

INTERACTIONS AMONG SPATIAL FREQUENCY AND ORIENTATION CHANNELS ADAPTED CONCURRENTLY

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Abstract—Interactions between size and orientation-specific mechanisms in the human visual system were investigated using a sequential adaptation technique. Subjects adapted to a vertical, 4 c/deg high-contrast (0.7) sinewave grating that was interleaved at a rate of 0.5 Hz with another adapting grating differing either in (1) spatial frequency or (2) orientation. Before and after adaptation contrast thresholds were measured for a vertical 4 c/deg sinewave test grating. The resultant elevation in contrast threshold was plotted as a function of the (1) spatial frequency or (2) orientation differences between the first and second adapting gratings. Maximum threshold elevation was found when both adapting gratings shared the same spatial frequency and orientation. Minimum elevations were found when the second grating's spatial frequency or orientation differed by approx. 1.5 octaves or 45 deg, respectively. Beyond these values threshold elevations reapproached the baseline value measured in a control condition, where the 4.0 c/deg adapting grating was interleaved with a blank. The minimum threshold elevations were 0.2–0.3 log units below the baseline level. The results suggest the existence of inhibitory interactions between neural mechanisms tuned to the size and orientation of retinal images.

Spatial vision Adaptation Channels Lateral inhibition Spatial frequency Orientation

INTRODUCTION

Several lines of evidence converge to support the theory that the visual system of the cat, monkey and man contains spatially localized neural mechanisms, or “channels”, responding only to a restricted range of sizes (spatial frequencies) and orientations (Braddick *et al.*, 1978; Rose and Dobson, 1985; Shapley and Lennie, 1985). The most convincing psychophysical evidence for such channels come from selective adaptation experiments, wherein the observer views a high-contrast grating of a particular spatial frequency and orientation and the pre- and post-adaptation contrast thresholds are determined for test gratings of various spatial frequencies and orientations. The range of test stimuli over which a threshold elevation is observed is thought to reflect the bandwidth of the underlying neural mechanism for the stimulus parameter under investigation (Blakemore and Campbell, 1969; Blakemore and Nachmias, 1971; Georgeson and Harris, 1984). Experiments using complex gratings containing two or more spatial frequencies or orientations indicate that composite adapting stimuli may induce less

contrast threshold elevation at either component frequency/orientation than when these components are adapted to alone (Tolhurst, 1972; Nachmias *et al.*, 1973; Stecher *et al.*, 1973; Tolhurst and Barfield, 1978; Georgeson, 1980). These results led to the suggestion that the neural channels underlying this stimulus selectivity are not completely independent, but that each channel receives inhibitory input from channels coding neighbouring spatial frequencies and orientations. Further psychophysical evidence for this type of spatial frequency and orientation-specific lateral inhibition comes from analogous studies on the suprathreshold tilt aftereffect (Magnussen and Kurtenbach, 1980; Kurtenbach and Magnussen, 1981) and from simultaneous contrast experiments studying the effects of spatial frequency (Klein *et al.*, 1974) and orientation (Carpenter and Blakemore, 1973; Kurtenbach and Magnussen, 1981).

However, the interpretation of the composite adaptation experiments in terms of inter-channel inhibition assumes that the processing of stimulus components is independent of the context in which they are embedded. Such a

view is complicated by several factors. For example, the weak effect of a squarewave adapting grating on the third harmonic frequency (Tolhurst, 1972; Nachmias *et al.*, 1973) could be due to the fact that the edges of the squarewave grating may be less effective in adapting mechanisms which would normally respond to one or more harmonic frequencies of the squarewave (Greenlee and Magnussen, 1987, 1988; von der Heydt *et al.*, 1986; von der Heydt, 1987). Klein and Stromeyer (1980) have shown that the first and third harmonics of a squarewave can be effective adaptors, if they are "separately visible" during adaptation. Swift and Smith (1985) have argued that weak adaptation effects following composite adaptation could be caused by the local contrast beats occurring in the physical luminance profile of complex gratings whenever the component frequencies approach a similar value. These experiments therefore suggest that complex adapting stimuli in which two or more sinewaves are superimposed may not be adequate to test the inter-channel interaction hypothesis.

