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RESEARCH ARTICLE

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Short-term changes in movement frequency do not alter the spatial tuning of saccade-related neurons in intraparietal cortex

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Abstract Modulations of the firing rates of neurons in the lateral intraparietal area (LIP) have been observed during experiments designed to examine decision-processing, movement planning, and visual attention. These modulations have been assumed to reflect a uniform scaling of spatially stationary response fields, which describe firing rate as a function of either visual target location or movement metrics. However, because complete response fields are rarely collected, the possibility exists that these modulations may reflect shifts in response field location or changes in response field size. Moreover, many of these observed changes in LIP neuronal activity are also correlated with experimental practices that alter the frequency with which particular visual stimuli are viewed and particular movements are produced. The effects of repeatedly presenting a particular target and eliciting a particular movement on the response fields of LIP neurons warrant closer inspection because manipulations of this type are known to alter both the location and size of the receptive fields of many cortical sensory neurons. To address this issue, we measured the response fields of neurons in intraparietal cortex under two conditions over a period of up to 2 h: one in which each of nearly 200 stimulus locations was equally likely to serve as the saccade target on a trial, and a second in which one stimulus location was up to 750 times likelier to serve as the saccade target on a trial than were any of the other stimulus locations. We found no shifts in response field location or changes in response field size when we altered the frequency with which particular movements were produced or particular visual stimuli were presented. These data suggest that the response fields of intraparietal neurons are stationary over short periods of time and under conditions similar to those typically used to study LIP neuronal activity.

Key words Saccade · Parietal cortex · Probability · Spatial tuning · Plasticity

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Introduction

Neurons in the lateral intraparietal area (LIP), like neurons in many cortical sensory and motor areas, fire action potentials in a graded fashion as a function of visual target position or saccadic amplitude and direction (Gnadt and Andersen 1988; Barash et al. 1991b; Gnadt and Breznen 1996; Platt and Glimcher 1998). Specifically, when animals are trained to shift gaze into alignment with a visual stimulus, each LIP neuron is most active in association with a particular target-movement pair (a *best target-movement pair*); neuronal activity decreases gradually as the location of the target and the metrics of the accompanying movement deviate from this best target-movement pair. The graded relationship between firing rate and target location/movement metrics defines the response field of each LIP neuron.

Both we (Platt and Glimcher 1998) and Gnadt and Breznen (1996) have shown that the response fields of LIP neurons can be well-described by two-dimensional gaussian functions. Each gaussian function is defined by an *x*, *y*-coordinate pair specifying the center of the function (and thus the best target or movement for the neuron), a *z*-coordinate specifying the maximum increase in firing rate produced by the neuron (and thus the modulation in the activity of the neuron for the best target or movement), sigma-parameters specifying the width of the gaussian function (and thus how quickly firing rate drops off as targets or movements deviate from the best target-movement pair), and a baseline rate specifying the tonic activity of the neuron.

In many experiments, however, it is impractical or difficult to derive estimates of all of these parameters. As a result, it is common to test experimental hypotheses by first estimating the best target-movement pair and then by examining activity associated with this target-movement pair under a variety of conditions (cf. Duhamel et al. 1992; Bracewell et al. 1996; Colby et al. 1996; Mazzoni et al. 1996; Shadlen and Newsome 1997; Platt and Glimcher 1997, 1999). Observed changes in activity are then assumed to reflect a uniform scaling of the activation of the neuron for all possible target-movement pairs.

Unfortunately, measurements of the responses of a neuron under these conditions can be ambiguous. While a decrease in firing rate may indeed indicate a decrease in the maximal response of the neuron under study, it may also indicate a shift either toward a new best target-movement pair or a change in the sigma-parameters of the neuronal tuning function. For example, the peri-movement firing rates of saccade-related neurons in both the superior colliculus (Mays and Sparks 1980; White and Sparks 1986) and LIP (Gnadt and Andersen 1988; Barash et al. 1991a) have been observed to be lower for memory-guided saccades than for visually guided saccades, and these modulations are consistent with a spatially uniform scaling of maximum firing rate. Relatively complete response field data gathered from collicular neurons studied with both visually guided and memory-guided saccades (Stanford and Sparks 1994), however, suggest that memory-dependent modulations in collicular neuron activity might be more precisely described as dynamic changes in the horizontal and vertical amplitude of the best movement of each neuron, rather than a uniform scaling of maximum firing rate for all movements.

