SSC. This procedure reduces the background (as determined by the amount of DNA bound to a blank filter) to less than 1 percent of the input radioactivity. After this incubation, H^3-labeled nascent DNA fragments in 150 μl of 3 × SSC were added. Incubation was continued for 10 hours at 65°C; the temperature was lowered to 55°C, and the reaction mixture was kept at that temperature for another 4 hours. The filter was washed on both sides with 60 ml of SSC and dried, and the radioactivity was determined by counting the filters. Knowing the specific activity of C^{14}-thymidine, the labeled strands on the filter, and the relative number of thymidine in each strand of phage DNA (*5*), one can determine the exact amount of each DNA strand on the filter. These estimates always gave more than 96 percent of the input.

The results of hybridizing isolated DNA fragments to the separated strands of phage DNA, to unfractionated phage DNA, and to DNA from the host, *B. subtilis*, are presented in Table 1. Even after 2 seconds of exposure to the isotope, the labeled phage DNA fragments are complementary to both strands of phage DNA. There is no significant asymmetry in the proportion of fragments that bind either strand. Results from two other time points also agree with this observation. These results show that, within the limits of resolution of the experiments (a few seconds), short nucleotide sequences complementary to both strands of SPP-1 DNA are synthesized.

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Size Adaptation: A New Aftereffect

Abstract. *If, after prolonged observation of a striped pattern, one views a grating of the same orientation with somewhat narrower bars, then the bars seem even thinner than in fact they are. Broader bars seem broader still. This finding implies a system of size-detecting channels in human vision. The phenomenon may underlie many of the classical figural aftereffects.*

After observation of a high-contrast grating pattern, the intensity difference between light and dark bars necessary just to detect a grating is markedly elevated (*1*). This rise in contrast threshold occurs only for gratings similar to the adapting pattern in orientation and in spatial frequency (the number of cycles of the grating per degree of visual angle). This finding argues for the presence, in the human visual system, of neurons selectively sensitive to a limited range of spatial frequency. Such units have indeed been found in the visual pathway of cat and monkey (*2*). The optimal spatial frequency varies from neuron to neuron, and the sensitivity maxima are closely spaced along the spatial frequency continuum. It is possible that these neurons constitute a system of channels involved in the analysis of the size of retinal images.

A grating of some spatial frequency will arouse a distribution of activity in the population of size-detecting neurons. If the identity of the most active neuron or the shape of this distribution is used by the brain to recognize the size of the bars, then previous adaptation and depression of sensitivity at some other spatial frequency (which will shift the peak and skew the distribution of activity away from the adapting frequency) should make the grating seem different. In short, gratings with narrower bars than the adapting pattern should appear to be of even higher spatial frequency, and lower-frequency gratings should seem lower than in fact they are. We have found this to be the case and take it to be additional evidence for size-selective neurons in man.

You may observe this phenomenon for yourself by inspecting Fig. 1. First convince yourself that the two gratings on the right are identical in spatial frequency by looking from one to the other. Now place the illustration at a distance of about 2 m and look between the two gratings on the left for about a minute, allowing the gaze to wander back and forth along the horizontal bar. (This maneuver avoids the formation of a conventional after-

