkeys. We defined visual neurons as those having a statistically significant (ANOVA, $P < 0.05$) increase in activity in response to stimulus presentation at any test location. Of those, 202 neurons were tested at all nine grid locations with a single stimulus and an array and displayed differential responses to single stimuli appearing at the nine grid locations (one-way ANOVA, $P < 0.05$). These neurons were included in further analysis. Results in this paper are based on the analysis of responses to the first stimulus (cue) appearing in each behavioral trial. Responses to subsequent stimuli are presented in the companion paper.

Responses to Salient Stimuli

Neuronal responses to single stimuli and arrays presented as cues in the match-to-sample task were compared and the effect of distractors was assessed. A representative example is shown in Figure 4. This neuron responded to a single stimulus and to

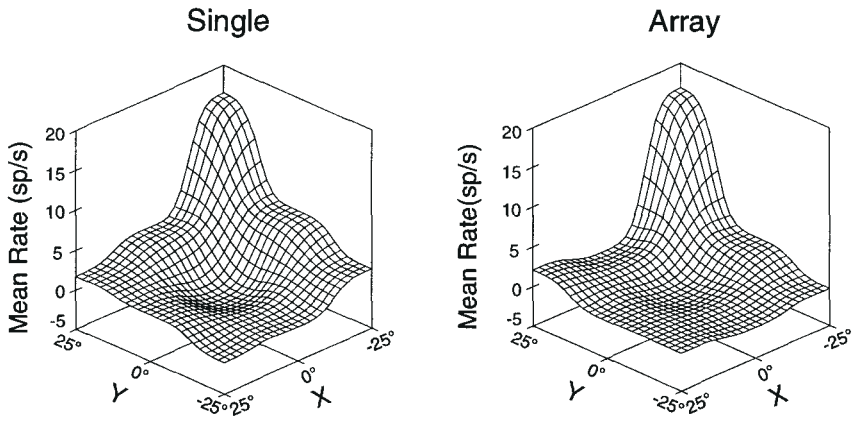

Figure 5. Surface plots represent the mean firing rate of the neuron shown in Figure 3 during the cue presentation period as a function of the coordinates of a salient stimulus presented alone (left) or in a multiple-stimulus array (right). Nine locations were tested; intermediate points were interpolated using an inverse power function.

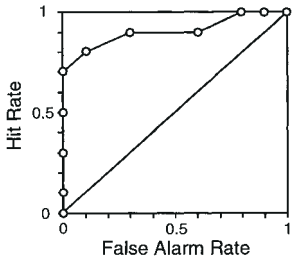

Figure 6. ROC curve based on the responses to the salient stimulus and distractors is shown for one area 7a neuron. The area under the ROC curve was 0.9 for this example.

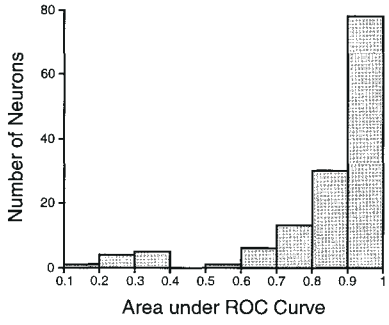

Figure 7. The distribution of the area under the ROC curve is shown for the population of area 7a neurons studied. ROC analysis was performed to compare the responses to salient stimuli and to distractors appearing inside the receptive field.

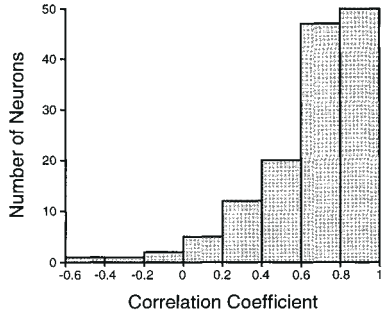

Figure 8. Coefficients of correlation between the responses to single and multiple stimuli presented with the salient stimulus at each of the nine grid locations.

stimulus arrays of either color when the salient stimulus was presented inside the receptive field (left panels). This same neuron did not respond when the salient stimulus was presented outside of the receptive field even though distractors fell inside the receptive field (right panels). The spatial tuning of this neuron derived from the responses of the salient stimulus alone and among distractors for each of the nine grid locations is shown in Figure 5. The correlation coefficient between the two spatial profiles was 0.95. Despite the high degree of similarity, some suppression around the peak is evident when distractors are present.

Differential responses to the location of the salient stimulus in the array was observed in 68% (138/202) of the neurons tested (one-way ANOVA, $P < 0.05$). This result indicates that the majority of area 7a neurons responded more strongly to salient stimuli than to distractors in their receptive fields. The remaining neurons responded similarly to salient stimuli and distractors and therefore could not provide a spatial signal for the position of the salient stimulus; their response properties were examined separately.

The ANOVA results demonstrate that a population of neurons responded differentially to the location of the salient stimulus in the array. We quantified the reliability of individual neurons in discriminating between salient stimuli and distractors by performing a ROC analysis. Responses to arrays of stimuli with the salient stimulus or distractors appearing inside the receptive field were compared in the 138 neurons that exhibited significant spatial preference for the location of the salient stimulus. The ROC curve is shown in Figure 6 for one area 7a neuron. The area underneath the ROC curve indexes the ability of an individual neuron to discriminate between a salient stimulus and a distractor. An area of 1.0 indicates a perfect discrimination; an area of 0.5 indicates a neuron that cannot discriminate between a salient stimulus and a distractor. The histogram in Figure 7 shows the value of the area under the ROC curve for all 138 neurons tested. The mean probability value of the population was 0.86. Eighty-three per cent (114/138) of the neurons exceeded a ROC value of 0.75.

