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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.

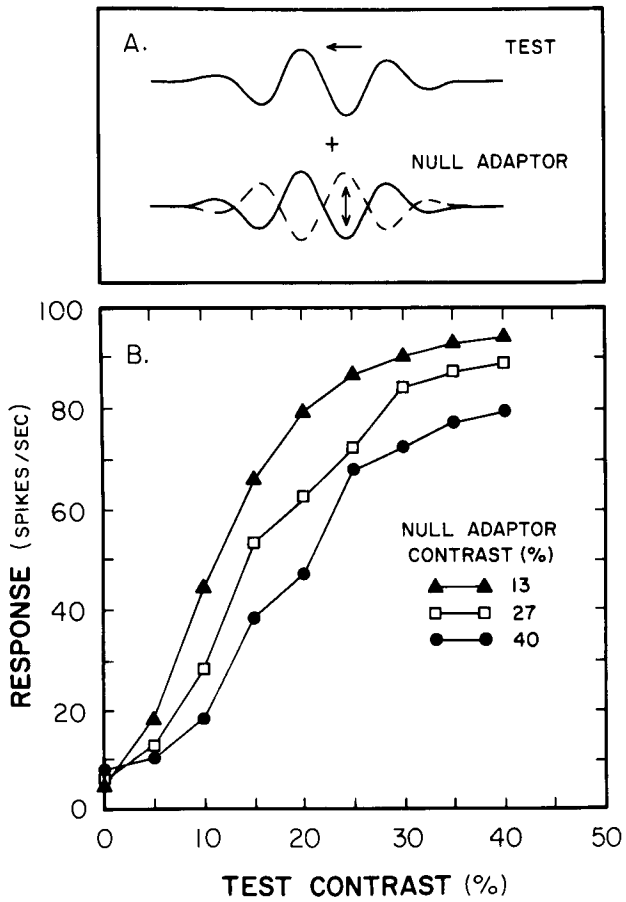

FIGURE 1. (A) The stimulus configuration used to isolate the contrast–gain control mechanism. A drifting grating was superimposed upon a stationary counterphase grating of the same spatial and temporal frequency. The counterphase grating (the null adaptor) was placed at the null position of the receptive field for the neuron being tested. The contrast of the counterphase grating was parametrically varied. At the null position, the counterphase grating evoked little or no response no matter what the contrast. The adaptation effect produced by a given null adaptor was then measured by varying the contrast of the superimposed drifting grating (the drifting test). Note that because total contrast cannot exceed 100%, the individual contrasts of the drifting and stationary gratings were each restricted to a maximum of 50%. (B) Responses of a nondirection–selective simple cell recorded from cat striate cortex as a function of the contrast of a drifting grating (contrast–response functions) measured in the presence of three different adapting contrasts (13, 27 and 40%). The adapting gratings at the null position produced little response (see responses at zero test contrast), nonetheless, as the contrast of the adapting grating increased, the contrast–response functions shifted. This pattern of results is consistent with what would be expected from a multiplicative contrast–gain mechanism.

temporal frequency, and null position were determined and held constant throughout the experiment.

The responses of 21 simple cells were recorded in the cat striate cortex. The contrast–response functions of a representative cell are shown in Fig. 1(B), for three different null-adaptor contrasts. As can be seen, the null adaptor had little or no effect on the response when presented alone (see the data points at zero contrast of the drifting test grating). However, the null adaptor had a substantial effect on the response when the drifting grating was superimposed. Specifically, as the contrast of the null adaptor increased, sensitivity to contrast was reduced. The contrast–response functions primarily shifted to the right, with some decrease in peak response. This pattern of results (which we found in 17 of the 21 cells) is what one would expect from a multiplicative contrast-gain control mechanism.*

Because we did not use transient presentations, it was not possible to precisely determine the time–course of the gain change. However, the shifts in the contrast–response functions were present at full strength within the first one or two temporal cycles (100–200 msec).†

The shifts in the contrast–response function illustrated in Fig. 1(B) cannot be explained by fatigue due to prolonged spike generation, or by static nonlinearities associated with spike generation, because the null adaptor produces almost no spikes. The shifts cannot be explained by the type of adaptation which requires prolonged exposure to high contrasts because the shifts are present at full strength within a few hundred milliseconds. The shifts could possibly be explained by spatial-frequency and orientation-selective inhibition; however, this seems unlikely because both the null adaptor and the drifting test were set at the optimal spatial frequency and orientation, and were spatially confined to the conventional receptive field. The results could possibly be explained by direction-selective inhibition; however, this seems unlikely because large shifts in the functions occurred in both direction-selective and nondirection-selective cells [e.g. the cell in Fig. 1(B) was not direction selective, yet the shifts were substantial].

In sum, the results provide strong support for the hypothesis that there is a fast-acting contrast–gain control governing the sensitivity of cortical neurons. This contrast–gain control could be the result of mechanisms in the retina (Shapley & Enroth-Cugell, 1984), the LGN, the cortex, or all three (c.f. Albrecht & Geisler, 1991).

*We verified this by fitting the data with the contrast-gain model described in Albrecht and Geisler (1991), where the only adaptation mechanism is a multiplicative contrast gain. Note that because the null adaptor and the drifting test were both presented for 10 contiguous cycles, the contrast gain was determined by the sum of the two contrasts. Under these circumstances a contrast-gain mechanism produces a change in the shape and a slight decrease in the peak of the contrast response function in addition to a rightward shift.

†Note that the *null-adaptor* technique could be used to measure the time–course with greater precision by using transient presentations.

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