Responses of Intraparietal Neurons to Saccadic Targets and Visual Distractors

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Platt, Michael L. and Paul W. Glimcher. Responses of intraparietal neurons to saccadic targets and visual distractors. *J. Neurophysiol.* 78: 1574–1589, 1997. Current evidence suggests that neuronal activity in the lateral intraparietal area (LIP) reflects sensory-motor processes, but it remains unclear whether LIP activation participates directly in the planning of future eye movements or encodes data about both sensory events and the behavioral significance of those sensory events. To examine this issue, 31 intraparietal neurons were studied in awake, behaving monkeys trained to perform two tasks that independently controlled the location of a saccadic target and the location and behavioral relevance of a visual distractor. In both of these tasks, two eccentric light-emitting diodes (LEDs) were illuminated yellow, one above and one below a fixation stimulus. Shortly after the eccentric LEDs were illuminated, a change in the color of the fixation stimulus indicated which of these LEDs served as the saccadic goal and which served as a visual distractor. In the first or distractor-irrelevant task, fixation offset indicated that the subject must initiate a saccade shifting gaze to the saccadic goal. In the second or distractor-relevant task, distractor offset served as the saccade initiation cue. Intraparietal neurons responded more strongly in association with an LED that served as a saccadic target than in association with the same LED when it served as a visual distractor. Neuronal responses in association with either target or distractor stimuli on distractor-relevant and distractor-irrelevant blocks of trials were statistically indistinguishable. When the location of either the target or the distractor was varied across trials, the response of each neuron in association with a particular stimulus location was always greater for targets than for distractors and the magnitude of this response difference was independent of distractor relevance; however, distractors were nearly always associated with some intraparietal neuronal activity. A target/distractor selectivity index was computed for each neuron as the difference between responses associated with targets minus responses associated with distractors divided by the sum of these values. When the selectivity of each neuron on the distractor-relevant task was plotted against the selectivity of the same neuron on the distractor-irrelevant task, activity in the population of intraparietal neurons was found to be independent of distractor relevance. These data suggest that LIP neuronal activation represents saccadic targets and, at a lower level of activity, visual distractors, but does not encode the relevance of distractor stimuli on these tasks.

INTRODUCTION

Several covert psychological processes have been postulated to participate in the cascade of neural events that begins with the transduction of a visual stimulus and ends with an eye movement. For example, coordinate transformations, which shift signals gathered by the sensory epithelium into coordinate systems appropriate for the guidance of movement, have been identified as processes that intervene between sensation and action (cf. Gnadt and Andersen 1988; Hallett and Lightstone 1976; Mays and Sparks 1980). The explicit planning of an eye movement for future execution also has been proposed as a neurobiologically separable element in the sensory-motor process (Glimcher and Sparks 1993; Gnadt and Andersen 1988). It has even been argued that the psychological process of selective attention, which is presumed to participate in sensory-motor processing, might be observable at the single-neuron level as sensory responses that are modulated by the relevance of saccade-related stimuli (Bushnell et al. 1981; Goldberg and Wurtz 1972; Goldberg et al. 1990; Robinson et al. 1978; Wurtz and Mohler 1976).

Several groups of researchers have argued that neurons in the lateral intraparietal area (LIP) of primate posterior parietal cortex may participate in some of these covert processes (Gnadt and Andersen 1988; Goldberg et al. 1990; Shadlen and Newsome 1996). LIP receives direct projections from multiple extrastriate visual areas (Andersen et al. 1990; Blatt et al. 1990) and projects directly to principal oculomotor control areas in the frontal eye fields and the superior colliculus (Andersen et al. 1985, 1990; Cavada and Goldman-Rakic 1989a,b; May and Andersen 1986). LIP thus seems appropriately situated anatomically to intervene between sensation and action in the generation of saccades guided by visual targets.

Gnadt and Andersen (1988) were among the first to suggest that neurons in area LIP participate in a specific covert presaccadic process. In a series of studies (Andersen et al. 1990; Barash et al. 1991a,b; Bracewell et al. 1996; Gnadt and Andersen 1988; Mazzoni et al. 1996), these investigators and colleagues examined the activity of single neurons while monkeys made saccades that shifted gaze into alignment with the locations of previously viewed targets. Gnadt and Andersen (1988) demonstrated that most neurons in area LIP responded strongly before saccadic eye movements having a limited range of amplitudes and directions. Further, these authors found that for many cells in area LIP an increase in firing rate that was correlated with the onset of an eccentric visual target was maintained after target offset if a gaze shift to the eccentric location was required. Because this activity accurately predicted the amplitude and direction of a future saccade and was maintained in the absence of the visual stimulus, these authors suggested that neurons in LIP might encode the metrics of planned future movements.

This hypothesis was strengthened when it was demonstrated that the information these units carried was encoded in a motor coordinate framework appropriate for eye movement control and not in a sensory coordinate framework anchored to the locus of retinal stimulation (Barash et al.

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1991b; Gnadt and Andersen 1988; Mazzoni et al. 1996). These studies employed a double-saccade task (cf. Hallett and Lightstone 1976; Mays and Sparks 1980) in which subjects were required to make two saccades that sequentially fixated two briefly flashed visual targets. In one of these studies, Mazzoni et al. (1996) arranged the targets so that one stimulus was illuminated within and the other outside of the response field of the neuron under study. By varying the sequence in which the two targets were presented, Mazzoni et al. could compare the responses of LIP neurons on trials in which the first saccade was directed toward the response field with trials in which the first saccade was directed away from the response field. The authors reported that most (77%) LIP neurons were more strongly activated when the first saccade was directed toward the response field than when the first saccade was directed away from the response field, even though a visual stimulus had appeared within the response field in both conditions. These data led the authors to suggest that most LIP neurons encoded the direction and amplitude of the next saccade the animal intended to make, although it was noted that in a minority of LIP neurons (16%) the neural response was identical for either saccade.

In an attempt to demonstrate that LIP neurons specifically encode the metrics of intended movements and generate only minimal activity associated with the locations of sensory stimuli, Bracewell et al. (1996) designed a task in which subjects were instructed to plan a movement for future execution and then, on occasion, to change that plan before the movement was executed. While a monkey maintained fixation of a central stimulus a target was flashed briefly at an eccentric location. If the central target was extinguished, the subject was rewarded for shifting gaze to the eccentric target location. If, however, a second eccentric target was briefly presented, then, on fixation stimulus offset, the animal was rewarded for making a saccade that shifted gaze into alignment with this second target. Thus a subject could be sequentially instructed to prepare saccades of different metrics simply by illuminating multiple eccentric visual targets in series. Bracewell et al. determined that most LIP neurons responded with maintained activation after the presentation of a target placed at the center of the neuronal response field but became inactive as soon as a new saccadic target was flashed at a location outside of the neuronal response field. From these data, Bracewell et al. concluded that the activity of most LIP neurons principally signals the intention of an animal to generate saccades having a limited range of directions and amplitudes.

Using a very similar body of tasks, Goldberg and colleagues (1990) reached quite different conclusions regarding the functional role of LIP activity. For example, in one experiment, monkeys maintained steady fixation of a central stimulus while an eccentric visual stimulus was presented to the animal. The animal received a reward for indicating, with a lever press, the time at which the fixation stimulus dimmed. Although no movement was required by the task and the eccentric stimulus was completely irrelevant to the task, Goldberg et al. demonstrated that LIP neurons responded if the eccentric stimulus was placed in the response field of the neuron. Further, these investigators found that responses associated with the eccentric stimulus were strengthened when the monkey was rewarded for identifying, with a lever press, the time at which the eccentric stimulus dimmed rather than the time at which the central fixation stimulus dimmed. From these data, Goldberg et al. concluded that modulating the behavioral relevance of an eccentric stimulus modulated the activity of LIP neurons that were active in association with that stimulus. They further hypothesized from these and other data that LIP neuronal activation might encode an attentionally modulated representation of the local visual environment.

In fact, the hypotheses of both groups are consistent with nearly all available data on LIP neuronal activity and with the hypothesis that deterministically ties all planned eye movements to shifts in attention (cf. Sheliga et al. 1994). In the experiments of Gnadt and Andersen (1988), the single light-emitting diode (LED) that served as both the visual stimulus and the saccadic target was also the only behaviorally relevant eccentric visual stimulus. Thus neurons may have responded after the onset of the saccadic target because it was a behaviorally meaningful stimulus or because it specified the metrics of a future saccade. Even in the experiments of Bracewell et al. (1996), LIP neurons may have signaled the relevance to the animal of each sequentially illuminated stimulus rather than the actual metrics of a planned movement. Similarly, in the experiments of Goldberg et al. (1990), LIP neurons may have represented the metrics of saccades that the animal planned but never produced, just as many LIP neurons in the study by Bracewell et al. (1996) responded for saccades that were instructed but never executed.

One way to further examine these two hypotheses would be to develop a behavioral task or tasks that combine, in a single experiment, the experiments of Bracewell et al. in which monkeys plan and execute movements that align gaze with an eccentric visual target and the experiments of Goldberg et al. in which the relevance of a nontarget stimulus is altered systematically. If a task provided independent control over both the relevance of a nontarget and the precise metrics of a required saccade, then it might be useful for associating neural activity with movement plans and/or changes in attentional state. In the experiments described here, animals were presented with two eccentric visual stimuli on each trial. One of the two visual stimuli served as the target, whereas the other served as a distractor. On some trials, the distractor was completely irrelevant to the task, whereas on other trials offset of the distractor signaled to the animal that a saccade shifting gaze to the target must be completed within 750 ms. The data indicated, first, that the irrelevant distractor was always represented in intraparietal cortex, but with a less vigorous discharge than was associated with a saccadic target; second, that the relevance of the distractor stimulus on these tasks had no effect on intraparietal neuronal activation.

METHODS

Two juvenile male rhesus macaques (*Macaca mulatta*) served as subjects in the following experiments. All animal procedures were developed in association with the University Veterinarian and these procedures were approved by the New York University Institutional Animal Care and Use Committee. These procedures

were designed and conducted in compliance with the Public Health Service's Guide for the Care and Use of Animals.

Surgical and training procedures

In an initial sterile surgical procedure performed under isoflurane and nitrous oxide inhalant anesthesia, a head restraint prosthesis and scleral search coil (Fuchs and Robinson 1966) were implanted. First, the rostral dorsum of the skull was exposed and four 2.5-mm holes were drilled through the skull with standard orthopedic surgical instruments. These holes were then tapped for 3.5-mm fine-thread orthopedic cortical bone screws. Four titanium screws (Zimmer) were inserted into the tapped holes and a custom-fabricated titanium bar was lowered to just above the skull surface between these screws. The restraint bar and the four screws were then bonded together with sterile orthopedic bone cement (Smith and Nephew: Palacos). The Teflon-insulated stainless steel scleral search coil was implanted underneath the conjunctiva, passing just rostral to the insertions of the extraocular muscles (Judge et al. 1980). The search coil wire exited the conjunctiva temporally, formed a subdermic stress-relief loop just inside the temporal bone of the orbit, exited the orbit subdermically, passed through the temporalis muscle, and then passed through the bone cement that formed the restraint prosthesis, terminating in a gold and plastic electrical connector. After surgery, animals received analgesics for a minimum of 3 days. Antibiotic prophylaxis was initiated intraoperatively and continued for a minimum of 3 days.