The effect of distractors on the spatial tuning of area 7a neurons was determined by computing the correlation of responses to a stimulus appearing alone and among distractors. Correlation coefficients for the 138 neurons tested are shown in

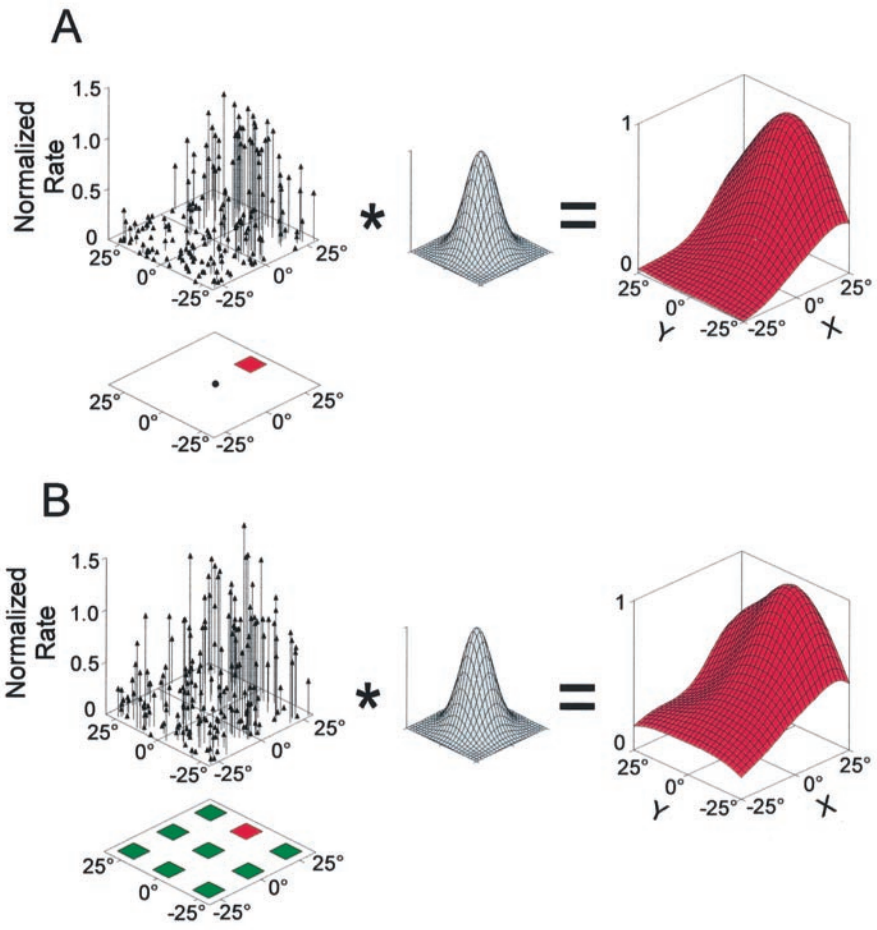

Figure 9. Population model of responses to single stimuli and multiple-stimulus arrays. Each vector represents the response of one neuron to the stimulus appearing to the right of fixation. The location of the vector represents the neuron's preferred stimulus location. The height of the vector is proportional to the neuron's normalized response to the stimulus. The population of vectors was convolved with a two-dimensional Gaussian with a standard deviation of 10° to produce the continuous population response function to the right. (*A*) Population responses to a single stimulus. (*B*) Responses to a multiple-stimulus array with the salient stimulus appearing to the right of fixation. Stimulus size (4°) not drawn to scale.

Figure 8. The mean correlation value was 0.67. The distribution of correlation values was normalized by transforming r values to Fisher's z, as follows:

$$z = \frac{\ln(1+r) - \ln(1-r)}{2} \qquad (3)$$

The positive correlation of the transformed data was statistically significant by t-test ($P < 10^{-5}$). A small percentage of neurons (3%, 4/138) displayed negative correlation coefficients, and 10 neurons displayed ROC values less than 0.5 (see Fig. 7). These data suggest that activity in a small population of area 7a neurons was suppressed by the appearance of salient stimuli in their receptive fields.

Population Response

The similarity in spatial tuning between single-stimulus and multiple-stimulus array responses indicates that individual area 7a neurons are capable of representing the location of the salient stimulus in the multi-stimulus displays. Previous studies have shown that these neurons are broadly tuned for spatial location with receptive fields that are typically 40° in diameter or more (Motter and Mountcastle, 1981; Motter *et al.*, 1987). We examined the population response in order to assess the ability of these broadly tuned neurons to signal the location of single stimuli, and to determine if the presence of distractors in and around the receptive fields had an adverse effect on the ability to encode the location of salient stimuli in multiple-stimulus arrays.

A model was constructed to evaluate the ability of the population to encode the location of a salient stimulus in a multiple-stimulus array. First, a two-dimensional Gaussian curve was fitted to the single stimulus responses at the nine grid locations. The peak of the fitted function was used to extrapolate the neuron's preferred location. The goodness-of-fit criterion (see methods) was exceeded in 98 (71%) of 138 neurons; only these neurons were included in the model. The population response was computed separately for nine conditions corresponding to a stimulus appearance at each of the grid locations. The responses of all neurons to a stimulus at one grid location were plotted on a single plane (Fig. 9*A*). Each neuron was plotted at an X–Y position corresponding to its preferred location. The Z-axis corresponds to the mean response across repeated stimulus presentations and normalized to the neuron's best single-cue stimulus response (Fig. 9*A*, left). The responses of all neurons were convolved with a two-dimensional Gaussian to produce a smoothed function of the population response to a particular stimulus presentation (Fig. 9*A*, right). The population response profile can be viewed as the degree of activation of neurons in a putative spatial map.

