

THE PERCEIVED
SPATIAL FREQUENCY SHIFT: EVIDENCE FOR FREQUENCY-
SELECTIVE NEURONES IN THE HUMAN BRAIN

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SUMMARY

1. Prolonged observation of a high-contrast grating pattern causes an apparent shift in the spatial frequency of gratings subsequently viewed with the same retinal region. Gratings of higher and lower frequency than the adapting pattern seem, respectively, higher and lower than in fact they are.

2. There is no significant after-effect at the adapting frequency itself nor at frequencies more than two octaves away.

3. For very low adapting frequencies, the after-effect remains centred at about 3.0 c/deg and declines in strength as the adapting frequency is successively lowered.

4. The magnitude of the after-effect increases with the contrast of the adapting grating and the length of time spent in adaptation. It takes several hours to recover completely from 30 min adaptation.

5. The phenomenon is orientation-specific: a horizontal adapting grating has no effect on vertical test gratings. There is partial interocular transfer of the after-effect.

6. These findings provide further evidence that the visual system of man, like those of the cat and the monkey, contains neurones 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.

INTRODUCTION

Within the last few years, evidence has come to light that the visual system of man is organized rather similarly to that of the cat and the monkey. Neurophysiological studies in these animals have shown that

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individual neurones of the visual cortex are selectively sensitive to the orientation of linear targets such as black-white edges and narrow bright slits (Hubel & Wiesel, 1962, 1968). They are also rather critically sensitive to the dimensions of the targets. Campbell, Cooper & Enroth-Cugell (1969) used moving grating patterns of variable spatial frequency to study the selectivity of the cat's cortical units, and they report that some neurones require gratings of a rather specific bar width, or period, for the optimal response. Moreover, the preferred spatial frequency varies from cell to cell over a wide range. There is some preliminary evidence (Campbell, Cooper, Robson & Sachs, 1969) that neurones in the monkey cortex are similarly organized and that some of them can resolve gratings of high spatial frequency, quite near the limit of acuity in man.

The evidence that the brain of man contains similar cells comes from psychophysical experiments. Campbell & Kulikowski (1966) discovered that a grating of one orientation interferes with the detection of added gratings of similar orientation: the contrast necessary to detect the grating is raised. But there is very little masking effect of one grating on another one of a very dissimilar orientation. An even more direct indication that the neurones responsible for threshold detection in man are orientation-selective comes from a recently discovered sensory adaptation phenomenon. Gilinsky (1968) and Blakemore & Campbell (1969*a, b*) found that prolonged observation of a high-contrast grating subsequently causes a considerable rise in the contrast threshold for gratings of similar orientation. The latter authors found that this psychophysical after-effect is accompanied by a marked reduction in the amplitude of the occipital potential evoked by a low contrast grating of the same orientation. Campbell & Maffei (1970) have extended this electrophysiological evidence. Presumably adaptation to a high-contrast grating depresses the sensitivity of a limited set of neurones in the human brain.

It is of interest, then, that this phenomenon is also specific for the spatial frequency of the adapting grating (Blakemore & Campbell, 1969*a, b*; Pantle & Sekuler, 1968). The threshold is only elevated significantly for gratings whose spatial frequency is rather similar to that of the adapting pattern. The human neurones whose sensitivity is being depressed seem, therefore, to be frequency-selective as well as orientation-selective, just like those in the cat and the monkey.

An obvious question that arises is whether the orientation and frequency-selectivity in man (and for that matter in the other animals) is functional. Do the neurones actually encode and signal the orientation and dimensions of suprathreshold retinal images or are those properties of their receptive fields merely incidental to some other function?

There is at least one critical test of whether the neural elements revealed

by adaptation are really involved in the analysis and perception of spatial dimensions. When a grating of suprathreshold contrast is viewed, it activates frequency-selective neurones in proportion to their sensitivity to the grating's frequency. Imagine that the brain distinguishes, say, the repetition period of a grating by the identity of the most active frequency-selective neurone in the visual cortex, or by some other measure of central tendency derived from the distribution of activity among the whole population of neurones. Assume that prolonged stimulation reduces the over-all sensitivity of a neurone without altering its characteristic frequency—the frequency to which it is most sensitive. Consequently, adaptation at one particular spatial frequency selectively depresses the sensitivity of neurones whose characteristic frequencies are in the vicinity of that frequency. Subsequent observation of a test grating of somewhat different spatial frequency will produce a distribution of excitation different from normal. The central tendency of the distribution will be shifted away from the adapting frequency, and hence so should the *perceived* frequency of the test grating.

In short, after adaptation, a grating with narrower bars than those of the adapting pattern should seem to be of an even higher spatial frequency, and a lower frequency grating should seem lower still. But this prediction only holds if the neurones are actually responsible for the encoding of spatial dimensions. Blakemore & Sutton (1969) have presented preliminary evidence that this expected phenomenon actually occurs and here we examined the after-effect in more detail.

Definitions

I_{\max} = luminance of the brightest part of the grating.

I_{\min} = luminance of the dimmest part.

$$\text{Contrast} = \frac{I_{\max} - I_{\min}}{I_{\max} + I_{\min}}.$$

$$\text{Mean luminance} = \frac{I_{\max} + I_{\min}}{2}.$$

Spatial frequency: the number of cycles of a repetitive grating pattern per degree of visual angle.

Spatial period: the visual angle subtended by a single cycle of the grating. Period = 1/spatial frequency.

Octave: one octave is a change in frequency by a factor of two. Octaves of spatial frequency are, therefore, equal increments on a logarithmic scale.

METHODS

We used the method of Schade (1956) as modified by Campbell & Green (1965) to generate vertical gratings of sinusoidal or square-wave form on oscilloscope screens. The spatial frequency and contrast of the pattern could be varied by altering the frequency and amplitude of the signal from an oscillator that was used to modulate the uniform raster on the screen.

From a distance of 114 in. the subject viewed two oscilloscope tubes, one directly above the other. The screens were masked down to rectangular areas each subtending 1.5° in width and 1.25° in height. The gap between the two screens was 25 mm wide and in the centre of it was a self-luminous, horizontal fixation bar, about 0.5° by 4 mm.

The experimenter could turn the gratings on and off and alter their spatial frequency and contrast, independently for the two screens. In addition, the subject held a ten-turn potentiometer that was coupled in series with the time-base velocity control of the lower oscilloscope. Turning this potentiometer therefore changed the spatial frequency on that screen. The period of the grating varied linearly with the voltage across the potentiometer, which was monitored on a digital voltmeter and displayed on a printer when the subject pressed a button.

It must be emphasized that none of these manoeuvres to switch the patterns on and off, and change their frequency and contrast, altered their mean luminance appreciably. The light adaptation of the subject was, therefore, held constant throughout these procedures.

For some experiments we used oscilloscopes with a blue-white (P-7) phosphor, and on other occasions the tubes used had a green-yellow phosphor (P-31). The type of phosphor, the mean luminance of the screen and other experimental details are noted in the Figure legends or the text. The luminance of the dim background was always about 0.07 cd/m^2 .

For the experiments on very low spatial frequencies the stimulus array and viewing distance were altered, as described in the text.

