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Thompson, Peter Gage and Murphy, Brian (1980) *Adaptation to a 'spatial-frequency doubled' stimulus*. *Perception*. pp. 523-528. ISSN 0301-0066

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## Adaptation to a 'spatial-frequency doubled' stimulus

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Received 4 February 1980, in revised form 6 May 1980

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**Abstract.** The perceived spatial frequency of low-frequency sinusoidal gratings is elevated when the gratings are temporally modulated sufficiently rapidly. Although this phenomenon is usually called 'spatial-frequency doubling', the magnitude of this spatial-frequency elevation depends on the spatial and temporal parameters of the grating and may be less than or greater than doubling. Adaptation to such a pattern produces contrast-threshold elevation whose spatial-frequency tuning is centred upon the grating's real rather than perceived spatial frequency. These results suggest that spatial-frequency elevation occurs later in the visual system than adaptation or that these two processes are independent of one another, at least under the conditions of these experiments.

### 1 Introduction

Blakemore and Campbell (1969) demonstrated size-selective threshold elevation following adaptation to a high-contrast sine-wave grating. This finding led them to propose that the underlying mechanisms of the effect were adaptable neurones in the visual cortex selective for stimulus size or spatial frequency.

When Blakemore and Sutton (1969) and Blakemore et al (1970) demonstrated a suprathreshold distortion in perceived spatial frequency following adaptation to a grating, the possibility arose that these spatial-frequency mechanisms provided a direct correlate with the experience of seeing. Furthermore the similarity between the properties of these spatial-frequency mechanisms in man and those of single neurones in the visual cortex of cat and monkey was striking. Indeed, Blakemore et al (1970) state:

"These findings provide further evidence that the visual system of man, like those of the cat and the monkey contains neurons selectively sensitive to the orientation and dimensions of retinal images, and that these adaptable cells are actually involved in the encoding and perception of the size of simple patterns."

The suggestion that seeing can be directly correlated with activity in neurones in the visual cortex is an important one which we have tried to test by a simple experiment. We have utilized the phenomenon of 'spatial-frequency doubling', first described by Kelly (1966), who reported that when a sine-wave grating of low spatial frequency is flickered sufficiently rapidly its perceived spatial frequency is twice its true value. Following adaptation to such a stimulus we have measured the threshold elevation produced on a range of test gratings. If the neurones "involved in the coding and perception of" size are those most adapted by a 'frequency doubled' stimulus then the greatest threshold elevation should occur at the perceived spatial frequency of the adaptation grating rather than at its true spatial frequency.

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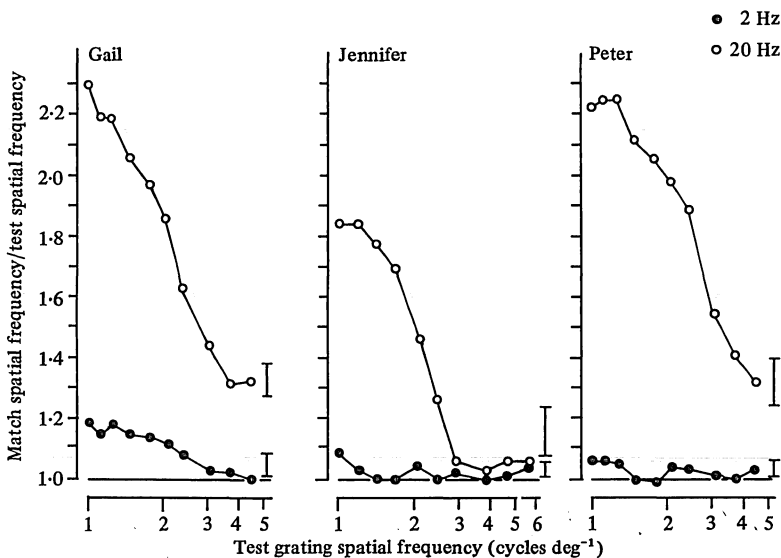
## 2 Methods

Two experiments were carried out. In both, the stimuli were sinusoidal gratings generated on the screen (P31 phosphor) of an oscilloscope by the method devised by J G Robson, as described by Campbell and Green (1965). Subjects sat 57 in from the screen, which was masked by a rectangular aperture 5 deg wide and 3 deg high. The area surrounding the aperture was matched for both colour and brightness to the mean luminance of the screen ( $15 \text{ cd m}^{-2}$ ). All gratings in experiment 1 and the adaptation gratings in experiment 2 had a Michelson contrast of 0.40. Subjects were instructed to fixate a small circle placed centrally on the screen throughout both experiments. Of the three subjects Gail and Jennifer were naive to the purpose of the experiment and, though given a good deal of practice in making settings by the method of adjustment, had not taken part in any experiment before. Peter, one of the authors, is a seasoned observer. All three have normal vision.

