6

Multiple Spatial Frequency Channels

In Chapter 5, we described the CSF, discussed the manner in which both high and low spatial frequency attenuation might occur in the visual system, and pointed out some consequences for visual perception of the shape of the CSF. In this chapter we address the question of whether a single broadly tuned mechanism underlies the CSF. Until the late 1960s, visual scientists had implicitly assumed that to be the case: the low frequency attenuation was attributed to center-surround antagonism in the RFs of ganglion cells, and all ganglion cells (and implicitly later cells as well) were assumed to have the same broad sensitivity profile as the CSF. In 1968, however, Campbell and Robson made the then revolutionary suggestion that the visual system might contain something like groups of independent, quasilinear band-pass filters, each of which was more narrowly tuned for spatial frequency than the overall CSF. The CSF would then reflect not the sensitivity of a single typical visual channel or cell, but some envelope of the sensitivities of all these multiple filters, or channels. Somewhat similar proposals were also put forth by Pantle and Sekuler (1968) and by Thomas (1970). These ideas had a large impact on vision because they provided a model of how the visual system might be analyzing spatial patterns which was quite different from the mechanisms previous workers had considered. In this new model, the visual system was considered to be operating not purely in the space domain, analyzing the amounts of light at different points in space or edges where the amount of light abruptly changes, but rather operating at least partially in the spatial frequency domain, responding to patterns on the basis of their underlying frequency content.

One of many attractions of this suggestion is its similarity to generally accepted ideas about the manner in which the auditory system operates. There is great appeal in (and some sound scientific grounds for) assuming that the nervous system solves analogous problems in similar ways. Thanks to more than a century of diligent work by auditory scientists, there is a large and impressive body of knowledge and highly developed theory about the ways in which the auditory nervous system might carry out a quasilinear frequency analysis in the temporal domain. If the visual system should be performing a similar analysis in the spatial domain, many of the ideas first developed by auditory theorists might be relevant to the visual system. (See Chapter 12 for a more extensive discussion of many reasons why the visual system might be performing a local spatial frequency filtering of visual information.)

In the initial formulations of ideas about multiple channels, and in almost all the early tests of the ideas, only one-dimensional stimulus patterns were used and the possible operation of one-dimensional filters considered. In this chapter, therefore, we confine our attention to such simple patterns. Two-dimensional channels will be considered in Chapter 9.

DEFINITION OF "CHANNEL"

There is now a considerable body of psychophysical, physiological, and anatomical evidence supporting the suggestion that the CSF represents the envelope of many more narrowly tuned channels. We shall consider several types of experiments bearing on this issue in turn, but we need first to address the question of what is meant by a "channel." The generalized notion of a channel refers to a filtering mechanism, something which passes some, but not all, of the information that may impinge upon it. Spatial or temporal frequency filters may transmit whatever input is present above a particular frequency (high-pass), below a particular frequency (low-pass), or within a restricted frequency region, with rejection at both ends (band-pass). A system that filters with multiple channels, then, would be one with a number of different band-pass channels tuned to different frequency ranges, plus possibly low-pass and high-pass channels at either end of the range. We can see that the concept has two essential components. One is that of spatial frequency filters sufficiently narrowly tuned that each is responsive to only some fraction of the total range encompassed by the organism's CSF (see Figure 6.1). The second is that of parallel processing of information, in which the pattern within a given limited spatial region is not analyzed on the basis of the point-by-point luminance level, but rather is simultaneously analyzed by multiple spatial frequency filters, each responding insofar as the spectrum of this spatial pattern contains energy within its particular spatial frequency band (see Figure 6.2).

Certain difficulties arise when one attempts to specify more precisely than we have above what constitutes a psychophysical "channel," or when one considers exactly what the physiological underpinnings may be of the hypothesized channels. One widely recognized definition of a "channel" is that it is composed of all those cells with receptive fields that are identical in every respect save retinal location (cf. Graham, 1980). A group of cells, each with a certain RF periodicity (giving it a particular spatial frequency bandwidth) and optimally sensitive to, say, 2 c/deg, would constitute the 2-c/deg "channel" which would detect the presence of energy at that spatial frequency in the stimulus pattern. Another group of cells similar except for being tuned, say, to 3 c/deg would be another, 3-c/deg channel. Representatives of each of these channels would have RFs located in each region of at least the central visual field. All of these spatially dispersed 2-c/deg units would together, then, form the 2-c/deg channel.
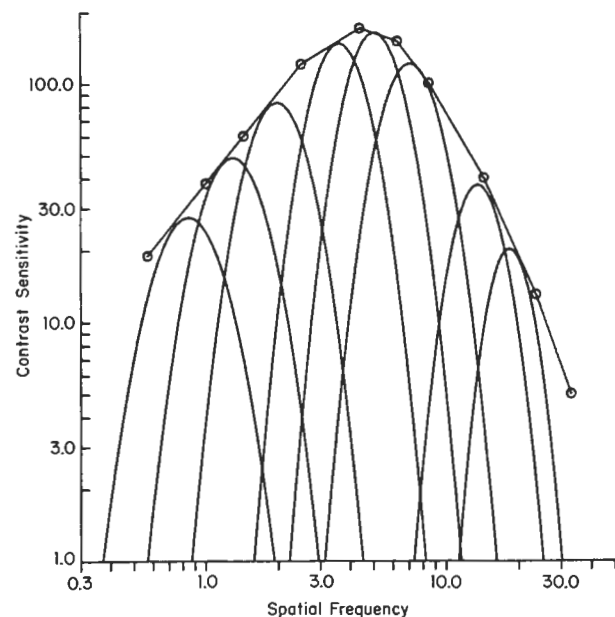
FIG. 6.1 Spatial contrast sensitivity function as the envelope of many more narrowly tuned spatial frequency selective channels.

It can be seen that this definition introduces still a third aspect of the channel concept, in addition to those of multiple parallel units and narrow spatial frequency tuning that we discussed earlier. This is that the underlying units have spatially restricted RFs and are somehow related to similar units with RFs in different spatial locations. Most psychophysical studies related to multiple channels—all the earlier ones and most still done today—used large, redundant stimulus displays, e.g., gratings covering a large part of the visual field, and they considered only the detection or appearance of the overall pattern. Given this, it was easy to think of the process as a global one, although few theorists (e.g., Kabrisky, 1966) explicitly proposed that the visual system might be doing a global frequency analysis. It is immediately obvious to anyone who has examined the properties of striate units that cells at this level have restricted RFs, as do those at earlier levels; any spatial filtering they do must be on a quite local basis. So a spatially extended 2-c/deg grating will be responded to by many units tuned to this frequency, but with RFs scattered across the visual field. Graham's (1980) definition of channel raises the important issue of how these spatially displaced units of similar tuning properties are related to each other. The implication is that their outputs may be combined in some more global 2-c/deg detector.
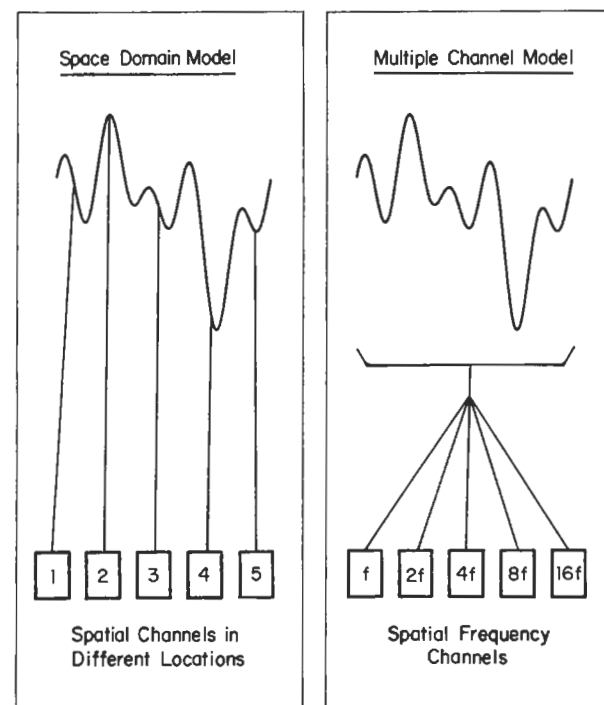
FIG. 6.2 Two simplified models of spatial analysis. In the space domain model (left), each point in space is analyzed by a separate filter which responds to the average luminance in a small region around that point. In the multiple spatial frequency channel model (right), a somewhat larger but still delimited region of space is analyzed by each of several fairly narrowly tuned spatial frequency filters, each of which responds to the power in the pattern which falls within its frequency band. In the space domain model the analysis is carried out serially across space on a point-by-point basis. In the multiple spatial frequency channel model the analysis over the same restricted region is carried out in parallel by different spatial frequency filters.