Our own work (Platt and Glimcher 1999) has indicated that the presaccadic firing rates of LIP neurons are modulated by the probability that the visually guided movement they encode will be required for reinforcement, as well as by the amount of reinforcement delivered for that same movement (see Basso and Wurtz 1997; Dorris and Munoz 1998, for similar effects in collicular neurons). In that experiment, movements guided by only two visual targets were studied: one specifying the best target-movement pair for the neuron, and a second specifying a movement of equal amplitude in the opposite direction. We then manipulated either the probability that the best movement would be required in order to receive a drop of juice or the volume of juice delivered for that movement. Our results suggested that LIP neurons encode the value of particular eye movements to an animal.

Unfortunately, that experiment cannot address the possibility that the response fields of LIP neurons may be non-stationary when the frequency with which particular stimuli are viewed or particular movements are produced is systematically manipulated during the course of an experimental session. This possibility warrants further inspection in the light of recent studies demonstrating non-stationarities in the receptive field structure of cortical sensory neurons when the normal pattern and frequency of sensory inputs is disrupted or when particular stimuli are repeatedly presented during behavioral training (cf. Merzenich et al. 1983a,b, 1984; Jenkins et al. 1990; Recanzone et al. 1992a,b, 1993; for a review see Buonomono and Merzenich 1998). For example, Jenkins and colleagues (1990) have shown that the receptive fields of cortical somatosensory neurons shift toward an increased representation of those particular sensory inputs that are most frequently stimulated. Moreover, dynamic changes in receptive field tuning can develop within minutes or hours, as demonstrated by Edeline and Weinberger (1992) for the representation of conditioned auditory stimuli by frequency-tuned neurons in auditory cortex and auditory thalamus. Thus, if it can be demonstrated that the frequency with which particular targets are viewed or particular movements are produced does alter the spatial tuning functions of LIP neurons, then the common experimental practice of limiting observations to the target-movement pair identified as the best target-movement pair at the beginning of an experimental session may itself induce changes in the response profile of the cell. In some measure, the interpretation of many previous experimental studies in LIP thus rests on the extent to which the spatial tuning functions of LIP neurons can be shown to be invariant when the frequency of viewing particular targets or producing particular movements is altered.

The goal of this study was to determine whether changes in the frequency with which a particular target was viewed or a particular movement was executed over the course of a single experimental session would systematically change the location or size of LIP neuronal response fields. In order to determine whether the response fields of LIP neurons can be modified by altering the frequency with which a particular target is presented or a particular movement is produced, we trained rhesus monkeys to make visually guided saccades under two conditions. In one condition, saccade targets were randomly selected on each trial from a grid of 199 possible stimulus locations (or in a small sample of neurons, a collinear array of 10 stimulus locations). In the second condition, one particular stimulus location was programmed as the saccade target on a high percentage of trials (typically 50%, but for some neurons, 75%), while on each of the remaining trials the saccade target was selected randomly from among the 199 possible target locations. If the response fields of LIP neurons are influenced by those stimuli most often viewed or those movements most often produced by an animal, then the best target-movement pairs of these neurons would be expected to shift under these conditions. We found that, across the population of LIP neurons, there was no systematic alteration in either the locations of the best target position nor in the metrics of the best movement when a particular visually guided movement was repeatedly evoked. We also found that the extent to which firing rate drops off as target-movement pairs deviate from the

best target-movement pair did not change. These data suggest that, across the population, LIP response fields are spatially stationary during short-term manipulations of the frequency with which particular targets are viewed or particular movements are produced.

Materials and methods

Three subadult to adult male rhesus macaques (*Macaca mulatta*) served as subjects in the following experiments. All animal procedures were developed in association with the University Veterinarian and 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; Judge et al. 1980) were implanted using standard techniques described in detail elsewhere (Platt and Glimcher 1997). After surgery, animals received analgesics for a minimum of 3 days. Antibiotic prophylaxis was initiated intraoperatively and continued for a minimum of 3 days.

Animals were trained to perform oculomotor tasks for a fruit-juice reward. Correct oculomotor responses were reinforced on a VR3 variable ratio schedule (on average, one juice reward for every three correct trials) or a VR1 variable ratio schedule. A 300-ms noise burst served as a secondary reinforcer on all correct trials.