## 3 Results

### 3.1 Experiment 1: the perceived spatial frequency of a counterphase modulated grating

The purpose of the first experiment was to select the spatial and temporal parameters of a counterphase modulated grating so that its apparent spatial frequency was approximately twice its true spatial frequency. The method of successive matching was used. A counterphase modulated grating was presented on the screen for 6 s, followed by 6 s of a temporally unmodulated grating whose spatial frequency could be varied by the subject. Alternation of these stimuli continued until the subject considered that the spatial frequency of the unmodulated grating exactly matched that of the counterphase grating. This value was then recorded and a new trial initiated. In any one session the rate of temporal modulation of the counterphase grating was unchanged but a range of spatial frequencies was investigated, each frequency being matched twelve times, in random order.



**Figure 1.** Apparent spatial frequency of sine-wave gratings sinusoidally modulated at 2 Hz and 20 Hz. The ratio of the apparent to the real spatial frequency is plotted as a function of spatial frequency. At 20 Hz low-spatial-frequency gratings have a greatly elevated apparent spatial frequency, which for subjects Gail and Peter exceeds doubling. Vertical bars indicate the mean standard deviation for each condition. There were no systematic or large differences in the standard deviations at different spatial frequencies.

Figure 1 shows the perceived spatial frequency of gratings counterphase modulated at 2 Hz and 20 Hz for three subjects. The results are clear. At the low rate of counterphase modulation (2 Hz) the perceived spatial frequency of gratings is generally veridical although there is a tendency to perceive low-spatial-frequency gratings as having an elevated spatial frequency (especially by Gail in figure 1).

At the high rate of counterphase modulation (20 Hz), as the spatial frequency is decreased its perceived spatial frequency is relatively increased. At a spatial frequency of 1–2 cycles  $\text{deg}^{-1}$  perceived spatial frequency is approximately twice its veridical value.

### 3.2 Experiment 2: contrast threshold elevation following adaptation to a counterphase modulated grating

From the results of experiment 1 it was possible to select a counterphase modulated grating of a suitable spatial frequency so that its perceived spatial frequency at a 2 Hz modulation rate was close to its true frequency and yet it had a perceived spatial frequency close to double this value at a 20 Hz modulation rate.

Experiment 2 investigated the contrast-threshold elevation of a range of temporally unmodulated (stationary) gratings following adaptation to such a 'frequency-doubled' stimulus. Three adaptation conditions were investigated.

- (i) Adaptation to a grating of low spatial frequency and 20 Hz counterphase modulation rate. This condition selected stimulus parameters from the results of experiment 1 so that the apparent spatial frequency of the grating was approximately twice its true value.
- (ii) Adaptation to a grating of low spatial frequency and 2 Hz counterphase modulation rate. The apparent spatial frequency of this grating was approximately equal to its true value.
- (iii) Adaptation to a grating of high spatial frequency and 2 Hz counterphase modulation. The spatial frequency was chosen to be equal to the apparent spatial frequency of the adaptation grating used in condition (i).

In condition (i) the apparent spatial frequency of the adaptation stimulus was approximately twice its true value. If those mechanisms in the visual system which determine the appearance of a grating are also those whose sensitivities are reduced by adaptation then the maximum threshold elevation after adaptation in this condition should occur at the apparent (doubled) spatial frequency and not at the true spatial frequency of the adaptation grating.

Adaptation conditions (ii) and (iii), described above, provide an indication of the spatial-frequency tuning of the threshold elevation following adaptation to gratings of spatial frequency equal to both the true (ii) and the perceived (iii) spatial frequency of the 'frequency doubled' adaptation stimulus in condition (i).

The spatial frequencies used in this experiment (1.26 and 2.9 cycles  $\text{deg}^{-1}$ ) were chosen after the collection of pilot data. Ideally the ratio of the perceived spatial frequencies of the 'frequency doubled' stimulus (20 Hz, 1.26 cycles  $\text{deg}^{-1}$ ) to the slowly flickering high-spatial-frequency grating (2 Hz, 2.9 cycles  $\text{deg}^{-1}$ ) should be unity. This latter grating is the control grating used in condition (iii) above. Actually the ratios used were 1.09 for Gail, 1.29 for Jennifer, and 1.04 for Peter.

The procedure was identical for each condition. Contrast thresholds were set by the method of adjustment both before and immediately after adaptation to a high-contrast counterphase modulated grating. In the adaptation phase of the experiment an initial exposure to the adaptation stimulus of 2 min preceded the threshold settings. Following this adaptation 4 s periods in which the subject adjusted the contrast of a test grating were alternated with 22 s 'topping-up' periods of adaptation. Threshold settings made before adaptation followed the same procedure with a blank field of the same mean luminance substituted for the adaptation grating.