While this aspect of multiple channels is an important issue, we would like to restrict our discussion of it here, because it takes us beyond our present knowledge of probable physiological substrates. Some complex striate cells show increased responses to increasing numbers of cycles of a grating of their optimal spatial frequency, but yet have quite broad spatial frequency bandwidths (Webster & R.L. De Valois, 1985). This suggests that these cells are integrating the outputs of more spatially restricted units (ones tuned to this spatial frequency) whose RFs are scattered over some distance. However, the total extent of the RFs of even such complex cells is only a small part of the whole visual field. If

more global spatial frequency channels exist, we can with considerable certainty state that they are not at or before the striate cortex. Cells at later levels, however, have increasingly extensive RFs, and it is possible that some poststriate cells may respond to the amount of energy at, say, 2 c/deg over a whole large part of the visual field. However, since at the present time evidence on this question is lacking, we would like to concentrate on questions on which physiological and psychophysical evidence converge.

The main problem we see with most definitions of "channel" is that they imply a limited set of properties, e.g., bandwidths, in the underlying units, and a static character to the channel properties. Such assumptions may be useful for modeling purposes, but they do not seem to us to be in accord with either the physiological or the psychophysical evidence. Striate cortex recordings (e.g., R.L. De Valois, Albrecht, & Thorell, 1982) have shown that the various cells that are maximally sensitive to a grating of, say, 2 c/deg vary greatly in the breadth of their spatial frequency tuning (and thus, by implication, in their RF profiles). It seems to us reasonable to assume that many if not all of those cells will be contributing to the detection of a 2-c/deg grating (or the amount of energy at 2 c/deg in a more complex pattern), rather than just a small subset of units with a particular RF shape. Also, as the contrast of a 2-c/deg pattern is raised many more units will be activated, some of which may have different properties than those responsive at a lower contrast level, e.g., a unit tuned optimally to 2.5 c/deg may now be responsive as well. With practice in detecting a particular pattern, one may learn to attend to some subset of the whole population initially involved, thus accounting for increases in sensitivity and narrower bandwidths over time (K.K. De Valois, 1977b). There are also inhibitory interactions among units (see Chapter 11). In some situations, such as masking, there may be more inhibitory activity than in other situations, thus different populations of units may be involved, and perhaps the individual properties of underlying units may change as well.

This heterogeneity among neurons and the variability in their properties are bothersome only if one considers that "channels" are discrete structural entities which are invariant with any stimulus parameter other than spatial frequency. While it is certainly easier to think in terms of models of channel behavior if one assumes channels that are cast in concrete, it seems very unlikely that this is in fact the case! We are thus led to the position that spatial frequency channels are composed of whatever cells are contributing to the transmission of information about a stimulus with power at particular spatial frequency at any given moment. They are thus not rigidly defined and certainly cannot be described under any and all circumstances by the specification of one or two parameters.

Some (e.g., Westheimer, 1981) have questioned whether the channel concept in spatial vision has been useful at all. Surely its success in the prediction of the detectability of complex visual patterns (e.g., Campbell & Robson, 1968; Campbell, Carpenter, & Levinson, 1969; Graham & Nachmias, 1971), or the explanation of perceptual changes with adaptation (e.g., Blakemore & Sutton, 1969) is sufficient justification. Another is that the notion of spatial frequency channels

and quasilinear frequency filtering has prompted a salutary reexamination of ill-specified but widely accepted models which assumed that the visual system performed a naturalistic feature analysis of spatial patterns. Such ideas, which have great intuitive appeal, can often blind one to considering other possibilities that may more accurately reflect the real characteristics of the system. Whether or not a frequency filtering model is eventually superseded by other ideas (as virtually any scientific model will be as our understanding increases), it will have played an important role in forcing us to reconsider readily accepted but perhaps ill-founded assumptions about how the visual system functions.

A final justification for the use of channel models in general is that they are in accord with much physiological evidence. Whether or not we understand completely why the visual system might choose to use multiple channels which are selective along the domain of spatial frequency (however, see the discussion in Chapter 12), the fact is that such selectivity is prominent in striate cortex cells. Whatever its function, spatial frequency filtering is something which the visual system seems indubitably to be doing. It behooves us to note and try to understand, not to ignore this.

Psychophysical Evidence for Multiple Spatial Frequency Channels

The initial ideas with respect to multiple spatial frequency channels, and most of the early evidence for the notions, came from psychophysical experiments of various sorts. These experiments bear on both of the related but distinct fundamental issues mentioned earlier: whether there are multiple (versus single) parallel spatial channels, and whether these channels are selective for spatial frequency (as opposed, for instance, to size or pattern width).

Detection of Patterns Based on Amplitude Spectra

In the initial paper that raised the possibility that the visual system spatial frequency filters patterns, Campbell and Robson (1968) measured the detection threshold for various complex patterns and related the detectability of these to their amplitude spectra and the observer's sine wave CSF. If detection depends on the activation of one (or more) independent narrow-band filters, a pattern should first be visible when (and only when) any one of its frequency components reaches its own threshold contrast. An alternative possibility, which was the dominant theoretical view earlier, is that the overall contrast of a pattern is the critical factor in determining its threshold. It will be remembered from Chapter 1 that contrast can be defined as $L_{max} - L_{min}/L_{max} + L_{min}$. Two different patterns, e.g., a square wave grating and a sine wave grating, can have equal contrasts—equal peaks and troughs—but very different amplitudes of the underlying frequency components. Only if the visual system were filtering patterns into multiple spatial frequency components would one expect the detec-

tion of various patterns to be related to their spatial frequency amplitude spectra rather than to their overall contrast, when these differ.

Campbell and Robson found that for a variety of periodic complex waveforms (square and rectangular wave gratings, sawtooth waveforms, etc.) the amplitudes of the individual spatial frequency components, not the overall contrasts of the patterns, determined threshold detection. Consider, for instance, the detectability of sine wave and square wave gratings. The fundamental component of a square wave (see Chapter 1) is a sine wave of the same frequency but of $4/\pi$ (= 1.27) times the amplitude of the square wave. If the overall contrast of the pattern is the crucial variable, a sine wave and a square wave grating should be detected at the same contrast; if the patterns are being detected on the basis of the outputs of various parallel, narrow-band spatial frequency channels, on the other hand, the square wave grating should be detectable at a lower pattern contrast. Campbell and Robson found the square wave grating in fact to be more detectable by precisely the ratio predicted from a consideration of the relative amplitudes of the square and sine wave fundamentals for all gratings except those of very low spatial frequencies (see below).

Another important observation that Campbell and Robson reported was that at threshold a sine wave and a square wave of the same fundamental frequency are perceptually indiscriminable. Only when the third harmonic of the square wave reaches its own (independent) threshold do the two patterns become discriminably different perceptually. This indicates that at threshold only the fundamental component of the square wave (which is of course of the largest amplitude) is being responded to by the visual system, as one would predict if the square wave were being broken down into its separate frequency components in multiple spatial frequency channels.

Campbell and Robson found the linear predictions to hold quite precisely when square waves of moderate to high spatial frequencies were studied. The human CSF shows marked attenuation at low spatial frequencies, however, which would lead to quite different predictions for low-frequency square waves. Since sensitivity to low spatial frequencies drops rapidly, it should be possible to find a frequency range in which the visual system would be more sensitive to the third harmonic of a square wave (which has only one third the amplitude of the fundamental) than to the fundamental frequency itself. At that point the $4/\pi$ relationship between threshold contrasts for sine and square waves should break down, with the square wave becoming progressively more detectable relative to the sine wave as the fundamental frequency is reduced, since the sine wave, of course, has no higher harmonics. Campbell and Robson found this to hold, as well, thus buttressing their argument.

Another demonstration that the amplitude of the individual spatial frequency components, not the overall contrast of the pattern, determines detection thresholds was presented by Graham and Nachmias (1971), who examined the detectability of a grating composed of two frequency components, f and $3f$, as a function of the relative phase of the two gratings. When the two gratings are combined in such a relative phase angle that their peaks coincide (peaks-add),

the contrast of the pattern is much greater than when they are combined so that their peaks are out of phase (peaks-subtract). Figure 6.3 shows the luminance profiles of two such patterns and their appearance. If the overall pattern contrast determines detection, the peaks-add grating should be far more detectable since it has greater overall contrast. However, Graham and Nachmias found that the patterns were equally detectable: the amplitudes of the individual spatial frequency components, not the overall contrast, determine detectability.

Frequency-Specific Adaptation

Perhaps the single most convincing psychophysical demonstration that the visual system contains multiple channels, each of which operates more or less as a band-pass spatial frequency filter, is spatial frequency specific adaptation. When, by selective adaptation, one can differentially affect either the sensitivity to or the appearance of two different patterns, then it may be assumed that the two patterns are processed by nonidentical underlying structures. If adaptation to pattern A reduces sensitivity to A but does not affect sensitivity to B, then there is the strong implication that the neural elements that were affected by the adaptation subserve the detection of A but not of B. Note that this does not carry any implication about the type of neural change that might underlie it, whether fatigue, prolonged inhibition, gain control, or whatever, although that is an interesting question in its own right.