We here present new evidence for inhibitory interactions between neural mechanisms based on the technique of sequential adaptation (Greenlee and Magnussen, 1987). This technique permits concurrent adaptation to two spatial frequencies or orientations in the same retinal region and separates genuine interactions between mechanisms from the confounding effects of stimulus complexity. The experimental rationale is simple: to build up an aftereffect, adaptation need not be continuous but can be interrupted for short periods of time without reducing the size of the resultant aftereffect, provided total adaptation time is kept constant (Magnussen and Greenlee, 1986). We take advantage of this feature of adaptation by presenting two adapting gratings alternating in time. These gratings would adapt the same or different mechanisms depending on their similarity on the stimulus parameter in question, e.g. spatial frequency or orientation. It follows that the degree to which one adapting grating affects the elevation in contrast threshold caused by the other adapting grating reflects the bandwidth of the adapted mechanism. More importantly, this method can be used to measure the extent to which that mechanism can be affected by adaptation occurring outside of the channel's own operating range, and thus can reveal interactions between neighbouring channels.

METHOD

Sinewave gratings were produced on a high-resolution cathode ray tube (Joyce Electronics, U.K.) under microprocessor control. The screen was masked off to a circular field of 11 deg visual angle, which was viewed at a distance of 114 cm. Viewing distance and head orientation was held constant using a chin-forehead rest. The mean luminance of the screen was 150 cd/m². The linearity of the voltage/contrast function was measured and controlled for on a regular basis using a spot photometer. Contrast thresholds were measured using a two-alternative forced-choice method where the test grating was presented randomly for 1 sec in one of two 2.5 sec temporal intervals. The brief pause before and after presentation of the test grating assured that the visual field was clear of any transient afterimages and that no form of forward and/or backward masking occurred. The intervals were delineated by auditory signals and the observer indicated in which interval he thought the grating appeared by pressing the appropriate button. According to the correctness of the observer's response, the computer then chose the next test contrast guided by a maximum-likelihood search algorithm (Lieberman and Pentland, 1982). All thresholds are based on 30 trials giving an average of 8–10 reversals of the contrast staircase. It has been shown that the reliability of this threshold search algorithm reaches an asymptote around 30 trials (Lieberman and Pentland, 1982). The data presented in Figs 2 and 4 are the means of at least two such measurements. The standard errors of the individual thresholds measurements usually do not exceed 1 dB in contrast.

The test gratings were vertically oriented with a constant spatial frequency of 4.0 c/deg and a temporal frequency of 1 Hz. Of the two adapting gratings, one was fixed at 4.0 c/deg in the vertical orientation and the spatial frequency or orientation of the second adapting grating was varied in constant half-octave steps, while the adapting contrast was held constant at 0.7. Contrast is defined as the ratio between the difference between the maximum and minimum luminance levels and their sum. The two adapting gratings were presented sequentially at a rate of 0.5 Hz over an 8 min adapting period. During adaptation the subject fixated along a small (1 deg) fixation circle and the spatial phase of the adapting grating was reversed at a temporal frequency of 1 Hz. This procedure was done to

avoid the induction of retinal afterimages and to create an adaptation effect that was independent of spatial phase. Post-adaptation thresholds were measured according to a test-readapt regime with 15 sec readaptation periods interleaved with test trials.

To be able to compare the extent of interaction between the effects of the two adapting gratings, a control condition was conducted which measured the elevation in contrast threshold resulting when the standard 4 c/deg adapting grating was interleaved at the same rate with a blank field of same mean luminance. Since there is no spatial contrast in such a blank field, we were thus able, in this way, to measure the extent of adaptation in the mechanism tuned to the 4 c/deg test grating under the assumption that the only effect, if any, of the interleaving exposures to a blank field would be a partial decay of adaptation.