The population response was computed for multiple-stimulus array presentations in a similar manner (Fig. 9*B*). Each neuron

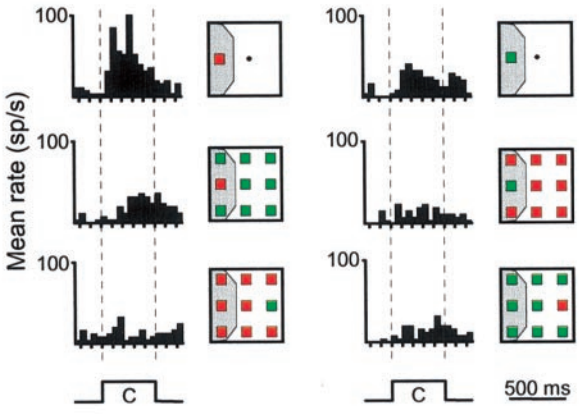

Figure 10

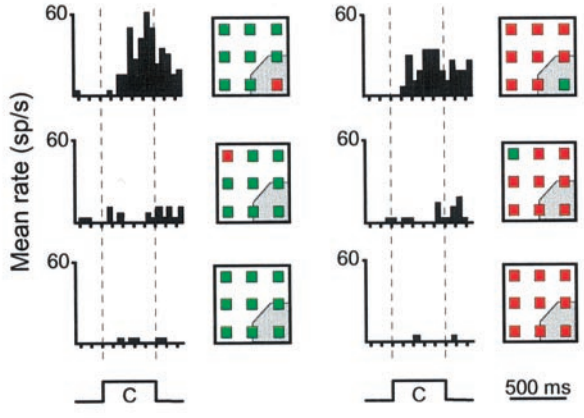

Figure 11

Figure 10. Response histograms show one of the rare examples of neurons displaying color selectivity. Conventions are the same as in Figure 4. The neuron responded best to a red single stimulus in the receptive field (top left). The neuron responded to a lesser degree to a salient red stimulus (middle left), but not to red distractors in the receptive field. The response to salient stimuli of either color (top and middle rows) was ordinarily significantly greater than the response to distractors (bottom row).

Figure 11. Response histogram shows responses of one area 7a neuron to displays with identical stimuli. Conventions are the same as in Figure 4. The neuron responded to salient stimuli of either color (top), but not to distractors (middle) appearing inside the receptive field. No response was elicited when the neuron was tested with arrays having nine identical stimuli (bottom row).

was again plotted as a vector at a position corresponding to the preferred location determined from the single stimulus responses and the discharge rate normalized to the maximum of the single stimulus responses. Some neurons responded more strongly to the array than to any single stimulus presentation resulting in values greater than 1. Neuronal responses were convolved with the same two-dimensional Gaussian. An underlying assumption in this analysis is that each neuron provides a spatial signal denoting its preferred location, regardless of its level of activity or the presence of distractors in the stimulus array.

We computed the population response separately for nine conditions corresponding to a stimulus presentation at each of the nine grid locations. The median correlation between single-stimulus and array population responses was $r = 0.96$. The median distance between the peak of the single and array population responses was 1.6°. The population response therefore accurately represented the location of the salient stimulus in the multiple-stimulus array. The results shown in Figure 9 were obtained when a Gaussian of 10° standard deviation was used for smoothing. Wider Gaussian curves (larger standard deviation values) produced marginal improvement. Similar results were obtained with narrower Gaussian functions; the median correlation between single and multiple-stimulus array responses was $r = 0.91$ for a 5° Gaussian.

Color Selectivity

Neuronal responses to salient stimuli of different colors were compared to ensure that the differential responses observed could not be explained simply by neuronal selectivity for the color of the salient stimulus. A total of 97 neurons displaying spatial selectivity for the salient stimulus were tested with green and red stimuli at the same location inside the receptive field. A significant preference for one of the two colors was observed for 14 (14%) of these neurons (*t*-test, $P<0.05$). An example of a neuron displaying significant selectivity for one of the two colors is shown in Figure 10. Color selectivity cannot explain the preferential responses to the salient stimulus because even among the neurons that preferred salient stimuli of one color over another, the majority (9/14) responded better to a salient stimulus of the non-preferred color than they did to a distractor of the preferred color. No overall preference was observed for green or red stimuli across the population of neurons (paired *t*-test, $P>0.1$), indicating that stimuli of the two colors were equally effective in eliciting responses. These results indicate that a small proportion of neurons in area 7a display significant color preference. The majority of area 7a neurons however respond to the salient stimulus in multi-stimulus arrays regardless of its color.

