Direction Selectivity of Synaptic Potentials in Simple Cells of the Cat Visual Cortex

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[1]*Laboratory of Neuropsychology, National Institute of Mental Health, National Institutes of Health, Bethesda, Maryland 20892;* [2]*Department of Neurobiology and Physiology, Northwestern University, Evanston, Illinois 60208; and* [3]*Smith-Kettlewell Eye Research Institute, San Francisco, California 94115*

Jagadeesh, Bharathi, Heidi Sue Wheat, Leonid L. Kontsevich, Christopher W. Tyler, and David Ferster. Direction selectivity of synaptic potentials in simple cells of the cat visual cortex. *J. Neurophysiol.* 78: 2772–2789, 1997. The direction selectivity of simple cells in the visual cortex is generated at least in part by nonlinear mechanisms. If a neuron were spatially linear, its responses to moving stimuli could be predicted accurately from linear combinations of its responses to stationary stimuli presented at different positions within the receptive field. In extracellular recordings, this has not been found to be the case. Although the extracellular experiments demonstrate the presence of a nonlinearity, the cellular process underlying the nonlinearity, whether an early synaptic mechanism such as a shunting inhibition or simply the spike threshold at the output, is not known. To differentiate between these possibilities, we have recorded intracellularly from simple cells of the intact cat with the whole cell patch technique. A linear model of direction selectivity was used to analyze the synaptic potentials evoked by stationary sine-wave gratings. The model predicted the responses of cells to moving gratings with considerable accuracy. The degree of direction selectivity and the time course of the responses to moving gratings were both well matched by the model. The direction selectivity of the synaptic potentials was considerably smaller than that of the intracellularly recorded action potential, indicating that a nonlinear mechanism such as threshold enhances the direction selectivity of the cell's output over that of its synaptic inputs. At the input stage, however, the cells apparently sum their synaptic inputs in a highly linear fashion. A more constrained test of linearity of synaptic summation based on principal component analysis was applied to the responses of direction-selective cells to stationary gratings. The analysis confirms that the summation in these cells is highly linear. The principal component analysis is consistent with a model in which direction selectivity in cortical simple cells is generated by only two subunits, each with a different receptive-field position and response time course. The response time course for each of the two subunits is derived for four analyzed cells. Each derived subunit is linear in spatial summation, suggesting that the neurons that comprise each subunit are either geniculate X-cells or receive their primary synaptic input from X-cells. The amplitude of the response of each subunit is linearly related to the contrast of the stimulus. The subunits are nonlinear in the time domain, however: the response to a stationary stimulus whose contrast is modulated sinusoidally in time is nonsinusoidal. The principal component analysis does not exclude models of direction selectivity based on more than two subunits, but such higher-order models would have to include the constraint that the extra subunits form a smooth continuum of interpolation between the properties derived from the two subunit solution.

INTRODUCTION

With the rise of ever more complex computational models of the brain, the question of how individual neurons perform their computational tasks has become increasingly important. Linear neurons hold appeal for the ease with which their computational function can be analyzed. Neurons that combine their inputs in a nonlinear way (prior to threshold) are capable of performing much more complex computations (Koch and Poggio 1992). Some of the most precise measurements of linearity in a neuronal system have been applied to the assembly of receptive fields in the visual system, in part because of the ease with which visual stimuli can be precisely controlled (Shapley and Lennie 1985). Layer 4 of the visual cortex has been of particular interest because it is the site of a radical transformation in the response properties of visual neurons. The simple cells of layer 4 will respond only to stimuli of the proper orientation, size, disparity, and often direction of motion, yet their afferent inputs, the relay cells of the lateral geniculate nucleus (LGN), will respond to a wide variety of visual stimuli by virtue of their circularly symmetric receptive fields. A great number of experiments have focused on the degree to which simple cells resemble linear filters and the degree to which they apply linear operators to their synaptic inputs in constructing their highly selective receptive fields.

The linearity of processing underlying the direction selectivity of simple cells has come under particular scrutiny in the past several years. All motion detectors must somehow compare the image from at least two different visual field locations at two different times. Early models of direction selectivity emphasized nonlinear interactions between the signals from different visual field locations, each of which had different response latencies (Barlow and Levick 1965; Poggio and Reichardt 1973; Reichardt 1961). More general models of motion processing, however, have shown that neurons could, in theory, become direction selective through linear combinations of such signals (Adelson and Bergen 1985; Burr 1981; Burr et al. 1986; Watson and Ahumada 1983, 1985).

Models of direction selectivity in simple cells have developed in parallel with the more general models of direction selectivity. Initial experiments were interpreted as evidence for nonlinear mechanisms of direction selectivity (Bishop et al. 1973; Emerson and Gerstein 1977; Ganz and Felder 1984; Goodwin et al. 1975). Subsequently, Reid et al. (1987,