EFFERENCE COPY FOR SACCADIC EYE MOVEMENTS CAN MODULATE RESPONSES TO VISUAL STIMULI IN THE VENTRAL VISUAL PATHWAY

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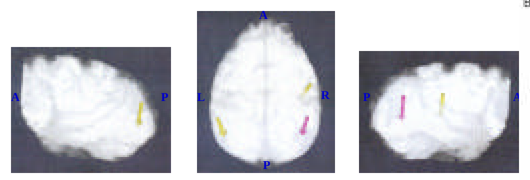
INTRODUCTION

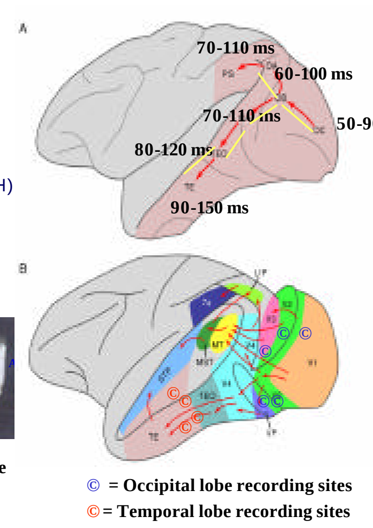
Complex visual tasks can be solved by combining active vision with feature analysis (Floreano et al., 2004). Active vision is a process of sequentially selecting different parts of the visual scene for analysis by the most sensitive regions of the visual system. Feature analysis presumably proceeds between the shifts in gaze utilizing the information gathered from the central visual fields. Here we examine the neural activity associated with a behavior where active vision was incorporated spontaneously into a pattern recognition task by the two monkeys in our study. The activity of cortical neurons in the ventral visual pathway is analyzed with respect to two task-related events: (1) transitions in the visual stimulus, (2) saccadic eye movements. The neural activity is also analyzed with respect to interactions between these events. Thus, we view our data as the expression of a 3-channel system, with stimulus, behavior and neural activity comprising the three channels. While the stimulus channel must be connected by unidirectional links to the other two channels, bidirectional interactions can exist between the neural activity and behavioral channels. In addition, the behavioral channel can modulate the link between stimulus and visual response. Examples of such modulation in the ventral visual pathway can be seen in the oculomotor signals that have been characterized by their relation to target selection (Sheinberg & Logothetis, 2001; Tolias et al., 2001; Mazer & Gallant, 2003), receptive field remapping (Nakamura & Colby, 2002), suppression and distortion (Santoro et al., 2002; Burr, 2004), and retinal reafference (Purpura et al., 2003). We note that the behavior we observe is coupled to the dynamics of the visual display. This behavior sometimes produces a minimum of eye movement-related distortion while enhancing the optimal transmission of visual information as defined by modulation in spike rates.

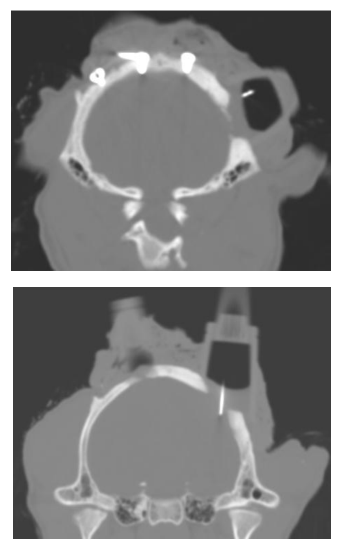
METHODS 1: Recording Locations

- **Monkey 1: Three Chambers**
  - Right hemisphere occipital and temporal lobes
  - **Left hemisphere occipital lobe**
- **Monkey 2: Two Chambers**
  - Right hemisphere occipital and temporal lobes
- Local field potentials & single - and multi-units from each site
- On-line spike detection using MEX system (LSR-NEI, NIH)
- ASL5000 IR video eye-tracking system for eye positions