Pattern-specific adaptation has provided a compelling argument for the existence of multiple spatial frequency channels. Spatial frequency specific adaptation was demonstrated initially by Pantle and Sekuler (1968) and by Blakemore and Campbell (1969). The former used square wave patterns, while the latter used sinusoidal gratings. Since square waves are more complex (i.e., they have more frequency components), the experiment using sine waves is more straightforward. We will therefore consider sine wave adaptation as in the Blakemore and Campbell experiment in more detail.

In order to produce a baseline against which to measure possible adaptation effects, contrast sensitivity is first measured for a variety of different spatial frequencies, thus defining an unadapted CSF. The subject then adapts to a high contrast grating of a single spatial frequency, following which the CSF is measured again. During the retest period the subject must periodically readapt for a short period in order to maintain a high, constant level of adaptation.

Before adaptation, the CSF typically has an inverted U shape, with highest sensitivity to middle spatial frequencies. If there were a single channel underlying the CSF, as was implicitly assumed by early investigators, the effect of adaptation should be to lower the overall CSF uniformly. On the other hand, if the overall sensitivity were some envelope of the sensitivities of multiple channels tuned to different spatial frequency ranges, adaptation to some one spatial frequency might produce a loss in contrast sensitivity over a restricted range of spatial frequencies. This is what Blakemore and Campbell in fact found, as did
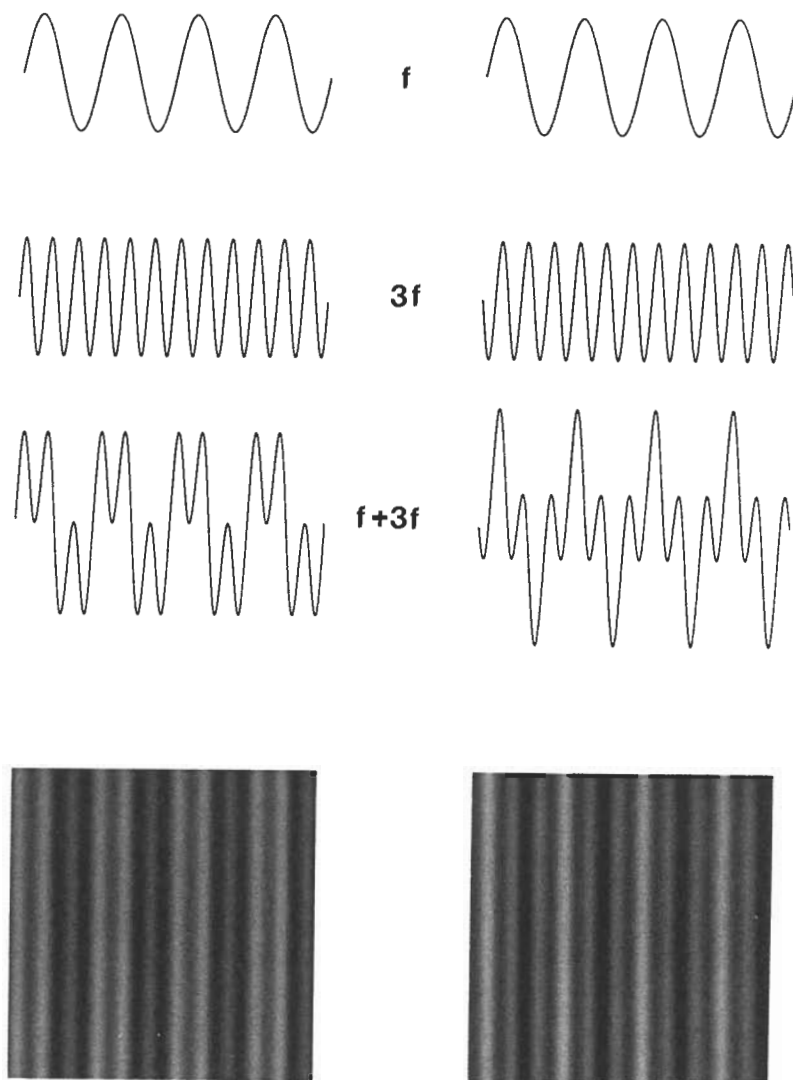
FIG. 6.3 Luminance profiles and patterns produced by adding *f* and 3*f*. The addition of equal-amplitude components at *f* and 3*f* in either peaks-subtract (left) or peaks-add (right) phase produces the luminance profiles shown above. Below each profile is a photograph of the corresponding pattern.

Pantle and Sekuler; see Figure 6.4. If the subject adapts to a middle-range spatial frequency, say, 5 c/deg, the CSF will show a band-limited depression centered at the adaptation frequency, with a loss at the adaptation frequency of as much as 1 log unit. According to Blakemore and Campbell, spatial frequencies on either side of the adaptation frequency will show a smaller loss, decreasing as the test frequency is further removed from the adaptation frequency. The loss generally falls to zero, the postadaptation contrast sensitivity being the same as the preadaptation contrast sensitivity, when the test frequency is about an octave (different by a factor of 2) on either side of the adaptation frequency, and frequencies further removed are not affected. Blakemore and Campbell reported that the function describing the adaptational loss is asymmetric, having a steeper high-frequency fall-off, with a full bandwidth at half amplitude of about 1.2 octaves. They found the effect to be centered on the adaptation frequency for all frequencies above 3 c/deg. Below that, the loss remained centered at 3 c/deg. They also reported that adaptation to high spatial frequencies produced slightly narrower adaptation functions than did adaptation to low frequencies.

It is also interesting to note that the apparent contrast of a suprathreshold grating may also be affected by adaptation to a high-contrast grating of similar spatial frequency (Blakemore, Muncey, & Ridley, 1971, 1973). Following adaptation to a grating of 2 c/deg, for example, subsequently viewed gratings of 2 c/deg, even though clearly suprathreshold, will appear to be of reduced contrast. The magnitude of the reduction in apparent contrast is a function of the similarity of test and adaptation gratings along the dimensions of spatial frequency and orientation and of the contrast of the adaptation grating. Thus the effects of
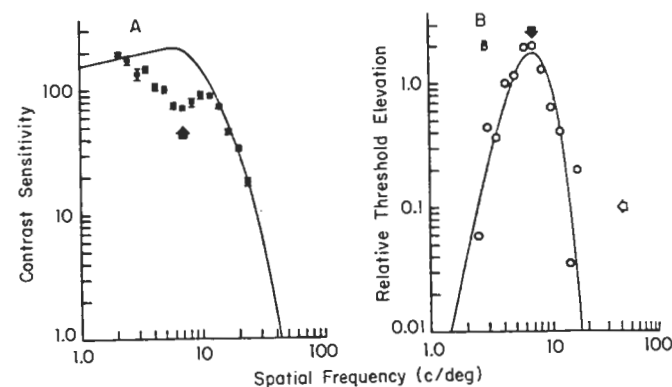

FIG. 6.4 (A) CSF before (solid line) and after (data points) adaptation to a grating of a single spatial frequency. (B) Threshold elevation at different spatial frequencies produced by the adaptation . Note the band-pass loss in contrast sensitivity around the adaptation frequency (indicated by arrows) (from Blakemore & Campbell, 1969. Reprinted by permission).

spatial frequency adaptation are not restricted to the detection of near-threshold patterns but can be seen in the appearance of high-contrast patterns, as well.

Several subsequent investigations have modified the description of one or more of the characteristics of the spatial frequency specific adaptation described by Blakemore and Campbell, as discussed below, but none of them has challenged the central finding—namely, that adaptation to a single spatial frequency produces a band-limited loss in contrast sensitivity centered at that frequency rather than depressing the entire CSF. The fact that adaptation produces a loss so profound yet so restricted indicates that the CSF does *not* describe the filtering characteristics of a single, broadly tuned analyzer. That any given part of the function can be selectively depressed demonstrates that the different spatial frequency regions are subserved by different structural elements with some considerable degree of independence.

One of the most puzzling aspects of the Blakemore and Campbell report was the finding that adaptation to frequencies lower than 3 c/deg produced a loss centered on 3 c/deg. It seems unlikely that there should be no low-frequency channels, given the fact that we can discriminate among various low frequencies with reasonable ease. If there were only one detector responding to all low frequencies, then such patterns should be indiscriminable if properly matched for contrast above threshold. Jones and Tulunay-Keesey (1975) showed that this finding of Blakemore and Campbell's was an artifact resulting from the small size of the grating display they used. If the display is sufficiently large, the adaptational loss follows the adapting frequency down to much lower spatial frequencies (see Figure 6.5). They pointed out that in a restricted stimulus display, with too few cycles, the power spectrum is spread over a broad range. For instance, an adaptation pattern with a nominal frequency of 1 c/deg on such a small display would have considerable power even beyond 3 c/deg. Since one is considerably more sensitive to 3 than to 1 c/deg, the maximum adaptation might well occur at 3 rather than at 1 c/deg.