Eye position signals were sampled at 500 Hz. Light-emitting diodes (LEDs) served as visual stimuli and were fixed on a tangent screen placed 57 inches from the eyes of the animal. Standard microelectrode recording techniques were employed using 10–12 MΩ tungsten electrodes (Frederick Haer).

Behavioral techniques

Delayed saccade trials were used to assess the spatial tuning of physiologically identified intraparietal neurons. Each trial began, in the dark, with the illumination of a central yellow LED which subjects were required to fixate within 1000 ms. A single eccentric yellow LED was illuminated 200–800 ms after gaze was aligned within 2° of the fixation stimulus. After a further 200–800 ms delay, the fixation stimulus was extinguished, cueing the subject to shift gaze to the eccentric target (±4°, monkeys HX and CH; or ±6°, monkey YY) within 350 ms in order to receive reinforcement.

Recording protocol

An electrode was lowered, under physiological guidance, until neurons with visual and/or saccade-associated activity were encountered. Based upon 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 or saccade-associated activity lying ventral to area 5 or lateral to the border of the intraparietal sulcus were considered likely to lie in area LIP, based upon our previously published histological localization of neurons with similar properties to the lateral bank of the intraparietal sulcus (Platt and Glimcher 1998). Neurons located within this physiologically identified area typically fired action potentials before visually guided saccades having a limited range of amplitudes and directions (Barash et al. 1991b; Platt and Glimcher 1998).

Once a cell was isolated, one block of 200–400 delayed saccade trials (*uniform probability condition*) was presented in which the fixation stimulus appeared at a central location and the location of the saccade target on each trial was drawn randomly, with replacement, from among a grid of 199 LEDs spaced at 2° intervals vertically and 4° horizontally. These trials were used to describe the neuronal response field at the beginning of the experiment and to estimate the location of the best target-movement pair. Based upon an on-line analysis of these data, a single privileged LED location, which was associated with firing rates that were less than 80% of the maximum firing rate exhibited by the neuron under study on delayed saccade trials and typically placed on a line segment connecting the best target and the fixation LED, was identified. Then a second block of 200–600 delayed saccade trials (*biased probability condition*) was presented. On a randomly selected 50% (or, for some neurons, 75%) of these trials, the privileged LED was programmed as the saccade target, while on the remaining 50% (or 25%) of trials the saccade target was drawn randomly, with replacement, from the pool of all possible target locations.

Analysis

After each experiment was finished, we computed, for each trial, the onset and offset times of all task-required movements, the locations of the visual targets, and the horizontal and vertical amplitudes of those movements. The number of action potentials was counted for each delayed saccade trial during two intervals: (1) target-onset, a 200-ms epoch beginning with the illumination of the eccentric visual target, and (2) premovement, a 100-ms epoch ending with saccade onset. For each cell, a database was constructed from these measurements.

These databases were used to construct response field plots for each neuron in both the uniform and biased probability conditions. Each response field plotted the firing rate during the measured interval against either the horizontal and vertical position of the target (response fields plotted in *target coordinates*) or horizontal and vertical amplitude of the subsequent saccade (response fields plotted in *movement coordinates*). In the uniform probability condition, all correctly executed trials were used to construct response fields during each interval. For the biased probability condition, response fields were plotted from data gathered on those trials in which each stimulus location was equally likely to be programmed as the saccade target. These response field plots were then used to assess the spatial tuning of each neuron during target-onset and premovement intervals during both uniform and biased probability conditions. For graphical display, two-dimensional response fields plotted firing rate data that had been averaged in 2°×2° bins using an arbitrary color scale.

In order to determine whether neuronal response fields systematically changed when the probability that a particular LED location would serve as the saccadic target was changed, the center of each neuronal response field, as well as the width of each response field, were estimated by fitting Cartesian two-dimensional gaussian models to the raw (unaveraged/unbinned) data, in both target and movement coordinates, from each neuron in each interval, during both uniform and biased probability conditions (for details of our models see Platt and Glimcher 1998; for a demonstration that these gaussian models perform as well as, or better than, many other models see Gnadt and Breznen 1996). The gaussian models had six free parameters: the horizontal and vertical position of the center, the horizontal and vertical standard deviations (sigmas), baseline (or tonic) firing rate, and peak firing rate above baseline. Response field radius was computed as the arithmetic mean of the x and y standard deviations of the gaussian model optimally fit to each neuron during each interval.

