INTRODUCTION

In alert monkeys, even in well-trained ones, small eye movements occur during fixation periods (**Fig. 1**). These movements constantly shift the retinal image, thus modifying the stimulus-generated responses during visual stimulation. Although now it is becoming widely appreciated that eye movements play an important role in shaping neuronal activity in behaving monkeys, the extent of the eye movements' impact on stimulus-evoked activity is not clear.

The aim of this study was to analyze the effects of fixational eye movement on responses of V1 neurons to drifting gratings and to estimate the magnitude of these effects. We have found previously that responses to gratings in alert monkeys do not distinguish between simple and complex cells, as it does in anaesthetized animals. Here we examine the same issue by quantifying the effects of various eye movements on responses of simple and duplex/complex cells.

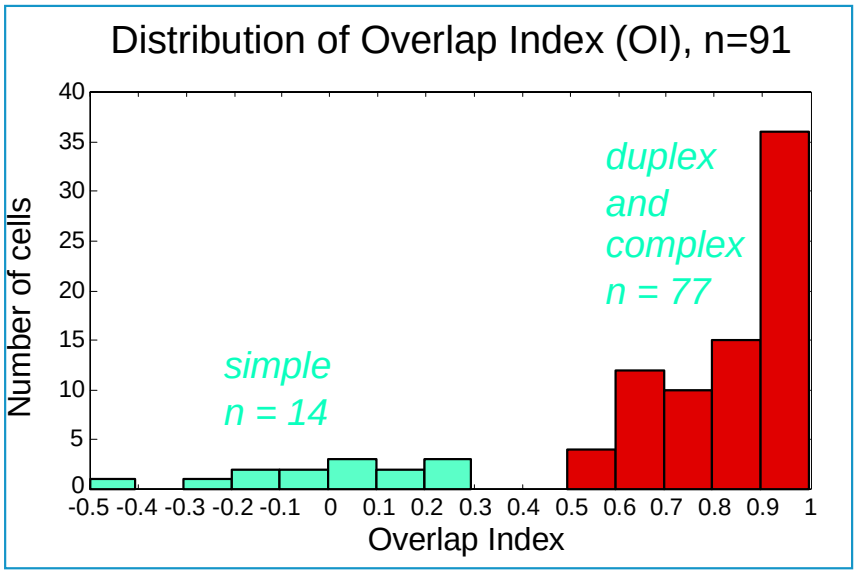
METHODS

Extracellular responses of V1 neurons and eye positions were recorded from alert monkeys during fixation. Stimuli were rectangular patches of drifting sinusoidal gratings. From the eye position records we identified epochs of fast movements (small fixational saccades), slow drifts and stable fixation (**Fig. 2**) and compared patterns of neuronal firing during various eye movement conditions. Spectral analysis was used to quantify the different modes of data selection. Cells were classified as simple or duplex/complex on the basis of spatial overlap of increment and decrement activating regions (Overlap Index, **inset**).

The Relative Modulation Index (RMI) -

$$RMI = \frac{AC_1}{DC - DC_{spont.}}$$

was taken as the principal response measure.



RESULTS

The responses of each cell (n=91, 14 simple and 77 duplex/complex) were subdivided into 200 ms segments (one temporal cycle of stimulus). RMI was estimated using 3 different modes of data selection (**Fig. 2**): 1) selecting all data *("All")*, 2) discarding saccade periods by automatic saccade detection *("Auto")*, and 3) manually discarding both saccades and slow eye movements *("Select")*. The RMI of "Select" data was also calculated using phase alignment of individual segments ("Align"). Eye movements decrease response modulation in both simple and duplex/complex cells (**Figs. 3, 4** - individual examples, **Figs. 5, 6, 7** -population characteristics). Duplex/complex cells are more affected by the slow eye movements than simple cells (mean difference between RMIauto and RMIselect is 0.17 (18%) and 0.02 (2%), respectively), but are similarly affected by saccades (mean difference between RMIauto and RMIall is 0.13 (18%) and 0.25 (18%), respectively). The overall impact of eye movements on response modulation, without phase alignment, is 0.3 (34%) for duplex/complex and 0.28 (21%) for simple cells. With phase alignment (mean difference between RMIalign and RMIall), the effect is 0.56 (49%) for duplex/complex and 0.62 (37%) for simple cells.

CONCLUSIONS

- Fixational eye movements consistently and substantially modify grating-elicited neuronal activity in V1.

- Exclusion of these effects *does not* lead to categorization of V1 cells on the basis of response modulation; *on the contrary*, it makes RMI distribution more uniform, shifting both simple and duplex/complex cells to more modulated values.

- *Unlike* response modulation, spatial mapping (OI) *does* categorize cells in V1 to simple and duplex/complex classes.