RESULTS

Demonstration of the phenomenon

Perhaps the reader should, first of all, convince himself that the after-effect really does occur. Look at the upper right-hand pair of gratings in Fig. 1*B* to be sure that they are identical in spatial frequency. Now hold the illustration at a distance of about 75 cm and stare at the horizontal bar in between the two vertical gratings on the upper left (Fig. 1*A*). Move your gaze back and forth along the bar, to avoid the formation of a conventional negative after-image of the patterns, but be sure not to look away from the bar itself. After about 20 sec quickly transfer your fixation to the small spot in between the two gratings on the upper right, and compare their spatial frequencies while fixating in between. Do they still seem identical? The top one should seem higher and the bottom one lower in spatial frequency because of adaptation of those retinal regions to low and high frequency gratings respectively.

Now, after recovering for at least 2 min, repeat the whole procedure,

but this time adapt to the pair of gratings on the middle left (Fig. 1C), which are identical in spatial frequency to those in Fig. 1A but are tilted at 45° to the vertical. When you now inspect the vertical test gratings in Fig. 1B they should hardly be altered in apparent frequency. But if you view the test gratings of the same orientation in Fig. 1D, after adapting to Fig. 1C, they will seem dramatically changed. Finally, adapt to the horizontal patterns in Fig. 1E, this time moving your gaze up and down over the bar to prevent after-images. There should be no disturbance at all of the vertical gratings of Fig. 1B. The phenomenon is, then, orientation-specific.

Measuring the after-effect

For ease of reproduction the gratings of Fig. 1 have square-wave form, but for the experiments we chose to use patterns with sinusoidal luminance profile because of their simplicity, in terms of Fourier theory. (Any wave form can be thought of, and described in mathematical terms, as the mixture of a number of sine waves.) Also, in this demonstration, two parts of the retina are adapted to different spatial frequencies to emphasize the phenomenon. In the actual experiments we adapted to only one frequency at a time.

Campbell, Nachmias & Jukes (1970) have measured the precision with which differences in spatial frequency can be detected, and it is very high: in the range of 1–20 c/deg of visual angle, two gratings can be just discriminated if their frequencies differ by 4%. Before our initial experiments we checked the exactitude with which two gratings could be matched in frequency. Similar vertical gratings were shown on the two screens and the subject attempted to match with the potentiometer the frequency of the lower grating to that of the upper, while fixating in between. He offset the potentiometer before each reading. The spatial frequency of these test gratings was varied in quarter octave steps, between 1.05 and 28.3 c/deg of visual angle. Three settings were made at each frequency, working up through the frequency spectrum, and three more on the way down. This whole procedure was repeated at the end of the first set of experiments to make sure that there had been no change in the equipment or the subject's criterion. There was no consistent difference between these two runs.

The means ($n = 12$) of the unadapted settings are shown as open circles in Fig. 2A (subject C.B.) and B (subject P.S.).

Let p_0 be the period of the standard grating on the upper screen;

p_1 be the period of the matching grating on the lower screen, without prior adaptation;

p_2 be the period of the matching lower grating during adaptation.

The logarithmic abscissa is the spatial frequency ($1/p_0$) of the upper grating and the ordinate is, for each spatial frequency, the ratio of the period of the matched lower grating to that of the upper (p_1/p_0). A perfect match would have a value of 1.0, marked with an open arrow on the ordinate. If the lower grating were set a little higher in frequency than the upper the match would have a value less than 1.0. The match can be made

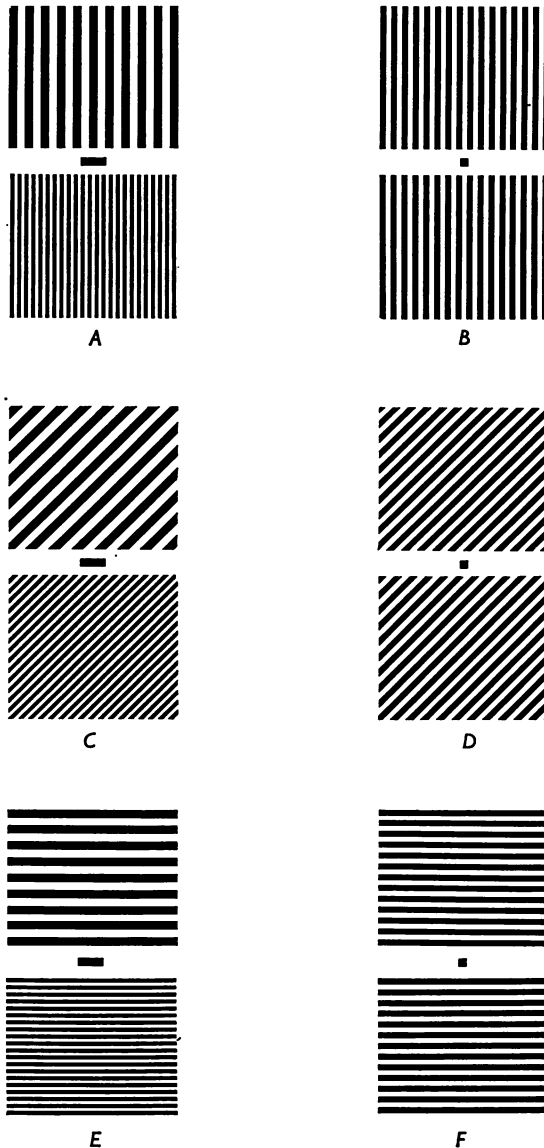


Fig. 1. For legend see opposite page.

very closely: the average s.e. ($n = 12$) of these settings was only about 0.02 on the ordinate.

In the adaptation experiments a pattern was shown on the upper screen while the lower one was blank and of the same mean luminance. The subject fixated in between, letting his gaze wander to left and right along the horizontal bar. After 3 min initial adaptation, the experimenter suddenly displayed a test grating on each oscilloscope and the subject quickly matched the lower grating (falling on unadapted retina) to the apparent frequency of the upper (which fell on adapted retina). He took about 2 sec to make this match, then he pressed the button to display the result on the printer, and the adapting array immediately reappeared. Ten seconds of re-adaptation were allowed before the next test was made. This sequence was repeated, taking six readings altogether at each test frequency, three on the way up through the frequencies and three more on the way down. This method of frequent interpolation of the same adaptation pattern was found to hold the adaptation level constant, for the settings on the ascending and descending runs were not consistently different.

In Fig. 2, the filled circles and vertical bars stand for the mean ($n = 6$) and the s.e. of the matches made while the subject was adapting to a grating of 10 c/deg (marked by a filled arrow on the abscissa). The ordinate is (p_2/p_0) , the ratio of the period of the matched lower grating during adaptation, p_2 , to that of the upper grating, p_0 . The contrast of the adapting pattern was 1.5 log units above the subject's psychophysical threshold contrast for 10 c/deg, measured while fixating the bar. There is a distinct elevation of apparent spatial frequency (decreased period ratio)

Legend to Fig. 1.

You can use this diagram, as described in the text to demonstrate the perceived frequency shift. Hold the illustration about 75 cm away and, after assuring yourself that the three pairs of gratings on the right (*B*, *D* and *F*) are equal in spatial frequency, adapt for about 20 sec to the pair of vertical gratings (*A*) on the left, by looking around the horizontal bar in between the upper (low frequency) and lower (high frequency) patterns. Then quickly transfer your gaze to the dot in between the identical vertical gratings (*B*) on the right. Do they still seem the same? Allow at least 2 min recovery before repeating your observation but this time adapt to the diagonal gratings (*C*) and look at the effect on the similarly tilted gratings (*D*) as well as upon the vertical ones (*B*). Finally, test the effect on all three pairs of test gratings (*F*, *D* and *B*) of adapting to the horizontal patterns (*E*). While adapting in this case move your gaze up and down over the bar, to avoid the generation of an after-image. Adaptation to the diagonal gratings (*C*) may cause some slight disturbance in the apparent spatial frequency of the vertical (*B*) but the horizontal adapting patterns (*E*) should have no effect on the vertical.