We performed all of our numerical analyses of individual neurons in both target and movement coordinates, allowing us to test the hypotheses that either target representations or movement representations in area LIP are plastic under these conditions. Our previous studies of these neurons have shown that gaussian mod-

els fit to LIP response fields in movement coordinates account for more variance than gaussian models fit to LIP response fields in target coordinates (Platt and Glimcher 1998). For brevity, all graphical representations of the data are therefore presented in movement coordinates. As the following numerical analyses reveal, however, these two approaches yielded almost identical results for each of the neurons we studied.

To quantify whether the *population* of intraparietal neurons showed systematic shifts in either the location of the best target or the metrics of the best movement, the distance between the high-probability target location and the center of the response field of each neuron during each interval was computed during both the uniform and biased probability conditions, for response fields plotted in both target and movement coordinates. A *distance contrast index* was then computed for each neuron in each interval by first computing the magnitude of the difference between the values obtained for the horizontal and vertical amplitudes of the best movement and the values of the horizontal and vertical position of the high-probability target, during both the uniform and biased probability conditions (a second set of distance contrast indices comparing the distance between the location of the high-probability target and the best target location was also computed for each neuron). A distance contrast index, for each neuron in each interval, was then computed from these measures as: (uniform–biased)/(uniform+biased). This index spans the range –1 to 1. Thus, if the metrics of the best movement (or best target location) of a neuron measured in the biased probability condition had shifted toward the high-probability target location when movement frequency was biased, then the distance contrast index would be positive. If, on the other hand, the metrics of the best movement (or best target location) of a neuron had shifted away from the high-probability target location, then the distance contrast index would be negative. If the metrics of the best movement (or best target location) were the same under the two probability conditions, then the distance contrast index would equal 0. Histograms of the distance contrast index in each interval were constructed for the population of recorded neurons to determine whether the horizontal and vertical amplitudes of the best movements (and, separately, the best target locations) of the population of intraparietal neurons were systematically shifted toward the values of the x and y locations of the high-probability target (see below), as would be expected if the response fields of intraparietal neurons were biased toward representing high-probability movements (or high-probability targets).

Response fields were also examined for changes in the extent to which firing rate dropped off as movements deviated from the best movement (or, separately, targets deviated from the best target) in both uniform and biased probability conditions. For each neuron, during each interval, a *tuning radius contrast index* was computed by subtracting the response field radius estimated during the biased probability condition from the response field radius estimated during the uniform probability condition, and then dividing by the sum of these two response field radii. This analysis was performed for response fields plotted both with respect to the horizontal and vertical amplitude of the saccade, as well as the horizontal and vertical position of the visual target. This index ranges from –1 to 1. Thus, if the response field radius estimated for the uniform probability condition was broader than the response field radius estimated for the biased probability condition, then the tuning radius contrast index would be negative; whereas if the response field radius estimated for the uniform probability condition was narrower than the response field radius computed for the biased probability condition, then the tuning radius contrast index would be positive. No change in response field radius between probability conditions would result in a tuning radius contrast index of 0. Histograms of the tuning radius contrast index in each interval were constructed for the population of recorded neurons to determine whether response fields became systematically broader or narrower when the probability that a particular target location would guide a movement was increased (see below).

High-density sampling in one dimension

For several neurons, one-dimensional response fields were constructed after a conventional two-dimensional neuronal response field had been measured on-line. In this procedure, a vertical column or horizontal row of ten targets spaced at 4° intervals and passing through the center of the neuronal response field was identified. One block of 150–400 delayed saccade trials (*uniform probability condition*) was then presented in which the fixation stimulus appeared at a central location and the location of the saccade target on each trial was drawn randomly, with replacement, from among the ten canonical LEDs. A one-dimensional response field, or tuning curve, was then constructed from these data. Based upon this on-line analysis, a single privileged LED location, lying between the best target and the fixation LED and which was associated with firing rates that were less than 80% of the maximum firing rate exhibited by the neuron under study, was selected from among the ten canonical target locations. A second block of 150–400 delayed saccade trials (*biased probability condition*) was then presented. On a randomly selected 50% of these trials, the privileged LED was programmed as the saccade target. On the remaining 50% of trials the saccade target was drawn randomly, with replacement, from the pool of ten canonical target locations. The response field of the neuron was then replotted from those trials in which the saccade target was randomly drawn from the pool of ten LED locations.