In the experiments on orientational effects, the screen was viewed monocularly through a two-channel optical system. In one channel the test and standard adapting grating were presented and in the other channel the orientation of the second adapting grating was varied in constant angular steps by changing the orientation of a Dove prism (see Fig. 1). Computer control of electronic shutters guaranteed proper synchronization of the test and adapting fields. Due to the optics, the mean luminance was reduced to 30 cd/m² at the eye. Four observers (MWG, SM, FH and WD) with normal or corrected-to-normal vision participated. All subjects had extensive training in similar experiments; WD was naive with respect to the aims of the study.

RESULTS

Spatial-frequency interactions

Figure 2 shows the results of the first experiment for the three observers tested, where the elevation in contrast threshold for the 4 c/deg grating is plotted as a function of the spatial frequency of the second (variable) adapting grating. The horizontal arrow and dashed line present the threshold elevation induced when the standard adapting grating was interleaved with a blank field of mean luminance.

The dual-grating adaptation function has a "sombbrero" shape with a central range of spatial frequencies showing summation of adaptation effects between the two adapting gratings.

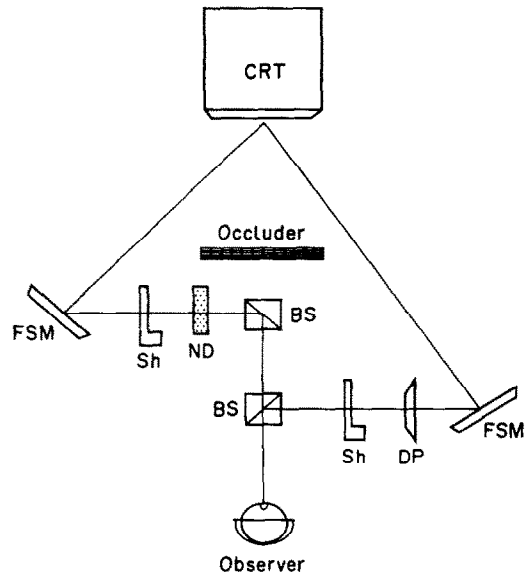


Fig. 1. A schematic representation of the optical system developed to test the effect of orientation on threshold elevation. Abbreviations: FSM = front surface mirror; Sh = shutter; ND = neutral density filter; BS = beam splitter; DP = Dove prism.

Clearly, adapting gratings having a similar spatial frequency as that of the fixed adapting grating should stimulate the same mechanism centered at the test frequency of 4 c/deg. For gratings of the same spatial frequency, the additional build-up of adaptation can be predicted based on the time course of adaptation to a single grating. Previous experiments indicate a difference between 0.2 and 0.4 log units in threshold elevation resulting from 4 and 8 min of adaptation for different observers (Magnussen and Greenlee, 1985). Beyond this central summing range there is a second range where the elevation in threshold is reduced below the baseline level of the control condition, where the fixed adapting grating was interleaved with a blank field. This is followed by a third range, where the threshold elevation again approaches the baseline. There is a slight (approx. 0.1 log unit) difference in threshold elevation obtained between the control condition and the condition where the two adapting gratings differed by 2 octaves or more for all three subjects tested. This finding suggests a slight global effect of the second adapting grating of the same orientation irrespective of spatial frequency. Correcting for this effect, the profiles show an approximate 2 octave summative region, surrounded by approximate 1 octave subtractive regions to either side. The full bandwidth of the central adapting region (1.2 octaves