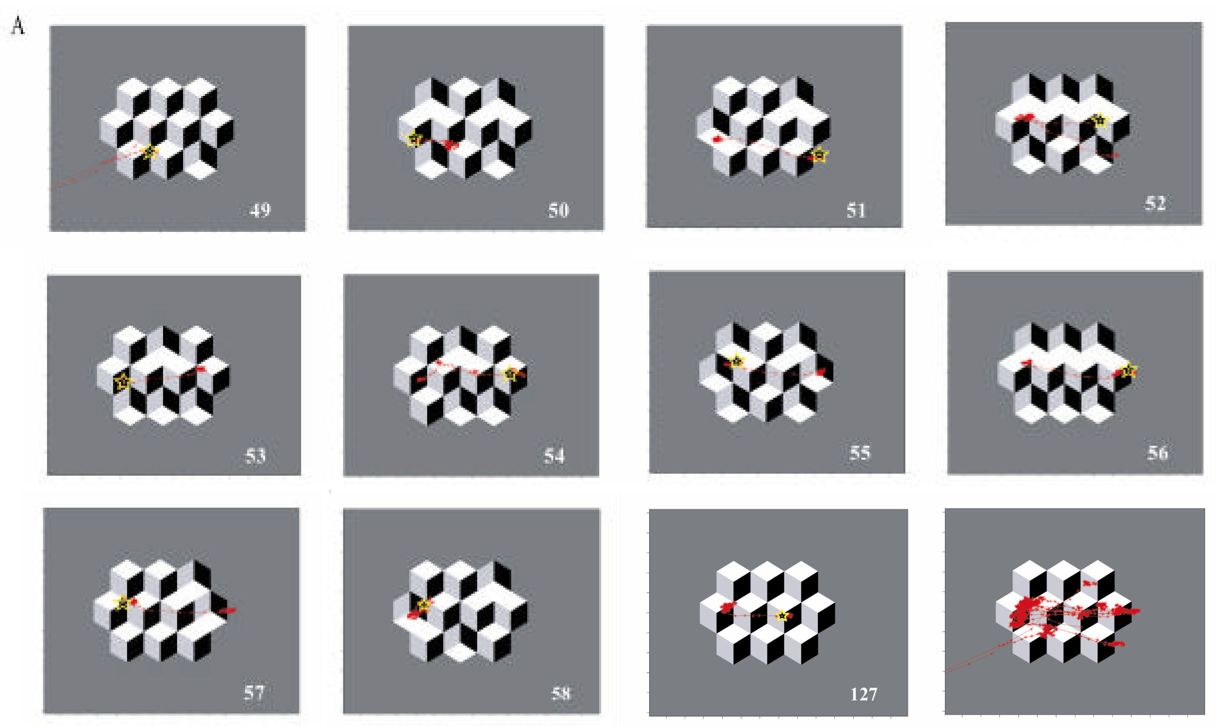


Monkey 1: MRI





Monkey 2: CAT Scan

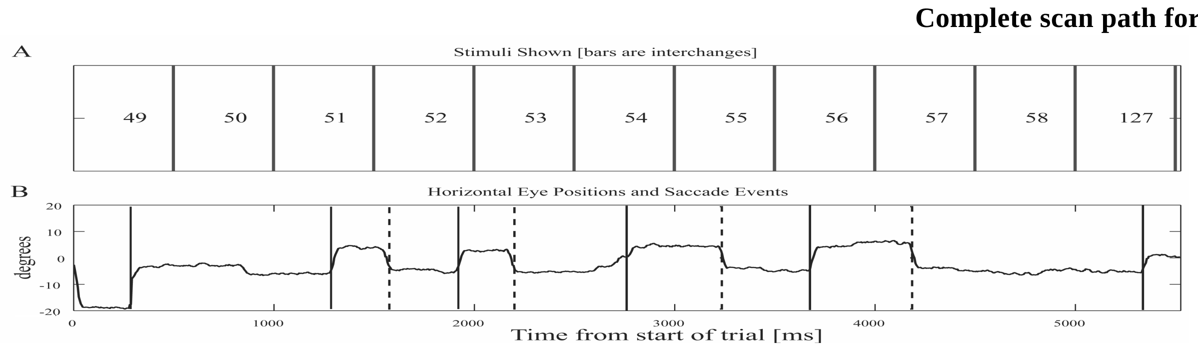


Complete scan path for trial

METHODS 2: Task

Example of eye movement behavior produced during one, 6 second trial.