There have been several other amendments and corrections to Blakemore and Campbell's original findings. Their results suggested completely independent channels: adaptation to one spatial frequency appeared to have no effect on contrast sensitivity to frequencies farther than one octave away from the adaptation frequency. Careful measurements have revealed, however, that contrast sensitivity to frequencies farther away may actually be increased by spatial frequency adaptation (K.K. De Valois, 1977b; Tolhurst & Barfield, 1978); see Figures 6.5 and 6.6. This suggests that spatial frequency channels are not truly independent, but rather may be mutually inhibitory. If so, reducing the activity of one channel would reduce the inhibition it exerts on channels tuned to other spatial frequencies, thus increasing their sensitivity. Similar suggestions of inhibitory interactions among different spatial frequency channels come from studies that have examined the effect of simultaneously adapting to more than one spatial frequency (e.g., Nachmias, Sansbury, Vassilev, & Weber, 1973; Stecher, Sigal, & Lange, 1973; Tolhurst, 1972b; K.K. De Valois & Switkes, 1980). The general finding is that adaptation to a pattern containing more than one spatial fre-
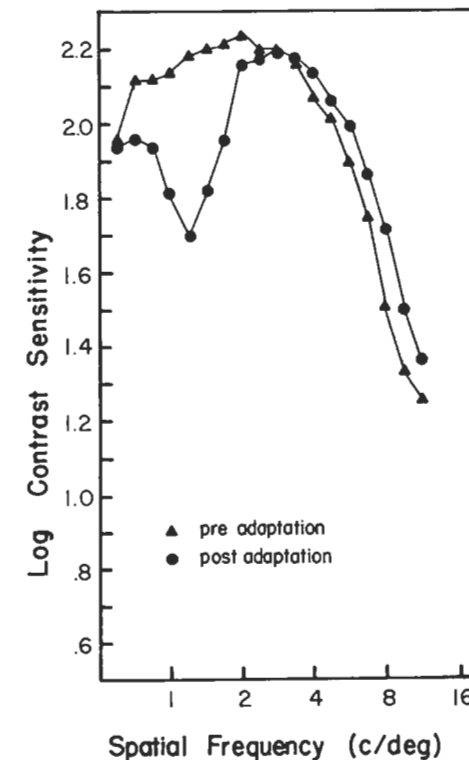
FIG. 6.5   Spatial frequency adaptation effect following adaptation to a low spatial frequency. Note that when a large display is used the loss in contrast sensitivity remains centered on the adaptation frequency (from K.K. De Valois, 1977b, *Vision Res., 17,* 1057-1065. Copyright 1977, Pergamon Journals, Inc. Reprinted by permission).

quency produces a smaller loss in contrast sensitivity than one would predict from a similar model that posited independent channels. The apparent inhibitory interactions revealed by such studies, however, are clearly relatively minor compared to the large loss of sensitivity at and around the adaptation frequency. These findings are important, though, in allowing us to understand better the physiological interactions (e.g., K.K. De Valois & Tootell, 1983) and organization underlying spatial frequency specific channels.

Other criticisms of the Blakemore and Campbell (1969) study deal with either psychophysical techniques or other aspects of the experimental methodology. For example, the method of adjustment, which they used, is often roundly condemned for being subject to criterion effects. While this certainly is true, replications of the study using more sophisticated forced-choice methods produce
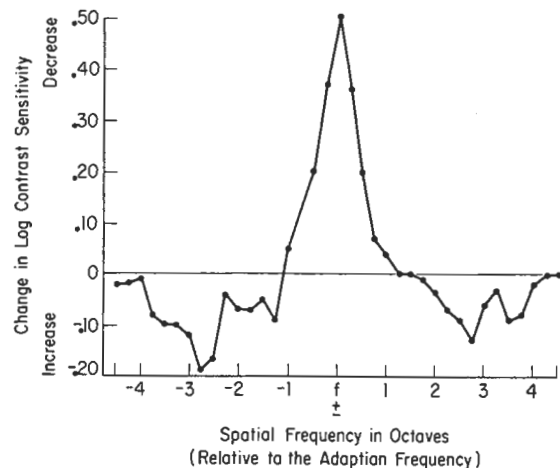
FIG. 6.6   Change in contrast sensitivity produced by spatial frequency specific adaptation. Note that in addition to the loss in contrast sensitivity for frequencies near the adaptation frequency, there is also an enhancement in contrast sensitivity for frequencies further removed (from K.K. De Valois, 1977b, *Vision Res., 17,* 1057–1065. Copyright 1977, Pergamon Journals, Inc. Reprinted by permission).

very similar results. The central finding of a band-limited, frequency-specific loss in contrast sensitivity following adaptation remains unchanged. Similarly, the free-scan viewing of a stationary grating has been shown to produce a small amount of patterned retinal adaptation, which might lead to retinal afterimages (Arend & Skavenski, 1979). However, the use of steady fixation and either drifting or phase-reversing (counterphase-flickering) adaptation gratings does not materially alter the findings of the experiment; nor does stabilization of the pattern on the retina combined with controlled modulation significantly change the effect (Jones & Tulunay-Keesey, 1975).

Spatial Frequency Specific Aftereffects

If, in a selective adaptation experiment such as those we have been discussing, prolonged inspection of a grating selectively depresses the sensitivity of just that restricted population of cortical cells tuned to the adaptation frequency (thus selectively inactivating one channel), there should also be measurable effects on the perceptual character of patterns seen later. (By perceptual character we mean to imply more than just the apparent contrast of a pattern, which, as we discussed above, also changes.) Blakemore and Sutton (1969) first noticed that there is a striking change in the appearance of certain grating patterns following adaptation: gratings of other nearby spatial frequencies were shifted in apparent

spatial frequency. Specifically, gratings of a spatial frequency lower than the adaptation frequency appeared perceptually to be lower still after adaptation; higher frequencies appeared shifted still higher in spatial frequency after adaptation. This effect can be observed by inspecting the patterns in Figure 6.7. Note that the two gratings to the right are identical. Now adapt for a minute or two to the patterns on the left by staring at the fixation line, being careful to move your eyes constantly back and forth along the fixation line to reduce selective retinal adaptation and the formation of afterimages. Then glance briefly at the fixation point between the two gratings at right. Do they still appear identical? Most people readily see that the top grating, which now stimulates a region that had been adapted to a low spatial frequency; appears to be of a higher spatial frequency than the physically identical pattern at bottom right, which stimulates a region that had been adapted to a high frequency.
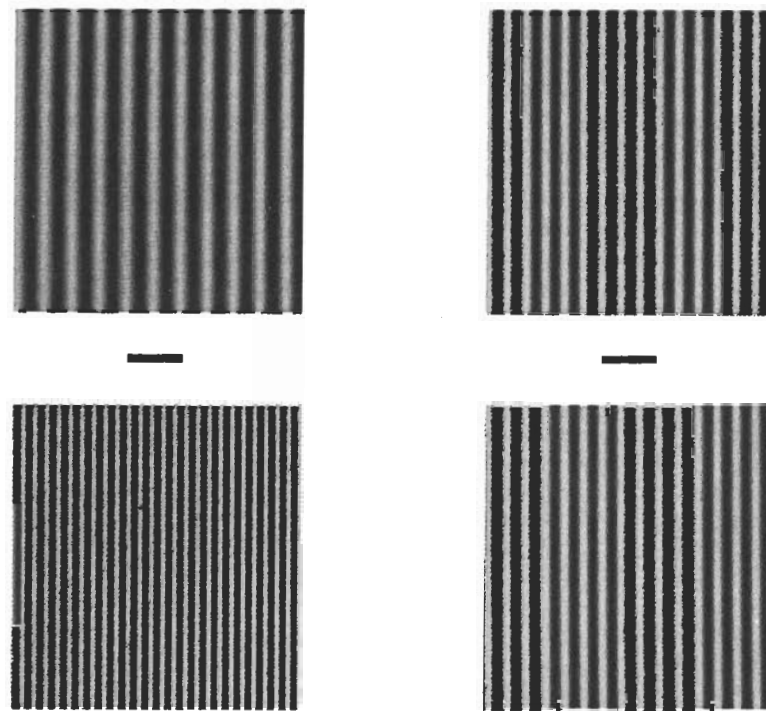

FIG. 6.7   Demonstration of the Blakemore-Sutton effect. First note that the two test gratings on the right are identical. Now adapt for about 1 min while scanning back and forth along the fixation bar between the two gratings on the left, then quickly shift your gaze to the fixation line between the test gratings on the right. They should now appear different in spatial frequency, each one being shifted away from the frequency of the adaptation grating that occupied the same retinal area.