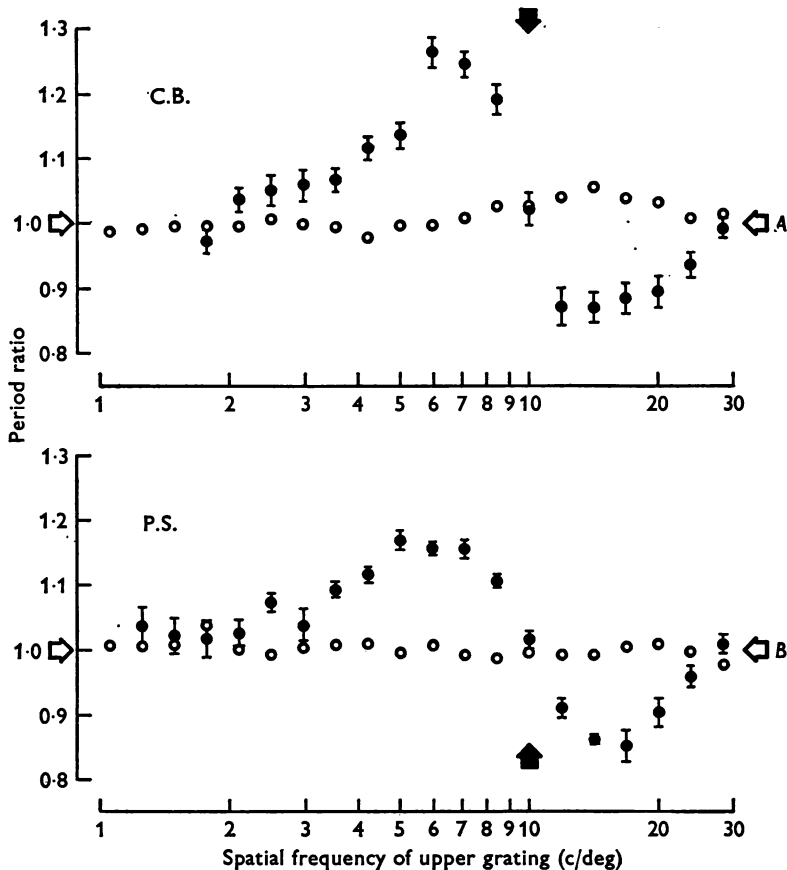


Fig. 2. The effect of spatial adaptation upon spatial frequency discrimination. The results for the two subjects C.B. and P.S. are plotted separately in Fig. 2A and 2B. The subject, fixating in between the two oscilloscopes, altered the spatial frequency of the grating on the lower screen until it seemed to match that of the grating on the upper screen. The test spatial frequencies, at which judgements were made, were spaced at $1/4$ octave intervals. The ordinate is the ratio of the periods of the gratings on lower and upper oscilloscopes, when they appeared matched. The open circles are means ($n = 12$) of settings made with no pre-adaptation. (Period ratio = p_1/p_0 .) The filled circles are the means with their s.e. ($n = 6$) of settings made after adapting to a grating of 10 c/deg on the upper screen alone, at a contrast of 1.5 log units above the subject's contrast threshold. (Period ratio = p_2/p_0 .) For test frequencies below 10 c/deg a greater period (lower spatial frequency) is needed on the lower screen to match the apparent period of the upper grating. Above 10 c/deg the apparent period of the upper pattern is reduced. The effect is limited to spatial frequencies near that of the adapting grating, marked with a filled arrow, but at the adapting frequency itself there is no significant disturbance of spatial frequency.

Oscilloscope phosphor: P-7. Mean luminance: 1.7 cd/m^2 . Contrast of test gratings: 0.6.

for gratings higher than 10 c/deg, up to about 25 c/deg, and a decrease of apparent frequency for patterns lower than 10 c/deg, down to about 2.5 c/deg.

The spatial frequency of the adapting grating

Middle frequencies. Fig. 3A and B show the results of adapting to a number of different spatial frequencies for the two subjects. Different symbols are used to plot the results for adapting frequencies of 2.5, 3.5, 5.0, 7.1, 10.0 and 14.2 c/deg, marked with filled arrows on the abscissa. In each case the contrast of the adapting pattern was 1.5 log units above the subject's threshold.

In Fig. 3 the ordinate expresses the period of the matching grating relative to the unadapted settings shown in Fig. 2: the period ratio p_2/p_1 is plotted for each test spatial frequency on the upper screen. This way of plotting the results takes account of the occasional slight mis-matches made even in the absence of adaptation (Fig. 2).

The shape of the adapting function is rather similar for all these adapting frequencies, except perhaps for 2.5 and 3.5 c/deg, where the whole after-effect is somewhat smaller. To demonstrate just how much alike they are, the results of Fig. 3, except those for 2.5 and 3.5 c/deg, are normalized for the adapting frequency in Fig. 4.

Lower spatial frequencies. The fact that the after-effects for adaptation to 2.5 and 3.5 c/deg were rather less than those for higher frequencies led us to explore the low adapting frequencies a little more closely.

The subject, C.B., moved in to a distance of 57 in. from the oscilloscopes, thus doubling their angular subtense to 3° by 2.5° . This ensured that, even with the very lowest spatial frequencies used here, there were several cycles of the grating on the screen. In order to avoid the possibility of vernier alignment of the bars on the lower screen with those on the upper, for these low spatial frequencies, we chose not to have the two gratings directly one above the other. The two oscilloscopes were moved so that, by means of a suitably placed front-silvered mirror, the two screens appeared side by side some 0.5° apart. The horizontal fixation bar was now situated in the centre of this gap between the screens. The adapting pattern was shown on the right-hand oscilloscope and when test patterns appeared on both screens the subject adjusted the grating on the left-hand tube. The subject adapted in exactly the same way as before, while fixating the bar. We tried adapting frequencies of 3.0, 2.5, 2.1, 1.8 and 1.5 c/deg. all set at 1.5 log units above their own contrast thresholds. The results are shown in Fig. 5. Strangely enough, the after-effect is not only smaller for these low frequencies but the function is no longer centred about the adapting frequency itself. The effect remains centred at between

3 and 3.5 c/deg. This result was not totally unexpected, for Blakemore & Campbell (1969*b*) found that adaptation to these very low spatial frequencies causes an elevation of threshold at about 3 c/deg and not at the adapting frequency itself.

