Receptive fields and quasi-linear response modulation in V1 of alert macaques

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Although it has long been routine to classify neurons in V1 of anesthetized animals into simple and complex categories, it has not been easy to apply the original criteria to alert animals because of the omnipresent eye movements. In our experiments, effects of eye movements were minimized by compensating for them and by data processing. Activating regions (ARs) of 228 cells in parafoveal V1 of alert monkeys were mapped with increment and decrement moving and flashing bars. Most cells had two ARs, one responsive to increments (INC) and one responsive to decrements (DEC). The majority of the cells (78%, "duplex") had completely or partially overlapping INC and DEC ARs. Simple cells with minimal spatial overlap of INC and DEC ARs comprised 14% of our sample. 114 neurons were also studied with drifting gratings of varied spatial frequencies and window widths. Responses to the stimulus condition generating the maximal harmonic (F0 or F1) and the one generating the maximal relative modulation, RM (F1/F0), were analyzed. Most duplex cells responded with considerable modulation at the stimulus temporal frequency in both the maximal harmonic condition (mean RM 0.60±0.41 to 0.92±0.45) and the maximal RM condition (RM = 0.79±0.43 to 1.12±0.46), with the range dependent on the method of correcting for eye movements. A subset of duplex cells had RM >1, the traditional criterion for identifying simple cells, even though variations in stimulus conditions evoked clearly nonlinear behavior. There was little or no correlation between the degree of overlap of INC and DEC ARs and the value of RM, indicating that neither linearity nor the spatial organization of receptive fields can be predicted reliably from RM values. Our results suggest that nonlinear duplex cells represent the largest neuronal class in primate V1, whereas the linear simple cells are less numerous, more homogeneous, and probably preferentially associated with the magnocellular pathway.

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