INTRODUCTION

In alert monkeys, even in well-trained ones, small eye movements occur during fixation periods. 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.

In this study we analyze the effects of fixational eye movements on responses of V1 neurons to drifting gratings, that have been used to distinguish between simple and complex cells in anaesthetized animals. Then we test whether the same classification scheme can be applied in alert monkeys, using both spatial mapping and response modulation measures. Our results demonstrate that many cells in our preparation (duplex cells) have properties that are intermediate between simple and complex cells.

METHODS

Extracellular responses of V1 neurons and eye positions were recorded from alert monkeys during fixation. Cells were classified as simple or duplex/complex on the basis of spatial overlap of increment and decrement activating regions, mapped with drifting bars and flashes (**Fig. 1**). The responses of each cell to rectangular patches of drifting sinusoidal gratings were subdivided into 200 ms segments (one temporal cycle of the 5 Hz stimulus, **Fig. 2**).

The Relative Modulation Index (RMI) was estimated using 3 different modes of data selection (**Fig. 3**): **1)** selecting all data *("All")*, **2)** discarding saccade periods by automatic saccade detection *("Auto")*, and **3)** discarding periods with saccades or manually detected slow eye movements *("Select")*. The RMI of "Select" data was also calculated by taking the mean of individual segments' first harmonic (AC1) *("Align")*.

RESULTS

Eye movements decrease response modulation in both simple and duplex/complex cells (**Figs. 4, 5** - individual examples, **Fig. 6** - population). Duplex and complex cells are more affected by the slow eye movements than simple cells, but are similarly affected by saccades. 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, the effect is 0.56 (49 %) for duplex/complex and 0.62 (37 %) for simple cells. Based on the "Select" data, many duplex cells, similar to simple cells (**Fig. 7**), respond to drifting gratings with a significant modulation at the stimulus temporal frequency (**Figs. 8, 9**), whereas counterphase gratings yield frequency-doubled rerponses. In a large portion of duplex/complex cells (n=29) frequency doubling occurs also in response to drifting gratings of low spatial frequency (**Fig. 10**). The harmonic content of the responses depends upon the combination of the grating spatial frequency and window size (**Fig. 11**).

CONCLUSIONS

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

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

- Most (83%) cells in the V1 of alert monkeys have overlapping increment and decrement zones. Of these, most (duplex cells) show considerable modulation at the driving frequency.

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