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Response-locked changes in auto- and cross-covariations in parietal cortex☆

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Abstract

Action potentials from small groups of physically adjacent neurons were recorded from the parietal cortex of two rhesus macaques performing a memory saccade task. Recordings were made using tetrodes and sorted into spike trains from individual cells. Auto- and crosscovariograms of spike times for individual cells and simultaneously recorded pairs of cells, respectively, show modulations synchronized with behavioral events consistent with visual, memory, and perisaccadic activity.

Keywords: Tetrode; LIP; Covariogram

1. Introduction

Computation within a single cortical area is likely to be a dynamic process, involving local recurrent circuitry, which can be revealed through simultaneous multiple single unit recording. Of particular interest are cells that lie within tens of microns of each other. These cells are often members of single functional unit (a column or micro-column), and are likely to have connectivity to sustain synchronous coding or cooperative computation. The lateral intraparietal area, or LIP, as an

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example, shows a variety of responses to visual stimuli, and saccade planning and execution amongst neighboring cells [3], suggesting that it contains rich local circuitry.

For this experiment, we sought to examine dynamics in spike firing for individual neurons and between neighboring cells within LIP. We used the tetrode technique as introduced by Recce and O'Keefe [4], adapted to the awake, behaving monkey preparation [2] to simultaneously collect spike trains from multiple neighboring cells. We recorded from the intraparietal sulcus of rhesus macaques while the animals performed memory saccades, and computed covariograms from the collected data to track changes in neural response.

2. Methods

The behavioral task for this experiment was the memory saccade [3]. Stimuli were points of light approximately 1° in diameter projected on a tangent screen, the first of which to appear for each trial was a central fixation point. The animal was required to foveate this light as long as it was illuminated. 1–2 s after fixation commenced, a second point, the target, was flashed for 150 ms in one of eight equally spaced positions around a circle of radius 10° centered on the fixation point. After a 1000 ms memory period delay, the fixation point was extinguished. At this cue, the animal was required to saccade in the dark to the remembered target location. Upon successful completion of the cued saccade, the target was reilluminated for 500 ms, and the animal rewarded with a drop of juice. Targets were randomly interleaved and a set of 96 or 120 trials collected at each recording site.

Data were recorded from the parietal cortex from each of the two animals (with two hemispheres total) using tetrodes [2]. Stereotaxic coordinates and observed neural responses were consistent with recordings having been made in the lateral intraparietal area (LIP), although recording sites have not, as yet, been verified histologically. Simultaneous spike trains were derived from continuous analog recordings digitized to 16 bits and sampled at 20 kHz using previously reported statistical techniques [5,6].

Sets of auto- and crosscovariograms [1], binned to 1 ms over a delay of $\pm$ 50 ms, were computed at each target position for each cell and pair of simultaneously recorded (neighboring) cells for non-overlapping 200 ms windows spanning the range of behavioral time. Each covariogram was computed by forming the correlation of the two spike trains, subtracting the shift predictor, and normalizing by an estimate of the variance given the null hypothesis of independence.

Covariogram sets were rotated by target to bring the preferred directions into registration at a fixed position (column 3, as shown in Fig. 1). For autocovariograms, the preferred direction was determined from the target with maximum first-order firing rate (the spike count over time, or, equivalently, the integral of the PSTH) for the experimentally relevant epoch; for crosscovariograms, the preferred direction was determined similarly for the second-order firing rate (the integral of the convolution of the two PSTHs). The central bins on all covariograms were suppressed, and mean