Responses to Stimulus Arrays with Identical Elements

There are two alternatives that could explain the lack of responses to distractors presented inside the receptive field. One possibility is that the salient stimulus appearing outside of the receptive field suppresses responses to distractors in the receptive field. The other alternative is that identical distractors produce a mutual suppression of their responses. These two alternatives were examined in 42 neurons tested with array patterns containing nine same-color stimuli (i.e. no salient stimulus). A representative response is shown in Figure 11. This neuron responded to salient stimuli of either color appearing inside the receptive field (upper panels) but not to distractors (middle panels). The neuron also did not respond when arrays of nine identical elements were presented. These data demonstrate that the absence of response to a distractor stimulus does not require the presence of a salient stimulus somewhere outside of the receptive field.

We quantified the response to an array with nine identical stimuli by computing a 'No-Cue Index' (NCI) for each neuron, according to the formula:

$$\mathrm{NCI} = \frac{\mathrm{NoCue} - \mathrm{Min}}{\mathrm{Max} - \mathrm{Min}} \qquad (4)$$

where NoCue is the mean firing rate evoked by an array without a salient stimulus, Min is the minimum response to a multiple-stimulus array with the salient stimulus outside the receptive field, and Max is the best response to an array with the salient stimulus inside the receptive field. NCI values close to 1 indicate

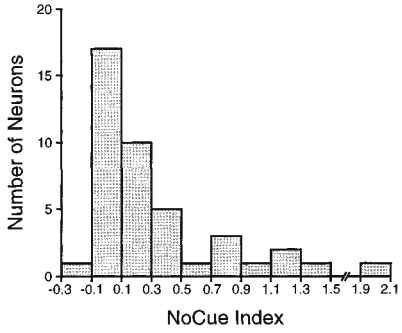

Figure 12. Histogram shows the distribution of the No-Cue index (see text for details) in the population of neurons tested with arrays of nine identical stimuli. The majority of neurons have values close to zero, indicating that the response to a display with no salient stimulus was approximately equal to that when the salient stimulus was outside of the receptive field.

that a salient stimulus is necessary to suppress distractor responses; NCI values near 0 would support the mutual inhibition hypothesis.

A histogram summarizing the NCI values for all 42 neurons is shown in Figure 12. The majority of the neurons responded to an array with no salient stimuli with approximately the same firing rate as to an array with the salient stimulus outside of the receptive field (NCI value close to 0). A few neurons did respond maximally to arrays of identical stimuli (NCI values close to 1). The median NCI value was 0.17. These results indicate that distractor responses are most often inhibited by the presence of other identical stimuli.

Time Course of Salient Stimulus Selectivity

The time course of single and array stimulus responses are shown in the population post-stimulus time (PST) histograms of Figure 13*A*. Results are averaged from the 138 neurons selective for the location of the salient stimulus in an array. We examined the difference in the time course of responses to the salient stimulus and distractors by comparing the responses on a bin-by-bin basis. The population response to an array with the salient stimulus inside the receptive field first became significantly greater than the response to an array with distractors inside the receptive field 110 ms after the array onset (paired *t*-test, $P < 0.05$). The population response to the array stimuli with the salient stimulus at the preferred location rose to a similar level but with a slower time course than the response to a single stimulus at the same location. The slower rise time apparent in the population response of Figure 13*A* can also be observed in the single-neuron PSTH of Figure 4. The reduced responsiveness to the array of stimuli is apparent from the onset of the response. The mean response rate during the presentation of the stimulus was 27.9 impulses/s for the single stimulus, 23.9 for the salient stimulus and 10.5 for the distractors. Figure 13*A* also illustrates the weak response to distractors across the population of area 7a neurons.

Non-selective Neurons

The majority of area 7a neurons responded differentially to salient stimuli and distractors in multiple-stimulus arrays but a few neurons responded with equal intensity when either a salient stimulus or a distractor appeared in the receptive field. The neuron depicted in Figure 14*A* responded best to a single stimulus in the lower right quadrant (axes have been rotated for clarity in the figure). The same neuron fired with much higher

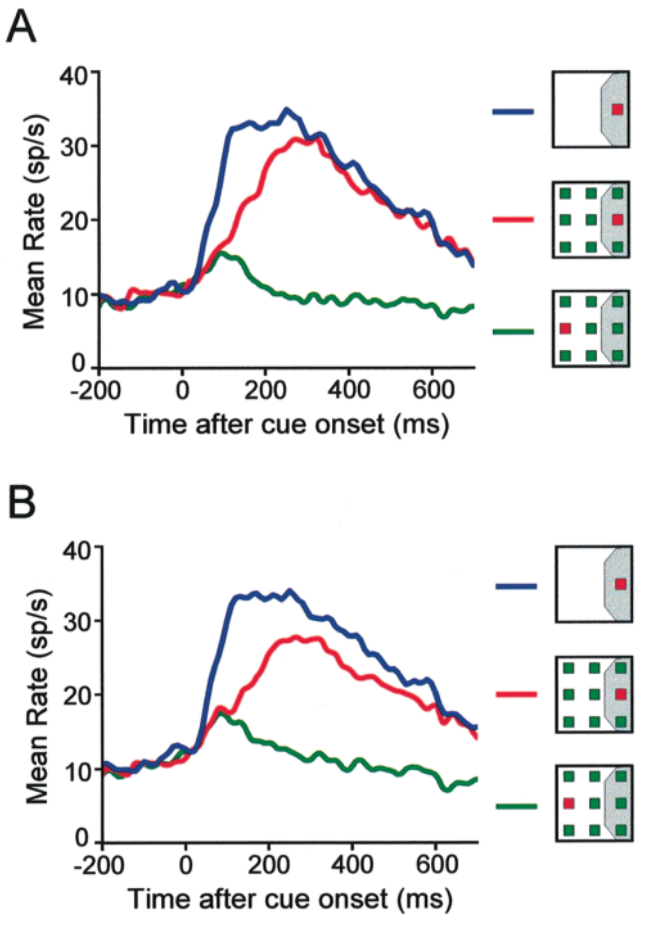

Figure 13. Population PST histograms display single and array stimulus responses. Responses are shown for single stimuli presented at the most responsive location for each neuron (blue line), for stimulus arrays with the salient stimuli at that location (red line), and for stimulus arrays with a distractor at the most responsive and the salient stimulus at the least responsive location (green line). The stimulus positions shown are examples; the actual location of the stimulus differed for each neuron. (*A*) Responses of the 138 neurons selective for the location of the salient stimulus. (*B*) Responses of all 202 neurons in our sample.