After a 6-wk recovery period that facilitated the osteointegration of the implanted bone screws, access to water was restricted and animals were habituated to head restraint and then trained to perform oculomotor tasks for a fruit juice reward. Correct oculomotor responses were reinforced on a VR3 variable ratio schedule (on average, 1 juice reward for every 3 correct trials). A 300-ms noise burst served as a secondary reinforcer on all correct trials.

During data collection, horizontal and vertical eye position signals were sampled at 500 Hz. Tristate LEDs (LEDtronics), which could be illuminated to appear red, green, or yellow to normal human observers, served as visual stimuli. LEDs were fixed on a tangent screen placed 57 in. from the eyes of the animal. Four hundred forty-one of these LEDs formed a grid of points, separated by 2°, spanning 40° horizontally and 40° vertically. The computer system controlling the experiments could illuminate these LEDs with a temporal precision of 1 ms and extinguish them with a precision of 7 ms.

After subjects had been trained to execute all the oculomotor tasks employed in this study, a second sterile surgical procedure was performed. During this second surgery, a stainless steel receptacle (Crist Instruments) was positioned stereotaxically over a 15-mm craniotomy and bonded to four additional orthopedic bone screws and the original implant with orthopedic bone cement. The receptacle was centered 3 mm caudal and 12 mm lateral to the intersection of the midsaggital and interaural planes. On one animal, the base of the receptacle was placed flat against the skull, deviating the central axis of the receptacle ~13° from vertical. On the second animal, the central axis of the receptacle was positioned perpendicular to the stereotaxic horizontal plane. The receptacle was kept sterile with regular antibiotic washes and sealed with replaceable sterile Teflon caps. Postoperatively, animals received both analgesics and antibiotics for a minimum of 3 days. Single-cell recording experiments began after a 1-wk postoperative period.

Microelectrode recording techniques

Before each experimental recording session, the stainless steel receptacle was opened under aseptic conditions and flushed repeatedly with sterile saline, and then an *X*-*Y* micropositioner (Crist Instruments) and hydraulic microdrive (Kopf) were mounted to the receptacle. A 23-gauge hypodermic tube, into which was withdrawn a tungsten steel 6- to 8-MΩ electrode (Frederick Haer), was used to puncture the intact dura. Electrophysiological signals were amplified and band-pass filtered to exclude both power line noise and the signals of the magnetic fields (passband ~200–5,000 Hz). Individual action potentials were identified in hardware by time and amplitude criteria. Times of spike occurrence were recorded by computer with the use of a 1-μs internal clock.

Behavioral techniques

To ascertain whether intraparietal neurons encode the behavioral relevance of an eccentric visual stimulus when the metrics of a reinforced saccade have been specified by a second eccentric visual stimulus, we used a two-part process to study each cell. First, we measured the basic response properties of each neuron as a function of target location/movement metrics with the use of a delayed saccade task. After this basic analysis was completed, each neuron was studied with a pair of tasks that presented animals with two eccentric visual stimuli, one of which would be identified as the eventual saccadic goal and the other as a visual distractor. In the cued saccade task, offset of the fixation stimulus cued the animal to initiate a movement that shifted gaze into alignment with the specified saccadic goal an unpredictable time after the saccadic goal was identified to receive reinforcement. In the distributed cue task, offset of the distractor stimulus provided the saccade initiation cue. Data collected on cued saccade and distributed cue trials were compared to determine whether the neuron under study responded differentially when the behavioral relevance of the visual distractor was altered.

DELAYED SACCADE TASK. Delayed saccade trials (Fig. 1*A*) were used to assess the spatial tuning of physiologically identified intraparietal neurons. Each trial began with the illumination of a central yellow LED that subjects were required to fixate within 1,000 ms. Two hundred to 800 ms after gaze was aligned within 3° of the fixation stimulus, a single eccentric yellow LED was illuminated. After a further 200- to 800-ms delay, the fixation stimulus was extinguished, cueing the subject to shift gaze to the eccentric target (±6°) within 350 ms to receive a reinforcer.

CUED SACCADE TASK. These trials (Fig. 1*B*) began with the illumination of a central yellow fixation LED to which subjects were required to direct gaze (±3°) within 1,000 ms. After a variable fixation interval of 200–800 ms, two eccentric yellow LEDs were coilluminated (200–800 ms), one above and one below the fixation stimulus. The saccadic goal, however, was not specified until the fixation stimulus changed color to either red or green. A change to red indicated that eventually a saccade that shifted gaze to the upper eccentric LED would be rewarded and that the lower eccentric LED was an irrelevant visual distractor. A change to green identified the lower eccentric LED as the saccadic target and the upper eccentric LED as an irrelevant visual distractor. Subjects were required to withhold the cued saccade for 200–800 ms. After this delay, the fixation LED was extinguished, indicating that the subject should direct gaze to the location of the cued target (±6°) within 500 ms to receive a reinforcer.[1] The precise target and distractor locations and the color of the fixation stimulus were varied randomly from trial to trial.

This task permitted us to compare visually similar pairs of trials on which the same two eccentric LEDs were presented. We could compare trials on which a particular LED served as a target with trials on which the same LED served as a distractor. Because the trials being compared differed only in the color of the fixation

[1] In typical data sets, *monkey YY* (*YY960305*) made these responses with a mean latency of 137 ± 39 (SD) ms and *monkey HX* (*HX951128*) with a mean latency of 207 ± 119 (SD) ms.

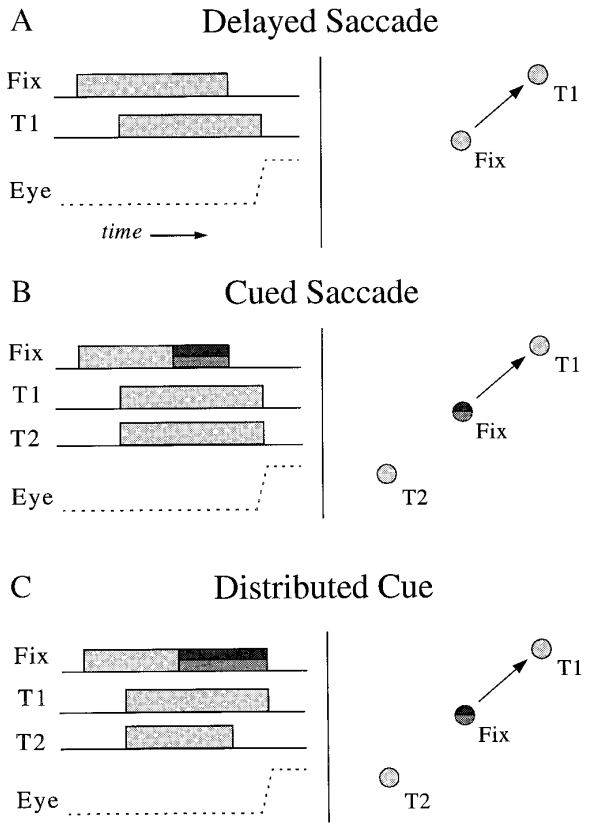

FIG. 1. *A*: delayed saccade trials began with onset of centrally located fixation light-emitting diode (LED). Subjects had 1,000 ms to align gaze with this stimulus, after which eccentric LED (T1) was illuminated. After 200–800 ms, fixation stimulus was extinguished and animals had 500 ms to shift gaze from alignment with now-extinguished fixation position into alignment with eccentric target. *B*: cued saccade trials began with illumination of central yellow fixation stimulus with which subjects aligned gaze within 1,000 ms. After delay of 200–800 ms, 2 eccentric LEDs (T1 and T2) were coilluminated yellow, 1 above and 1 below fixation. After 2nd delay of 200–800 ms, fixation stimulus changed color to either red or green. Change to red identified upper eccentric LED as saccadic goal and lower eccentric LED as irrelevant distractor; change to green identified lower eccentric LED as saccadic goal and upper eccentric LED as irrelevant distractor. After final delay of 200–800 ms, fixation stimulus was extinguished and subjects had 500 ms to shift gaze into alignment with eccentric LED specified by color of extinguished fixation LED. *C*: distributed cue trials began with onset of centrally located yellow fixation LED, with which subjects had 1,000 ms to align gaze. After delay of 200–800 ms, 2 eccentric LEDs were coilluminated yellow, 1 above and 1 below horizontal meridian. After 2nd delay of 200–800 ms, fixation stimulus changed color to either red, identifying upper eccentric LED as saccadic target and lower eccentric LED as distractor, or green, identifying lower eccentric LED as saccadic target and upper eccentric LED as distractor. After final delay of 200–800 ms, eccentric LED identified as distractor by color of fixation LED was extinguished and animals had 750 ms to shift gaze into alignment with saccadic target.

LED, differences in activity occurring after the change in the color but before the offset of the fixation LED could be attributed specifically to which eccentric stimulus served as a saccadic goal and which served as an irrelevant distractor.

DISTRIBUTED CUE TASK. Although the cued saccade task enabled us to assess whether LIP neurons responded differentially to targets and distractors, it alone could not determine the effects of altering the behavioral relevance of nontarget stimuli (distractors) on the firing patterns of LIP neurons. To examine whether LIP neurons encode the behavioral relevance of distractors, we employed the distributed cue task. This task (Fig. 1*C*) was identical to the cued saccade task except that the offset of the visual distractor, rather than the offset of the fixation stimulus, cued the subject to initiate a saccade shifting gaze to the location of the specified saccadic goal. Thus a change in the color of the fixation stimulus to red specified that the upper eccentric LED would be the eventual target of the saccade and that the offset of the lower eccentric LED would provide the cue to initiate the required saccade. Similarly, a change in the color of the fixation stimulus to green specified that the lower eccentric LED would be the eventual saccadic goal and that the offset of the upper eccentric LED would indicate the time at which the required saccade must be initiated. After the offset of the distractor LED, the subject was required to redirect gaze into alignment with the cued target LED ($\pm 6°$) within 750 ms to receive a reinforcement.[2]

Together, the cued saccade and distributed cue tasks permitted us to compare trials on which an LED was an irrelevant visual distractor with trials on which the same LED was a relevant distractor cueing the initiation of a saccade. Differences in activity elicited from the neuron on these two types of trials before fixation or distractor offset could be attributed to the altered behavioral relevance of the distractor LED.