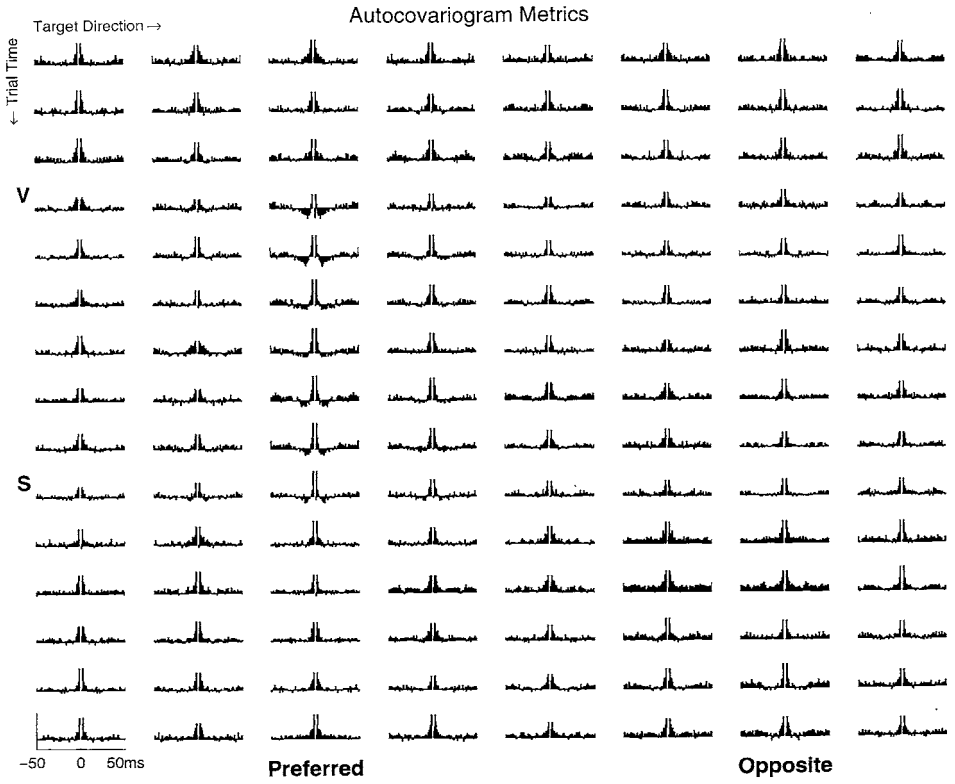

Fig. 1. Mean autocovariogram. Each column is for one target direction after registration, with the preferred direction in the third column, and target positions moving around the circle from left to right. Each row corresponds to one 200 ms window, with trial time increasing from top to bottom along rows. Row V is the first window containing visual target response; row S is the first window after the saccade. From the start of the trial to the row before S, trials were temporally aligned to the target presentation, from that row onwards, trials were aligned to the measured saccadic event. Column Preferred was used to register preferred directions; column Opposite is 180° away. Each autocovariogram is binned at 1 ms and covers ± 50 ms of delay. Vertical scales in arbitrary units related to significance. $n = 124$ cells.

auto- and crosscovariograms were computed over all cells and pairs of neighboring cells, respectively, after preferred-direction registration. Finally, for the preferred direction, first- and second-order mean firing rates were computed in the same 200 ms windows as the covariograms.

3. Results

The mean autocovariogram is shown in Fig. 1. All of the subplots exhibit positive sidelobes 1–2 ms wide at the peak, flanking zero delay, and a few exhibit negative sidelobes approximately 20 ms wide, at slightly larger delays. The inner positive

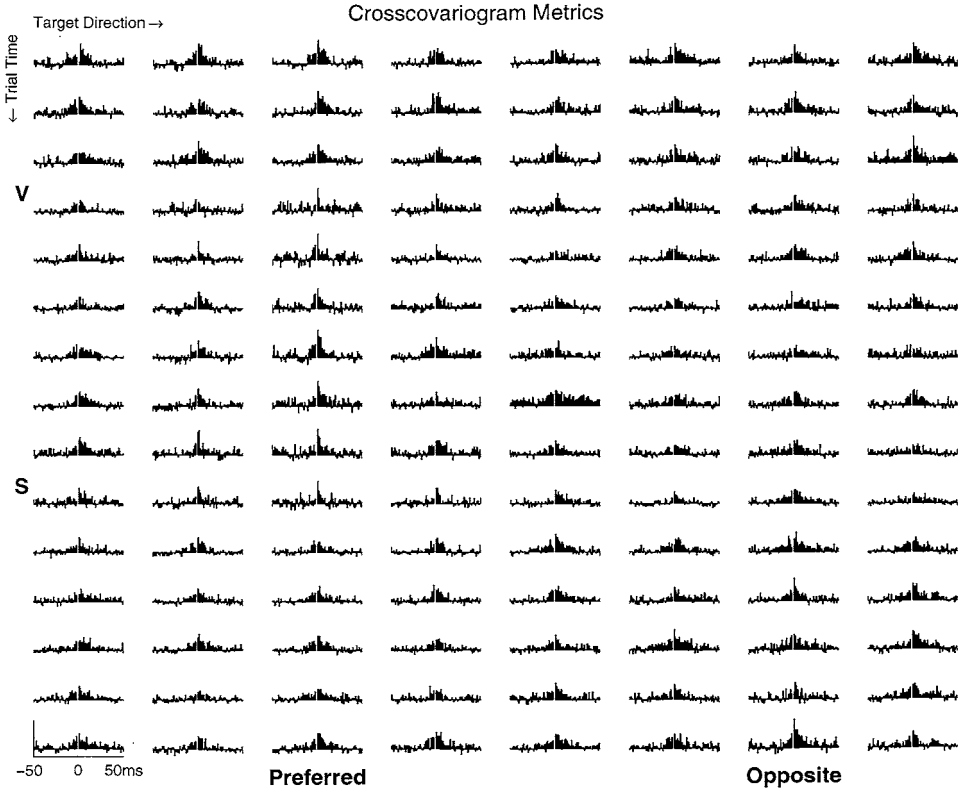

Fig. 2. Mean crosscovariogram. Columns, rows, and axes as described in the previous figure. $n = 169$ pairs of neighboring cells from 37 sites.