For analysis, the firing rate of each neuron studied with high-density one-dimensional response field mapping was computed during the target-onset and premovement intervals, as described above. A one-dimensional gaussian model was fit to the response fields measured for each neuron in each interval, in the both the uniform and biased probability conditions in both target and movement coordinates, and distance contrast indices and tuning radius contrast indices were computed as described above. Because there were no significant differences between the either the distance contrast indices or the tuning radius contrast indices computed for the neurons studied with one-dimensional response field mapping and those neurons studied with two-dimensional response field mapping, in each interval these values were combined for all neurons studied in this experiment.

Results

Analysis of single neurons

Thirty intraparietal neurons were studied in this experiment. Nineteen neurons were studied with two-dimensional response field mapping, using an average of 361 (SD 61) delayed saccade trials in the uniform probability condition and 277 (SD 114) delayed saccade trials in the biased probability condition. Eleven additional intraparietal neurons were studied with one-dimensional response field mapping, using an average of 137 (SD 47) delayed saccade trials in the uniform probability condition and 112 (SD 28) delayed saccade trials in the biased probability condition.

Figure 1 plots response fields (in movement coordinates) for an intraparietal neuron studied in both the uniform (Fig. 1a) and biased (Fig. 1b) probability conditions, in both the target-onset and premovement intervals. In each graph, the firing rate of the neuron is plotted in color as a function of the horizontal and vertical amplitude of the saccade made at the end of the trial. As shown in the figure, this neuron was most strongly activated on trials in which movements were directed toward

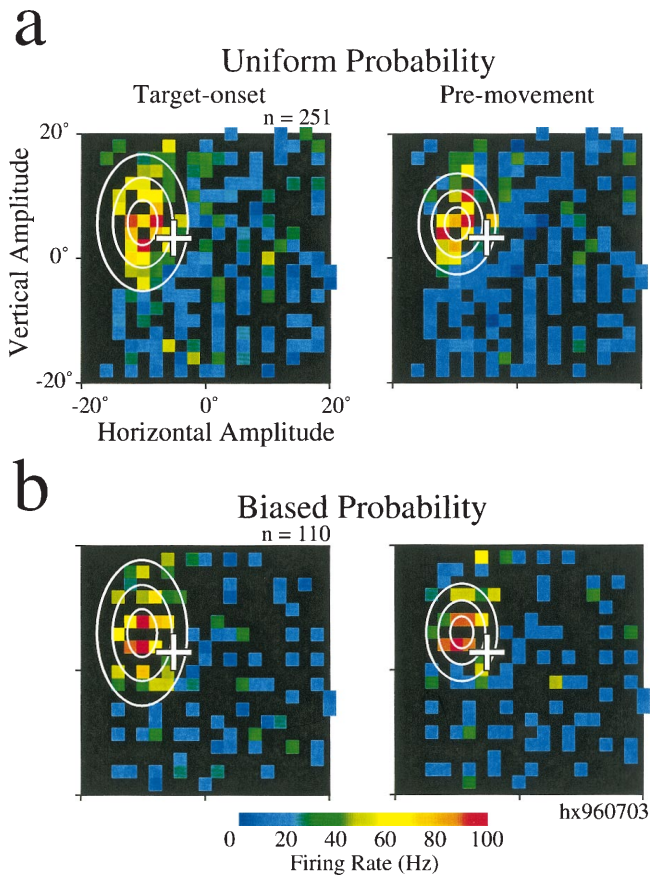

Fig. 1a,b Response field plots of an intraparietal neuron during conditions of uniform and biased movement probabilities, measured immediately after target onset and immediately preceding saccade onset. Each graph plots the firing rate of the neuron in color as a function of the horizontal and vertical amplitude of the saccade made at the end of the trial. Data are averaged in 2°×2° bins, and *black pixels* indicate unsampled regions. The *concentric white ellipses* plot iso-firing rate contours at one-third standard deviation steps from the center of the response field, as estimated by the two-dimensional gaussian model fit to the raw data in each interval. **a** Uniform probability condition: each of 199 stimulus locations was equally likely to serve as the saccade target on a given trial. **b** Biased probability condition: one stimulus location, indicated by the *white cross*, was programmed as the saccade target on a randomly selected 75% of trials, while each of the other stimulus locations was equally likely to serve as the saccade target on the remaining trials