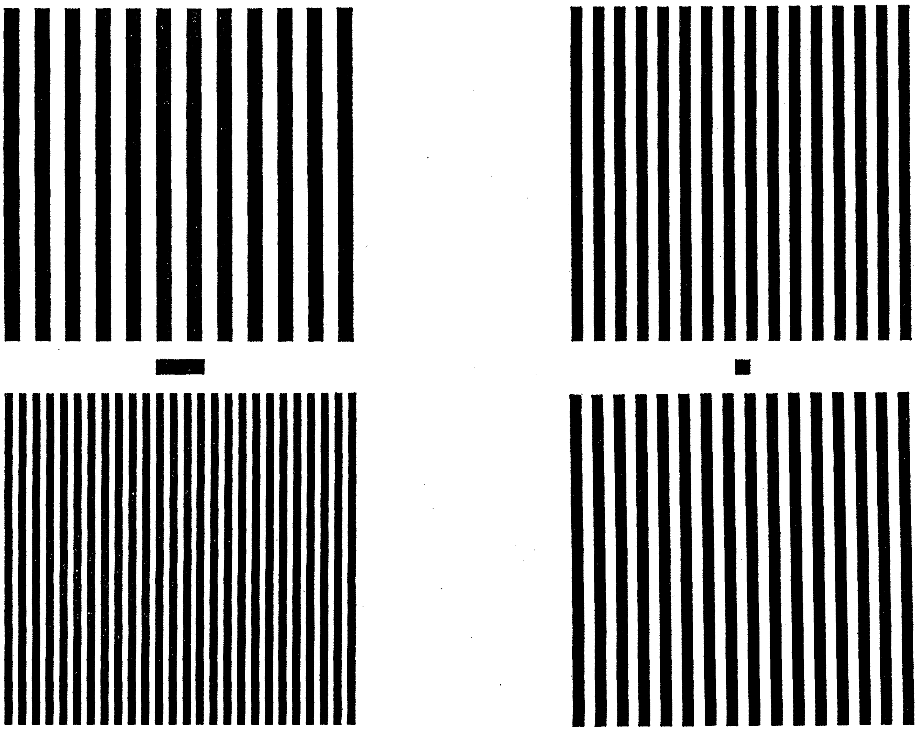

Fig. 1. Follow the instructions in the text to observe the aftereffect for yourself.

image.) At the end of the period of adaptation, quickly transfer your gaze to the fixation point between the two gratings on the right. They should no longer seem identical in spatial frequency. The grating above the fixation point appears higher in spatial frequency because of adaptation of that retinal region to the low-frequency grating, and that below seems lower in frequency after adaptation to the high-frequency pattern.

In our experiments the subject viewed two oscilloscope screens from a distance of 2.9 m. Each screen subtended 1.75° in width and 1.25° in height and they were about 0.5° apart, one directly above the other, with a horizontal fixation bar in between. The method of Campbell and Green (*3*) was used to display vertical gratings, with sinusoidal intensity distribution (*4*), on the screens. The patterns could be turned on and off and their contrasts and spatial frequencies changed by the experimenter without appreciable variation of mean luminance. In addition the subject could alter the spatial frequency of the lower grating by turning a potentiometer controlling the time-base of that oscilloscope. He could display the voltage across the potentiometer by pressing a button. This reading gave a measure of the spatial frequency of the lower grating.

