A model for the early stages of motion processing based on spatial and temporal edge detection by X-cells

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Abstract—A model for the early stages of motion processing in the visual cortex is presented. The 'building block' for this model is the 'rebound response', which is the neuronal response evoked when a sufficient inhibitory stimulus is turned off. This response enables detection of temporal changes when the stimulus involves spatial changes. The model suggests that adjacent subunits in primary cortical cells have different weight functions for rebound responses, and thus a synergistic type of response is evoked in the preferred direction, which is predicted for both light and dark stimuli. Predictions of the model for different stimuli and receptive field structures are discussed. It appears to be more economical than previous motion models.

1. INTRODUCTION

Directional selectivity is one of the prominent features of neurons in the visual cortex. Different directional selectivity models have been suggested, but only some of these are directly relevant to electrophysiological findings from the primary visual cortex (Reichardt, 1961; Foster, 1971; Marr and Ullman, 1981; Van Santen and Sperling, 1984; Adelson and Bergen, 1985; Koch and Poggio, 1985; Watson and Ahumada, 1985; Grossberg and Rudd, 1989). The different models can be divided into three main groups: correlation models, energy models (or so-called linear models), and gradient models (see reviews by Nakayama, 1985; Koch and Hildreth, 1987). Although many theoretical models have emerged, the precise properties and mechanism of the processes which lead to motion selectivity are still a subject of debate. A number of recent physiological studies which tested simple cells in the primary visual cortex with contrast reversal and drifting gratings have supported the proposal that the initial stage of direction selectivity could be achieved with linear spatio-temporal filters (Reid et al., 1987, 1991; Hamilton et al., 1989; Albrecht and Geiser, 1991;
Tolhurst and Dean, 1991). However, these results do not rule out alternative hypotheses, such as the one presented here (see Discussion). In this study we propose a new theoretical model for the early stages of motion processing in the visual cortex.

Many of the neurons in the primary visual areas of the cat (areas 17 and 18) and the monkey (areas V1 and V2) are selective with regard to the direction of the motion of visual stimuli. These primary visual areas are the first station where directional selectivity is acquired in cats and monkeys (Nakayama, 1985). Hubel and Wiesel were the first to describe the properties of direction-selective cortical receptive fields (Hubel and Wiesel, 1959, 1962). They suggested an electrophysiological mechanism arising from the coinciding responses of an Off region and an adjusted On receptive-field region when a moving visual stimulus drifts in the preferred direction. This overlapping response from the two receptive-field regions does not occur in the reverse direction. Accordingly, they suggested that the specific arrangement of the excitatory and inhibitory receptive-field regions determines the properties of directional selectivity for the striate cells and the prestripate units.

Hubel and Wiesel found support for this idea when they identified simple cells which showed a directional preference for a light bar moving from an Off region to an On region. Additional support was obtained from the results of Bishop and his colleagues, who found boundary responses to a moving light stimulus when it leaves the receptive field (Camarda et al., 1985). They showed that there is also a boundary response to a moving dark bar as it leaves an On receptive-field region. Thus directional preference can also be obtained through the same mechanism, with dark stimuli drifting across the receptive field. In other words, a response to the turning off of a stimulus can also be evoked from an On region with regard to a dark stimulus, just as a response to a light stimulus is evoked from an Off region (Spitzer et al., 1993). (This response to a dark stimulus was not taken into account in Hubel and Wiesel's original qualitative suggestion.)

Hubel and Wiesel's physiological explanation was rejected by other investigators for several reasons. The main criticism of their explanation was that a cell does exhibit the same directional preference for both light and dark bars — 'real directional cells' (Goodwin et al., 1975; Nakayama, 1985; Baker and Cynader, 1986). Another objection related to the findings that a single subregion can show directional selectivity. We will show in this study that when Hubel and Wiesel's explanation is expanded and transformed into a model, the preceding and other objections are no longer valid. We present a quantitative motion model which is based on the rebound response model (Spitzer et al., 1993). The rebound response is defined as the increased rate of spike discharge which is evoked when an inhibitory visual stimulus is turned off. The rebound response model broadens the significance of this type of response and leads to additional physiological predictions. The model takes into account the contribution made by the duration of the stimulus and the rate at which it is turned off, factors which have both been neglected in previous receptive-field models (Rodieck, 1965; Enroth-Cugell and Robson, 1966; Richter and Ullman, 1982).

The model has been applied, for simplicity, to a unidimensional receptive-field profile. Directional selectivity was studied on the assumption that the stimuli are presented at the preferred orientation. Since the cortical receptive fields are sensitive