The monkeys had to release a bar after the appearance of a learned target pattern within the stimulation sequence and were free to move their eyes over the visual display.



Temporal coupling between stimulus transitions (A) and eye movements (B).

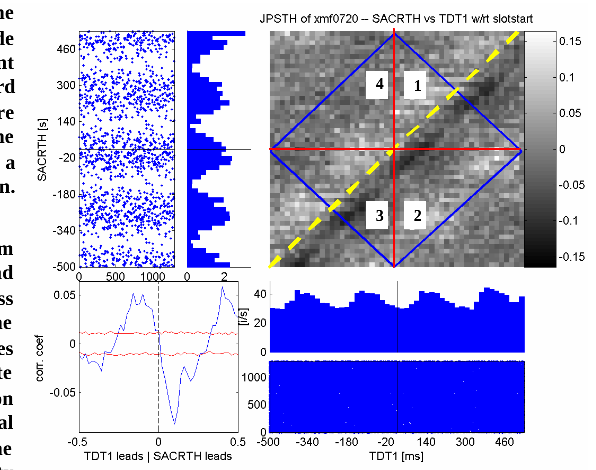
Experiments were conducted in two rhesus monkeys performing a pattern recognition task. Recordings were made at a number of sites in the ventral visual pathway (METHODS 1). For the pattern recognition task (METHODS 2) a multi-element luminance contrast image changed configuration at a rate of 2, 3, or 4 Hz. The monkeys had to release a bar after the appearance of a learned target pattern within the stimulation sequence and were free to move their eyes over the visual display during the course of the trials. Note that the monkey makes about one saccade per stimulus frame in this selected trial (here the time between transitions is 500 ms).

METHODS 3: Joint Peri-Stimulus Time Histogram

The single and multi-unit data were analyzed by computing the Joint Peri-Stimulus Time Histogram (JPSTH), and the normalized cross-correlogram (see Aertsen et al., 1989; Brody, 1999; Vaadia et al., 1995). A set of JPSTH calculations demonstrates the strength and direction of normalized covariance between the three channels in our system: neurons, behavior (saccades), and external stimuli. Normalized cross-correlograms between any two of the channels is estimated by averaging along central, consistent length sub-diagonals of the JPSTH formed by temporally referencing the activity of the two channels by an event in the third channel. The activity of and interactions between the three channels are estimated by analyzing neuronal activity time-locked to three different temporal references: (a) stimulus interchanges, (b) saccade onsets, and (c) firing times of a neuron. The probability of obtaining a mutual rate of activity in, for example, the neural channel and eye movement channel is computed from the joint frequency of occurrence in bins created by referencing the activity of these two channels to the time of stimulus transition. The joint probability estimates are corrected by removing the product of the strengths of the activity in two of the channels; i.e. subtracting the product of the PSTHs of the two channels.

PSTH (rate) and raster (time of occurrence) for saccade onset in eye movement channel (here leftward directed saccades are isolated). Time zero is the time of occurrence of a stimulus transition.

Normalized cross-correlogram between leftward saccades and neural activity formed across the yellow diagonal within the blue box in the JPSTH. Values above the red curves indicate significant levels of correlation between saccades and neural activity. The right side of the graph indicates the probability of generating a spike at some time after a leftward saccade.



PSTH (rate) and raster (time of occurrence) for a spike in the neural channel (here isolated in the occipital lobe). Time zero is the time of occurrence of a stimulus transition.

JPSTH

Zone 1: joint probability of finding a particular saccade rate and spike rate after a stimulus transition.

Zone 2: joint probability of finding a particular saccade rate before a stimulus transition associated with a spike rate after a stimulus transition.

Zone 3: joint probability of finding a particular saccade rate before the stimulus transition associated with a spike rate before the transition.