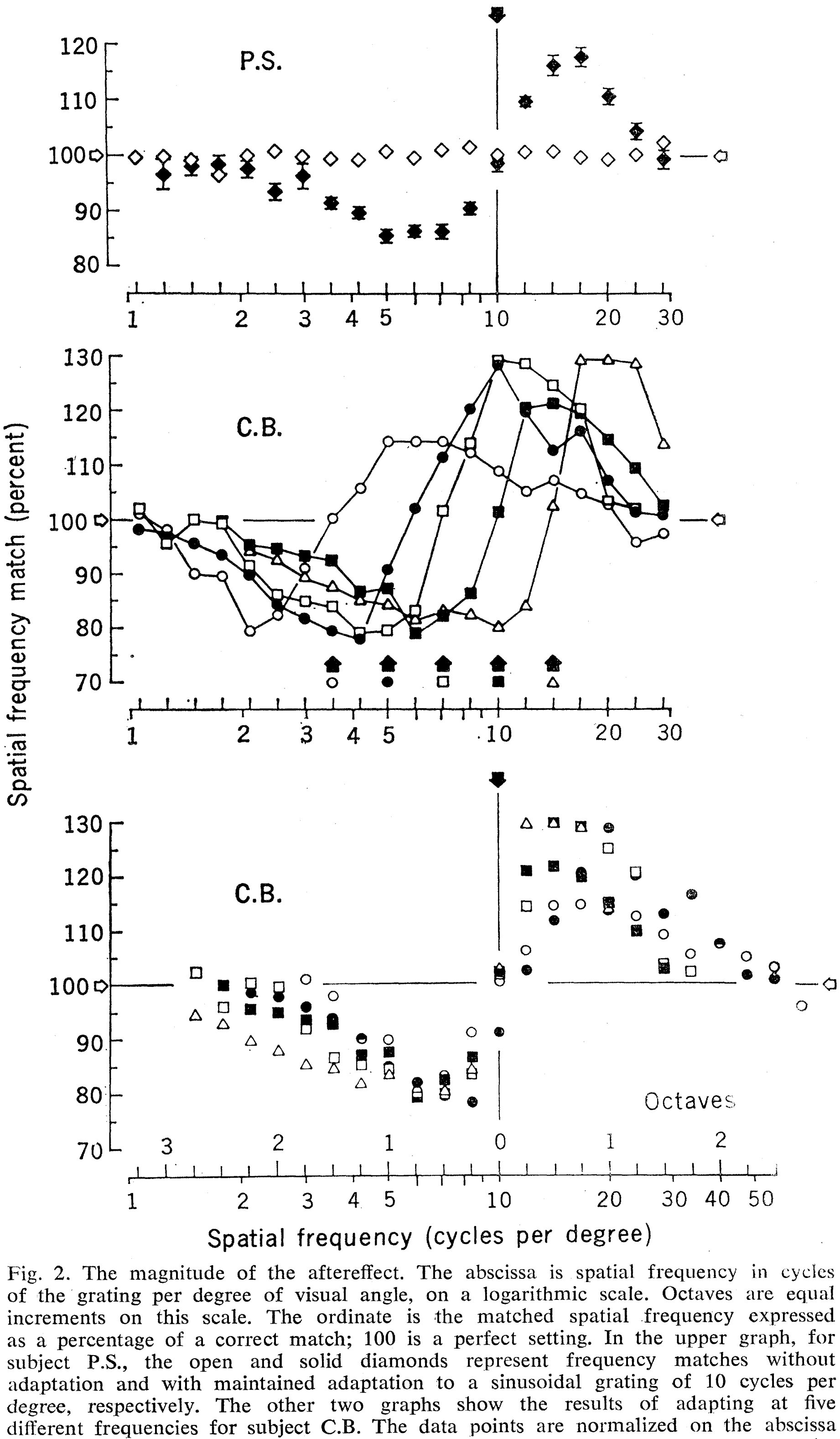

Fig. 2. The magnitude of the aftereffect. The abscissa is spatial frequency in cycles of the grating per degree of visual angle, on a logarithmic scale. Octaves are equal increments on this scale. The ordinate is the matched spatial frequency expressed as a percentage of a correct match; 100 is a perfect setting. In the upper graph, for subject P.S., the open and solid diamonds represent frequency matches without adaptation and with maintained adaptation to a sinusoidal grating of 10 cycles per degree, respectively. The other two graphs show the results of adapting at five different frequencies for subject C.B. The data points are normalized on the abscissa in the bottom graph, with all the adapting frequencies superimposed at 10 cycles per degree.

In a preliminary experiment the subject attempted to match the lower pattern to the upper while fixating in between the two. A range of spatial frequencies from 1.05 to 28.3 cycles per degree was studied in quarter octave steps. (One octave is a change by a factor of 2.) The contrast was fixed at about 60 percent for all test gratings. At each frequency the subject made six attempts to match the patterns, offsetting the potentiometer and looking away between each. Further sets of six readings were taken in this way after the experiments described below.

In the upper graph of Fig. 2 the open diamonds represent the means of the twelve estimates at each spatial frequency for subject P.S. The results are expressed as the percentage difference from true equality:

$$\frac{\text{Spatial frequency on lower screen}}{\text{Spatial frequency on upper screen}} \times 100$$

A perfect match gives a value of 100, marked with an open arrow on the ordinate. Clearly the judgment can be made with great accuracy.

In the adaptation experiments, before each frequency match made in the manner described, the subject viewed a high-contrast grating on the upper screen and a blank field of the same space-average luminance [about 0.5 ft lam (0.54 mlam)] on the lower oscilloscope. The adapting pattern was set at a contrast of 1.5 log units above the subject's threshold contrast for that spatial frequency. Initially this display was viewed, by fixation between the screens, for about 3 minutes. After this initial period of adaptation, a test grating appeared on both screens and the subject made a frequency match as quickly as possible, taking about 2 seconds. The adapting display was substituted for a further 10 seconds before each additional match was made. The subject held his fixation between the two screens throughout the procedure. Three settings were made at each test frequency, working up through the spatial frequency spectrum, and then three more at each, working down again. The settings obtained on the descending run were similar to those on the ascending run.