This aftereffect, examined in further quantitative experiments by Blakemore, Nachmias, & Sutton (1970), can readily be explained on the basis of multiple spatial frequency channels. If, as shown in Figure 6.8, our perception of a pattern as having a particular spatial frequency is based on the relative activity rate in overlapping spatial channels, and if the effect of adaptation is to selectively depress the sensitivity (and responsiveness) of the channel(s) activated by the adaptation stimulus, the predicted shift in the apparent frequency of gratings away from that of the adaptation grating can be predicted. Note that this involves an important additional assumption—namely, that the outputs of the various spatial frequency channels are somehow labeled. In other words, it assumes that activity within a given mechanism does not just signal the presence of some contrast in the stimulus, but rather that it also signals a specific spatial frequency. Thus, one could unambiguously conclude that the stimulus contained energy at or near 2 c/deg if the 2-c/deg channel was active. Such an assumption is not required to explain the results of most of the detection experiments. As applied to the Blakemore and Sutton experiment, it requires some additional assumption about the way in which one interprets the outputs of multiple, simultaneously active detectors. A high-contrast pattern of a particular spatial frequency will activate many cells, only some of which are maximally sensitive at that spatial frequency (see our earlier discussion about the makeup
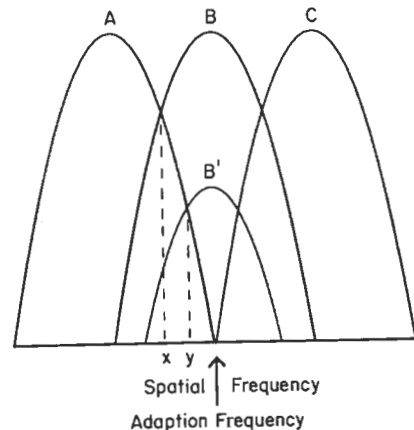

FIG. 6.8   A model of spatial frequency channels and the effects of adaptation, to account for the Blakemore-Sutton apparent spatial frequency shift. Three spatial frequency channels (A, B, and C) are presumed to signal the apparent spatial frequency in this region by their relative activity rates. For instance, *x* will have a certain apparent spatial frequency because it equally stimulates channels A and B. Following adaptation to a grating of the middle frequency, the sensitivity of channel B is reduced to B'. Now, a grating of frequency *y* will equally stimulate channels A and B (now B'), and thus will look the same as *x* had looked before adaptation.

of channels). In order to assign a spatial frequency to such a pattern, based on the output of a large, varied collection of cells, one might assume either that the frequency of the stimulus was the peak spatial frequency of the most active cell, or that the stimulus frequency was reflected by some central tendency of the distribution of peak frequencies of the active cells. In either case, the underlying assumption is that cells (or perhaps very small cortical regions) are tagged in such a way that activity in a given cell somehow signals a particular spatial frequency (or perhaps a narrow range of spatial frequencies). Some such assumption is necessary to explain the Blakemore and Sutton experiment, but any of a number of similar models would suffice.

Blakemore and Nachmias (1971) also measured both the loss in contrast sensitivity and the apparent spatial frequency shift produced by grating adaptation as a function of the orientation of the test grating relative to that of the adaptation grating. They found that when the test grating was tilted about $6\frac{3}{4}°$ with respect to the adaptation grating, the decline in the magnitude of *both* effects could be matched by a reduction in contrast (of the adaptation grating) by a factor of two. This quantitative similarity strongly suggests that a common underlying mechanism is responsible for both of these phenomena.

A similar shift in the apparent spatial frequency of a grating was demonstrated by Klein, Stromeyer, and Ganz (1974), using two simultaneously presented gratings rather than an adaptation pattern and a subsequent test pattern. They showed that the apparent spatial frequency of a grating within a small central test region depends, to some extent, upon the spatial frequency of a grating seen in a surrounding (but not overlapping) annulus. Gratings which are higher in frequency than the surrounding pattern appear to be still higher. Those which are lower in frequency than the surrounding pattern appear to be lower yet. The shifts in apparent spatial frequency as a function of the frequency of a surrounding grating section are similar to those seen in the Blakemore and Sutton adaptation experiment.

It is important to distinguish between these experiments and the earlier figural aftereffect demonstrations of Kohler and Wallach (1944). In the latter case, the subject steadily fixates an adaptation pattern, without (intended) eye movement, and then inspects a test pattern. The contours of the test pattern now appear to be displaced away from those of the adaptation pattern. It can be seen that the figural aftereffects of Kohler and Wallach consist of changes in the apparent position of contours after adaptation to nearby contours, but such a phenomenon cannot explain the Blakemore and Sutton aftereffect. Since the eyes are moving back and forth during adaptation to the pattern in Figure 6.7, the contours of the grating will stimulate all retinal areas approximately equally. There is no selective adaptation of certain discrete *spatial locations*, as there is in figural aftereffects (although the adaptation is restricted to a general retinal region). Rather, the selective adaptation is in the *spatial frequency domain*. Insofar as striate units have both spatially localized RFs and have spatial frequency selectivity, however, the same essential mechanism could be involved in each case.

It is well known that if one stares for a time at a bright light and then looks

away, various aftereffects of the stimulation are seen for several seconds. Such afterimages can be partly attributed to selective bleaching of receptor photopigments or gain control changes in the receptors, and partly to the afterdischarge of receptors or later neural elements. Some afterimages (e.g., negative color afterimages) can most readily be accounted for on the basis of neural rebound (see R.L. De Valois & K.K. De Valois, 1975). After prolonged excitation a neuron tends to exhibit a refractory period when it is less likely to fire; after prolonged inhibition it may rebound into excitation. If similar postadaptation processes occur in cortical neurons activated by various spatial patterns, one might expect to see patterned afterimages on blank surfaces after prolonged inspection of certain figures. Georgeson (1976) has reported seeing such spatial afterimages, which he called "hallucinations." He reported that after looking at a pattern of one orientation, one spontaneously sees gratings of slightly different orientations when staring at a blank field. He also reported that "hallucinatory" gratings of slightly different spatial frequencies appear after inspecting a grating of a particular spatial frequency. It should be emphasized that in this situation, as in the Blakemore and Sutton aftereffect tests, the adaptation patterns were inspected with moving fixation, so the aftereffects cannot be attributed to luminance adaptation in certain spatial locations. They occur within the spatial frequency domain.

These spatial afterimages find a ready explanation in multiple spatial frequency and orientation channels. We presumably can identify the orientation and spatial frequency of a grating because units tuned to that particular frequency and orientation are more active than are those units tuned to other spatial frequencies and orientations. A uniform or blank field, correspondingly, would normally appear uniform because all channels are equally active (or inactive). But after prolonged exposure to a particular spatial frequency and/or orientation of pattern, the various channels would no longer be equally sensitive, so that uniform, broad-band stimulation might well produce more activation in some spatial frequency and/or orientation channels than in others. Alternatively, if some spatial frequency and orientation channels had been inhibited by the cells most responsive to the inspection pattern, rebound excitation would result in these units' firing more rapidly, even in the absence of subsequent stimulation, thus producing "hallucinatory" gratings of other orientations and frequencies. The fact that the patterns seen are slightly off in orientation and spatial frequency from the inspection pattern is consistent with the nature of cortical inhibitory interactions (see Chapter 11).

An explanation for such spatial afterimages is fairly straightforward. What is not obvious, however, is an explanation for the paucity and faintness of these afterimages. When compared to retinal afterimages (negative color afterimages, for example), they are poor fare indeed. The reason may lie in the much lower levels of spontaneous activity found in the cortex as compared to retinal ganglion cells and LGN cells. Indeed, the sharp reduction in spontaneous neural activity is among the most noticeable differences between cells in the striate cortex and those at earlier neural levels. Suppose now that in the cortex the identity

of a visual stimulus is signaled by the relative firing rates of various neurons. If the effect of adaptation is to hyperpolarize some cells and concomitantly depolarize others, the relative firing rates of the two groups will now differ significantly if both groups of cells have unadapted spontaneous activity rates greater than zero. The cells that were excited by the stimulus will now show an abnormally low spontaneous rate, and those that were inhibited will rebound to a higher-than-normal spontaneous rate.

Consider what the result would be, however, if these same groups of cells were strongly hyperpolarized in the resting state so that they showed no spontaneous firing. Their spontaneous rates can be considered as being below zero. Their resting levels would have to be raised considerably before random fluctuations in ionic currents would produce action potentials. Thus, even if these cells were depolarized to some extent following prolonged inhibition, the rebound effect might not be sufficient to raise the resting level enough to allow random fluctuations to produce frequent action potentials. Sensitivity to subsequent stimulation (measured in terms of stimulus amplitude necessary to produce firing) would be increased, but afterimages that depended on rebound firing in the absence of stimulation would not be seen.