Recording protocol

Electrodes were lowered, under physiological guidance, until units with visual and/or saccade-associated activity were encountered. Most penetrations were made so that electrodes first passed through tissue containing neurons with skeletomuscular related activity, presumably located in Brodmann's area 5 and therefore dorsal to area LIP. This increased the probability that subsequently encountered visual or saccade-related neurons were located in area LIP and not in area 7a (cf. Barash et al. 1991a,b). When penetrations did not pass through area 5, neurons with vigorous visual/saccade-associated activity could be recorded for up to 8 mm, presumably because the electrode was traveling parallel to the surface of the cortical sheet within the lateral intraparietal sulcus. Because the electrode guide tube was constructed to penetrate 2–3 mm into cortex, neurons with visual/saccade-associated activity in the gyral portion of area 7a were probably not encountered. On the basis of the physiological characteristics and relative depths of recorded neurons, the lateral border of area 5 and the medial and lateral borders of area LIP were drawn on a map of the recording chamber grid. Neurons with visual/saccade-associated activity lying ventral to area 5 or located lateral to the border of the intraparietal sulcus were considered to lie in area LIP. Neurons located within this physiologically identified area LIP typically fired action potentials before visually guided saccades having a limited range of amplitudes and directions. Moreover, many of these neurons fired action potentials during the delay period on memory saccade trials for saccades having a similar range of metrics, as has been documented previously for LIP neurons (cf. Barash et al. 1991b; Gnadt and Andersen 1988).

Once a cell was isolated, 100–400 delayed saccade trials were presented in which the locations of the eccentric target varied randomly from trial to trial and the location of the fixation stimulus was fixed at a central location. On-line analysis of these trials was used to assess the visual and saccade-related spatial tuning of each neuron.

After conducting these delayed saccade trials, we presented subjects with 100–400 cued saccade trials. At the beginning of this block of trials, one of the two eccentric LEDs was fixed at a location that, on delayed saccade trials, did not elicit a response

[2] In typical data sets, *monkey YY* (*Y Y960305*) made these responses with an average latency of 252 ± 128 (SD) ms and *monkey HX* (*HX951128*) with an average latency of 325 ± 250 (SD) ms.

from the neuron under study. The location of the other eccentric visual stimulus varied randomly among >200 possible locations comprising the hemifield (upper or lower) for which the neuron under study was most responsive. Which of these two eccentric stimuli served as the saccadic target and which served as the visual distractor varied randomly from trial to trial. Because one eccentric LED was fixed at a location that did not elicit modulations in the activity of the neuron, we could attribute any change in neuronal activity observed on a particular trial to the effects of the variable eccentric LED, irrespective of whether it served as a saccadic target or as a visual distractor.

After the animal had completed this block of cued saccade trials, we conducted a block of 100–400 distributed cue trials. These trials differed from those of the preceding block only in the relevance of the distractor, the offset of which now served as the movement initiation cue.

Single-trial analysis

We compared reinforced single cued saccade trials in which the locations of the eccentric LEDs were the same but the color of the fixation LED was different. Because these trials used displays that differed only in the color of the fixation LED, which was outside the response field of the neuron, changes in neuronal activity could be attributed to whether the variable eccentric LED served as a saccadic target or a visual distractor. This attribution could be strengthened by comparing delayed saccade trials and cued saccade trials that shared a common eccentric LED as the saccadic goal. If the responses of a neuron on delayed saccade trials were similar to those elicited by cued saccade trials with the same saccadic target, it could be inferred that the neuron encoded some saccade-associated aspect of the task and not simply the color of the fixation LED.

We could then use the distributed cue task to ask whether intraparietal neurons encoded the relevance of LEDs that did not serve as saccadic goals. To accomplish this, a set of distributed cue trials could be compared with a set of cued saccade trials employing the same pair of eccentric LEDs. This permitted the assessment of neuronal responses as a function of whether movement initiation was cued by the offset of either the distractor or the fixation stimulus.

Target and distractor field analysis

Comparison of single trials can provide qualitative evidence about relative neuronal responses to a particular pair of eccentric LEDs, but it provides neither quantitative data regarding the effects of the spatial location of LEDs identified as targets and distractors nor estimates of average LIP neuronal responses to a particular stimulus/movement configuration. To provide systematic, quantitative analyses of the effects of varying the locations of target and distractor LEDs on LIP neuronal activity, we subjected the trials recorded from each neuron to a two-stage analysis.

In the first stage of this analysis, we computed, for each reinforced trial, the onset and offset times of all task-required movements, as well as the amplitudes and directions of those movements. Action potentials were counted during three intervals: *1*) a visual interval, the 200-ms interval following the illumination of the eccentric visual stimuli; *2*) a cue interval, the 200-ms interval immediately preceding the initiation signal (either fixation offset for cued saccade trials or distractor offset for distributed cue trials); *3*) a premovement interval, the 100-ms interval preceding saccade onset. From these spike counts, mean firing frequencies during each of these intervals were computed. For each unit, a data base was constructed from these measurements.

In the second step of this analysis, we sorted, for each neuron, both cued saccade and distributed cue trials into two groups: target trials, on which the LED that varied in spatial position was identified as a saccadic target; and distractor trials, on which the variable LED was identified as a distractor. These data sets were then used to construct six three-dimensional plots for each neuron for both cued saccade and distributed cue trials. Data from target trials were used to construct three target field plots, graphs of the firing rate during each of the measured intervals as a function of the horizontal and vertical location of the variable LED when it served as a saccadic target. The three complementary graphs were distractor fields, which plotted the firing rate during the measured intervals as a function of the horizontal and vertical location of the variable LED when it served as a visual distractor. Comparison of target fields and distractor fields during visual, cue, and premovement epochs enabled us to determine whether LIP neurons encoded targets and distractors differentially in association with informationally distinct task events. Further, comparison of distractor fields gathered during cued saccade trials with distractor fields gathered during distributed cue trials permitted us to quantify the effects of changes in distractor relevance on intraparietal neuronal activity.

Statistical analysis of target/distractor selectivity

Although generating target and distractor fields permits us to assess whether intraparietal neurons respond differentially to LEDs identified as targets and distractors, it does not provide a quantitative measure of this discrimination. To quantify the differential activation of intraparietal neurons by the variable LED when it served as a target versus when that same LED served as a distractor, a measure of target/distractor selectivity was calculated for trials during which either the target or the distractor was located within the center of the response field of each unit. To accomplish this, the spatial tuning of each intraparietal neuron was estimated by fitting a Cartesian two-dimensional Gaussian model to the combined target and distractor data sets measured for each cell during each interval (Gnadt and Breznen 1996). The Gaussian model had six free parameters: horizontal and vertical position of the center, horizontal and vertical SDs, baseline firing rate, and peak amplitude. The model was constrained so that the center of the Gaussian lay within ±40° of the plot origin (the location of the fixation LED).

The mean responses for targets located within the rectangle defined by ±1 horizontal sigma and ±1 vertical sigma of the center of the response field and the mean response for distractors located within the same region were then calculated for each interval for each neuron. Target/distractor selectivity was computed as (Mean Target Response − Mean Distractor Response)/(Mean Target Response + Mean Distractor Response). In principle, the minimum selectivity was −1, indicating that the neuron under study responded infinitely more strongly for distractors than for targets located within the estimated center of the response field. The theoretical maximum selectivity was +1, indicating that the neuron under study was activated infinitely more strongly for targets than for distractors located within the center of the estimated response field. A selectivity of 0 indicated that the unit under study responded equally to targets and distractors. Selectivity ratios were compared across visual, cue, and premovement intervals to determine whether intraparietal neurons discriminated between stimuli that would eventually serve as saccadic targets and those that would eventually serve as distractors, and if so, whether this discrimination was associated with any trial events.

Effects of distractor relevance

Although selectivity indexes provide an estimate of intraparietal neuronal target selectivity on each task, they cannot provide a direct estimate of the effects of altering the relevance of the distractor on the selectivity of a particular neuron. To determine whether individual LIP neurons represent stimuli differently when distractor relevance is altered, selectivity ratios computed from distributed cue trials for each neuron during each interval were plotted as a

function of selectivity on cued saccade trials for that same neuron during that same interval. If intraparietal neurons did not alter their responses to distractors when distractor relevance was changed, then a graph of distributed cue task selectivity as a function of cued saccade task selectivity would describe a diagonal line passing through the origin and having a slope of 1. If intraparietal neurons were more strongly activated by distractors that cued movement initiation than by irrelevant distractors, then selectivity should be lower on distributed cue trials than on cued saccade trials, and the points on a bivariate plot of selectivity would fall below the line having a slope of 1. Thus, by generating a two-dimensional plot of selectivity on distributed cue trials as a function of selectivity on cued saccade trials, we can determine whether, on our tasks, intraparietal neurons encoded the behavioral significance of distractor stimuli that did not serve as saccadic goals.

RESULTS

Single-trial data

Thirty-one intraparietal neurons with saccade-associated activity were examined while subjects were presented with a minimum of 100 cued saccade trials and 100 distributed cue trials. The mean number of cued saccade trials performed correctly was 245 ± 57 (SD) (minimum = 103; maximum = 398). The mean number of correctly executed distributed cue trials was 278 ± 96 (SD) (minimum = 91; maximum = 584).

Figure 2 presents data for a single intraparietal neuron during 12 cued saccade trials. Figure 2, *A* and *C*, plots two trials that differed visually only in the color of the fixation LED. In these trials, the two eccentric LEDs were located, in Cartesian degrees of visual angle from the central fixation stimulus, at (−2,4) and (0,−10), respectively. Figure 2, *A* and *C*, *left*, each plot the horizontal and vertical position of the eye above an instantaneous frequency histogram of neuronal activity for a single trial. Arrows below the time axis identify events during the trial. The first arrow indicates the onset of the eccentric LEDs, the second arrow indicates the change in the color of the fixation stimulus, and the third arrow indicates the offset of the fixation stimulus. Figure 2, *A* and *C*, *right*, plot the point of gaze at successive 2-ms intervals during each trial. The disk shaded in dark gray identifies the boundaries of the response field at ±1 SD from the center as estimated by the sigma parameters of the Gaussian model for this cell (see METHODS).

Note in Fig. 2, *A* and *C*, that on both trials the neuron began firing action potentials immediately after the presentation of the two eccentric LEDs. In *A*, the neuron continued to fire action potentials at a high frequency after the fixation stimulus changed color from yellow to red (at the arrow marked cue), identifying the upper LED as the saccadic goal. The neuron maintained this high firing rate until after the completion of the required saccade. In *C*, however, the firing rate of the neuron diminished after the fixation stimulus changed color to green, indicating that a saccade shifting gaze to the lower LED would be required. It is important to note that only the color of the fixation cue, which indicated the direction of the required saccade, differed between these two cued saccade trials.

In Fig. 2*B*, spike rasters are plotted for five additional trials on which the saccadic target was located within 1 SD of the center of the response field; Fig. 2*D* plots five trials on which the irrelevant distractor was located within 1 SD of the center of the response field. In each raster plot, *T* indicates time of onset of the eccentric LEDs, *C* indicates the change in color of the fixation stimulus, *G* indicates offset of the fixation stimulus, and *S* indicates the time of saccade onset. Spike rasters were not averaged to produce a peristimulus time histogram. Horizontal and vertical movement amplitude are not plotted for these 10 additional trials.