intensity when either a salient stimulus or a distractor in an array appeared in the receptive field. The neuron depicted in Figure 14*B* was unresponsive to an array of stimuli regardless of the location of salient stimuli. These two examples represent the extremes of the distribution of responses among neurons that did not differentiate between salient stimuli and distractors. Sixty-four of 202 neurons (32%) did not have significantly different responses to arrays with the salient stimulus appearing at each of the nine locations, as described above (one-way ANOVA, $P > 0.05$). Thirty-seven of those neurons exhibited mean response rates that were higher for the array (Fig. 14*A*) and 26 higher for the single stimulus (Fig. 14*B*).

We examined the effect of including neurons that were non-selective for the location of the salient stimulus in a multiple-stimulus array in the population response by repeating the analysis using all 202 neurons in our sample (Fig. 13*B*). The difference in responses between the salient stimulus and distractors was somewhat diminished but became statistically significant 120 ms after the onset of the cue (paired *t*-test, $P < 0.05$). This represents an increase of only one bin relative to the population of spatially selective neurons.

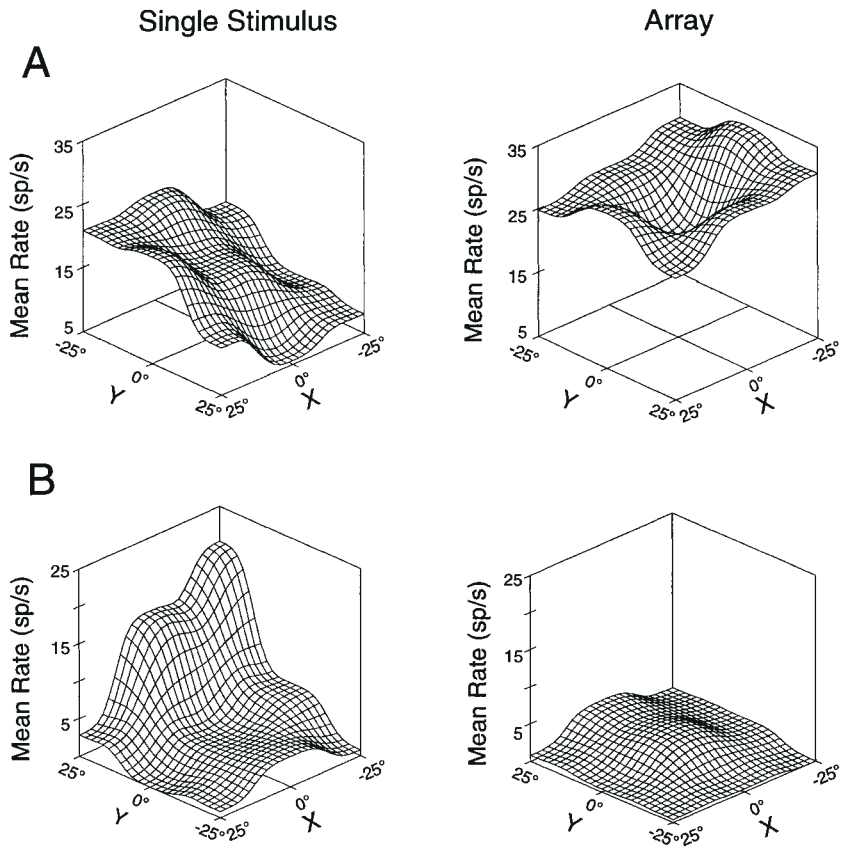

Figure 14. Surface plots showing receptive field profiles of two different neurons that did not discriminate between salient stimuli and distractors in multiple-stimulus arrays. Conventions are the same as in Figure 5. (*A*) An example of a neuron that showed similar responses to the presentation of a multiple-stimulus array regardless of the position of the salient stimulus. (*B*) An example of a neuron with responses that were suppressed by the presentation of the multi-stimulus array.

Eye Position

All responses we are describing here were recorded while the animal maintained central fixation. The behavioral task required the animal to release a lever when a subsequent stimulus appeared at the position of the salient stimulus in the cue presentation; the motor response was identical in all trials. Selectivity for the location of the salient stimulus therefore cannot be attributed to motor planning. We also tested whether the animals systematically deviated their eyes towards the location of the salient stimulus during the cue presentation to ensure that the selectivity for the salient stimulus was independent of eye movements. We recorded the eye position during the presentation of the display and measured the deviation from fixation. The average deviation was 0.01° and 0.05° for the two animals and was not significantly different for the nine stimulus locations (ANOVA, $P > 0.6$). Eye movements made by the animal at the termination of fixation control were also examined. Neither of the animals made systematic saccades towards the location of the salient stimulus at the end of the trial.