The results of experiment 2 are shown for the three subjects in figure 2. Regrettably condition (iii) was not run on one subject (Peter). The results show that the slow flicker (2 Hz) adaptation gratings gave rise to spatial-frequency-specific threshold elevation with the peak elevation at the adaptation spatial frequency. The fast flicker (20 Hz) adaptation grating also produced threshold elevation which, though smaller than that produced by the other adaptation gratings, also appears to have its peak at the real spatial frequency of the adaptation pattern ( $1.3 \text{ cycles deg}^{-1}$ ) rather than at its perceived spatial frequency.

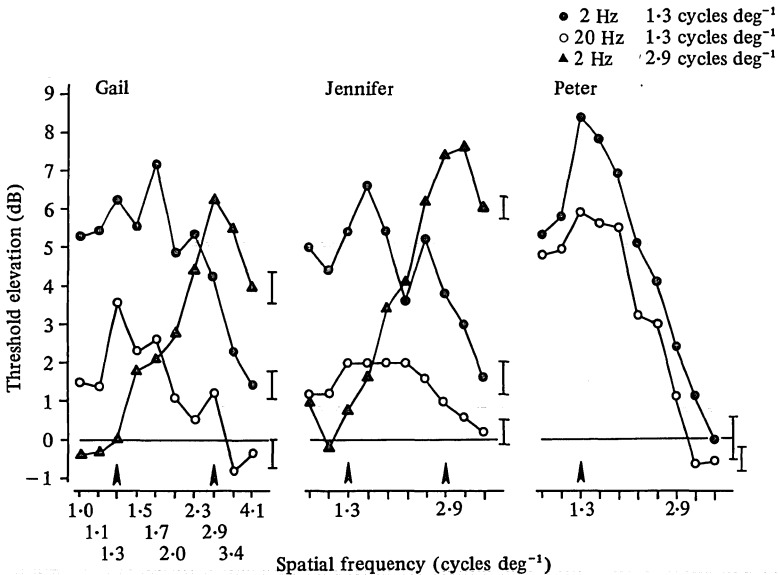


Figure 2. Detection-threshold elevation following adaptation to a frequency-doubled stimulus (open circles). For comparison the threshold elevation following adaptation to a slowly modulated grating of the same spatial frequency (filled circles) and a slowly modulated grating of a higher real spatial frequency (triangles) are also shown. Vertical bars indicate the mean standard deviation in each condition. Further details are in the text.

#### 4 Discussion

Three interesting points can be made from the two experiments described.

- (i) The appearance of objects is not necessarily determined by the activity in those neural mechanisms which manifest adaptation of the type described by Blakemore and Campbell (1969) and Blakemore et al (1970).
- (ii) The term 'spatial-frequency doubling' is a misnomer. Temporal modulation of a low-spatial-frequency pattern leads to 'spatial-frequency elevation' which may be increased up to and even extended beyond doubling (see also Virsu et al 1974).
- (iii) This spatial-frequency elevation is mediated by a mechanism which is either more central than or independent of the site of adaptation.

These latter two points provide some information as to the nature of the mechanism underlying spatial-frequency elevation. Virsu (Virsu and Nyman 1974; Virsu et al 1974) has provided strong evidence that two different kinds of spatial effects can be produced by flickering gratings. One type, which is manifest only at low temporal frequencies and produces modest increases in perceived spatial frequency, is attributed by Virsu to the increase in sensitivity to low spatial frequencies brought about by temporal modulation (Robson 1966; Nachmias 1967). A similar explanation is invoked by Tynan and Sekuler (1974) to explain the perceived spatial-frequency elevation of briefly presented gratings.

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The present experiments cannot address themselves to this mechanism of spatial-frequency elevation. Our adaptation pattern in experiment 2, a fast flickering counterphase grating of low spatial frequency, gives rise to Virsu's second type of spatial-frequency elevation, that mediated by temporal summation of nonlinearly filtered intensity signals (Kelly 1966). It is this mechanism which our experiments suggest must be more central than or independent of the site of adaptation.

Richards and Felton (1973), in an experiment somewhat similar to that reported here, found that disparity-specific adaptation occurs to the real and not to the doubled spatial frequency of a temporally modulated grating. Their conclusion that frequency doubling either occurs more centrally or is independent of disparity processing has been thoroughly examined by Tyler (1974), who has elegantly demonstrated that frequency doubling does indeed occur independently of disparity detection. This finding suggests that spatial-frequency elevation also occurs independently of the site of spatial adaptation.