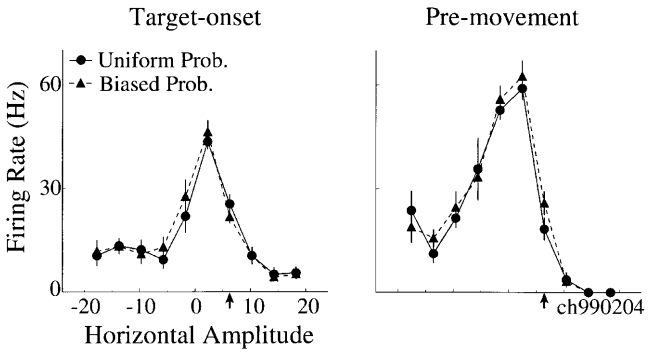

Fig. 2 Plots of firing rate, measured immediately after target onset and immediately preceding saccade onset, as a function of the horizontal amplitude of a movement (in 4° bins centered on each target), guided by targets fixed 8° below the central fixation stimulus. During the uniform probability condition (*filled circles*), each of ten stimulus locations, spaced 4° apart and spanning 36° of horizontal visual angle, were equally likely to serve as the saccadic target on each trial. During the biased probability condition (*filled triangles*), one stimulus, located 6° to the right of the fixation stimulus (*arrow*), served as the saccade target on approximately 50% of trials; the same ten stimulus locations utilized in the uniform probability condition were used and were each equally likely to serve as the saccade target on each of the remaining 50% of trials. In the biased probability condition, response fields were constructed from the 50% of trials in which target locations were randomly selected

targets located in the upper left quadrant. The white cross indicates the location of the stimulus (6° leftward and 4° upward from fixation) programmed as the saccade target on 75% of trials (n=407) during the biased probability block. For this condition, response fields were plotted from data gathered on the remaining 25% of trials (n=110), in which each stimulus location was equally likely to serve as the saccade target. The concentric white ellipses plot iso-firing rate contours at one-third standard deviation steps from the center of the response field, as estimated by the two-dimensional gaussian model fit to the raw data in each interval. Like many of the neurons we examined, the response fields of this neuron shifted between probability conditions, although the direction and magnitude of the shifts we observed were variable. (Estimated best *movement*: target-onset: uniform probability, 10.19° leftward, 5.64° upward; biased probability, 10.01° leftward, 5.98° upward; premovement: uniform probability, 9.67° leftward, 5.47° upward; biased probability, 9.01° leftward, 5.95° upward. Estimated tuning radius, *movement* coordinates: target-onset: uniform probability, 6.44°; biased probability, 6.65°; premovement: uniform probability, 4.98°; biased probability, 4.74°). When data from this same neuron were plotted in target coordinates, we measured a smaller shift in the response field center during the biased probability condition. (Estimated best *target*: target-onset: uniform probability, 13.54° leftward, 7.02° upward; biased probability, 13.35° leftward, 7.30° upward; premovement: uniform probability, 13.07° leftward, 6.99° upward; biased probability, 12.47° leftward, 7.57° upward. Estimated tuning radius, *target* coordinates: target-onset: uniform probability, 7.72°; biased probability, 7.34°; premovement: uniform probability, 6.52°; biased probability, 6.09°). Of course, determining whether these shifts reflect a small but systematic deviation induced by biasing target frequencies, or random variance amongst a stationary population of neurons, can only be addressed by the population-level analysis that follows.