After the two eccentric stimuli were illuminated, but before the cue LED identified one as the saccadic target, the neuron was strongly activated irrespective of whether the LED located within the center of the neuronal response field would eventually serve as a saccadic target or a visual distractor. After the saccadic target had been identified, however, the neuron under study continued to respond strongly if the LED aligned with the neuronal response field served as the saccadic target but fired at a reduced rate if that same LED served as an irrelevant visual distractor. Whether this was because a movement shifting gaze into alignment with the distractor LED was no longer being planned or whether it was because that stimulus became less relevant once it was identified as a distractor cannot be determined from an analysis of these trials.

Figure 3 presents the behavior of this same neuron on 12 distributed cue trials. On the two single trials presented in Fig. 3, *A* and *C*, the eccentric LEDs were illuminated at the same locations employed for the trials shown in Fig. 2, *A* and *C*. As in Fig. 2, Fig. 3*A* plots a single trial on which the upper eccentric LED served as the saccadic goal and Fig. 3*C* plots a trial on which the upper eccentric LED served as a visual distractor. Below the single trial presented in *A*, *B* plots spike rasters for five additional trials on which the saccadic target was located within 1 SD of the center of the neuronal response field. Beneath the single trial presented in *C*, *D* plots five additional trials on which the relevant distractor was located within 1 SD of the center of the neuronal response field.

To assess the effects of altering distractor relevance on the activation of this neuron, the single trials presented in Figs. 2*C* and 3*C* can be compared. Trial events are indicated by arrows below the time line: at the first arrow the two eccentric LEDs were illuminated, at the second arrow the fixation stimulus changed color to green, and at the third arrow either the fixation LED (Fig. 2*C*) or the LED identified as the distractor (Fig. 3*C*) was extinguished (the *go* command). Notice that neuronal activity during the last 200 ms of these two trials (light gray box) was largely identical. In both cases the response of the neuron under study was reduced after the cue signaled that the upper LED was a distractor, regardless of the relevance of the distractor to the task. Comparison of the spike rasters presented in Figs. 2*D* and 3*D* suggests that the activity of this neuron was not modulated by changes in distractor relevance across trials.

Figures 4 and 5 plot, for a second neuron, data during a similar set of cued saccade and distributed cue trials. Figure 4, *A* and *C*, presents two cued saccade trials during which the two eccentric LEDs were illuminated at (10,8) and (−10,−10). One eccentric LED was positioned in the center of the neuronal response field (indicated by the dark gray ellipses at *right*), whereas the other was located

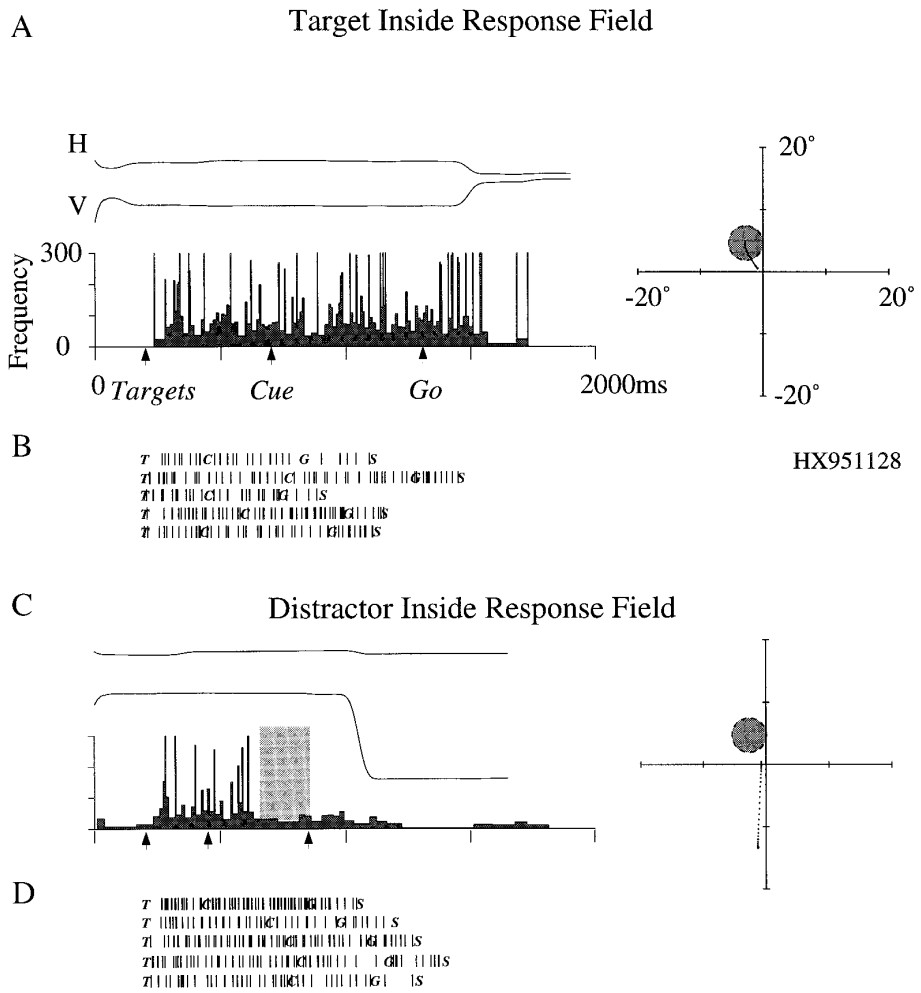

FIG. 2. Responses of single intraparietal neuron (*unit HX951128*) during 12 single cued saccade trials. In *A* and *C*, horizontal and vertical eye position are plotted as functions of time above instantaneous frequency histogram for 2 single trials. The 3 arrows under each histogram indicate, respectively, time of onset of eccentric LEDs (*Targets*), change in color of fixation LED (*Cue*), and offset of fixation LED (*Go*). In *C*, light gray box highlights cue interval for comparison with Fig. 3*C*. *Right*: point of gaze is plotted every 2 ms. Dark gray disk: center of response field (±1 horizontal and ±1 vertical SD) of neuron estimated by 2-dimensional Gaussian fit to combined cued saccade and distributed cue data. In *A*, fixation stimulus changed color to red, identifying upper eccentric LED (located 2° to left and 4° upward from fixation stimulus) as saccadic target and lower eccentric LED (located 10° straight down from fixation stimulus) as irrelevant distractor. In *C*, fixation stimulus changed color to green, identifying lower eccentric LED as saccadic target and upper eccentric LED as irrelevant distractor. Below single trial presented in *A*, *B* plots spike rasters for 5 additional trials on which target was located within ±1 horizontal and ±1 vertical SD of center of response field. In all spike raster plots, *T* indicates onset of eccentric LEDs, *C* indicates time at which fixation stimulus changed color, *G* indicates offset of fixation stimulus, and *S* indicates saccade onset. Below single trial presented in *C*, *D* plots spike rasters for 5 additional trials on which distractor was located within ±1 horizontal and ±1 vertical SD of response field center. Note that on all 12 trials, neuron responded briskly after presentation of 2 eccentric LEDs and continued to respond at high frequency when color of fixation stimulus cued movement that aligned gaze with upper eccentric LED (*A* and *B*); when color of fixation stimulus cued movement that would align gaze with lower eccentric LED (*C* and *D*), however, neuron responded at diminished frequency.

in the lower left visual hemifield, where it elicited no increased response from the cell on delayed saccade trials. The two trials presented in Fig. 4, *A* and *C*, differed visually only in the color of the fixation stimulus: in *A*, a change in the color of the fixation stimulus to red (at the time-marked cue) indicated that the upper eccentric LED would be the saccadic goal, whereas in *C* a change in the color of the fixation stimulus to green indicated that the upper eccentric LED would be an irrelevant distractor. In *A*, the neuronal response became elevated after a change in the color of the fixation stimulus indicated that the upper LED would be the saccadic goal. In contrast, when the same LED was specified as an irrelevant distractor in *C*, the neuron was only weakly activated.

Figure 5 presents data for this same neuron on 12 distributed cue trials. On the single trials presented in Fig. 5, *A* and *C*, the two eccentric LEDs were illuminated at the same locations as in Fig. 4, *A* and *C*. As in Fig. 4, Fig. 5*A* plots an instantaneous spike frequency histogram, as well as eye position as a function of time, for a single trial on which the upper eccentric LED served as the saccadic goal; Fig. 5*C* plots a trial on which the same upper eccentric LED served as a visual distractor. Below the single trial presented in Fig. 5*A*, Fig. 5*B* presents spike rasters for five additional

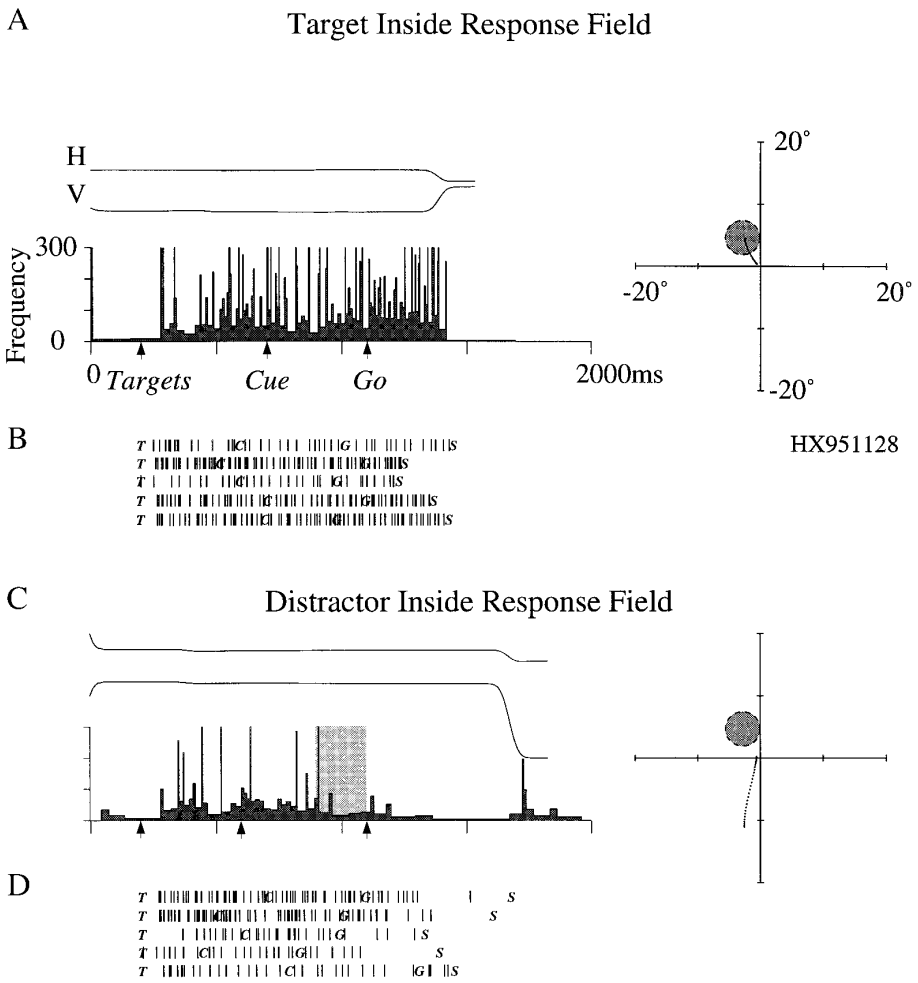

FIG. 3. Responses of single intraparietal neuron (*HX951128*) on 12 distributed cue trials. *Go*: offset of distractor LED. For single trials presented in *A* and *C*, eccentric LEDs were located in same positions as on trials presented in Fig. 2, *A* and *C*. Below single trial presented in *A*, *B* presents spike rasters for 5 additional trials on which target was located within ±1 horizontal and ±1 vertical SD of center of neuronal response field. Beneath single trial presented in *C*, *D* presents spike rasters for 5 additional trials on which distractor was located within ±1 horizontal and ±1 vertical SD of center of neuronal response field. As in Fig. 2, neuron responded strongly after presentation of 2 eccentric LEDs and continued to respond when color of fixation stimulus cued movement that would align gaze with upper eccentric LED (*A* and *B*); when color of fixation stimulus cued movement that would align gaze with lower eccentric LED, neuron responded at reduced frequency (*C* and *D*). Note that neuronal activity during cue interval (light gray box) was largely identical in Figs. 2*C* and 3*C*.

distributed cue trials on which the saccadic target was located within 1 SD of the center of the response field. Beneath the single trial presented in *C*, *D* plots spike rasters for five additional trials on which the relevant distractor was located within 1 SD of the center of the response field.