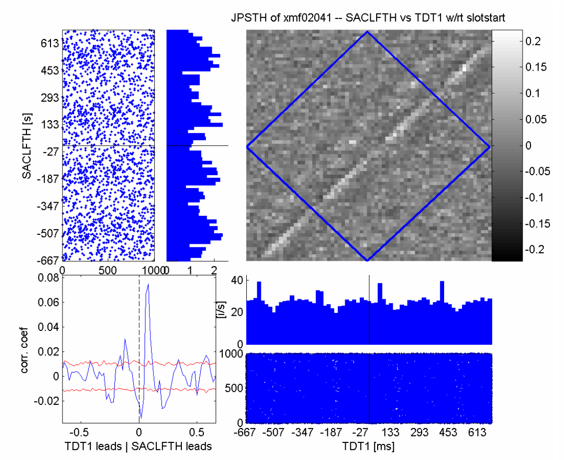
Zone 4: joint probability of associating a particular saccade rate after the stimulus with a spike rate before the transition.

RESULTS

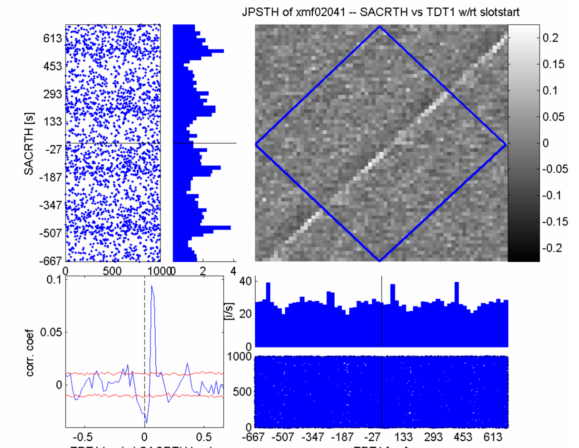
We analyzed neuronal activity time-locked to three different temporal references: (a) stimulus interchanges, (b) saccade onsets, and (c) firing times of the neuron.

a. JPSTH organized by transitions in the visual stimulus.

Occipital Lobe Recording Site

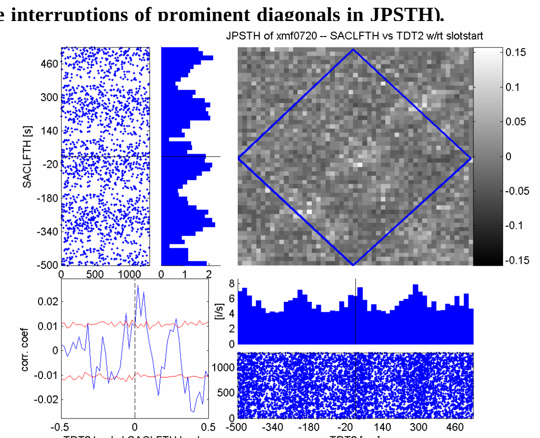


RESULTS 1. Normalized covariance (JPSTH) computed for leftward saccades (left PSTH) and neuronal spikes (bottom PSTH), organized around transitions in the visual stimulus. The normalized cross-correlogram (lower left) averages the interaction between saccade and spikes over all times before and after a stimulus transition. Saccades can generate a transient neural response. Coupling between stimulus and behavior can influence these transients (notice interruptions of prominent diagonals in JPSTH).

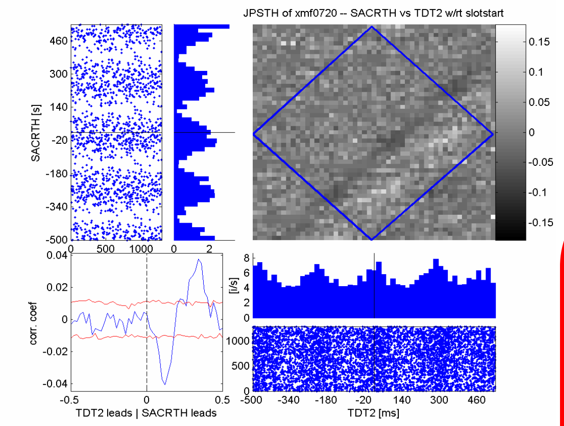


RESULTS 2. Normalized covariance computed for rightward saccades (left PSTH) and neuronal spikes (bottom PSTH), organized around transitions in the visual stimulus. In the occipital lobe, rightward saccades generate a transient neural response that is very similar to the response generated by leftward saccades.

