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Research Note

Cortical Neurons: Isolation of Contrast Gain Control

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The selectivity of cortical neurons remains invariant with contrast, even though the contrast–response function saturates. Both the invariance and the saturation might be due to a contrast-gain control mechanism. To test this hypothesis, a drifting grating was used to measure the contrast–response function, while a counterphase grating was simultaneously presented at the null position of the receptive field (where it evokes no response at any contrast). When the contrast of the counterphase grating increased, the contrast–response function shifted primarily to the right. This result is consistent with the hypothesis that there is a fast-acting gain-control mechanism which effectively scales the input contrast by the average local contrast.

Visual cortex   Receptive fields   Contrast sensitivity   Spatial frequency   Contrast adaptation

The selectivity of cortical cells generally remains invariant with contrast, despite the fact that the contrast–response function saturates (e.g. Albrecht & Hamilton, 1982; Sclar & Freeman, 1982). Both the invariance and the saturation could be due to a fast-acting gain-control mechanism which scales the input contrast by the average contrast, pooled over space and time. There is recent evidence consistent with this hypothesis (Albrecht & Geisler, 1991; Bonds, 1991; Heeger, 1991; Robson, 1991). However, the contrast-gain mechanism is difficult to study in a simple adaptation or masking paradigm because there are other factors that might affect response sensitivity: slow adaptation, response fatigue, static response nonlinearities, orientation and spatial-frequency inhibition. This report describes a new technique (a *null-adaptor* technique) for isolating and studying contrast-gain control. Using this technique, we find strong evidence for a fast-acting gain-control mechanism.

To isolate contrast-gain control and eliminate (or hold constant) the other factors, we made use of the fact that in simple cells it is generally possible to find a position for a counterphase grating‡ that evokes little or no response (i.e. the null position). By varying the contrast of a counterphase grating placed at the null position, it is possible to vary average contrast, and hence contrast-gain control, without producing a response.

There are several advantages of this *null-adaptor* technique. First, because the null adaptor alone does not generate a response from the neuron, it does not produce response fatigue, and it avoids the static response nonlinearities. Second, orientation and spatial-frequency inhibition can be minimized by using the optimal stimulus confined (in length and width) to the conventional receptive field. Third, fast contrast-gain control can be distinguished from slow adaptation by analyzing the responses as a function of time after onset of the null adaptor. This technique should be suitable for any visual neuron whose responses to a counterphase grating can be nulled.

The basic paradigm is illustrated in Fig. 1(A). A stationary counterphase grating of fixed contrast (the null adaptor) was placed and held at the null position of the receptive field. A drifting sinusoidal grating (the drifting test) was then superimposed upon the null adaptor in order to measure response as a function of contrast. These measurements were repeated for null adaptors of several contrasts. Both the null adaptor and the drifting test were confined in spatial extent (length and width) to lie within the conventional receptive field. Because it is generally not possible to find a position where the response to the counterphase grating is exactly zero (cf. Albrecht & Geisler, 1991), the starting position of the drifting test was set such that the response added constructively (in phase) with any residual response to the counterphase grating; when the response to the counterphase grating was exactly zero, the spatial and temporal phases were equated. Each presentation consisted of a block of 10 contiguous temporal cycles, and each block was separated by a period of time equal to the block length. A minimum of 4 blocks were obtained for each stimulus condition. The different stimulus conditions were randomly interleaved. The procedure for electrophysiological recording and stimulus display have been described elsewhere (see Albrecht & Geisler, 1991). Once a single neuron was isolated and classified as a simple cell, its optimal orientation, spatial frequency,

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‡A counterphase grating is a stationary spatial sinewave whose contrast is modulated sinusoidally through time.