Discussion

We demonstrate that area 7a neurons encode the location of the stimulus that attracts attention in multiple-stimulus displays. We used displays that consisted of one stimulus differing in color from eight distractors. Human psychophysical studies demonstrate that attention is shifted directly to the location of the salient stimulus in similar displays, without a serial search through every element, although these experiments are typically conducted with target eccentricities considerably smaller than those we have used here (Treisman and Gelade, 1980; Duncan and Humphreys, 1989). Monkeys have also been shown to detect such a target in parallel (Bichot and Schall, 1999).

Our data suggested that individual area 7a neurons exhibit the same spatial tuning for a salient stimulus within an array as they do for a stimulus presented alone, suggesting that they encode the location of the salient stimulus in a complex visual scene. Such a preferential representation could be the result of the mere physical salience of the target stimulus or the effect of attention and the mnemonic demands of the task. The animal was required to attend to the location of the salient stimulus in the array and to maintain that location in working memory in order to perform the match-to-sample task. In either case, a population of area 7a neurons was able to encode the location of the salient stimulus despite the presence of distractors in and around their receptive fields.

Effect of Multiple Stimuli

The appearance of multiple stimuli in the visual field elicited an initial response that did not differentiate between a salient stimulus and a distractor within the first 100 ms after the cue onset (Fig. 13). This response was weaker compared with a single stimulus, suggesting that the initial effect of multiple stimuli was to suppress neuronal responses across area 7a. The discharge rate continued to increase when the stimulus that attracted attention was present inside the receptive field; the response declined to background levels when only a distractor

was present (Fig. 13). Analysis of responses to displays consisting of identical elements indicates that the suppressive effect is due to the presence of multiple identical stimuli rather than a salient stimulus outside of the receptive field.

The presentation of multiple-stimulus arrays evoked moderate responses in neurons with receptive fields centered away from the salient stimulus and higher levels of activity in neurons tuned for locations near the salient stimulus (Fig. 9). The presence of distractors in and around the receptive fields influenced the discharge rate, but did not alter appreciably the spatial tuning of the majority of neurons. Although individual neurons in area 7a are broadly tuned for spatial location, the population as a whole accurately encoded the location of the salient stimulus.

The role of neurons non-selective for the location of the salient stimulus is unclear. Their effect on the ability of the overall population to distinguish between a salient stimulus and a distractor is not substantial in that they respond either with equal intensity to arrays with the salient stimulus in any position or not at all to the multiple-stimulus arrays. It is possible that neurons not responding to any array presentation (Fig. 14*B*) would be excited by arrays with salient stimuli appearing at eccentricities greater than those used in these experiments. Neurons responding to all salient stimulus locations (Fig. 14*A*) could represent the inhibitory neurons providing the mutual suppression when distractors are present in the display. Alternatively, it is possible that non-discriminating units represent a distinct class of neurons that do not contribute to the network that computes the position of the salient stimulus. This seems unlikely given that they were selective for the location of a stimulus appearing alone.

Color Preference and Saliency

Early studies of the PPC showed that posterior parietal neurons are fairly insensitive to stimulus attributes such as form, luminance and size (Mountcastle *et al.*, 1975; Robinson *et al.*, 1978). This view has been challenged by more recent experiments, indicating some broad selectivity for stimulus shape in area LIP (Sereno and Maunsell, 1998). Our results show that a small proportion of area 7a neurons do respond better to stimuli of one color versus another. Most area 7a neurons, however, respond preferentially to a salient stimulus and do not discriminate between stimuli based on their color alone.

Responses to stimuli are enhanced in the presence of contrasting backgrounds at many stages of the visual system (Knierim and van Essen, 1992; Lamme, 1995). Mutual inhibition has been proposed as a possible mechanism that could generate selective responses to a salient stimulus differing from the distractors in color. Such inhibition could occur among color-selective neurons in area 7a or cortical areas providing input to area 7a. Mutual inhibition among similar stimuli is consistent with our finding that displays with nine identical stimuli do not evoke strong responses.

Our stimulus displays involved identical distractors that differed unambiguously from a single salient stimulus. Saliency in natural environments is rarely so clear. Normally there are many potential targets with various degrees of saliency competing for attention. Winner-take-all circuitry could ensure that activity from only one stimulus survives in area 7a while the activity to the background is suppressed (Koch and Ullman, 1985).

Functional Implications

The functional importance of the spatial information carried in the PPC is vividly illustrated by lesion studies. Patients with posterior parietal lesions are characterized by a severe inability to perceive or identify stimuli in the hemifield contralateral to the lesion (Critchley, 1966; Ratcliff and Davies-Jones, 1972; Weinstein and Friedland, 1977; Heilman, 1979). The constellation of deficits associated with bilateral posterior parietal lesions, known as Balint's syndrome, includes a narrowing of visual attention around the fovea and an inability to orient gaze into the peripheral field (Hecaen and de Ajuriaguerra, 1954). Patients suffering from such bilateral lesions are unable to correctly identify objects defined by combinations of features and report illusory conjunctions instead (Friedman-Hill *et al.*, 1995).