Spatial Frequency Selective Masking

Psychophysical evidence for the existence of multiple spatial frequency selective channels also comes from masking studies, in which the detectability of a particular pattern is measured alone and then in the presence of another, masking pattern. If the presence of the mask has no effect on the detectability of the test pattern, then one can assume that mask and test are detected by independent mechanisms. The interpretation of the condition in which a significant masking effect is seen, however, is rather more complicated. There are at least two straightforward ways in which such a result could be produced. The most commonly assumed one is that both the mask and test stimuli excite some of the same units. The detectability of a 2-c/deg grating, for instance, presumably measures the activity of a channel centered at 2 c/deg. Suppose that a grating of 3 c/deg also excites that channel to some extent. If the contrast-response function for that channel is compressive (e.g., it shows a Weber fraction relationship), then the presence of one suprathreshold excitatory input (here the 3-c/deg mask) would increase its threshold for detection of an additional input (the 2-c/deg test grating). The "mask" grating here acts as a stimulus pedestal upon which the test increment must be detected. By measuring the spatial frequency range over which masking interactions are found, one can derive an estimate of channel bandwidth and shape. Since we know that similar relationships do hold for very many neural systems, this is not an unreasonable assumption.

There is another, perhaps equally likely, possibility, however. Assume now that there are mechanisms centered at 2 and 3 c/deg, respectively, which have nonoverlapping excitatory ranges but which are mutually inhibitory such that

activity in one directly inhibits the other, thus effectively increasing the threshold of the second mechanism. The presence of a masking grating of 3 c/deg, whether or not it excited the mechanism centered at 2 c/deg, would increase the threshold for detecting the simultaneous presence of a 2-c/deg grating by virtue of the increased inhibition it produces. Thus, the existence of spatial frequency specific masking does not provide unambiguous information about the shape or bandwidth of the detection channel under consideration. The fact that masking extends only over a limited spatial frequency range, however, does imply the presence of multiple channels that are considerably more narrowly tuned than the overall CSF.

Several investigators have found evidence for spatial frequency specific masking effects. Carter and Henning (1971), Stromeyer and Julesz (1972), and Henning, Hertz, and Hinton (1981) examined the detectability of grating patterns in the presence and absence of band-limited noise patterns. These experiments are similar in logic and design to critical band masking experiments in audition, in which one determines the width of the band of frequencies around the test frequency that can mask it. They found evidence for spatial frequency selective masking, in that the detectability of a grating pattern of a particular spatial frequency was severely degraded by a noise pattern of the same or nearby spatial frequency range, but little affected by the presence of noise patterns that were an octave or more distant in spatial frequency.

The use of a noise mask allows one readily to derive an estimate of the critical band. Masking by a single spatial frequency grating, however, allows a more precise determination of interactions between individual frequencies. If the mask is, say, a 1-octave-wide noise band, it is not clear whether the masking is due to the power present in a narrower band, to the interactions among the various frequencies present in the noise band, or to something like the integrated power over the entire masking bandwidth.

Several experiments (e.g., Pantle, 1974; Legge & Foley, 1980; K.K. De Valois & Switkes, 1983; Switkes & K.K. De Valois, 1983; H.R. Wilson, McFarlane, & Phillips, 1983) have measured masking of a single spatial frequency grating by another single frequency grating. Figure 6.9 presents data from one such experiment (K.K. De Valois & Switkes, 1983), in which both test and masking gratings were luminance-varying patterns of identical space-averaged luminance and chromaticity. It can be seen that masking—i.e., the decrease in contrast sensitivity—is profound when test and mask are identical or very near in spatial frequency and the mask is of high contrast. Masking decreases as mask and test frequencies diverge, falling to zero by about f +/− 2 octaves. The function is peaked, centered at f, and asymmetric, with higher frequencies masking a given test frequency more effectively than do lower frequency masks.

These masking results might be attributed to a pedestal mechanism, in which the added contrast is less effective by being superimposed on an existing contrast, its effectiveness being decreased because of a compressive contrast-response relationship. Alternatively, it could be due to direct inhibitory interactions. Whatever the mechanism, band-limited masking functions such as that
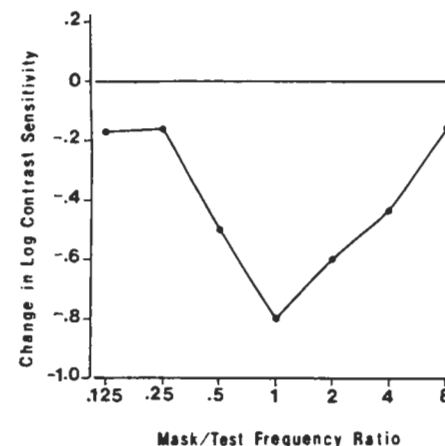
FIG. 6.9 Spatial frequency specific masking. A high-contrast mask of a given frequency selectively reduces contrast sensitivity to gratings of nearby spatial frequencies but has little effect on those which are further removed. The data plotted here show the change in log contrast sensitivity at a given spatial frequency as a function of the mask/test frequency ratio (redrawn after Switkes & K.K. De Valois, 1983. Reprinted by permission).

shown in Figure 6.9 imply multiple spatial frequency channels of finite bandwidth.

Subthreshold Summation

A paradigm methodologically similar to suprathreshold masking is one which measures subthreshold summation. The logic and procedure are as follows. Suppose that there exists a channel with a linear input-response relationship and two or more different excitatory stimuli. The output of that channel will be detected if and only if its response reaches some criterion level, but a subthreshold stimulus might still produce a small response even though it does not reach the detection threshold. Now assume that the input-response function for the first stimulus is known, such that one can produce a stimulus of half threshold contrast. Add to that a second stimulus which is also of half threshold contrast. Neither alone would be detected (since the response to neither would reach the criterion level), but one might well expect their combination to be detected. If the channel only needs n response units to reach threshold, and if it makes no difference to the channel whether those n units came from the same or different stimuli, then two stimuli, each of half threshold contrast, should combine to produce a threshold response.

This is easiest to imagine in the case of two identical gratings which are added together in phase, where the procedure reduces to one of merely increasing the

contrast from a subthreshold to a threshold level. The same logic may be applied, however, to the case in which the two gratings differ in spatial frequency. If the channel shows linear summation within its passband, then two excitatory stimuli, each of which is of 0.5 times threshold contrast, should sum to produce a threshold response. Thus, by measuring the frequency range over which subthreshold summation occurs, one can derive an estimate of channel bandwidth.

In a subthreshold summation experiment similar to that described above, Sachs, Nachmias, and Robson (1971) did indeed find subthreshold summation between gratings of closely spaced spatial frequencies but not between more widely spaced ones. This again implies the existence of multiple channels, each of which is more narrowly tuned than the overall contrast sensitivity function. In a later section we will consider the actual estimates of bandwidth that are derived from these various types of experiments.

Retinal Inhomogeneity

Almost all of the experiments we have been discussing above have used stimulus patterns that covered a considerable portion of the central retina. This raises a problem for the evaluation of the evidence discussed above for multiple channels. It is well known that our sensitivity to high spatial frequencies or very fine detail is greatest in the central fovea and decreases drastically with increasing retinal eccentricity. Given this progression, it is conceivable that the supposed high spatial frequency channels just reflect foveally related activity, that the near periphery is the site of detection of medium spatial frequencies, and that low frequencies are detected only in the far periphery (van Doorn, Koenderink, & Bouman, 1972). Much of the classical discussion of acuity, as well as many accounts of variation in RF size as a function of eccentricity (e.g., Hubel & Wiesel, 1974b), suggests such an organization. An arrangement like that, however, would produce a strange visual system indeed. Large (blurry) objects, for example, would only be perceived, or at least would be detected best, in the periphery. If such a suggestion were correct, it would compromise the interpretation of the psychophysical evidence for multiple spatial frequency channels. Analyzing complex patterns into their individual spatial frequency components in a spatially local frequency analysis would demand that these multiple channels all be processing information from the same retinal region. Thus establishing whether there are multiple channels all located within a given retinal region is an important question.

Robson (1975b); Graham, Robson, and Nachmias (1978); Watson and Nachmias (1980); Robson and Graham (1981); and Watson (1982) attempted to determine whether different spatial frequency channels are present in a given location or whether they merely correspond to different retinal eccentricities. Robson and Graham examined the detectability of spatially delimited grating patterns of a constant number of cycles, of various spatial frequencies, presented

at various eccentricities. Thus the size of the stimulus patch was inversely related to its spatial frequency. Their evidence suggests that every small region in visual space is in fact analyzed by channels tuned to a variety of spatial frequencies. The high spatial frequency channels do tend to drop out with increasing eccentricity, but the entire range of visible spatial frequencies is detected within the foveal projection itself, and smaller, but still broad ranges of spatial frequency are detected more peripherally. Furthermore, they found sensitivity to all spatial frequencies, low as well as high, to be greatest in the fovea.