Temporal Lobe Recording Site



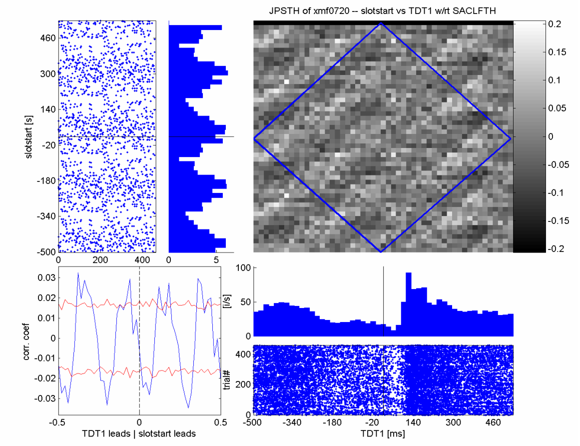
RESULTS 3. Normalized covariance computed for leftward saccades (left PSTH) and neuronal spikes (bottom PSTH), organized around transitions in the visual stimulus. See RESULTS 4.



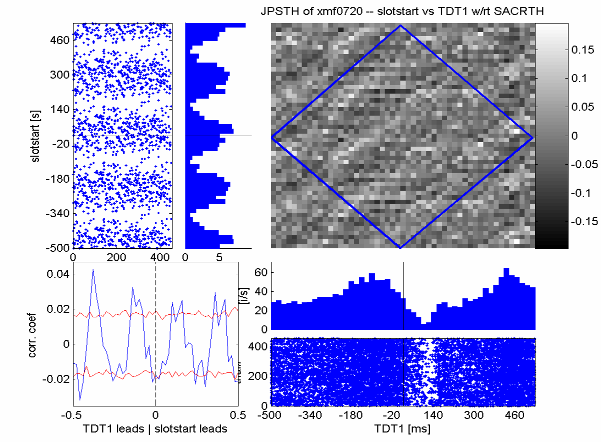
RESULTS 4. Normalized covariance computed for rightward saccades (left PSTH) and neuronal spikes (bottom PSTH), organized around transitions in the visual stimulus. Notice that saccade direction has a significant effect on the transient neuronal response, unlike in the occipital lobe where little influence due to saccade direction is evident (compare with RESULTS 1 and 2). Coupling between behavior and stimulus appears to have less influence on saccade-related neural activity in these temporal lobe recordings. RESULTS 1-4 can be interpreted as evidence for efference copy of motor command.

b. JPSTH organized by saccade onsets.

Occipital Lobe Recording Site

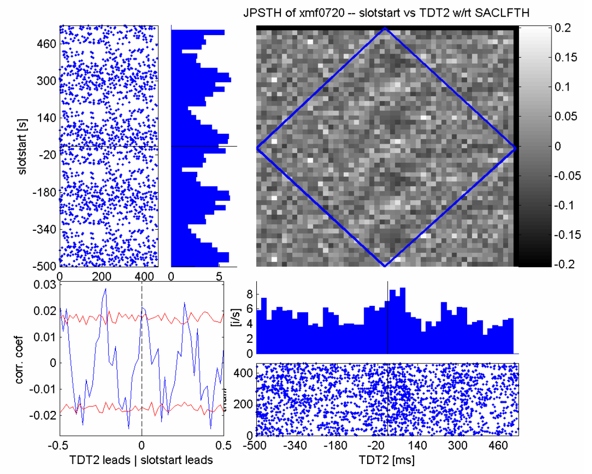


RESULTS 5. Normalized covariance computed for stimulus transitions (left PSTH) and neuronal spikes (bottom PSTH), organized around the onset of leftward saccades. The normalized cross-correlogram (lower left) averages the stimulus driven response over all times before and after a leftward saccade. The periodic modulated response, evident in the cross-correlogram, is interrupted during the saccade and recommences ~140 after saccade onset (see JPSTH).