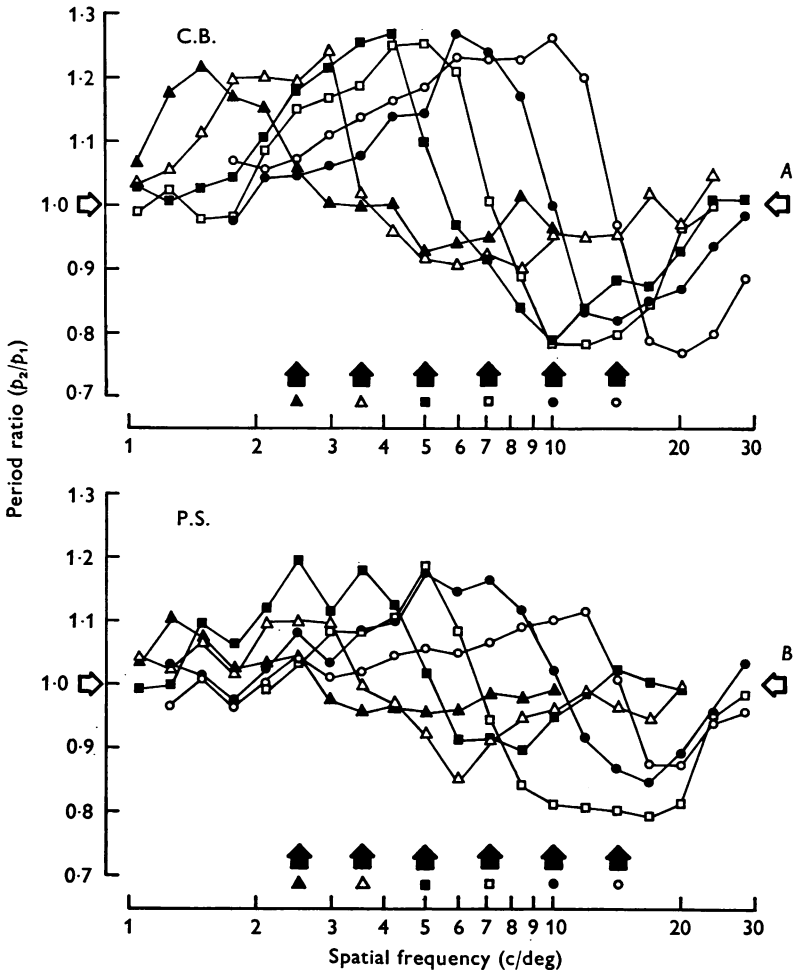


Fig. 3. The effect of adapting at six different frequencies for the two subjects. The filled arrows indicate the adapting frequencies of 2.5, 3.5, 5.0, 7.1, 10.0 and 14.2 c/deg, and below each arrow is the symbol used to plot the period matches made during adaptation. The adapting pattern was always set at a contrast of 1.5 log units above the subject's contrast threshold. In this case the ordinate is p_2/p_1 , the ratio of the mean matching period ($n = 6$) during adaptation to the mean unadapted match ($n = 12$).

Phosphor: P-7. Mean luminance: 1.7 cd/m². Contrast of test gratings: 0.6.

Adapting to a square wave grating

The Fourier spectrum of a square-wave distribution consists of all the odd-harmonics of the repetition frequency, the amplitude of each harmonic being inversely proportional to its number. There is evidence that, at threshold, the recognition of the wave form of a grating is determined by its harmonic content. Campbell & Robson (1968) found that the contrast

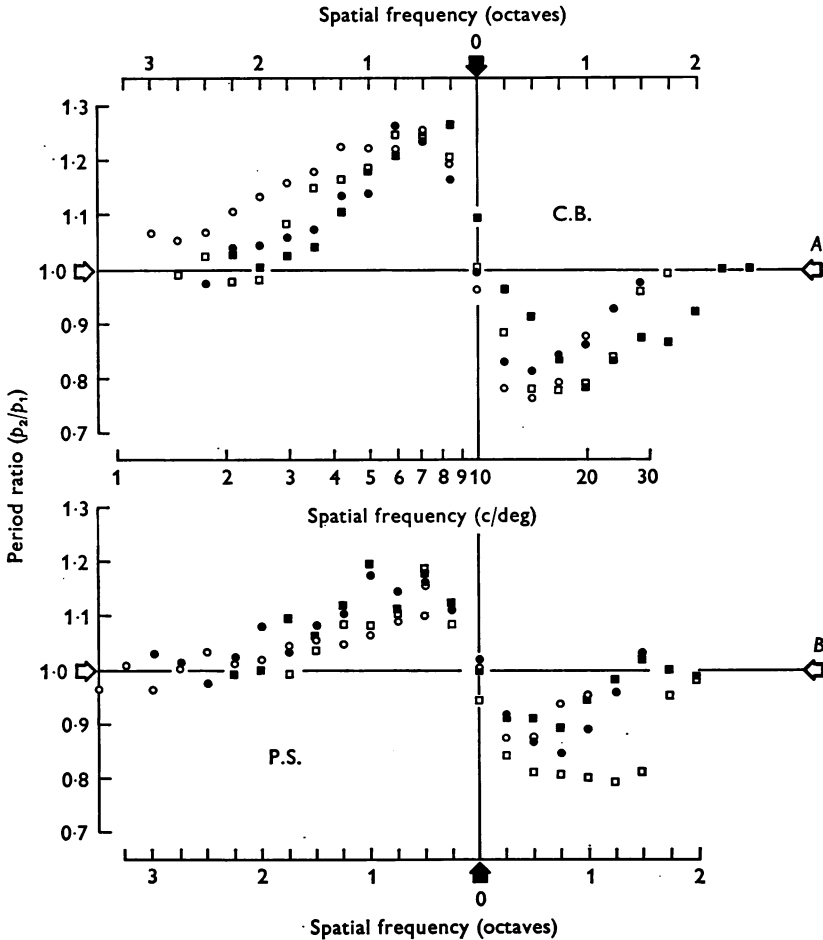


Fig. 4. The results from Fig. 3 are normalized on the abscissa for the adapting spatial frequency. The same symbols as in Fig. 3 are used to plot the effects of adapting to 5.0, 7.1, 10.0 and 14.2 c/deg, but the points have been shifted along the abscissa until all the adapting frequencies lie at 10 c/deg. marked with a filled arrow. The upper and lower abscissae are expressed in octaves of spatial frequency on each side of the adapting frequency. The middle abscissa is conventional spatial frequency.

of a square-wave grating must be raised to the point at which the amplitude of the third harmonic reaches its own threshold before the grating can be distinguished from a sinusoidal grating. This finding is compatible with the assumption that different and independent 'channels' are responsible for detection of the fundamental and third harmonic frequencies. Blake-more & Campbell (1969*b*) measured the threshold elevation after adapting to a square-wave grating and found that threshold is markedly elevated

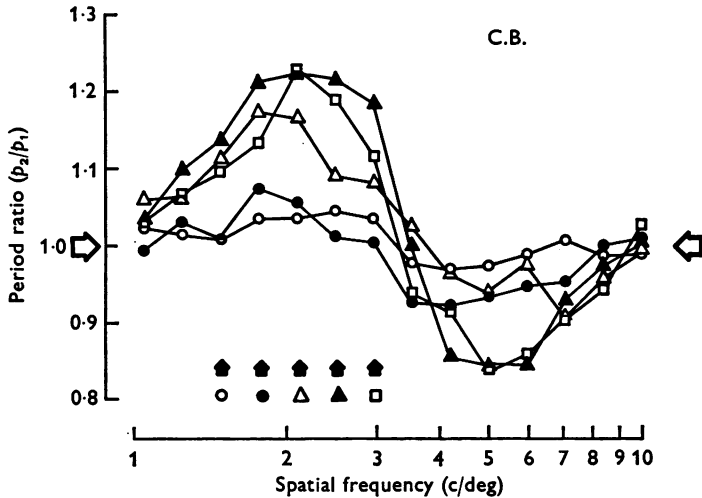


Fig. 5. Low adapting spatial frequencies. Subject C.B. viewed the two screens side by side from a distance of 57 in. He adapted to gratings, appearing on the right-hand screen, of 3.0 (□), 2.5 (▲), 2.1 (△), 1.8 (●) and 1.5 (○) c/deg, each one set at 1.5 log units above his contrast threshold. At each test frequency the period of the matching grating during adaptation (mean of $n = 4$) is expressed as a ratio of the period of a matching grating (mean of $n = 4$) without adaptation, the ordinate being the ratio p_2/p_1 . Oscilloscope phosphor: P-31. Mean luminance: 2.2 cd/m². Contrast of test gratings: 0.32.

for gratings of frequencies near the third harmonic of the square-wave grating as well as for frequencies near the fundamental. It is just as if each harmonic in the pattern adapts out its own detection system.