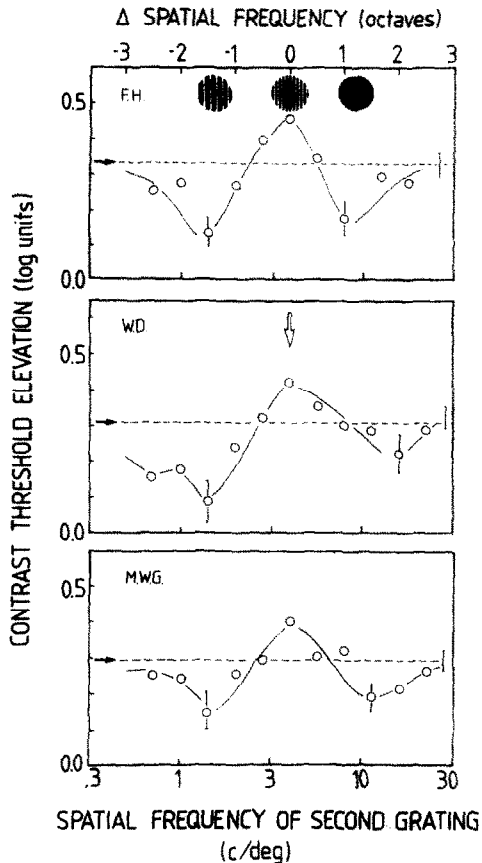


Fig. 2. The elevation in contrast threshold for detecting a 4 c/deg vertical grating following 8 min sequential adaptation to a high-contrast 4 c/deg vertical grating alternating with a second grating, as a function of the spatial frequency of the second grating. Dashed lines indicate the threshold elevation produced by adapting to a 4.0 c/deg grating alternating with a blank field. The data points are the mean values of, at least, two separate measurements and the error bars represent ± 2 SEM. The grating insets (above) depict the spatial frequency of the second adapting grating when it was identical to the first grating (centre), or when it had its most pronounced subtractive effect on the resultant elevation in threshold (left and right). Results shown separately for subjects FH, WD and MWG.

at half height) corresponds approximately to the tuning width of threshold elevation in single grating experiments (Blakemore and Campbell, 1969; Björklund and Magnussen, 1981; Georgeson and Harris, 1984).

To facilitate comparisons between subjects the findings shown in Fig. 2 have been normalized by assigning the maximum elevation in threshold the value of 1 for each subject separately and plotting all remaining threshold elevations as a ratio of the maximum value. The results of this reanalysis are shown in Fig. 3 for all three observers. Normalized threshold elevation is now plotted as a function of the octave difference between the first and second

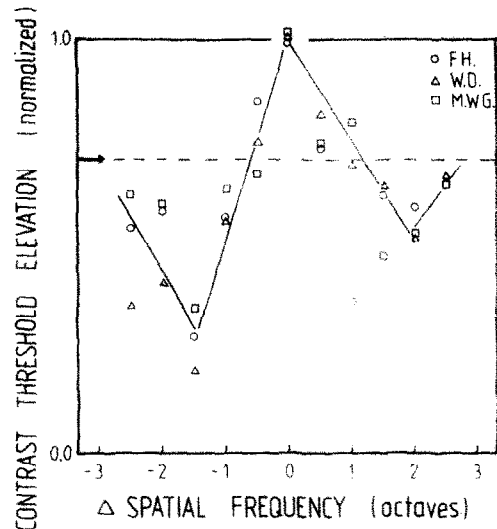


Fig. 3. The data in Fig. 2 are replotted after normalizing by assigning the value of 1 to the maximum threshold elevation and relating all other values to that maximum. Data for the three observers are shown. The straight lines have been fitted by eye.

adapting gratings. The straight lines have been fitted by eye and reveal that the reduction of threshold elevation is an asymmetric function of spatial frequency. For adapting frequencies above the 4 c/deg standard, the reduction in threshold elevation is less than for adapting gratings having a lower spatial frequency. Such an asymmetry may reflect differences in inhibitory interactions depending on the preferred spatial frequency of the underlying neural mechanisms.

Orientation interactions

We next investigated the effect of varying the orientation of the second adapting grating on the resultant elevation in contrast threshold. The results are shown for observer SM for two different adapting and test spatial frequencies: 4 c/deg (upper panel) and 8 c/deg (lower panel). Contrast threshold elevation (in log units) is plotted as a function of the orientation difference between the first and second adapting grating. A maximum threshold elevation occurs when both gratings have the same orientation as the test grating (vertical). For both spatial frequencies tested, minima occurred when the first and second adapting gratings differed by 45 angular deg. As has been reported earlier (Movshon and Blakemore, 1973; Greenlee *et al.*, 1988), the bandwidth of orientational selectivity appears to be fairly independent of spatial frequency. The full bandwidth of the central