Figure 2 plots mean neuronal firing rate (± SE) measured during the target-onset and premovement intervals as a function of horizontal movement amplitude for a second intraparietal neuron. This neuron was most strongly activated before downward and rightward saccades. In this experiment, the vertical position of the tar-

get on each trial was fixed 8° downward from the fixation stimulus, while the horizontal position of the target on each trial was varied among ten locations from 18° to the left to 18° to the right of the fixation stimulus. Movement endpoint was constrained to be within 4° of the target on all trials. The solid lines connecting filled circles indicate the firing rate of this neuron, plotted in 4° horizontal amplitude bins, measured when each of the ten possible target locations was equally likely to serve as the saccadic target on each trial (uniform probability; *n*=118). The dashed lines connecting filled triangles plot the firing rate of this same neuron during a block of trials (biased probability) in which a stimulus located 6° to the right and 8° down from fixation (arrow) was programmed as the saccadic target on 50% of trials (*n*=87), while on each of the remaining 50% of trials (*n*=119) each of the ten LEDs was equally likely to be programmed as the saccadic target. For the biased probability condition, response fields were plotted from data gathered on the 50% of trials in which the saccade target was drawn randomly from among the ten canonical LED locations. The response fields of this neuron were shifted 0.40° leftward in the target-onset interval, but were unshifted in the premovement interval, when saccade target probabilities were altered in this manner. When the response fields were plotted with respect to the horizontal position of the visual target, we observed a 0.50° leftward shift in the target-onset interval and a 0.12° rightward shift in the premovement interval.

Population analysis

To determine whether response field tuning remains stationary across the *population* of intraparietal neurons when the probabilities of a particular target/movement occurring are systematically altered, we examined the magnitude and direction of all the response field shifts we observed. Figure 3a plots population histograms of the distance contrast index based on gaussian fits computed in movement coordinates. On average (arrows), the distance between the high-probability target location and the best movement did not change significantly, in either the target-onset (mean shift 0.97° *toward* the high-frequency target; Wilcoxon test, Z=0.79, P>0.43; mean distance contrast index 0.03) or premovement (mean shift 0.35° *away* from the high-frequency target; Wilcoxon test, Z=0.34, P>0.72; mean distance contrast index 0.02) intervals, when target/movement frequency was altered. When these analyses were repeated for response fields plotted in target coordinates, the distance between the high-probability target location and the best target also did not change significantly, in either the target-onset (mean shift 0.68° *away* from the high-frequency target; Wilcoxon test, Z=0.48, P>0.62; mean distance contrast index –0.04) or premovement (mean shift 0.56° *toward* the high-frequency target; Wilcoxon test, Z=1.10, P>0.27; mean distance contrast index 0.03) intervals.

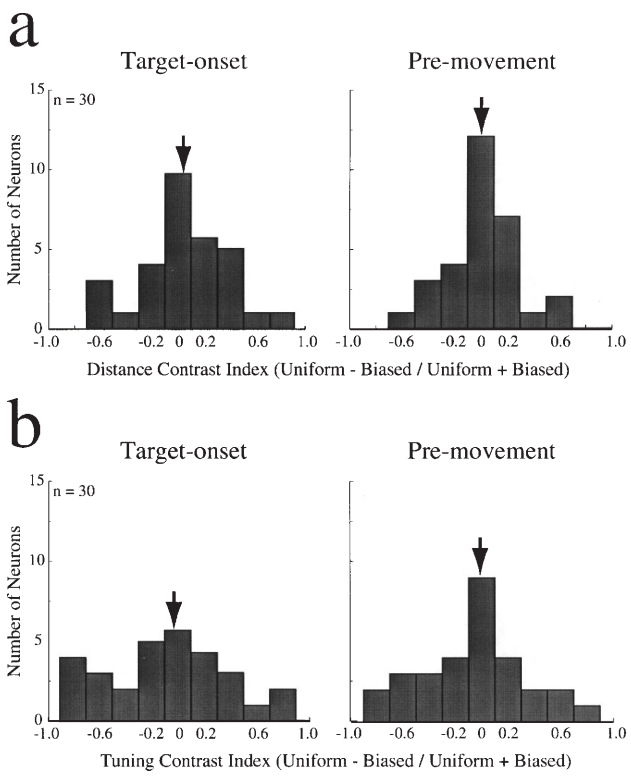

Fig. 3a,b Effects of changing saccade target probabilities on spatial tuning in a population of 30 intraparietal neurons. **a** Histograms of distance contrast index, computed for response fields plotted in movement coordinates, during the target-onset and premovement intervals. A systematic shift in the best movement, either toward or away from the high-probability target, would result in either a positive or a negative distance contrast index, respectively. On average (*arrow*), there were no systematic changes in the metrics of the best movement when movement frequencies were systematically altered. **b** Histograms of tuning contrast index for the same population. A systematic change in the tuning radius, toward either sharper or broader tuning, would result in either a positive or a negative tuning contrast index, respectively. On average (*arrow*), there were no systematic changes in the spatial tuning of intraparietal neurons when movement frequencies were systematically altered