In Fig. 5*A*, as in Fig. 4*A*, the neuron responded after the identification of the upper LED as the saccadic goal. In Fig. 5*C*, however, the neuron showed reduced activity after the change in the color of the fixation stimulus from yellow to green identified the lower eccentric LED as the saccadic goal. Note that in both Figs. 5*C* and 4*C* the neuron showed little activity after the change in the color of the fixation stimulus signaled that the upper LED was a distractor, irrespective of the behavioral significance of the distractor to the task. The spike rasters presented in Figs. 4*D* and 5*D* suggest that the neuronal activation associated with LEDs identified as distractors remained unmodulated by changes in the relevance of the distractor to the task across trials, despite differences in the timing of task events and the precise location of the distractor LED within the neuronal response field.

Target and distractor fields

The trials presented in Figs. 2–5 suggest that the neurons in our sample did not discriminate relevant from irrelevant distractors in our tasks. These results further indicate that distractors of both types were represented by our parietal population. Single trials, however, cannot tell us how intraparietal neuronal activity varies as a function of the spatial position of the target or distractor, nor can they provide a sense of the mean response of the neuron on many similar trials. To provide that information, we generated three target fields and three distractor fields for each neuron from both the cued saccade and distributed cue sets of trials.

Figure 6 presents these six response field plots during cued saccade trials for the single neuron described in Figs. 2 and 3. On these trials, one eccentric LED was located in the lower hemifield at $(0,-10)$ while the location of the other eccentric LED varied within the upper hemifield from trial to trial. Figure 6*A* presents trials on which the eccentric LED that was fixed in the lower hemifield served as the distractor and on which the eccentric LED located in the upper hemifield served as the target. These graphs plot neuronal activity as a function of target position (in Cartesian degrees of visual angle relative to fixation) during the visual, cue, and premovement epochs. Figure 6*B* presents the trials on which the eccentric LED fixed in the lower hemifield served as the saccadic target and the variable upper hemifield LED served as the irrelevant distractor. In these graphs, neuronal activity is plotted as a function of the position of the distractor.

During the visual interval, at which time targets and distractors were indistinguishable, the neuron responded if ei-

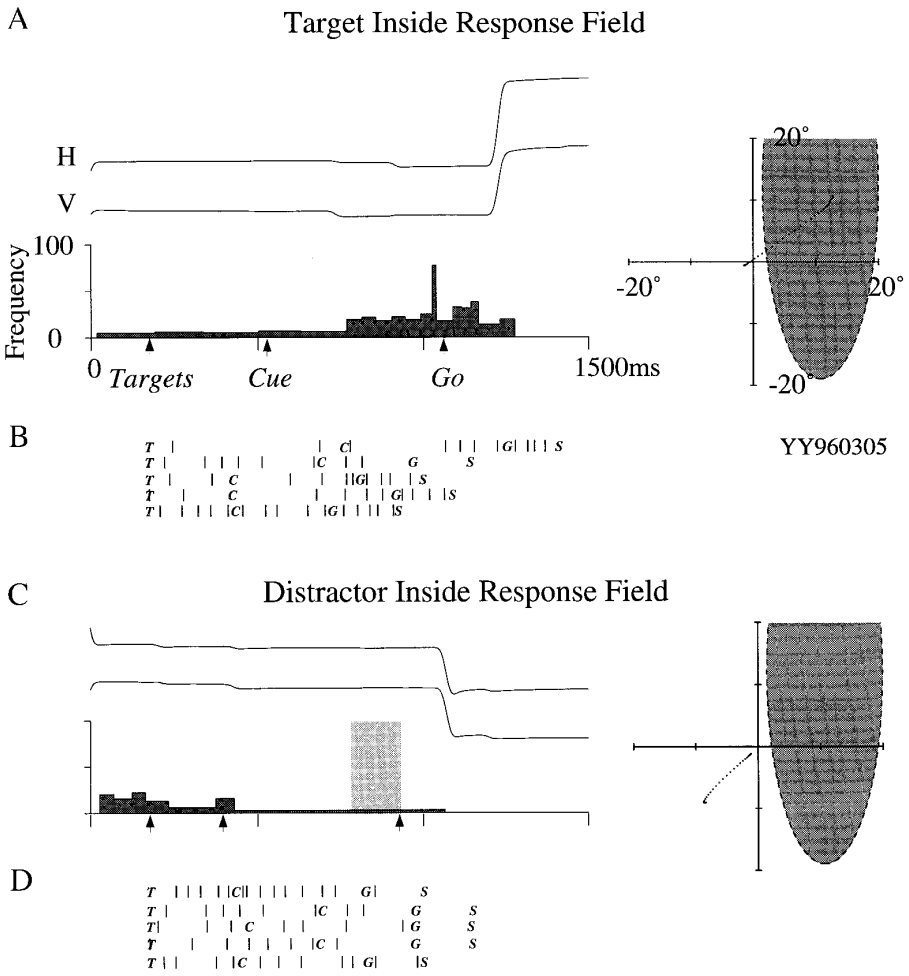

FIG. 4. Responses of single intraparietal neuron (*unit YY960305*) on 12 cued saccade trials. For single trials presented in *A* and *C*, eccentric LEDs were located at (10,8) and (−10,−10), respectively. In *A*, color of fixation LED changed from yellow to red, indicating that animal would be rewarded for shifting gaze into alignment with upper eccentric LED. In *C*, color of fixation LED changed from yellow to green, identifying lower eccentric LED as saccadic goal. Below single trial presented in *A*, *B* presents spike rasters for 5 additional trials on which target was located within ±1 horizontal and ±1 vertical SD of center of neuronal response field (indicated by dark gray ellipse in point-of-gaze plot on *right*). Neuron responded with increase in activity when cue identified upper LED as saccadic goal (*A* and *B*) but fired at reduced rate when cue identified lower LED as saccadic goal (*C* and *D*).

ther the (future) target or distractor was located within the center of the upper visual hemifield. During the cue interval, after one of the eccentric LEDs had been identified as the saccadic goal, the neuron continued to respond if the spatially varying LED was located in the middle of the upper visual field and served as a target but showed reduced activity when the variable LED served as a distractor in this same region. This differential activation for targets and irrelevant visual distractors became more pronounced in the immediate premovement interval.

Compare the responses plotted in Fig. 6 with those shown in Fig. 7. Figure 7 plots the behavior of the same neuron shown in Fig. 6, but during distributed cue trials. Notice that the selectivity of the neuron for saccadic targets over distractors on distributed cue trials is similar to the selectivity of the neuron on cued saccade trials. In particular, compare the activity on the distractor plots during the cue epoch, the 200 ms before the movement initiation cue was presented. In both Figs. 6 and 7, the activity of the neuron showed a similar target-to-distractor ratio of activity within the upper hemifield.

Figures 8 and 9 present target and distractor fields for a second neuron (single trials presented in Figs. 4 and 5) on cued saccade and distributed cue trials, respectively. On these trials, one eccentric LED was fixed in the lower left quadrant at (−10,−10) while the location of the other LED varied within the upper hemifield across trials. Target fields were constructed from trials on which the LED located within the upper hemifield was identified as the target, whereas distractor fields were constructed from trials on which the LED located in the upper hemifield was identified as a distractor. In contrast with the activity of the neuron presented in Figs. 6 and 7, this neuron was characterized by a tonic firing rate that was influenced only weakly by the initial presentation of the two eccentric visual stimuli. During the cue and premovement intervals, however, this neuron responded at an increased frequency in association with targets located in the upper right visual hemifield but responded weakly in association with distractors located in this same region. Note that the response of this neuron to distractors during the cue interval also appears not to depend on the relevance of the distractor.

Population data

To quantify the relative responses of each neuron to targets and distractors across trials, we computed the average response of the neuron on all trials on which either the target or the distractor was located within ±1 horizontal SD and ±1 vertical SD of the center of the response field (see METHODS). Figure 10 plots the population mean ± SE of the average neuronal response in association with targets