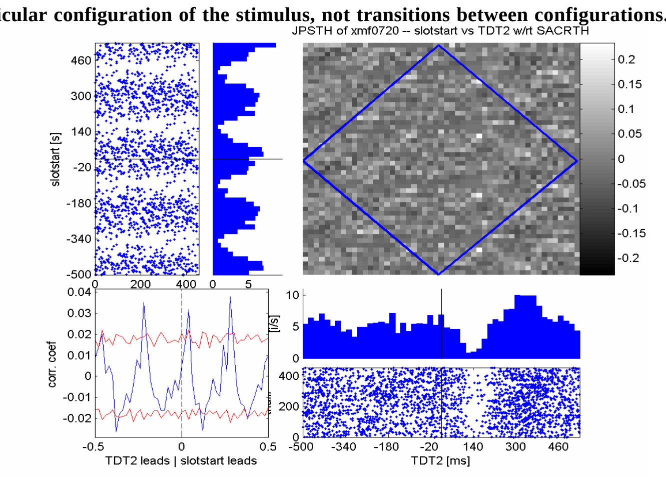


RESULTS 6. Normalized covariance computed for stimulus transitions (left PSTH) and neuronal spikes (bottom PSTH), organized around the onset of rightward saccades. As with RESULTS 5, the eye movements occur near the time of the stimulus transitions (left PSTH). This behavioral coupling may be useful in that the stimulus transitions occur during a brief period of suppressed neural activity following the saccade: the monkey is looking for a particular configuration of the stimulus, not transitions between configurations.

Temporal Lobe Recording Site



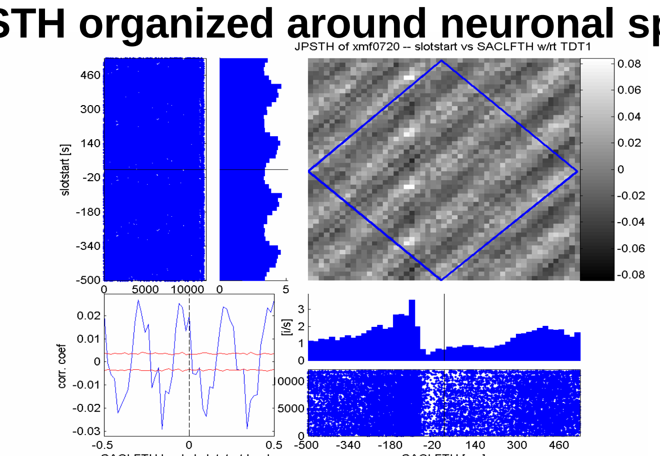
RESULTS 7. Normalized covariance computed for stimulus transitions (left PSTH) and neuronal spikes (bottom PSTH), organized around the onset of leftward saccades. Recordings in the temporal lobe (area TE) were made simultaneously with those shown in RESULTS 5. Here the coupling between behavior and the visual stimulus becomes evident in the JPSTH only at the time of the saccade when neural activity is enhanced. Enhancing neural activity at the time of a motor command in a sensory pathway may be one way to capture sensory signals during active vision.



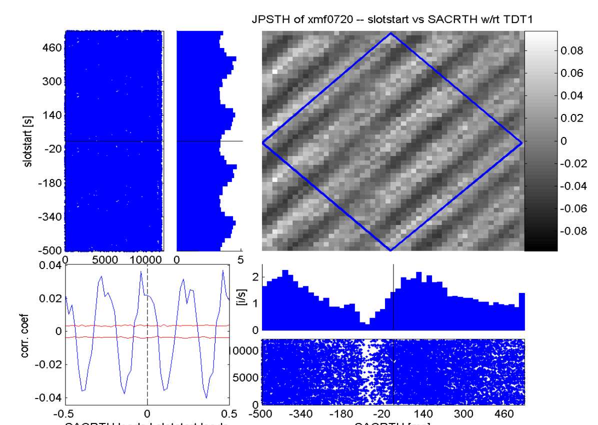
RESULTS 8. Normalized covariance computed for stimulus transitions (left PSTH) and neuronal spikes (bottom PSTH), organized around the onset of rightward saccades. Recordings in the temporal lobe (area TE) were made simultaneously with those shown in RESULTS 6. The periodic modulation of the neural activity by the visual stimulus (normalized cross-correlogram) is more robust than in RESULTS 7. The suppression of neural activity following the saccade is delayed with respect to the suppression in the occipital lobe (RESULTS 6).

c. JPSTH organized around neuronal spikes.