The selectivity we observed for the salient stimulus in a display could provide a signal to redirect visual attention and focus neuronal resources to one of several stimuli in the field of view. It has been proposed that focusing attention at a particular location in space involves selective routing of neuronal activity from occipital to IT cortex (Olshausen *et al.*, 1993). The routing can be achieved with a set of control neurons that receive input from a saliency map indicating the locations of stimuli of interest. Our present results indicate that area 7a selectively represents the location of a salient stimulus and could provide such a map. Alternatively, selectivity for the salient stimulus in area 7a could be thought as an enhanced representation of the stimulus, after attention has been directed to it through a process of competition between the stimuli in the display (Desimone and Duncan, 1995; Reynolds and Desimone, 1999). Several psychophysical experiments have studied the time course of the guidance of visual attention (Muller and Rabbitt, 1989; Nakayama and Mackeben, 1989; Egeth and Yantis, 1997). It is difficult, however, to classify the target selection we observed in area 7a as a pre- or post-attentive phenomenon based on the time course of neural responses.

A representation of the position of a salient stimulus in a visual scene could also serve to direct eye movements. Indeed, covert attention has been shown to influence the metrics of saccades elicited by microstimulation of the superior colliculus, suggesting that the two processes share common neural circuitry (Kustov and Robinson, 1996). A signal for the location of a particular saccadic target among several stimuli in the visual field has been previously demonstrated in the superior colliculus and the frontal eye fields (Glimcher and Sparks, 1992; Schall and Hanes, 1993; Schall *et al.*, 1995; Bichot *et al.*, 1996). Area 7a could be involved with these processes via its direct and indirect anatomical connections with areas specifically involved in eye movement control.

Finally, a selective representation of the salient stimulus may be necessary to register its location in memory. Area 7a is situated at the top of the hierarchy of the dorsal pathway and it is directly connected with the prefrontal and parahippocampal cortex, both of which are critically involved with spatial memory (Ungerleider and Mishkin, 1982; Felleman and Van Essen, 1991). The spatial signal represented in area 7a may represent the final stage of a sensory selection process that is then transferred into memory.

Notes

We thank Marlin Kreger for technical assistance and R. von der Heydt, K.O. Johnson and S.S. Hsiao for helpful suggestions and comments. Supported by National Institutes of Mental Health Grant MH55029 to M.A.S.

Address correspondence to Michael A. Steinmetz, Zanvyl Krieger Mind/Brain Institute, Johns Hopkins University, 3400 N. Charles Street/Krieger Hall, Baltimore, MD 21218, USA.

References

Andersen RA, Asanuma C, Cowan WM (1985) Callosal and prefrontal associational projecting cell populations in area 7A of the macaque monkey: a study using retrogradely transported fluorescent dyes. J Comp Neurol 232:443–455.

Bichot NP, Schall JD (1999) Saccade target selection in macaque during feature and conjunction visual search. Vis Neurosci 16:81–89.

Bichot NP, Schall JD, Thompson KG (1996) Visual feature selectivity in frontal eye fields induced by experience in mature macaques. Nature 381:697–699.

Bushnell MC, Goldberg ME, Robinson DL (1981) Behavioral enhancement of visual responses in monkey cerebral cortex. I. Modulation in posterior parietal cortex related to selective visual attention. J Neurophysiol 46:755–772.

Constantinidis C, Steinmetz MA (1996) Neuronal activity in posterior parietal area 7a during the delay periods of a spatial memory task. J Neurophysiol 76:1352–1355.

Corbetta M, Miezin FM, Shulman GL, Petersen SE (1993) A PET study of visuospatial attention. J Neurosci 13:1202–1226.

Corbetta M, Shulman GL, Miezin FM, Petersen SE (1995) Superior parietal cortex activation during spatial attention shifts and visual feature conjunction. Science 270:802–805.

Corbetta M, Kincade JM, Ollinger JM, McAvoy MP, Shulman GL (2000) Voluntary orienting is dissociated from target detection in human posterior parietal cortex. Nat Neurosci 3:292–297.

Critchley M (1966) The parietal lobes. New York: Hafner.

Desimone R, Duncan J (1995) Neural mechanisms of selective visual attention. Annu Rev Neurosci 18:193–222.

DiCarlo JJ, Lane JW, Hsiao SS, Johnson KO (1996) Marking microelectrode penetrations with fluorescent dyes. J Neurosci Methods 64:75–81.

Duncan J, Humphreys GW (1989) Visual search and stimulus similarity. Psychol Rev 96:433–458.

Egeth HE, Yantis S (1997) Visual attention: control, representation, and time course. Annu Rev Psychol 48:269–297.

Felleman DJ, Van Essen DC (1991) Distributed hierarchical processing in the primate cerebral cortex. Cereb Cortex 1:1–47.

Friedman-Hill SR, Robertson LC, Treisman A (1995) Parietal contributions to visual feature binding: evidence from a patient with bilateral lesions. Science 269:853–855.

Fuchs AF, Robinson DA (1966) A method for measuring horizontal and vertical eye movement chronically in the monkey. J Appl Physiol 21:1068–1070.

Glimcher PW, Sparks DL (1992) Movement selection in advance of action in the superior colliculus. Nature 355:542–545.

Gottlieb JP, Kusunoki M, Goldberg ME (1998) The representation of visual salience in monkey parietal cortex. Nature 391:481–484.

Hecaen H, de Ajuriaguerra J (1954) Balint's syndrome (psychic paralysis of visual fixation) and its minor forms. Brain 77:373–400.

Heilman KM (1979) Neglect and related disorders. In: Clinical neuropsychology (Heilman KM, Valenstein E, eds). New York: Oxford University Press.