sidelobes range in size, but are largest for the memory period, found between visual target presentation and the saccade, in the preferred direction. Further, there is a suppression over all directions during the response to the visual target. The negative sidelobes are nearly non-existent except during the memory period for the preferred direction, and for the last two or three post-saccadic windows in the opposite direction.

The mean crosscovariogram is shown in Fig. 2. Most subplots show a tendency towards a broad, if shallow, central peak 30–50 ms wide. Subplots in the preferred direction covering the memory period (between V and S in the figure) show a narrow central peak, 1–2 ms wide, which weakens shortly after the saccade. This same peak can be observed in other subplots as well, as seen for the opposite direction towards the end of trial time.

The mean first- and second-order response along the preferred direction are shown in Fig. 3. Both exhibit a primary peak directly after target presentation followed by sustained activity during the memory period and a secondary peak spanning

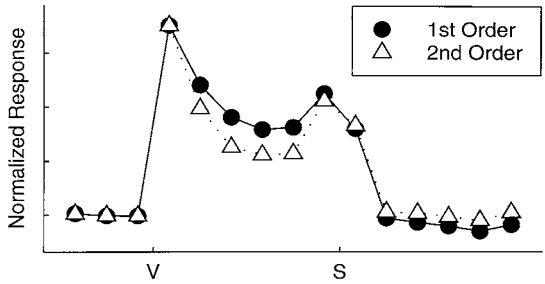

Fig. 3. Mean firing rate responses along the preferred direction. Filled symbols show the response for individual cells, as computed by the mean of all 200 ms-binned PSTHs. Open symbols show the response for pairs of neighboring cells, as computed by the mean of all 200 ms-binned shift predictors. Both have had the mean of the first three points subtracted, and then have been normalized by the maximum value.

execution of the saccade, while sustained memory activity is slightly stronger for the first-order metric.

4. Discussion

Response-locked changes in autocovariogram profiles over time and target position are relatively straightforward to interpret. The increase in the central peaks of the autocovariograms along the preferred direction start one 200 ms window after the response to the visual target begins, and continue through to about one window after the saccade. As these peaks correspond to bursts of spikes, their growth during the preferred-direction memory period reflects a rise in the proportion of spikes occurring in bursts despite the increased overall firing rate therein. Central peak modulations in this same period correspond quite well to the time a memory structure would need to retain information about the target: initialized by a volley of visual response spikes (within the first 200 ms period), it would be reset by the saccadic event.

The changes observed in the autocovariogram negative sidelobes track the mean neural response for the corresponding condition: it is highest along the preferred direction, strongest at the visual response, weakened slightly during the memory response, and re-elevated perisaccadically, but also slightly elevated late in trial time for the opposite direction. This lattermost effect we interpret to be due to uncued post-trial saccades returning to the fixation point, which, for the opposite direction, will be the same retinocentrically-expressed saccade as the one from central fixation to the preferred target. If the recorded cells are oscillating at slightly different frequencies, the mean autocovariogram would exhibit negative side lobes during periods of oscillation exactly as seen; although unpresented, some individual autocovariograms support this conclusion.

Similar changes in crosscovariogram profiles are less clearly interpretable. Again, we find one feature, namely a fine central peak, which tracks the experimental epoch, rising in the preferred direction directly after the target presentation, and maintaining

activity until approximately 200 ms after the saccade. This only coarsely matches the time course of mean firing rates for these cells. We also see a modulation of the broader central peak across target directions, present at the start of the trial, suppressed during the 200 ms after the display of the visual target, returning during the memory period, again being suppressed directly after the saccade, and finally returning once the saccade has been completed.

5. Conclusions

The apparent disparity in temporal response between the two autocovariogram and two crosscovariogram effects suggests multiple independent mechanisms may be at work in LIP mediating different phases of the response. Additional work with classification of cells based on responses in different parts of the task, we hope, will help elucidate these.

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