Occipital Lobe Recording Site

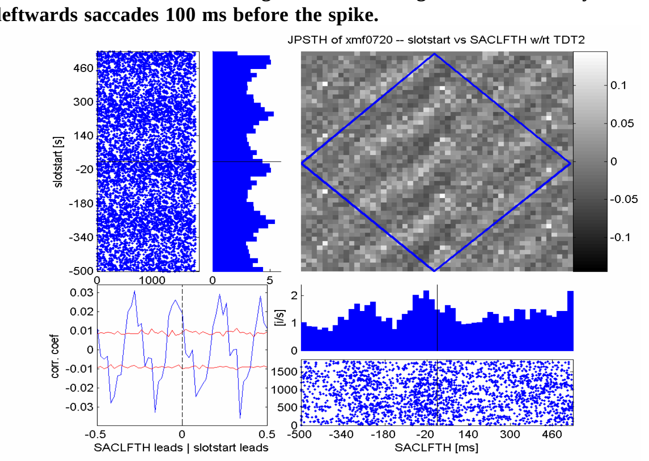


RESULTS 9. Transitions in the visual stimulus plotted against left-directed saccades, organized around neuronal spikes. The coupling between behavior and stimulus is evident in the normalized cross-correlogram (bottom left). The spiking activity captures the synchronization between saccades and stimuli. The likelihood of observing a stimulus change is accentuated by the occurrence of the leftwards saccades 100 ms before the spike.

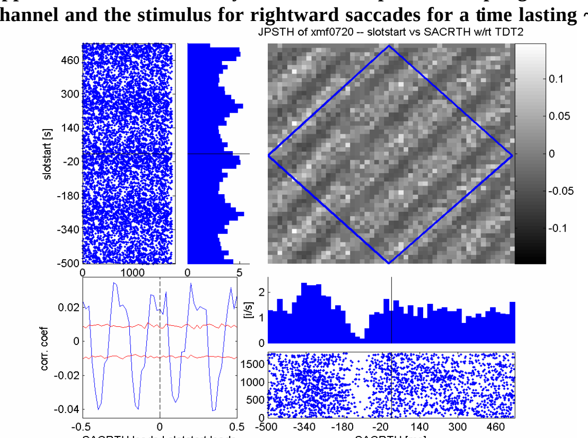


RESULTS 10. Transitions in the visual stimulus plotted against right-directed saccades, organized around neuronal spikes. The coupling between saccades and stimulus is just as tight as with the leftward saccades (RESULTS 9). However, neuronal activity is associated with a decrease in the number of rightward saccades suggesting that their occurrence leads to a suppression of neural activity. There is a drop in the coupling between the eye movement channel and the stimulus for rightward saccades for a time lasting ~50 ms.

Temporal Lobe Recording Site



RESULTS 11. Transitions in the visual stimulus plotted against left-directed saccades, organized around neuronal spikes. The likelihood of observing a simultaneous stimulus change and saccade is modulated in the time period directly preceding a neuronal spike.



RESULTS 12. Transitions in the visual stimulus plotted against right-directed saccades, organized around neuronal spikes. The likelihood of observing a simultaneous stimulus change and saccade is modulated in the time period directly preceding a neuronal spike.

CONCLUSIONS

- To study active vision we analyze the interactions between three channels: stimulus, saccades and neural activity.
- Interactions are evaluated through estimates of the probability of joint occurrences between channels with reference to the activity in a different channel.
- A range of relationships between the three channels becomes evident when occipital lobe recordings are compared with those made in the temporal lobe, and when saccade direction is used to organize the calculations.
- Saccades modulate single-unit responses in the ventral visual pathway of the alert monkey, strengthening the evidence for an efference copy of the motor command to move the eyes in sensory processing areas of the cortex. This efference copy can be modulated by the coupling between the eye movements and visual stimulus.

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