We were interested to see whether the current phenomenon is determined solely by the period of the adapting pattern and, say, its peak-to-trough contrast, or whether the harmonic components of a complex wave form act independently upon the nervous system.

The subject made spatial frequency matches while constantly adapting to a square-wave grating of 3.5 c/deg, indicated in Fig. 6 by a filled arrow, and at a contrast of 0.59. Then we repeated the measurements for adaptation to a sinusoidal grating of the same frequency at a contrast of 0.75.

This is the effective amplitude of the fundamental frequency in the square-wave pattern, $4/\pi$ times the amplitude of the square wave. For both types of adapting grating, the test gratings had sinusoidal profiles. The results

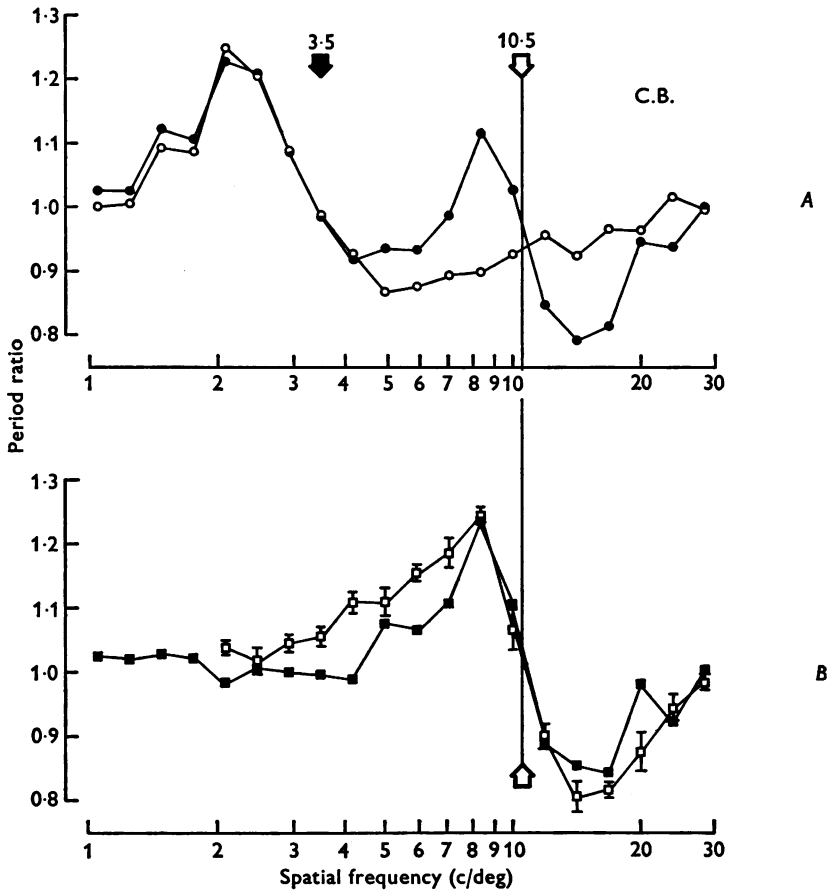


Fig. 6. The effect of the harmonic components of a square-wave adapting grating. *A*. Subject C.B. adapted to a square-wave grating of 3.5 c/deg and at a contrast of 0.59 and the results are plotted as filled circles. The open circles show the effect of adapting to a sinusoidal grating of the same frequency but at a contrast of 0.75. In each case the effect is expressed, as in Fig. 3, as the ratio of the mean ($n = 6$) matching period during adaptation to that during the original unadapted experiments of Fig. 2*A* ($n = 12$). *B*. The filled squares plot the difference between the sine and square-wave results of Fig. 6*A*, as explained in the text. The open squares show the mean result with the s.e. ($n = 6$) of adapting to a sinusoidal grating of the third harmonic frequency, 10.5 c/deg, and at a contrast of 0.25. In this case the ordinate is the ratio of the period setting to the mean matching period ($n = 12$) in the first unadapted settings (Fig. 2*A*). Phosphor: P-7. Mean luminance: 1.7 cd/m². Contrast of test gratings: 0.6.

are plotted in Fig. 6A, open circles for the sinusoidal and filled for the square-wave adapting grating. If, at each test frequency, p_2 is the average period of the matching grating on the lower screen during adaptation to the sinusoidal pattern, and p_3 during adaptation to the square wave grating, the units for the ordinate are p_2/p_1 and p_3/p_1 respectively; p_1 is the mean matching period at that test frequency in the original unadapted experiment (Fig. 2A).

There is an obvious difference between the two functions in the region of the third harmonic frequency, 10.5 c/deg, marked with an open arrow. It is as if this harmonic is causing its own after-effect. This feature of the results can be seen more clearly in Fig. 6B, where we have replotted the results of Fig. 6A as the ratio, $(p_3/p_1)/(p_2/p_1) = p_3/p_2$ (filled squares), and for comparison, the after-effect of adapting to a sinusoidal grating of 10.5 c/deg at a contrast of 0.25 (open squares). This is the effective amplitude of the third harmonic in the square-wave grating of Fig. 6A, one third the amplitude of the fundamental frequency component. For each test-frequency, the mean period of the matching grating during adaptation to this grating has been divided by the mean match without adaptation (Fig. 2A). Clearly the two curves in Fig. 6B resemble each other very closely.

The contrast of the adapting pattern

Blakemore & Campbell (1969b) have reported that the magnitude of the threshold elevation after adapting to a grating depends upon the supra-threshold contrast of the latter. They have also shown that the shape of the adaptation characteristic (log relative threshold increase versus test spatial frequency) stays constant as the contrast of the adapting pattern is raised.

We studied the effect of three contrast levels of adaptation at 8.4 c/deg. First of all subject C.B. made four unadapted frequency matches for gratings between 2.5 and 20 c/deg. He then adapted to a grating of 8.4 c/deg at a contrast of 0.022, 0.75 log units above his psychophysical threshold contrast for that frequency. Four readings were taken at each test frequency during adaptation. Then the contrast of the adapting grating was raised to 0.125 (1.5 log units above threshold), more settings were made, and finally the adapting contrast was set at 0.7 (2.25 log units above threshold) and a final set of observations made.

This whole procedure was repeated on four successive days and the pooled results are plotted in Fig. 7. The ordinate is the usual period ratio p_2/p_1 . Filled circles, squares and triangles show the effect for 0.022, 0.125 and 0.7 contrast respectively. The half-width of the stippled band is $2\sqrt{2} \times$ the average s.e. for the unadapted readings (calculated from the

four daily means). The band, therefore, marks the 95% confidence interval for deviations from a correct frequency match. Points falling outside this area denote significant mismatches ($P < 0.05$).

Evidently, even the lowest contrast level produces a measurable after-effect, and the general shape of the function does not change markedly as the contrast is raised. The mis-match is simply bigger at all affected frequencies.