This approach seems a reasonable one. There are, however, other methods that yield quite different answers. In particular, if the extent of the stimulus is increased with increasing retinal eccentricity (to compensate for the presumed CMF), the retinal region of greatest contrast sensitivity depends on the test spatial frequency (Rovamo et al., 1978; D.H. Kelly, 1984). See our earlier discussion of the variation of the spatial CSF with retinal locus (Chapter 5).

Physiological and Anatomical Substrates of Spatial Frequency Channels

Although spatial frequency channels are described on the basis of psychophysical experiments, they must, of course, have some physiological substrate. It is useful to consider the characteristics of psychophysically measured channels in relation to what is known about the properties of cells at various levels in the visual system. While the functioning of the system is specified by psychophysical experiments, the relevant physiology puts limitations on the types of models that can reasonably be suggested to explain the psychophysical findings. Much of the evidence relating to cell characteristics at the retinal, geniculate, and cortical levels has been summarized in the preceding chapters. Here we will consider only those findings which are directly relevant to the psychophysically measured spatial frequency channels.

Neural Level

Consider first the question of the neural level that is reflected in psychophysical "channel" experiments. It is generally accepted that psychophysically measured spatial frequency channels are cortical in origin. There are several reasons for this assumption. First, the channels are orientation selective. Adaptation to a grating of one spatial frequency at one orientation produces a temporary loss in contrast sensitivity for gratings of that and nearby frequencies only if they are at the same or similar orientations. Gilinsky (1968), in an early paper that led to much subsequent work with pattern-specific adaptation, demonstrated an orientation-specific loss in sensitivity to a low-contrast vertical grating following adaptation to a similar high-contrast grating. Adaptation to a horizontal grating had no effect on the detection of a vertical grating. Blakemore and Nachmias (1971) found that both the contrast sensitivity loss and the apparent frequency

shift with adaptation were sharply orientation specific. Sekuler, Rubin, and Cushman (1968) found a similar dependence on the relative adaptation and test orientations for the threshold elevation produced by adaptation. Since, as Hubel and Wiesel (1959, 1962) first showed, neurons in the striate cortex are the first in the geniculostriate pathway to show narrow orientation tuning, the orientation specificity of these processes implicates units at this level, or possibly still later levels.

A second reason for assuming that spatial frequency channels are of cortical origin is that there is considerable interocular transfer of spatial frequency adaptation effects. Blakemore and Campbell (1969) found interocular transfer of about 60%. It has been well established (e.g. R.L. De Valois, 1965; Wiesel & Hubel, 1966) that there is very little, if any, binocular interaction in LGN cells in primates. Indeed, the first cortical units may also be largely monocular (see Chapter 4). Thus the presence of significant interocular transfer implies a cortical locus for the effect being studied.

The third reason for concluding that psychophysical channels reflect the cortical, rather than retinal or LGN, organization is the narrowness of the spatial frequency tuning of cells at these various levels. The cells in striate cortex are the first in the path to show reasonably narrow spatial frequency tuning, as well as fairly narrow orientation tuning (see Chapters 3 and 4 and further discussion below).

Still another reason for attributing the characteristics of multiple spatial frequency channels as revealed in some of these psychophysical experiments to striate cortex cells is that cells at this level, but not at earlier levels, appear to show the appropriate adaptational changes. As we discussed in Chapter 3, LGN cells have very broad spatial frequency tuning. Since one might have thought a priori that both LGN and cortical cells could be subject to adaptation in the Blakemore and Campbell experiment, it is rather puzzling that one finds only narrow, spatial frequency specific (and orientation-specific) adaptation effects. If both broadly tuned geniculate units and narrowly tuned cortical units were adapted by the stimulus conditions in that experiment, one would expect to find a selective sensitivity loss around the adaptation frequency (due to cortical cells) superimposed on a general overall depression in the CSF (due to LGN cells). Nothing like this is in fact seen. Rather, at off spatial frequencies one can see an actual enhancement of sensitivity (K.K. De Valois, 1977b). The physiological basis for this appears to be that cortical cells show adaptation with prolonged presentation of an appropriate stimulus pattern (Maffei, Fiorentini, & Bisti, 1973; Vautin & Berkley, 1977; Movshon & Lennie, 1979a; Albrecht, Farrar, & Hamilton, 1984), but LGN cells do not (Movshon & Lennie, 1979b). The cortical evoked potential has also been found to show selective spatial frequency adaptation (Bonds, 1984).

The "adaptation" of cortical cells is often thought of as some sort of fatigue process resulting from overstimulation. The general assumption is that adapted cells are in a refractory state similar to that demonstrated in other neurons following repetitive stimulation. This is a simple and attractive hypothesis, both

because of its similarity to processes known to occur elsewhere in the nervous system and because it is easy to "explain" in terms of such relatively simple factors as transmitter depletion. (There is, however, some contrary evidence from both psychophysical [Dealy & Tolhurst, 1977] and physiological [Movshon, Bonds, & Lennie, 1980] experiments.)

Another possibility is that adaptation may reflect the contrast gain control process found to operate at striate levels among many cells. Ohzawa, Sclar, and Freeman (1982) showed that many cortical units adjust their sensitivity to the average contrast of test patterns present within their RFs. Such cells increase their sensitivity when presented with only low-contrast patterns, but decrease their sensitivity in the presence of high-contrast patterns (such as those used in the typical Blakemore and Campbell adaptation experiment). Such a mechanism has the clear functional advantage of extending the contrast range over which a cell can give useful information.

Narrow Spatial Frequency Tuning

The first study of the spatial frequency tuning of striate cells (Campbell, Cooper, & Enroth-Cugell, 1969) found most cortical units to be relatively broadly tuned (although more narrowly tuned than ganglion cells). However, recent studies (e.g., Maffei & Fiorentini, 1973; R.L. De Valois, K.K. De Valois, Ready, & von Blanckensee, 1975; R.L. De Valois, Albrecht, & Thorell, 1978; Movshon et al., 1978c; Kulikowski & Bishop, 1981; R.L. De Valois, Albrecht, & Thorell, 1982) based on many more cells (and perhaps with improved recording techniques) have found large numbers of more narrowly tuned units. (One might note parenthetically that the Campbell et al., 1969, study is one of the rare occasions in the history of science on which an investigator published data that appear to be biased *against* rather than in favor of his theory.)

The most relevant data are those from recordings made of the responses of cells in monkey striate cortex, in which (as discussed in Chapter 4) we find the average spatial frequency bandwidths of both simple and complex cortical cells to be about 1.4 octaves, with a significant number of units having a bandwidth of 1 octave or less. The most narrowly tuned striate cells have a bandwidth at half amplitude of about 0.6 octaves (R.L. De Valois, Albrecht, & Thorell, 1982). Other studies of monkey (Kulikowski & Vidyasagar, 1982; Foster, Gaska, & Pollen, 1983) and cat (Glezer, Ivanoff, & Tscherbach, 1973; Glezer & Cooperman, 1977; Movshon et al., 1978c) striate cells have reported similar tuning properties. The bandwidth of an average cell covers only a fraction of the total range of spatial frequencies to which the organism is sensitive (see Figure 6.10). In the fovea, the total CSF covers at least 6 to 8 octaves; the typical cell has a bandwidth of less than a quarter of that range. (We might note that this is actually somewhat less than the proportion of the total orientation range covered by the orientation bandwidth of a typical cortical cell.) In the periphery, the CSF may narrow, due to an absence of cells tuned to the highest spatial frequencies, and
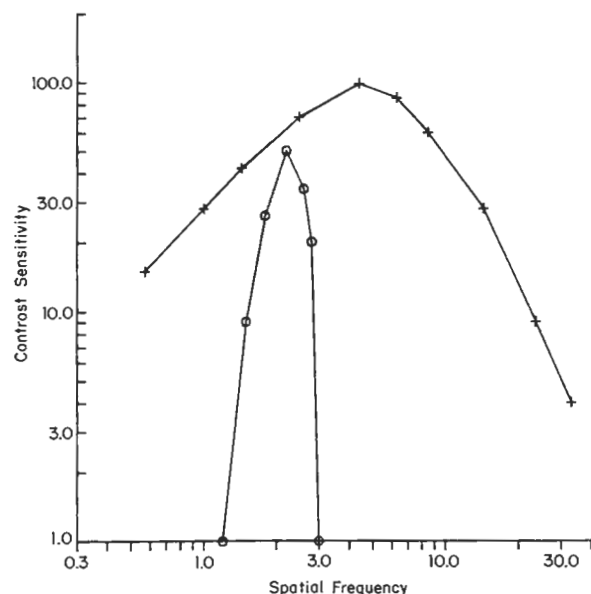
FIG. 6.10   Macaque behavioral CSF (crosses) and the CSF of a single macaque striate cortex cell (circles). Note that the cell's CSF has a very much narrower bandwidth than that of the overall behavioral CSF. The latter presumably reflects the activity of many more narrowly tuned individual cells, as depicted in Figure 6.1.

the cells there would cover a larger proportion of the total CSF if their bandwidths are no narrower than those in the fovea.