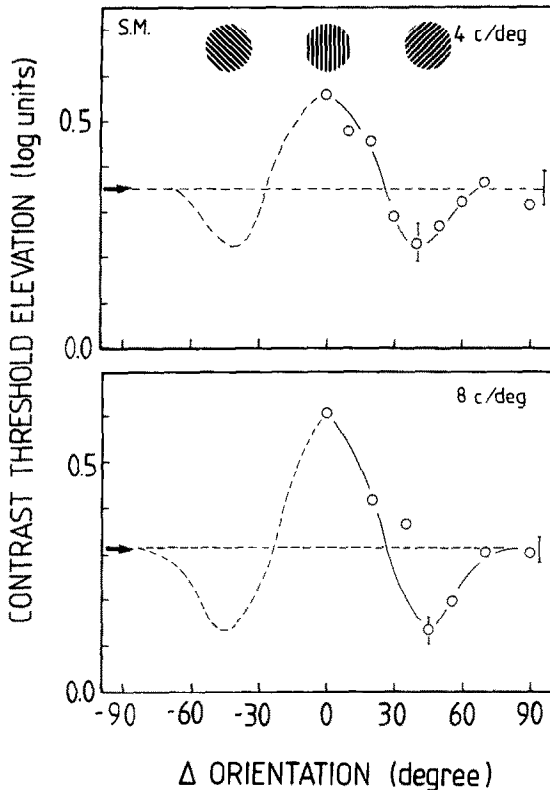


Fig. 4. The elevation in contrast threshold following adaptation to a 4 c/deg (upper panel) or a 8 c/deg (lower panel) vertical grating alternated with a grating of the same spatial frequency but of a different orientation as a function of the orientation difference between the first and second adapting gratings. The grating insets show the orientation of the second grating when it was identical to the first (centre) or when it had its most pronounced subtractive effect on adaptation (left and right). Data from observer SM.

adapting range is 45 deg, which corresponds well to that reported in single grating adaptation experiments (Blakemore and Nachmias, 1971; Movshon and Blakemore, 1973).

DISCUSSION

The technique of sequential adaptation enables us to isolate the neural interactions arising from adaptation to stimuli containing two spatial frequencies or orientations from the confounding effects of the luminance profile of complex gratings. Since the two adapting gratings were never simultaneously exposed in our experiments, any change in the resultant threshold elevation at the test frequency/orientation must reflect the effect of the second adapting frequency/orientation acting on the mechanism processing the test grating. The results of the present experiments show that the amount and direction of change in threshold elevation induced by the second grating depend

upon the relative difference in spatial frequency and orientation between the two adapting gratings. In both the spatial frequency and orientation domains sombrero-shaped adaptation profiles suggest that both facilitatory and inhibitory interactions occur.

Presumably, when the effects of the two adapting gratings sum they are both within the stimulus range responsible for adaptation in the mechanism tuned to the spatial frequency and orientation of the test grating. The width of this summative region is thus comparable to the spread of adaptation effects found in single-grating adaptation experiments. Such comparisons indicate good agreement between the width of the summation region and the stimulus selectivity estimated by the conventional adaptation experiments for both spatial frequency (e.g. Blakemore and Campbell, 1969; Björklund and Magnussen, 1981; Georgeson and Harris, 1984) and orientation (e.g. Blakemore and Nachmias, 1971; Movshon and Blakemore, 1973).

The second subtractive region (below the dashed lines in Figs 2 and 4) would not be readily observed in single-grating adaptation because of the obvious "floor" effect set by the unadapted contrast thresholds. In our dual-grating experiments, the baseline is raised by 0.3 log units, thus allowing modulation of the contrast threshold both above and below this level. The fixed adapting grating thus is analogous to the conditioning stimuli which raise the base rate activity in single cells measured in neurophysiological experiments (e.g. Blakemore and Tobin, 1972; Nelson and Frost, 1978; Heggelund, 1986). There have, however, been some reports of threshold facilitation in single-grating adaptation experiments (DeValois, 1977; Tolhurst and Barfield, 1978; Kelly and Burbeck, 1980). Furthermore, the illusory gratings which, after adaptation, briefly occur in blank fields, having apparent spatial frequencies and orientations remote from those of the adapting grating (Georgeson, 1976, 1980; Tyler and Nakayama, 1980), are probably manifestations of the same mechanism that yields subtractive effects in the present experiments (Georgeson, 1985).