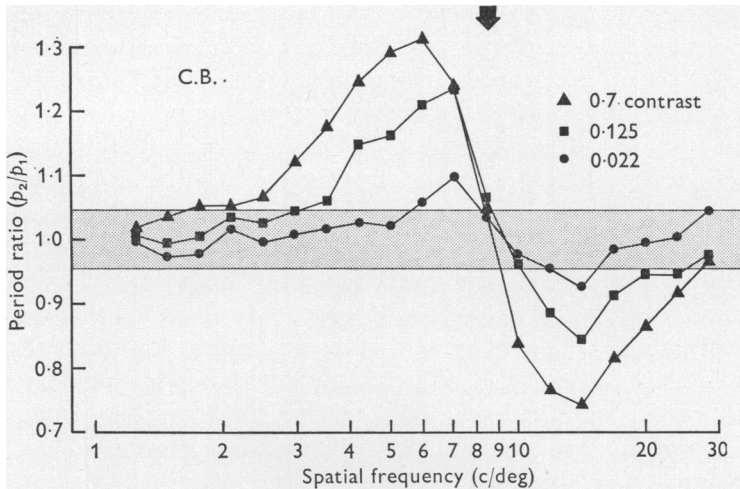


Fig. 7. Subject C.B. adapted to gratings of 8.4 c/deg at contrast levels of 0.022 (●), 0.125 (■) and 0.70 (▲). There were four separate experimental sessions, taking, at each test frequency, four unadapted settings and then four settings during adaptation. The effect plotted is the mean ($n = 16$) effect of adaptation and is expressed as a ratio of the mean unadapted match ($n = 16$). The stippled band delimits the 95% confidence level ($2\sqrt{2}$ times the mean s.e. of the unadapted settings) for significant deviation from the unadapted settings.

Phosphor: P-31. Mean luminance: 2.2 cd/m². Contrast of test gratings: 0.32.

The contrast of the test gratings

The magnitude of the change in apparent frequency does not seem to depend critically on the contrast of the test patterns, as long as they can be seen at all. Subject C.B. adapted continuously to a 10 c/deg grating at a contrast of 1.5 log units above threshold. Test gratings of 5.9 c/deg were interpolated and matched every 10 sec. Seven contrast levels of the test grating were used and six readings taken for each. For contrast levels of 0.5, 0.75, 1.0, 1.25, 1.5, 1.75 and 2.0 log units above the unadapted threshold, the mean ($n = 6$) apparent spatial frequency of the 5.9 c/deg grating was 5.23, 5.35, 5.43, 5.43, 5.32, 5.27 and 5.32 c/deg respectively.

The orientation of the adapting grating

The reader has seen for himself from Fig. 1 that this phenomenon is orientation-selective: a diagonal grating will hardly distort the apparent frequency of a vertical one, although it markedly influences a similarly tilted test grating. We were interested to know just how orientation-specific the after-effect is.

Our approach was similar to that in the experiment on adapting contrast. Because of difficulty in rotating the oscilloscope tubes, we took a photograph of a high-contrast sinusoidal grating and used the trans-illuminated negative as the adaptation pattern. This was mounted in a rotatable frame fixed to a sheet of opal Perspex (Lucite). By means of two projectors, with gelatine colour filters, directed from behind at unmasked portions of the Perspex, we mimicked the normal oscilloscope stimulus array in angular dimensions, mean luminance and colour. The rotatable grating appeared only in the upper aperture. Its contrast, assessed by matching it to a grating on an oscilloscope, was about 0.7 and its spatial frequency 8.4 c/deg. This whole apparatus was mounted directly above the two oscilloscopes so that the subject could adapt by fixating between the rotatable grating and the blank field and then quickly move his gaze down to the equivalent position between the two oscilloscopes to make the frequency matches.

The subject made four unadapted settings at each test frequency before every adaptation session. He adapted to gratings rotated 15, 25 and 35° clockwise, as well as at the vertical itself, with long rest periods in between. The results are shown in Fig. 8. Again the effect is expressed as the period ratio p_2/p_1 at each frequency, and the stippled band marks the 95% confidence interval.

There is, then, a distinct after-effect for vertical test gratings even after adapting to a grating of 35° to the vertical. Beyond about 45°, however, there is no significant effect (J. Nachmias & C. Blakemore, in preparation).

The time course of induction and recovery

We were interested in the rate of growth of the effect during adaptation and its decay afterwards. To obtain complete records of the decline of the after-effect for short adaptation times we displayed the voltage across the potentiometer controlling spatial frequency on the lower oscilloscope on a pen recorder (Brush Mark 220). We chose to adapt at 8.4 c/deg and to test frequency-matching only at 11.9 c/deg, one half-octave higher, where the effect is particularly large. After adaptation, the subject continuously followed his recovery, trying constantly to keep the test gratings matched.

In Fig. 9 there are three pen records each for adapting durations of 5, 10, 15, 30, 45, 60, and 120 sec.

The initial after-effect, immediately after adaptation, seems to grow for up to a minute or more of adaptation. It is also very clear that the recovery phase becomes progressively prolonged with increasing adaptation time.

Next we studied the effect of adapting at 8.4 c/deg for 6.5 min. We took readings on the voltmeter and printer as before and tested only at 11.9

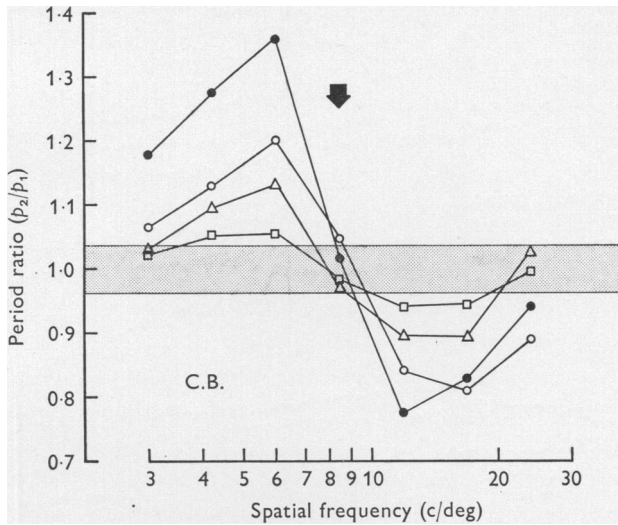


Fig. 8. The effect of tilting the adapting grating. Subject C.B. adapted to a grating of 8.4 c/deg and 0.7 contrast at 0° (vertical) (●) and tilted clockwise at 15° (○), 25° (△) and 35° (□) to the vertical. The after-effect upon a vertical test grating is plotted in the usual fashion, all the results superimposed. Each point is the mean of four readings and the change in apparent period is expressed as the ratio of the period setting during adaptation to the mean ($n = 16$) unadapted setting at each frequency. The stippled band again has a half-width of $2\sqrt{2}$ times the average s.e. of these unadapted values.

c/deg and at 8.4 c/deg itself. Throughout adaptation, we briefly interposed a test trial every 15 sec, alternating between 11.9 and 8.4 c/deg on successive tests. The subject made only one setting each time and made it as quickly as possible. After adaptation, one reading at 11.9 and another at 8.4 c/deg were taken in quick succession every 30 sec and the subject stared between the blank screens in between observations. This whole routine was repeated on two other days and Fig. 10 shows the mean results.

The effect grows for about the first 2 min of adapting and after 6.5 min of adaptation the complete recovery phase takes several minutes.