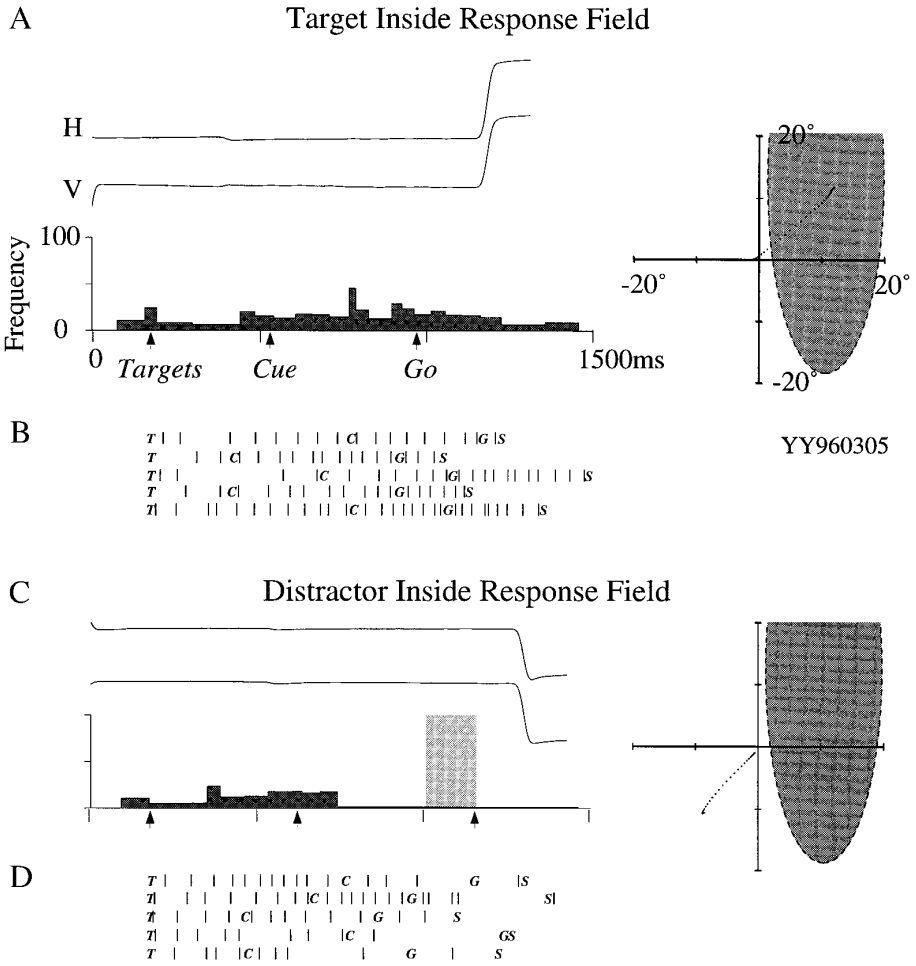

FIG. 5. Responses of single intraparietal neuron (*unit YY960305*) on 12 distributed cue trials. On trials presented in *A* and *C*, 2 eccentric LEDs were located in same positions as in Fig. 4, *A* and *C*. In *A*, cue identified upper eccentric LED as saccadic goal, whereas in *C*, cue identified lower eccentric LED as saccadic target. As in Fig. 4, neuron responded with increase in activity when cue identified upper eccentric LED as target (*A* and *B*) but responded with diminished activity after cue identified lower eccentric LED as target (*C* and *D*). Neuronal activity was approximately equal during cue interval (light gray box) in Figs. 4*C* and 5*C*, regardless of which task animal was performing.

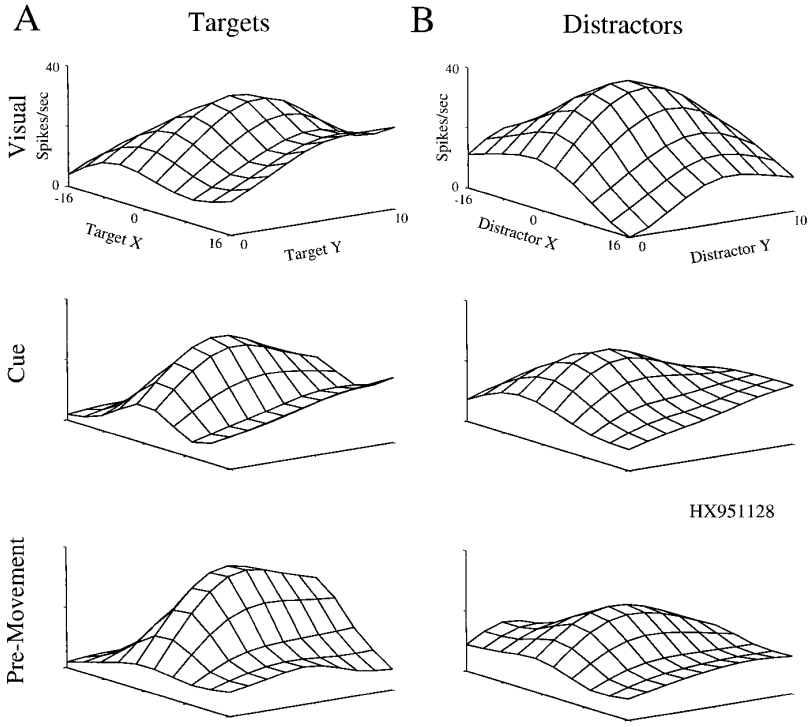

FIG. 6. Target and distractor fields from 194 cued saccade trials for *unit HX951128*. *A*: trials on which eccentric LED that varied in position was identified as saccadic target. *B*: trials on which variable eccentric LED was identified as irrelevant distractor. Data were averaged in 4 × 4° blocks and smoothed by interpolation (Axum). In *A*, firing rate is plotted as function of location of saccadic target. In *B*, firing rate is plotted as function of location of irrelevant distractor. Target and distractor fields are plotted for 3 time intervals: visual (200 ms from eccentric targets onset), cue (200 ms preceding fixation LED offset), and premovement (100 ms preceding saccade onset). Note that neuron responded briskly in association with both targets and distractors located within central upper hemifield during visual interval, but response for distractors became reduced during cue and premovement intervals (*B*). Maximum firing rate for surfaces: 32.0, 30.0, and 36 Hz (*A*); 38, 27.0, and 25 Hz (*B*). Mean firing rates within ±1 horizontal and ±1 vertical SD of center of neuronal response field: 26.8, 27.7, and 34.6 Hz (*A*); 31.6, 26.8, and 25 Hz (*B*). Spatial tuning radii (see METHODS): 3.6, 3.2, and 3.0° in visual, cue, and premovement intervals, respectively.

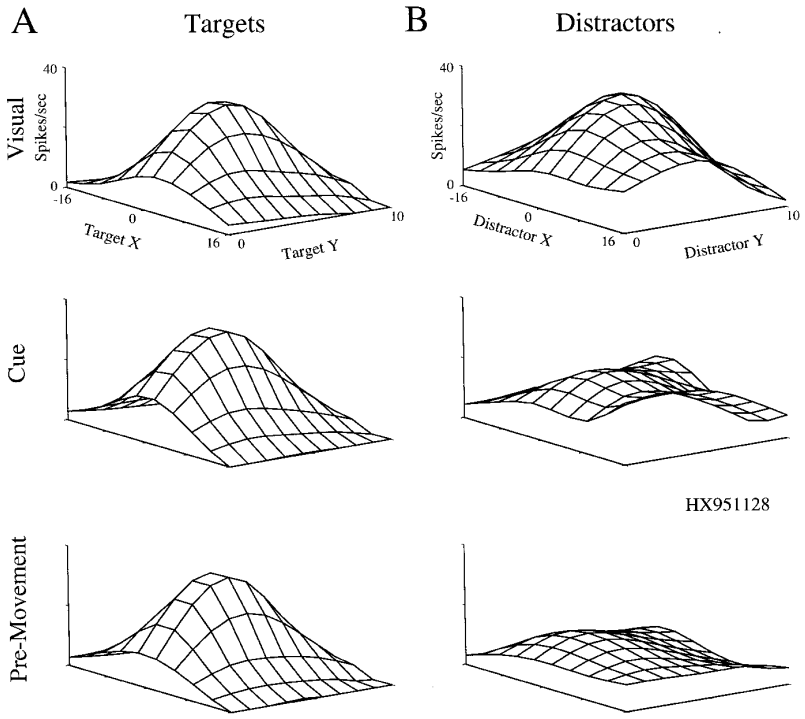

FIG. 7. Target and distractor fields computed from 91 distributed cue trials for *unit HX951128.* Note that neuronal response was similar during cue interval whether distractor was relevant (Fig. 7*B*) or irrelevant (Fig. 6*B*) to task. Maximum firing rate for surfaces: 32.0, 33.0, and 33 Hz (*A*); 32, 20, and 14 Hz (*B*). Mean firing rates within center of neuronal response field: 35.7, 30.7, and 50 Hz (*A*); 29, 21.6, and 12.2 Hz (*B*). Spatial tuning radii: 3.4, 3.0, and 1.6° during visual, cue, and premovement intervals, respectively.

(——) and distractors (– – –) located within the center of the response field for our population of 31 neurons during visual, cue, and premovement intervals on both cued saccade (●) and distributed cue (▲) trials. The average neuronal response in association with targets and distractors was equivalent during the visual interval on both tasks. During the cue and premovement intervals, average responses increased in association with targets but decreased in association with distractors on both tasks. In a three-way analysis of variance, the main effect of target/distractor was significant ($F = 22.12$, df = 1, $P < 0.00001$), as was the interaction between target/distractor and task interval ($F = 6.30$, df = 13, $P < 0.005$). The average neuronal response, however, was unaffected by modulations in distractor relevance ($F = 0.38$, df = 1, $P > 0.5$).

To ascertain whether the increased response in association with targets and decreased response in association with distractors shown in Fig. 10 was characteristic of individual neurons in our population, we plotted the average response of 10 randomly selected neurons during visual, cue, and

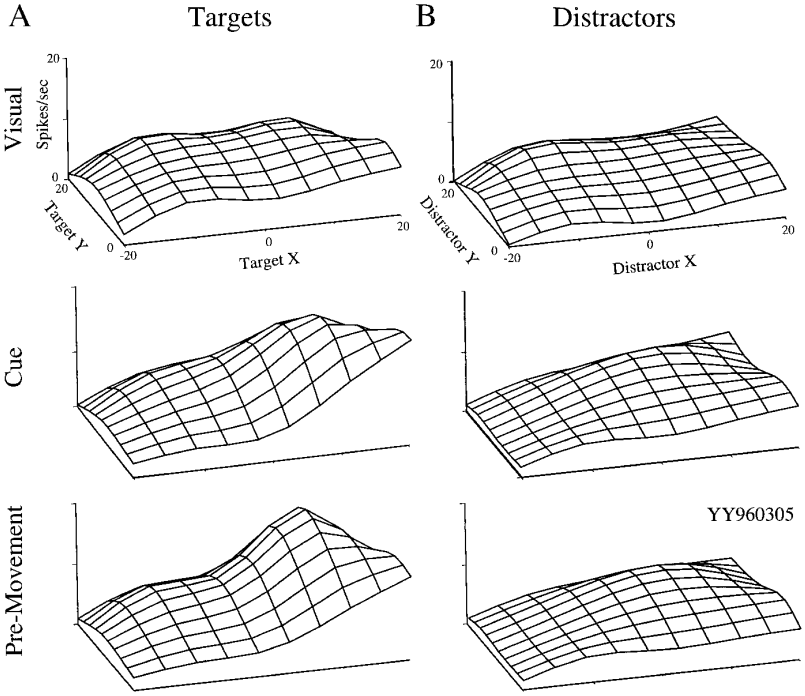

FIG. 8. Target and distractor fields computed from 239 cued saccade trials for *unit YY960305.* Note that neuron responded when LEDs located in right upper hemifield were identified as saccadic targets but responded weakly when LEDs located in same region were identified as irrelevant distractors. Maximum firing rate for surfaces: 10.0, 17.0, and 19.0 Hz (*A*); 9.4, 10.2, and 9.5 Hz (*B*). Mean firing rates within center of neuronal response field: 10.8, 14.1, and 16.2 Hz (*A*); 10.5, 9.7, and 9.5 Hz (*B*). Spatial tuning radii: 10.8, 23.1, and 24.1° during visual, cue, and premovement intervals, respectively.