Studies of suprathreshold aftereffects, which involve changes in the perceived size or orientation of stimuli also provide a non-zero baseline. Experiments on the tilt aftereffect have demonstrated interactions between adapting and test stimuli across the complete range of 90 deg difference in orientation, with negative

(repulsion) aftereffects occurring up to 45–60 deg adapting angles and positive (attraction) aftereffects beyond (e.g. Campbell and Maffei, 1971). In addition, there is substantial evidence that similar inhibitory/disinhibitory processes are involved in the tilt aftereffect (Magnussen and Kurtenbach, 1980; Kurtenbach and Magnussen, 1981).

The subtractive sidebands evident in the results shown in Figs 2 and 4 provide a decisive test of two competing theories of spatial adaptation, namely the fatigue vs inhibition theory of adaptation. If threshold elevation were the result of neural fatigue (Swift and Smith, 1982; Georgeson and Harris, 1984), then one would not expect additional adaptation at more remote spatial frequencies or orientations to cause *less* adaptation. However, if one assumes that adaptation is an active process, which adjusts the contrast gain of the adapted mechanism (Ohzawa *et al.*, 1985; Greenlee and Heitger, 1988) and that this gain adjustment may be mediated, at least in part, by lateral inhibition from mechanisms selective to neighbouring spatial frequencies and orientations (Blakemore *et al.*, 1973; Dealy and Tolhurst, 1974), then interpretation of the results becomes simple. The central summative adaptation region in Figs 2 and 4 would be the result of inhibitory activity of neighbouring channels and the subtractive regions would be the results of these neighbours themselves becoming adapted and thus disinhibiting the mechanism tuned to the central frequency/orientation. The present results thus provide additional evidence for the inhibition theory of adaptation, which has been shown to account for a number of results concerning the tilt aftereffect (Kurtenbach and Magnussen, 1981; Magnussen and Johnsen, 1986). Objective evidence, which is based on visual evoked potential amplitude in human observers, for such inter-channel interactions in the orientation domain has been recently reported by Burr and Morrone (1987).

It is interesting to note here that, compared to the effect caused by an adapting grating interleaved with a blank, Klein and Stromeyer (1980, Fig. 3) found no difference in threshold elevation when a $f/3$ adapting grating was interleaved with a f adaptor using a f test grating. There are, however, some important differences between the stimulus conditions used in their and our present experiments. First, the test and first adaptor, had a spatial frequency of 7.5 c/deg, almost an octave above our 4 c/deg

standard test grating. Second, as Klein and Stromeyer (1980) were interested in the interactions between harmonically related frequencies (of a squarewave) they used adapting contrasts that differed by a factor of three, 63% for 2.5 c/deg and 21% for 7.5 c/deg, whereas we used an adapting contrast of 70% for both fixed and variable adapting gratings. The adaptation effect in their experiment was fairly small (about 0.2 log unit) owing to the low adapting contrast at the 7.5 c/deg frequency. Furthermore, their mean luminance was 5 cd/m² compared to our 150 cd/m². The absence of an effect on threshold elevations in their experiment may thus be due to any or all of these differences.

In conclusion, the results from our dual-grating experiments provide evidence that lateral inhibition in the human visual cortex is organized along the dimensions of orientation and size (spatial frequency). Each neural mechanism receives excitatory input over a band-limited range of spatial frequency and orientation and an inhibitory input beyond this range. Spatial adaptation experiments reveal the extent of this lateral inhibition. It is interesting to note here that such inhibitory interactions between neighbouring neurons plays an important role in recent models of the computation performed by neural networks (see Hopfield and Tank, 1986). There is increasing neurophysiological evidence for this type of inhibition in the visual cortex (Morrone *et al.*, 1982; De Valois and Tootell, 1983; Nelson, 1985; Romoa *et al.*, 1986), which might have its structural basis in an orderly organization of orientation columns and spatial frequency rows (Maffei and Fiorentini, 1977; Tootell *et al.*, 1981; Berardi *et al.*, 1982).

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