Finally, we had one marathon adapting session of 30 min. The subject first of all made four unadapted frequency matches at each of seven test frequencies in half octave steps, from 3.0 to 23.8 c/deg. He then adapted to 8.4 c/deg, continuously trying to hold fixation on the bar between the screens. At 5, 15, and 25 min after the start of adaptation we measured the after-effect at the seven test frequencies in the normal way, but taking

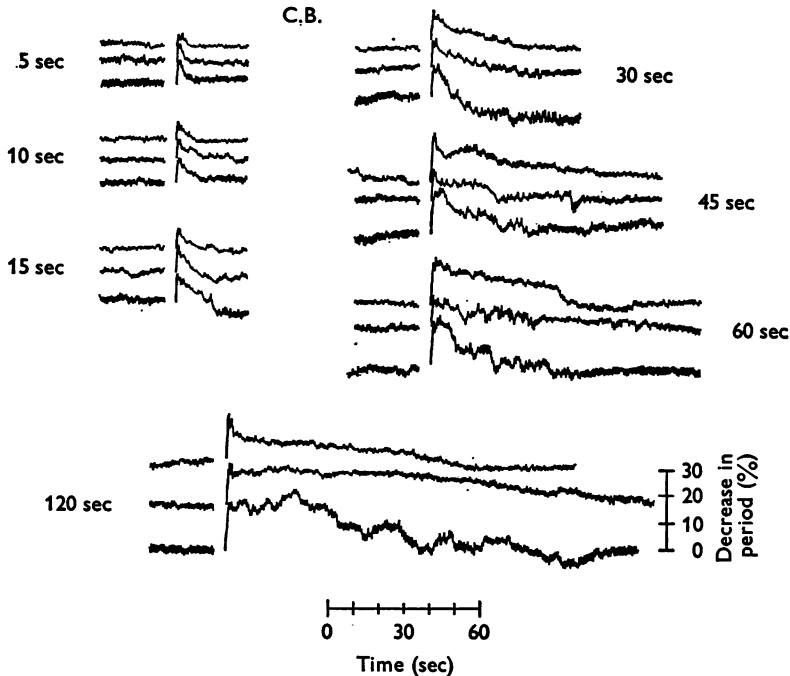


Fig. 9. The voltage across the potentiometer controlling the period of the lower grating was displayed on a pen recorder to produce these records of the complete recovery of the after-effect for short adaptation times. During the initial, fairly steady portion of each record the subject C.B. matched the grating on the lower screen to one of 11.9 c/deg, 0.32 contrast, on the upper screen. He tracked back and forth on the potentiometer over the range of subjective equality. The discontinuity in each record marks the break for adaptation during which a grating of 8.4 c/deg at a contrast of 0.72 was shown on the upper screen and the lower one was blank. The record restarts where the higher frequency test gratings appeared on both screens, and the subject attempted to keep the two matched throughout the period of recovery. The record was continued until the setting had returned to the approximate value of the unadapted record. Time is indicated on the horizontal scale. An upward movement of the pen indicates an increase in spatial frequency. The length of adapting time is shown against the records. There are three records for each different value of adapting time and they are slightly displaced vertically from each other. (Phosphor: P-31; luminance: 2.2 cd/m².)

only two readings at each. After this ordeal the subject was allowed to look wherever he pleased for the next few hours, but every now and then we took a pair of readings at each test frequency to see how his recovery was progressing.

Fig. 11 has some of the results for this experiment plotted as mismatches relative to the unadapted settings ($n = 4$), the period ratio being p_2/p_1 . It shows the results during adaptation (mean of the three determinations,

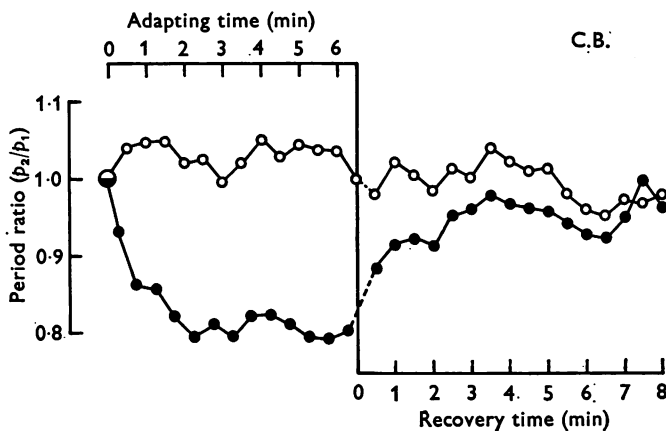


Fig. 10. Frequency matches were made as described in the text at 11.9 and 8.4 c/deg (contrast = 0.32) during and after adaptation to a grating of 8.4 c/deg (contrast = 0.72). Only one setting was made at a time but the whole procedure was performed three times. The ordinate is the ratio of the period of the lower grating during and after adaptation, to the mean period ($n = 12$) of four settings made without adaptation, before each session. The means of these unadapted settings are plotted with large symbols at zero adapting time and they have, of course, a value of 1.0 on the ordinate. The other open circles are the mean ($n = 3$) settings at 8.4 c/deg itself and the filled circles the mean ($n = 3$) readings for 11.9 c/deg. The abscissa is time and the vertical line through the graph marks the end of adaptation. (Phosphor: P-31; luminance: 2.2 cd/m².)

total $n = 6$), and at 10, 20, 100, 180 and 360 min, after the end of adaptation ($n = 2$ for each point). The after-effect has certainly outlasted the adaptation time by more than an hour.

The results for the two test frequencies half an octave on each side of 8.4 c/deg are plotted in detail in Fig. 12. Each point is the mean of a pair of readings and is expressed as the deviation from the unadapted match ($n = 4$). The stippled band again indicates the 95% confidence interval (on the basis of the average s.e. of the pairs of readings before adaptation).

There is a significant after-effect as long as 160 min after the end of half-an-hour's adaptation.

Interocular transfer

Subject C.B. made six unadapted frequency matches each at 4.2, 7.1 and 11.9 c/deg using only his right eye. He then adapted to a grating of 7.1 c/deg seen with the left eye alone, 1.5 log units above threshold, and periodically he made matches for the three frequencies in the right eye

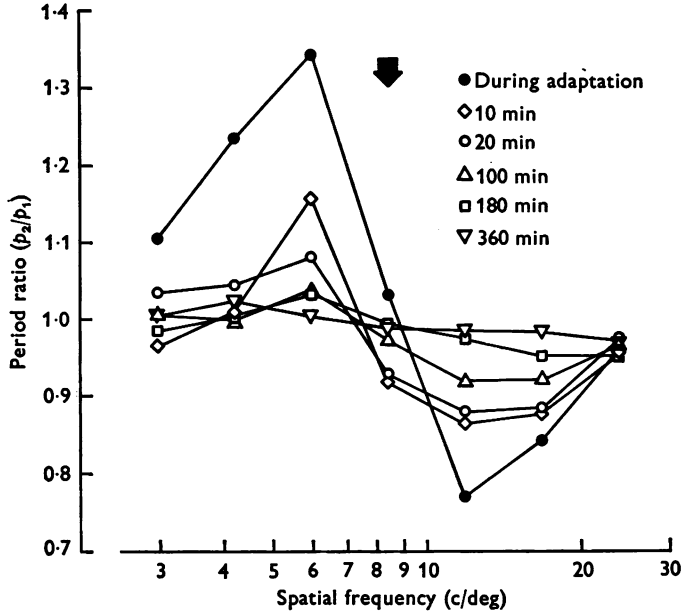


Fig. 11. The effect of adapting to a grating of 8.4 c/deg, 0.72 contrast, for 30 min. First, four unadapted matches were made at each test frequency (0.32 contrast). The ordinate is the ratio of the period of matching gratings, during and after adaptation, to the mean period of the unadapted settings. The filled circles show the means of 6 settings made during adaptation, at 5, 15 and 20 min after the start and the open symbols plot the means of two readings at each frequency taken at various times, shown in the legend, after the end of adaptation. (Phosphor: P-31; luminance: 2.2 cd/m².)

alone. After a rest period, this procedure was repeated, but using the right eye alone for both adaptation and testing. There was a distinct after-effect, even when adaptation and test gratings were seen with different eyes. However, when the gratings were seen with the same eye, the apparent change in period was 1.5 times greater.