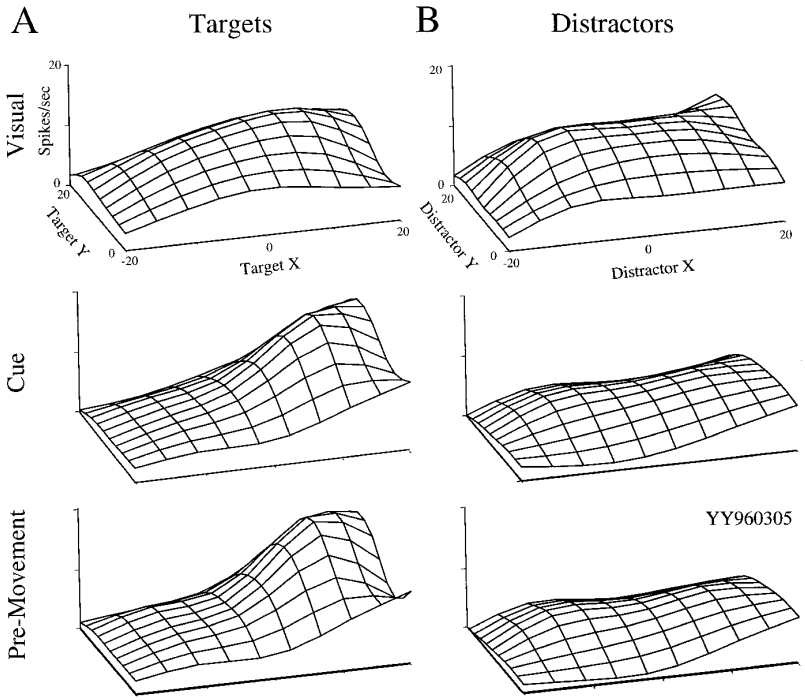

FIG. 9. Target and distractor fields computed from 275 distributed cue trials for *unit YY960305*. Note that ratio of target/distractor response was largely independent of whether visual distractor was relevant (Fig. 9) or irrelevant (Fig. 8). Maximum firing rate for surfaces: 13.0, 17.5, and 18.8 Hz (*A*); 12.2, 9.0, and 8.5 Hz (*B*). Mean firing rates within center of neuronal response field: 12.7, 13.7, and 14.6 Hz (*A*); 11.8, 8.1, and 7.6 Hz (*B*). Spatial tuning radii: 23.0, 15.4, and 24.8° during visual, cue, and premovement intervals, respectively.

premovement intervals on both cued saccade (Fig. 11*A*) and distributed cue (Fig. 11*B*) trials. Figure 11, *A* and *B*, *left* plot the average of neuronal responses produced by each neuron in association with targets located within ±1 horizontal and ±1 vertical SD of the center of the response field; the graphs at *right* plot the average of all neuronal responses that occurred in association with distractors located within this same area. Target-associated increases, and distractor-associated decreases, in mean neuronal firing rate were observed for most of these 10 neurons on both cued saccade and distributed cue trials.

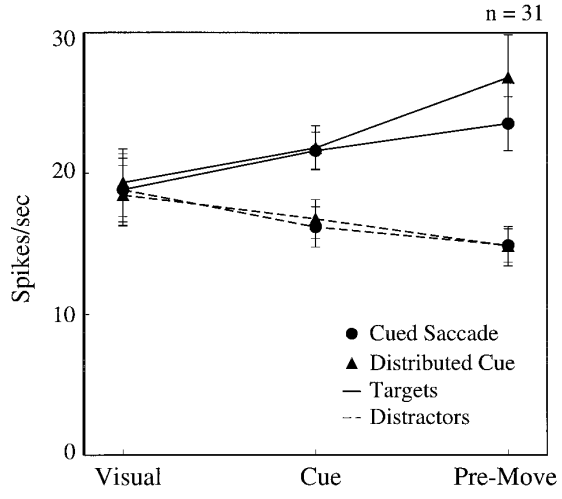

FIG. 10. Population mean ± SE of neuronal response rate in association with targets (——) and distractors (– – –) located within ±1 SD of center of each neuronal response field on both cued saccade (●) and distributed cue (▲) trials during visual, cue, and premovement intervals. On cued saccade trials, mean firing rate differed significantly between visual and premovement intervals on target plot (*t*-test, $P < 0.01$) but showed no significant differences across intervals on distractor plot. Responses differed significantly between target and distractor trials during cue ($P < 0.0001$) and premovement ($P < 0.0001$) intervals. On distributed cue trials, mean firing rate differed significantly between visual and premovement intervals on both target plot ($P < 0.01$) and distractor plot ($P < 0.05$). Responses differed significantly between target and distractor trials during cue ($P < 0.001$) and premovement ($P < 0.00001$) intervals. Mean firing rate did not differ significantly between the 2 tasks (analysis of variance: $F = 0.38$, df = 1, $P > 0.54$).

To quantify the differential responses of neurons to targets and distractors, selectivity indexes were computed from the average responses of each neuron (see METHODS). The selectivity indexes permit us to compare, for each neuron, how different task events modulate the relative strength of neuronal activation associated with an LED when it served as a target versus the activation associated with that same LED when it served as a relevant or irrelevant distractor.

Figure 12 plots histograms of the selectivity index for the visual, cue, and premovement intervals for the 31 neurons in our population. On cued saccade trials (Fig. 12*A*), the average neuron in the population responded approximately equally for targets and distractors during the visual interval, with a mean selectivity index of -0.01 ± 0.03 (SE). During the cue interval, the population was more active for targets than for irrelevant visual distractors (0.15, ± 0.03, mean ± SE), whereas during the premovement interval the population was even more selective for targets (0.21 ± 0.04, mean ± SE). The selectivity indexes for the cue and premovement intervals did not differ significantly by *t*-test ($t = -1.16$, df = 60, $P > 0.25$), but both were significantly different from the selectivity index calculated for the visual interval (cue: $t = 5.51$, df = 30, $P < 0.001$; premovement: $t = -4.42$, df = 60, $P < 0.001$).

Our population of intraparietal neurons responded similarly on distributed cue trials (Fig. 12*B*). During the visual interval, the average neuron responded equally strongly for targets and distractors (0.02 ± 0.02, mean ± SE). During the cue interval, the population responded more strongly for targets than for distractors (0.14 ± 0.03, mean ± SE). The

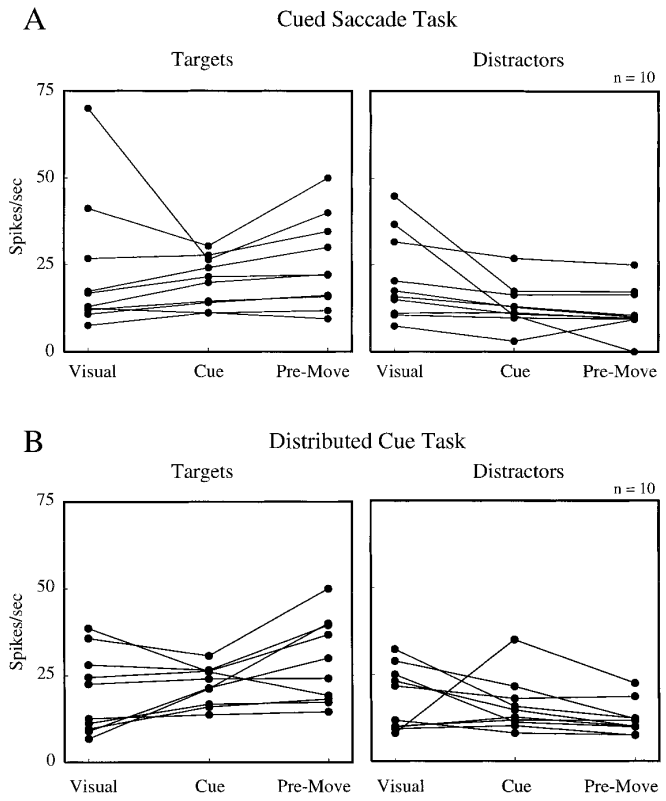

FIG. 11. Average neuronal response rates in association with targets and distractors located within ±1 horizontal and ±1 vertical SD of center of neuronal response field during visual, cue, and premovement intervals for 10 randomly selected neurons on cued saccade (*A*) and distributed cue (*B*) trials. Solid lines connect responses of each neuron across intervals. Most neurons showed both target-associated increases and distractor-associated decreases in mean firing rate on both tasks.

average neuron was most selective for saccadic targets during the premovement interval (0.27 ± 0.04, mean ± SE). The selectivity indexes for the cue and premovement intervals during distributed cue trials differed significantly ($t = -2.48$, df = 60, $P < 0.02$) and were significantly different from the selectivity index calculated for the visual interval (cue: $t = -3.34$, df = 60, $P < 0.005$; premovement: $t = -5.62$, df = 60, $P < 0.00001$).

Although these histograms confirm our initial observation that altering the relevance of the distractor by making its offset the movement initiation cue had little effect on the average responses of this population of intraparietal neurons, we were also interested in whether this result was reflected in the behavior of individual neurons in this population. To assess this, we plotted the selectivity index of each neuron on cued saccade trials against the selectivity index of the same neuron on distributed cue trials during each of our three epochs (Fig. 13, *A*–*C*). On these plots, the solid diagonal line indicates the expected distribution of neurons that showed an equivalent selectivity index on both trial types irrespective of the relevance of the visual distractor to the task. During the visual interval, most neurons clustered around a selectivity index of 0 on both tasks, indicating an equal response to targets and distractors. During the cue interval, however, most neurons shifted up into the first quadrant, indicating a greater response for targets than for distractors on both trial types. More importantly, most neurons fell along the diagonal line, indicating no change in selectivity when the behavioral significance of the distractor was altered. During the premovement interval, most neurons fell further out along the diagonal line within the first quadrant, with some points shifting up above the main diagonal. In fact, this enhancement of target/distractor selectivity during the premovement interval on the distributed cue task relative to the cued saccade task was due to an increase in mean response to targets without a concomitant change in mean response to distractors (see Fig. 10). The relative enhancement of the target representation on distributed cue trials may result from the fact that the two trial types were not visually identical during this epoch because the distractor had been extinguished as the cue to initiate a movement in the distributed cue task.