Figure 3b plots population histograms of the tuning radius contrast index computed in movement coordinates for the 30 studied intraparietal neurons. On average (arrows), tuning radius changed very little, during both the target-onset (1.41° *broader*; Wilcoxon test, Z=1.07, P>0.28; mean tuning radius contrast index –0.09) and premovement (0.62° *broader*; Wilcoxon test, Z=0.20, P>0.84; mean tuning radius contrast index –0.07) intervals, when movement frequency was altered. Similarly, when these analyses were computed for response fields plotted in target coordinates, tuning radius also was observed to change very little, in both the target-onset (0.19° *narrower*; Wilcoxon test, Z=0.16, P>0.87; mean tuning radius contrast index 0.02) and premovement (1.10° *narrower*; Wilcoxon test, Z=1.34, P>0.17; mean tuning radius contrast index 0.03) intervals.

Discussion

Across the population of saccade-related intraparietal neurons, increasing the frequency with which a particular movement was instructed by a particular target apparently had no systematic effect on either the coordinates of the best movement or the best target location encoded by the neuron under study. This manipulation also appeared to have no systematic effect on how firing rate decreased as movements deviated from the best movement or targets deviated from the best target. Taken together, these findings suggest that, at least across the hundreds of trials presented within a typical experimental session, LIP response fields are essentially stationary with regard to the frequency with which movements are produced and stimuli are viewed.

One issue that remains unaddressed by these observations is whether LIP response fields are stationary within a trial; that is, whether the best target-movement pair for a cell shifts transiently, immediately before or during a saccade. This is of interest because Duhamel and colleagues (1992) have reported that a visual target placed at a location that does not activate an LIP neuron can increase the activity of this cell immediately before the animal makes a movement that will shift the coordinates of the best target-movement pair into alignment with that visual target. Based upon these data, Duhamel and colleagues have suggested that LIP response fields are nonstationary around the time of a saccade, concluding that the best target-movement pairs of many LIP neurons shift presaccadically in a direction and amplitude determined by the direction and amplitude of the upcoming movement. While our data suggest that LIP response fields are stationary across trials, our data do not address stationarity during trials. Nonetheless, our analysis, and the work of Stanford and Sparks (1994) in the superior colliculus, does suggest that measuring complete response fields before, during, and after saccade onset may be an important test of the hypothesis of Duhamel and colleagues.

It is also possible that, although intraparietal response fields are stationary over the time courses we have examined here, these response fields might not remain stationary if a single movement were performed, or a single target were presented, at an elevated frequency for a much longer period of time. A growing body of evidence (reviewed in Buonomono and Merzenich 1998) suggests that the topological boundaries encompassed by the receptive fields of neurons in cortical sensory areas can be modified by long-lasting changes in the sensory epithelium or in the sensory environment. Plasticity in cortical motor areas, however, has only begun to be investigated (see, for example, Nudo et al. 1992). While it remains uncertain whether LIP should be considered either a sensory area, a motor area, or something distinct from either of these, our own data were gathered across so brief a time course that our findings cannot speak of the possibility of dynamic changes in response field tuning in response to long-term changes in either the frequency with which a particular movement is made or a particular stimulus is viewed.

While questions remain about the intrasaccadic stationarity and long-term stationarity of the response fields of intraparietal neurons, it does seem clear that across tens to hundreds of trials response fields in intraparietal cortex are essentially stationary, even when the frequency with which particular movements are made, or particular targets are viewed, is altered. This observation strengthens many of the conclusions that have recently been drawn about the role of LIP in the sensory-motor process (Duhamel et al. 1992; Bracewell et al. 1996; Colby et al. 1996; Mazzoni et al. 1996; Shadlen and Newsome 1997; Platt and Glimcher 1997, 1999), suggesting that many of the manipulations that have been observed to modify the activity of LIP neurons do so by uniformly scaling the responses of the neuron for all movements or target locations.

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