Kastner S, Pinsk MA, De Weerd P, Desimone R, Ungerleider LG (1999) Increased activity in human visual cortex during directed attention in the absence of visual stimulation. Neuron 22:751–761.

Knierim JJ, van Essen DC (1992) Neuronal responses to static texture patterns in area V1 of the alert macaque monkey. J Neurophysiol 67:961–980.

Koch C, Ullman S (1985) Shifts in selective visual attention: towards the underlying neural circuitry. Hum Neurobiol 4:219–227.

Kustov AA, Robinson DL (1996) Shared neural control of attentional shifts and eye movements. Nature 384:74–77.

Lamme VA (1995) The neurophysiology of figure-ground segregation in primary visual cortex. J Neurosci 15:1605–1615.

Motter BC, Mountcastle VB (1981) The functional properties of the light-sensitive neurons of the posterior parietal cortex studied in waking monkeys: foveal sparing and opponent vector organization. J Neurosci 1:3–26.

Motter BC, Steinmetz MA, Duffy CJ, Mountcastle VB (1987) Functional properties of parietal visual neurons: mechanisms of directionality along a single axis. J Neurosci 7:154–176.

Mountcastle VB, Lynch JC, Georgopoulos A, Sakata H, Acuna C (1975) Posterior parietal association cortex of the monkey: command functions for operations within extrapersonal space. J Neurophysiol 38:871–908.

Mountcastle VB, Andersen RA, Motter BC (1981) The influence of attentive fixation upon the excitability of the light-sensitive neurons of the posterior parietal cortex. J Neurosci 1:1218–1225.

Mountcastle VB, Motter BC, Steinmetz MA, Sestokas AK (1987) Common and differential effects of attentive fixation on the excitability of parietal and prestriate (V4) cortical visual neurons in the macaque monkey. J Neurosci 7:2239–2255.

Mountcastle VB, Reitboeck HJ, Poggio GF, Steinmetz MA (1991) Adaptation of the Reitboeck method of multiple microelectrode recording to the neocortex of the waking monkey. J Neurosci Methods 36:77–84.

Muller HJ, Rabbitt PM (1989) Reflexive and voluntary orienting of visual attention: time course of activation and resistance to interruption. J Exp Psychol Hum Percept Perform 15:315–330.

Nakayama K, Mackeben M (1989) Sustained and transient components of focal visual attention. Vision Res 29:1631–1647.

Nobre AC, Sebestyen GN, Gitelman DR, Mesulam MM, Frackowiak RS, Frith CD (1997) Functional localization of the system for visuospatial attention using positron emission tomography. Brain 120:515–533.

Olshausen BA, Anderson CH, Van Essen DC (1993) A neurobiological model of visual attention and invariant pattern recognition based on dynamic routing of information. J Neurosci 13:4700–4719.

Posner MI, Walker JA, Friedrich FJ, Rafal RD (1984) Effects of parietal injury on covert orienting of attention. J Neurosci 4:1863–1874.

Ratcliff G, Davies-Jones GA (1972) Defective visual localization in focal brain wounds. Brain 95:49–60.

Reynolds JH, Desimone R (1999) The role of neural mechanisms of attention in solving the binding problem. Neuron 24:19–29.

Richmond BJ, Optican LM, Podell M, Spitzer H (1987) Temporal encoding of two-dimensional patterns by single units in primate inferior temporal cortex. I. Response characteristics. J Neurophysiol 57:132–146.

Robinson DL, Goldberg ME, Stanton GB (1978) Parietal association cortex in the primate: sensory mechanisms and behavioral modulations. J Neurophysiol 41:910–932.

Robinson DL, Bowman EM, Kertzman C (1995) Covert orienting of attention in macaques. II. Contributions of parietal cortex. J Neurophysiol 74:698–712.

Schall JD, Hanes DP (1993) Neural basis of saccade target selection in frontal eye field during visual search. Nature 366:467–469.

Schall JD, Hanes DP, Thompson KG, King DJ (1995) Saccade target selection in frontal eye field of macaque. I. Visual and premovement activation. J Neurosci 15:6905–6918.

Sereno AB, Maunsell JH (1998) Shape selectivity in primate lateral intraparietal cortex. Nature 395:500–503.

Singer W, Gray CM (1995) Visual feature integration and the temporal correlation hypothesis. Annu Rev Neurosci 18:555–586.

Steinmetz MA, Constantinidis C (1995) Neurophysiological evidence for a role of posterior parietal cortex in redirecting visual attention. Cereb Cortex 5:448–456.

Steinmetz MA, Connor CE, Constantinidis C, McLaughlin JR (1994) Covert attention suppresses neuronal responses in area 7a of the posterior parietal cortex. J Neurophysiol 72:1020–1023.

Tolhurst DJ, Movshon JA, Dean AF (1983) The statistical reliability of signals in single neurons in cat and monkey visual cortex. Vision Res 23:775–785.

Treisman AM, Gelade G (1980) A feature-integration theory of attention. Cognit Psychol 12:97–136.

Ungerleider LG, Mishkin M (1982) Two cortical visual systems. In: Analysis of visual behavior (Ingle DJ, Goodale MA, Mansfield RJW, eds), pp. 549–586. Cambridge, MA: MIT Press.

Weinstein EA, Friedland RP, eds (1977) Hemi-inattention and hemisphere specialization. New York: Raven.

Yin TC, Mountcastle VB (1977) Visual input to the visuomotor mechanisms of the monkey's parietal lobe. Science 197:1381–1383.