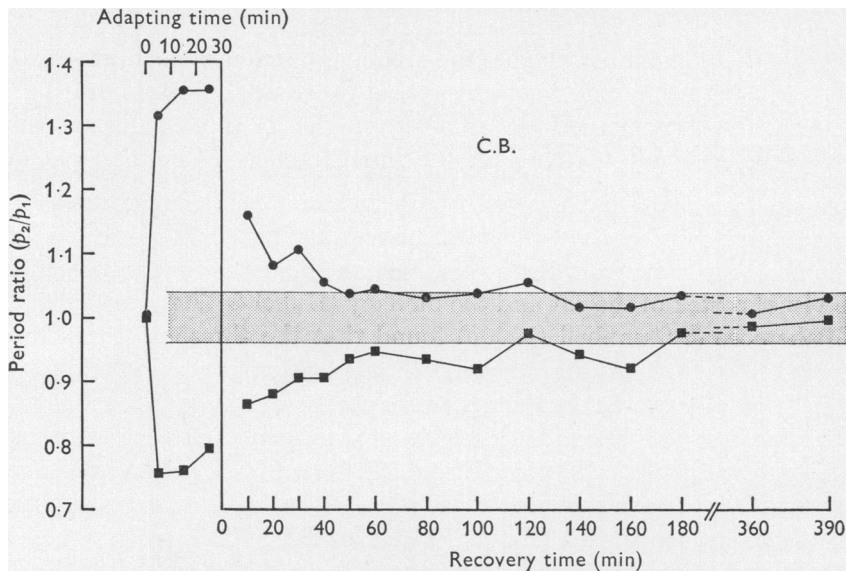


Fig. 12. The frequency matches at 5.9 (●) and 11.9 (■) c/deg made during the experiment described in Fig. 11, are plotted in detail. The ordinate is the ratio of the matching period on the lower screen during and after adaptation to the mean ($n = 4$) of the immediately preceding undapted settings. The latter settings (with, of course, a value of 1.0 on the ordinate) are plotted at zero adapting time. The half width of the stippled band is $2\sqrt{2} \times$ the average s.e. of pairs of readings.

DISCUSSION

Our principal finding is that prolonged observation of a grating, which is known to raise the contrast threshold for gratings of similar spatial frequency, also causes a disturbance of the apparent spatial frequency of other suprathreshold gratings. Spatial frequencies higher and lower than the adapting pattern seem, respectively, to be higher and lower than in fact they are. This phenomenon is predictable on the assumption that the frequency-selective neural mechanisms revealed by the threshold elevation after-effect (Blakemore & Campbell, 1969*a, b*) are actually involved in the signalling of the dimensions of retinal images. We take the existence of this effect as confirmation of the presence of such frequency encoding neurones in man.

The similarity, in every regard of the properties of the present after-effect and the threshold elevation effect, points to a common neural origin for the two phenomena. The two effects only substantially influence spatial frequencies up to 1.5 octaves away from the adapting frequency on the high frequency side, and 2 octaves away on the low side (Fig. 4). In-

creasing the suprathreshold contrast of the adapting pattern increases the magnitude of the after-effect just as with the threshold elevation effect. The effect is orientation-specific (Fig. 8) and so is the threshold effect (Gilinsky, 1968; Blakemore & Campbell, 1969*a*). The two phenomena even show interocular transfer to about the same extent. Here, then, is evidence that somewhere in the human brain, and probably in the visual cortex, there are neurones that are selectively sensitive to the orientation and spatial frequency content of retinal images, and a certain proportion of them have an input from both eyes. Just such cells are known to exist in the visual cortex of the cat and the monkey (Hubel & Wiesel, 1962, 1968).

Blakemore & Campbell (1969*b*) found that the threshold is no longer elevated about 1 min after the end of adaptation, for short adaptation times. It remains to be seen whether adapting for a much longer period of time produces such long term effects on threshold as we found it to have on frequency matching (Figs. 10, 11 and 12). Certainly other kinds of sensory adaptation have been shown to cause after-effects lasting a very long time. Adaptation to movement (Hepler, 1968; Masland, 1969) colour (Kohler, 1962; McCollough, 1965) and curvature (Gibson, 1933) can certainly produce illusory sensations hours or even days afterwards.

The results of adapting to low spatial frequencies (Fig. 5) are best explained by the hypothesis that, in foveal vision, the detection channel with the lowest preferred spatial frequency is optimally sensitive at about 3 c/deg. This hypothesis is supported by the finding of Blakemore & Campbell (1969*b*) that the threshold elevation caused by very low-frequency adapting patterns continues to peak at about 3 c/deg. But it is a very perplexing hypothesis because one can clearly detect patterns far below 3 c/deg in frequency, and what is more, these patterns can easily be discriminated (Campbell *et al.* 1970). In fact Nachmias, Sachs & Robson (1969) have shown by a mixed-grating detection technique that sinusoidal gratings at frequencies below 3 c/deg can be detected by separate neural channels. For some reason, then, these very low frequency channels are not adapted by a simple high contrast pattern. Perhaps gross movement of the retinal image is necessary for these neurones to be adequately driven for them to adapt.

The fact that spatial adaptation is orientation-specific, and that adaptation to a horizontal grating has no detectable influence whatever on a vertical test grating, implies that there is no significant adaptation of the cells in the visual pathway below the cortex, for the ganglion cells and lateral geniculate cells of the cat and the monkey almost all have round concentrically organized receptive fields (Kuffler, 1953; Hubel & Wiesel, 1960, 1961; Wiesel & Hubel, 1966). Since the orientation selectivity of cortical neurones must be synthesized from the input of fibres with round

receptive fields, substantial precortical adaptation would be expected to influence all orientations equally.

Rather than attempting to guess at a physiological function for these adaptation phenomena we must emphasize the unnatural nature of a high contrast sinusoidal grating. In a way, such a stimulus is a 'stabilized cortical image' for wherever one directs one's gaze within the pattern the population of cortical neurones being excited is virtually the same. Just as a physically stabilized retinal image appears to fade (Riggs, Ratliff, Cornsweet & Cornsweet, 1953) so does the grating pattern. The threshold and suprathreshold sensitivity are, however, completely normal for a fresh grating that stimulates a totally different group of cortical neurones, either because it lies well away from the adapted part of the visual field or because it is substantially different in spatial frequency or orientation.

One way to consider the decline of the after-effect with the change of orientation of adaptation is as if adapting to a grating of inappropriate orientation were equivalent to adapting to the correct orientation but at a reduced contrast. This is apparent from Figs. 7 and 8, and it is a point that we shall consider in more detail in a later paper (J. Nachmias & C. Blakemore, in preparation).

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