The solid diamonds in the upper graph of Fig. 2 show the mean matched frequency as a percentage of the true equality setting at each spatial frequency, while P.S. was adapting to a grating of 10 cycles per degree. The vertical lines through the points limited by short horizontal bars show one standard error on each side of the mean. There is a dramatic overestimate of spatial frequency above the adapting frequency and an underestimate below it. There is no significant effect at 10 cycles per degree itself, nor beyond about 3 and 25 cycles per degree.

The results for another subject (C.B.) are shown in the other two graphs of Fig. 2. Five different adapting spatial frequencies were used (from 3.5 to 14.2 cycles per degree), and they are marked with solid arrows on the abscissa. The symbol below each arrow is used to plot the frequency matches made during adaptation. In this case no unadapted settings are shown and the values plotted are

$$\frac{\text{Matched spatial frequency during adaptation}}{\text{Matched spatial frequency without adaptation}} \times 100$$

If adaptation has no effect this value will, of course, be 100.

In order to demonstrate the similarity of the functions at these five adapting frequencies, the third graph shows the data points normalized on the abscissa. All the adapting frequencies have been superimposed at 10 cycles per degree, marked with a solid arrow. In this case the abscissa is also expressed as octaves from the adapting frequency. The effect is negligible more than two octaves away on either side of the adapting frequency.

So far we have discussed only the initial effect (immediately after the adapting pattern is removed), which reaches a maximum value after only 2 or 3 minutes of adaptation. But what of the time-course of recovery? For short adapting times of about 60 seconds, recovery is complete in about the same time; but with the long periods of maintained adaptation used in these experiments (sometimes of more than 45 minutes) a significant aftereffect could be detected more than 4 hours later. Other long-term aftereffects have been reported for adaptation to movement (*5*), color (*6*), orientation, and curvature (*7*).

The magnitude of the initial effect increases with the contrast of the adapting grating, but it is not critically dependent upon the contrast of the test patterns, as long as they are distinctly visible.

If this phenomenon is due to adaptation of size-selective neurons it would be interesting to know where in the visual system these cells are. We have some evidence that they are central. First, if one adapts through one eye alone there is a transferred aftereffect, of about half strength, in the other eye. Second, adaptation to a horizontal grating produces no distortion of vertical gratings. This suggests that the size-detecting neurons are also orientation-selective and some of them at least have inputs from both eyes. Just such cells have been found in the visual cortex of cat and monkey (*8*).

The fact that threshold elevation after adaptation to a grating is also orientation-selective and shows interocular transfer (*1, 9*) suggests a common neural origin for that effect and the present phenomenon.

This size aftereffect is reminiscent of the classical figural aftereffects described by Köhler and Wallach (*10*). Prolonged observation of a single circle, for example, will make a subsequently viewed smaller circle appear smaller still. Current explanations of the phenomenon center on the concept of "contour displacement," but it may well be that a large component of these figural aftereffects is explicable on the basis of adaptation of size-detecting rather than position-detecting mechanisms. The concept of pattern recognition suggested by Blakemore and Campbell (*1*) certainly requires that size-detecting channels revealed by adaptation to a grating be involved in the analysis of the shape and size of much more complicated patterns.

It is possible that aftereffects of this type may provide a handle for the study of the "trigger features" or optimal stimuli of human sensory neurons. If one assumes that overexposure to a stimulus of one submodality differentially depresses its channel, during and after stimulation (*11*), then one expects certain perceptual phenomena: (i) The "strength" of the sensation should decline throughout adaptation; (ii) after adaptation it should be more difficult to detect a stimulus handled by that channel; (iii) because of imbalance in opponent channels a sensation of opposite value should arise spontaneously after adaptation; and (iv) the appearance of stimuli of different value but within the same stimulus submodality should be distorted by adaptation.

The phenomenon described here, along with figural and curvature aftereffects, is of class 4. The Waterfall Phenomenon and successive color effects are of class 3, and size-dependent threshold elevation is an example of class 2. Class 1 effects are common to all intense sensory stimulation.

Perceptual phenomena of this kind may help our understanding of human sensory neurophysiology.

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