Figure 13*D* plots (●) the average population selectivity index (mean ± SE on each axis) on each task during the three measured intervals. Notice that the average neuronal selectivity began near (0,0) in the visual interval, moved out along the main diagonal into the first quadrant during the cue interval, and peaked during the premovement interval, slightly above the main diagonal. The enhancement of neuronal selectivity during the premovement interval was due to a relative increase in the target representation on distributed cue trials (Fig. 10), whereas responses to distractors remained unchanged between the two tasks. Thus the re-

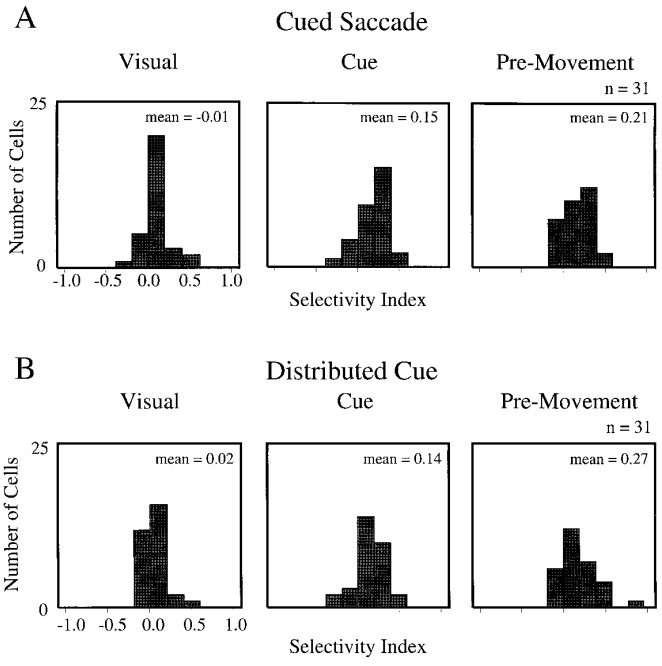

FIG. 12. *A*: frequency histogram for selectivity indexes on cued saccade trials during visual, cue, and premovement epochs calculated for 31 intraparietal neurons. Selectivity index: +1 for neurons responding infinitely more for targets than for distractors, −1 for neurons responding infinitely more for distractors than for targets, 0 for neurons responding equally strongly for targets and distractors. Average selectivity: visual interval, −0.01 ± 0.03 (SE); cue interval, 0.15 ± 0.03 (SE); premovement interval, 0.21 ± 0.04 (SE). *B*: frequency histogram for selectivity indexes computed during distributed cue trials for 31 intraparietal neurons. Average selectivity: visual interval, 0.02 ± 0.02 (SE); cue interval, 0.14 ± 0.03 (SE); premovement interval, 0.27 ± 0.04 (SE).

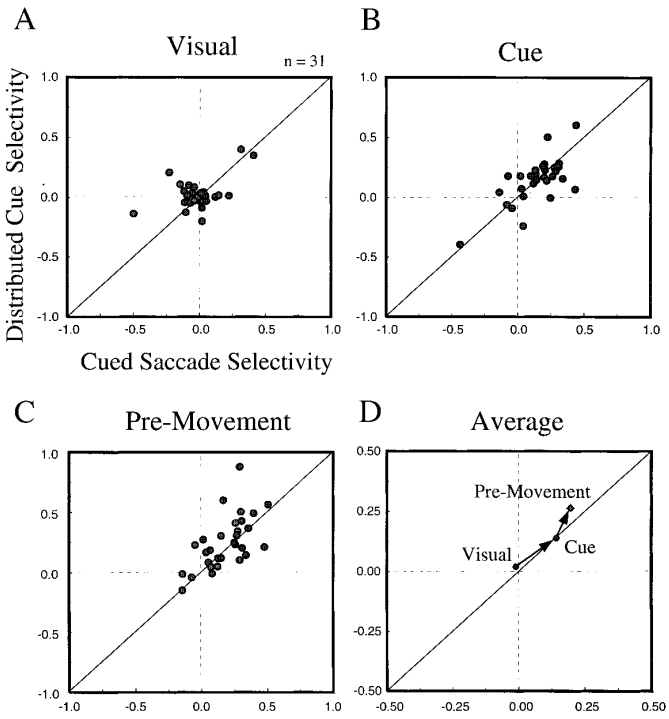

FIG. 13. Two-dimensional plot of selectivity on cued saccade trials as function of selectivity on distributed cue trials for each of 31 intraparietal neurons. Solid diagonal line: expected distribution of neurons showing equivalent selectivity index on both trial types irrespective of relevance of visual distractor. Neurons showing increased response to relevant distractors would fall below line. Note that in *A–C,* selectivity of most neurons was nonnegative and largely independent of behavioral significance of distractor. In *D,* average neuronal selectivity (mean ± SE) is plotted during all 3 sequential time epochs. Average selectivity was near 0 on both tasks during visual interval, shifted up along main diagonal into 1st quadrant during cue interval, and shifted up above main diagonal during premovement interval.

sponse of the population during both the cue and premovement epochs was largely unaffected by whether the distractor was irrelevant or served as the movement initiation signal at the end of the cue epoch (*t*-test: visual interval: $t = -0.88$, df = 60, $P > 0.38$.; cue interval: $t = 0.14$, df = 60, $P > 0.88$; premovement interval: $t = -1.07$, df = 60, $P > 0.29$).

To examine the possibility that a subpopulation of intraparietal neurons characterized by broad spatial tuning may show a sensitivity to distractor relevance in these tasks, we also assessed the relationship between spatial tuning breadth and target/distractor selectivity. For each neuron, a spatial tuning radius was computed by averaging the horizontal and vertical SDs generated by the two-dimensional Gaussian fit to the combined target and distractor data bases for each interval on both cued saccade and distributed cue tasks. The 31 neurons studied were found to be tuned across all spatial scales (minimum spatial tuning radius = 1.00°; maximum spatial tuning radius = 37.6°). During each interval on both tasks, the modal neuron had a spatial tuning radius of <5°. The mean spatial tuning radii of neurons in the cued saccade task were as follows: visual interval, 12.00 ± 1.92° (mean ± SE); cue interval, 11.17 ± 1.54° (mean ± SE); premovement interval, 12.61 ± 1.82° (mean ± SE). In the distributed cue task, mean spatial tuning radii were as follows: visual interval, 10.87 ± 1.69° (mean ± SE); cue interval, 10.53 ± 1.69° (mean ± SE); premovement interval, 11.23 ± 1.74° (mean ± SE). Linear regression analyses showed that there was no relationship between spatial tuning radius and selectivity on either cued saccade (visual interval, $r^2 = 0.001$; cue interval, $r^2 = 0.11$; premovement interval, $r^2 = 0.03$) or distributed cue (visual interval, $r^2 = 0.03$; cue interval, $r^2 = 0.007$; premovement interval, $r^2 = 0.09$) trials.

DISCUSSION

An examination of reinforced cued saccade trials indicated that intraparietal neurons responded more strongly in association with an appropriately placed LED when it was identified as the saccadic goal than when the same LED was identified as an irrelevant visual distractor. Comparison of distributed cue trials with cued saccade trials on which the same LEDs were identified as distractors showed that intraparietal neurons did not become more strongly activated when distractor offset cued movement initiation than when the same LED was completely irrelevant to the task.

Comparison of target fields and distractor fields, which plotted neuronal activity as a function of the position of the spatially variable eccentric stimulus, showed that the mean response of most intraparietal neurons during the cue interval was greater in association with LEDs that had been identified as targets than when the same LEDs had been identified as distractors. This differential response associated with targets versus distractors was enhanced in the 100 ms immediately preceding movement onset. Most neurons represented distractors with the same spatial tuning shown for saccadic targets, albeit at a lower level of activation. Finally, the magnitude of this differential response associated with targets versus distractors did not appear to vary as a function of the relevance of the distractor.

At the population level, the average neuronal response magnitude also differed in association with targets and distractors located within the center of the response field. A plot of mean neuronal activation in association with targets demonstrated a clear increase in response across visual, cue, and premovement intervals, whereas average neuronal activation decreased in association with distractors across the same intervals. Mean firing rate was not modulated by the relevance of the distractor. A plot of mean firing rate across measured intervals for 10 randomly selected neurons demonstrated that both target-associated increases and distractor-associated decreases in firing rate were characteristic of many individual neurons in our population.

The difference in activation level associated with targets and distractors was quantified by a selectivity index, which showed that most intraparietal neurons responded more for targets than for distractors on both of our tasks. We found that the precise selectivity index associated with each neuron in our population was largely unaffected by which task the subject performed. These selectivity index data indicate that on our tasks intraparietal neurons did not encode the relevance of stimuli that would not become saccadic goals, although these distractor stimuli were associated with the activation of these intraparietal neurons.

Comparison with previous studies

Previous studies that have attempted to relate LIP neuronal responses to attention typically employed tasks that pre-

sented subjects with only one eccentric visual stimulus, which was either completely irrelevant or provided information that the subject could use to obtain a reward (cf. Goldberg et al. 1990). Alternatively, attempts to relate LIP responses to planned movement metrics presented subjects with a single visual stimulus that specified the metrics of a required saccade (cf. Gnadt and Andersen 1988). Although these earlier studies suggested that LIP activity participated in some covert sensory-motor processes, significant uncertainty remains about whether LIP activity reflects the application of selective visual attention or simply represents the planning of an upcoming eye movement.

The tasks employed here presented subjects with two eccentric LEDs, one of which would be the eventual saccadic target and the other a visual distractor. By altering the behavioral relevance of the visual distractor and independently specifying the metrics of a required saccade, we hoped to gather evidence that would bear on sensory-attentional and movement planning hypotheses of LIP function. The single cued saccade trials presented here indicated that intraparietal neurons responded more strongly on trials in which an LED in the center of the response field of a neuron served as a saccadic target than when the same LED served as an irrelevant visual distractor. When we altered the relevance of the visual distractor by presenting animals with a block of distributed cue trials, intraparietal neurons did not show an enhanced response in association with the relevant distractor LED. The lack of an enhancement (Bushnell et al. 1981; Goldberg and Wurtz 1972; Robinson et al. 1978; Wurtz and Mohler 1976) in the neuronal spike rate associated with relevant versus irrelevant distractors suggests that, on our tasks, intraparietal neuronal responses were more strongly correlated with the metrics of upcoming saccades than with the relevance of a stimulus to the subject, although appropriately placed distractors were almost always associated with some intraparietal activity.

At least initially, our data would appear to be inconsistent with the hypothesis that LIP neuronal activation rates signal the behavioral relevance of visual stimuli (Goldberg et al. 1990). Of course we cannot exclude the possibility that LIP neurons respond to some manipulations of stimulus relevance but not to others and that our stimulus manipulation was simply not effective. If, as Goldberg et al. (1990) have proposed, LIP neuronal activity reflects the attentional state of the animal, then only direct measures of attentional state made simultaneously with direct measures of neuronal state can completely resolve this issue.

We did find that most intraparietal neurons were weakly activated by appropriately placed distractor LEDs regardless of their behavioral significance. Thus visual stimuli that will not become immediate saccadic goals appear to be represented in area LIP. How many distractor stimuli can be represented in LIP, and the significance of this information for parietal processing, cannot be discerned from the experiments reported here. These data do suggest, however, that a simple motor planning hypothesis of LIP activation may not provide a complete account of LIP function (Goldberg et al. 1990).

Summary

Our data suggest that when an animal is presented with two eccentric visual stimuli, two populations of LIP neurons become active, one activated in association with each of the two eccentric LED locations or with each of two simultaneously planned movements guided by these stimuli. After one of these LEDs has been identified as a saccadic goal, the population of LIP neurons associated with the target stimulus, or the movement it specifies, responds more strongly than the population of neurons associated with the irrelevant distractor. In the tasks examined here, this target-over-distractor selectivity was unaffected by changes in distractor relevance. These data provide some evidence in support of the hypothesis (Bracewell et al. 1996) that most LIP neurons carry a signal that has been filtered by the specification of a saccadic goal but is insensitive to the behavioral significance of visual distractors, although these stimuli are almost always represented (Goldberg et al. 1990).

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