Tyler himself proposed a flicker-detection model in which a full-wave rectification of the instantaneous input, performed perhaps by the amacrine cells, gives rise to frequency doubling. That adaptation to a frequency-doubled stimulus produces peak threshold elevation to the real rather than the perceived spatial frequency is explained on this model only if it is assumed that there are separate channels for pattern and flicker detection, the latter being responsible for the rectification and hence the doubling. Evidence for such channels has been provided by, amongst others, Tolhurst (1973).

Indeed, Tolhurst (1975) has proposed a model of frequency doubling based on sustained and transient channels. This model is essentially compatible with that of Tyler (1974) and may be the most satisfactory to date, but it does involve two very considerable assumptions: firstly that the doubled response of the amacrine cells (Tyler) or transient channels (Tolhurst) should result in a percept of a grating of twice its true spatial frequency and secondly that the relative responses of the two types of channel, flicker and pattern, are combined to produce an unambiguous percept of a grating of intermediate spatial frequency.

If these assumptions are accepted, our adaptation stimulus in experiment 2 had an elevated perceived spatial frequency because it was detected mainly by the transient channels. Therefore it would also adapt the transient channels to a far greater extent than the pattern channels. However, our stationary test gratings would be detected by the little-adapted pattern channels, hence the relatively little threshold elevation found, tuned to the real spatial frequency of the adaptation grating.

Two predictions can be made if this interpretation of our data is correct. Firstly, had we investigated the threshold elevation of flickering gratings following adaptation to the spatial-frequency doubled stimulus, the elevation would have peaked at the real spatial frequency of the adaptation grating, as both adaptation and test patterns would have undergone the same transformation. Secondly and more importantly, the amount of threshold elevation found should be far greater than that found in experiment 2 as it would now be the most adapted channels which were being tapped by the detection thresholds.

**Acknowledgements.** PT was supported by a Harkness fellowship from the Commonwealth Fund and BJM was the recipient of an NIH postdoctoral fellowship. This research was supported by NSF grant BMS75-07658 to Jacob Nachmias, with whose equipment and facilities the experiments were carried out and without whose help and guidance they could not have been carried out. I am most grateful to the wise comments of unknown referees.

This paper is dedicated to the memory of Brian J Murphy.

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**APPENDIX**
**The equivalence between orientation and length changes**

Assume that a line segment in the image plane (the plane perpendicular to the line of sight) rotates by  $\theta^\circ$ . Let  $l$  be the length of the line element in three-dimensional space,  $d$  be the projected length on the image plane, and  $\alpha$  be the angle between the line element and the image plane. The relation between the actual and the projected length is  $d = l \cos \alpha$ . Let  $\theta'$  be the rotation in space that produced the orientation difference of  $\theta$  in the image.

Straightforward trigonometry establishes that a rotation in the image by  $\theta$  can be produced by a rotation of  $\theta'$  in space if the following relation holds:

$$\sin \frac{1}{2} \theta' = \sin \frac{1}{2} \theta \cos \alpha .$$

(Comment: in fact, this is the minimal rotation in space that can produce the required image rotation, since an additional rotation about the line segment itself will not affect its final orientation. I shall use this minimal rotation since I can assume that small rotations are more likely than larger ones.)

A rotation by  $\theta'$  in space can also give rise to a pure length change (in the image) with no change in orientation. This will happen if the rotation axis is perpendicular to the line of sight. The initial length in the image plane was  $d = l \cos \alpha$ . The final length in the image plane, following the rotation, is  $d' = l \cos(\alpha + \theta')$ . The length ratio  $d'/d = \cos(\alpha + \theta')/\cos \alpha$  is thus independent of the length  $l$ . For a given initial orientation  $\alpha$ , this length ratio and an orientation difference of  $\theta$  are expected to be equivalent in terms of CS (i.e. a split motion can be expected), since both can be induced by the same rotation  $\theta'$  in space. To obtain a measure of the CS equivalence independent of the initial orientation of the line element, one can now average over all initial orientations. This can be done by numerical integration, or, for small angles, the integration can also be expressed analytically. The resulting expression is

$$\frac{d'}{d} = 1 - \frac{\theta^2}{4} - \frac{2\theta}{\pi} .$$

This relation gives us a measure of the length ratio  $d'/d$  (on the assumption that  $d' < d$ ) that is expected to be equivalent in CS to an orientation difference of  $\theta$  (expressed in radians). The analytic expression is fairly accurate for  $\theta$  between 0 and  $30^\circ$ . For  $\theta = 30^\circ$ , a numerical integration (averaging over  $\alpha$  every  $1^\circ$ ) yields  $d'/d = 0.61$ , compared with 0.598 obtained from the analytic expression.