Studies of the functional anatomy of the striate cortex also provide support for there being units tuned to limited spatial frequency ranges. As discussed in Chapter 4, if radioactively labeled 2-DG is injected into a cat while it binocularly observes a pattern containing all orientations (over time) but just a single spatial frequency, autoradiography on cortical sections reveals a clear columnar pattern of increased glucose uptake (Tootell et al., 1981); see Figure 4.24. Within a cortical region of about 1 mm x 1 mm, one group of cells has greatly increased activity and thus takes up a lot of the labeled 2-DG, whereas the other cells within the region do not. This indicates that only a subpopulation within the module is responsive to that particular spatial frequency: if each cell had the sensitivity of the overall CSF, each would respond to the pattern and uniform glucose uptake would result. When a binocular pattern made up of all spatial frequencies and all orientations is presented, just such a uniform pattern of uptake is in fact seen (Tootell et al., 1981). The same selective activation of the striate cortex by a pattern of just one spatial frequency is also found in monkey cortex (Tootell et al., 1982b). Although the overall anatomical arrangement of spatial frequency columns is different in monkey cortex from that seen in cat,

one finds again that patterns of a given single spatial frequency activate only a subpopulation of the cortical units.

Multiple Channels in a Given Region

Electrophysiological data are also available that are directly relevant to the question of whether there are cells tuned to multiple spatial frequencies within a given cortical area (the other possibility being that cells tuned to different spatial frequencies occur at different eccentricities). Here there are certain apparent contradictions in the physiological evidence. Two classic studies of the RF size of cells at different eccentricities (Hubel & Wiesel, 1974b; Albus, 1975a) both reported arrangements of cells within the striate cortex that are somewhat contrary to the requirements for multiple spatial frequency channels. Since these studies are widely accepted, the skepticism of many physiologists about spatial frequency models can be understood. Both of these studies reported that cells in the foveal (or central) projection region of cortex have small RFs, with RF size increasing with eccentricity. Some variability in RF size was found in each region, but much less than the variation with eccentricity. Thus some monkey foveally related striate cells were reported to have tiny RFs and others 2 or 3 times as large, but none to have nearly as large RFs as those seen in peripheral cells (Hubel & Wiesel, 1974b). Insofar as RF size, as measured in these experiments, is directly related to spatial frequency tuning (a very questionable jump, as we shall see), such findings clearly pose a problem for models of multiple spatial frequency channels processing information from a given retinal region.

On the other hand, two studies that specifically measured the optimal spatial frequency tuning of cells (as opposed to some measure of the overall RF size) reported quite different results. These studies in cat (Movshon et al., 1978c) and monkey (R.L. De Valois, Albrecht, & Thorell, 1982) found a wide range of spatial frequency peaks among foveally (or centrally) related units. In cat, the situation is complicated by the dual projection from the LGN to both areas 17 and 18. Movshon et al. (1978c) found that area 17 cells are tuned to a higher spatial frequency range than those in area 18, but within each of these areas the cell tunings cover considerably more than the 1-octave range of RF sizes reported by Albus (1975a). In our study of monkey striate cells (R.L. De Valois, Albrecht, & Thorell, 1982), we found an even wider range (ca. 4 to 5 octaves) of peak spatial frequency tuning among units in the near-foveal cortex, with the cells peaking everywhere from about 0.5 c/deg up to as high as 16 c/deg (see Figures 4.16 and 4.17). One might note in passing that there appears to be a continuous distribution of peak frequencies within this range, with no evidence for grouping into, for example, four distinct classes as the model of H.R. Wilson and Bergen (1979) would suggest.

Clearly those studies directly examining the spatial tuning of cells (Movshon et al., 1978c; R.L. De Valois, Albrecht, & Thorell, 1982) are the most relevant to questions of multiple spatial frequency channels, and they provide unequiv-

ocal evidence for cells within a given cortical region being tuned to each of a wide range of different spatial frequencies. Nonetheless, one would like to understand the apparent discrepancy between these studies and the others which measured RF size. Although the overall RF size of a cell should be somewhat related to its spatial frequency tuning (see Chapter 4), there is no reason to expect a one-to-one relationship. The width of the RF center of a simple cell should be equal to a half period of the optimal spatial frequency grating, but how each of these is related to the *overall RF size* is a more complex matter. It is important to note that Hubel and Wiesel (1974b) measured RF size not in terms of the optimal width bar, but by marking the locations at which a response was first elicited when a bar was moved towards the RF center from each side in turn. The resulting rectangle was taken as the RF size. For complex cells, the overall width of the RF is some amount greater than the optimum bar width, a relationship that varies from cell to cell and that may also vary with eccentricity. Many simple cells have periodic RFs, with multiple sidebands of decreasing sensitivity. If a rough RF mapping detected only the central excitatory region, one would conclude that the RF was a quite different size than one would if some of the sidebands were strong enough to be noticed. This could produce a very large difference indeed. Furthermore, the true RF size is a joint function of the optimum spatial frequency and the bandwidth (more narrowly tuned cells have more sidebands and thus larger total RF size than do broadly tuned cells with the same spatial frequency peak). Since cells tuned to high spatial frequencies are more narrowly tuned than low-frequency cells (see Chapter 4), the range in total RF size should be at least an octave less than the range in spatial frequency peak. These factors make reports of only a small range of RF sizes in foveal cortex less of a problem than they first seem. In addition, as stated initially, the crucial data are the actual spatial frequency tuning characteristics of cells.

Very clear anatomical evidence for a range of different spatial frequency tuning peaks within the central striate cortex has also been obtained in 2-DG studies of cat and monkey. When the 2-DG single spatial frequency experiment described above was repeated with single spatial frequencies ranging, in different animals, from 0.25 up to 2 c/deg (which cover a range from low to high spatial frequencies for the cat), columnar groupings of cells within each cortical module were found in each case (Tootell et al., 1981; Silverman, 1984). The columns of cells tuned to low spatial frequencies were found in all striate regions stimulated, including specifically the projection of the area centralis (which is homologous to the foveal projection in primate). When high spatial frequencies were used, however, columns were seen only in the central projection area. In studies of macaque monkey cortex (Tootell et al., 1982a), similar evidence was found for a grouping of striate cells by spatial frequency. Here again, it is clear that low spatial frequency patterns do *not* just activate peripheral cortex, but rather produce uptake all the way up to and including the foveal input region. High spatial frequency patterns produce uptake in these foveal regions as well, but the activation they produce falls off at some eccentricity, depending on how high a spatial frequency was used.

In summary, then, direct physiological and anatomical data support the psychophysical evidence that the overall behavioral CSF is made up of multiple subunits or channels with fairly narrow spatial frequency tuning. These studies indicate that each cortical module, which processes information from a given limited part of the visual world, has within it cells tuned to each of many spatial frequency ranges. These cells tuned to different spatial frequencies appear to be very systematically arranged in both cat and monkey cortex, in a columnar organization similar to that seen for cells tuned to different orientations.

CHANNEL TUNING CHARACTERISTICS

Any description of a system in terms of band-pass channels (along any dimension) raises questions concerning the tuning of those channels. A perfect, global, Fourier analyzing device, for example, would be composed of a set of band-pass filters, each of which was infinitely narrow. Activity in any one channel would unambiguously signal the presence of energy at one particular spectral point (in the case of spatial frequency analysis, at one particular spatial frequency). In practice, however, there is no truly ideal Fourier analyzer, and the visual system is certainly doing something far different from this: it does not do the global analysis required for extremely narrow channels at all. The nature of the analysis that can be carried out depends, among other things, upon the narrowness of the filters that transmit the necessary information. Thus, the question of the narrowness of tuning of visual spatial frequency channels is one of some importance.

Channel Bandwidth

There are two precautions that should be borne in mind in considering the bandwidth of spatial frequency channels. The first is that the precision with which one can measure such a function with a psychophysical experiment such as adaptation is not very great. A given subject may show considerable variability from day to day or even from session to session within the same day. This is true for criterion-free experimental paradigms (such as forced-choice methods), as well as for the faster method-of-adjustment paradigms. While long-term, repeated measures should allow one to converge on a reasonably accurate estimate, it is a mistake to assume a greater precision than one's psychophysical method (or even the visual system) allows. Extended practice and repeated measures can lead to greatly decreased fluctuations, but systematic changes (in sensitivity or bandwidth, for example) may result (K.K. De Valois, 1977b; McKee & Westheimer, 1978).

A second, more difficult problem with psychophysical estimates of spatial frequency bandwidths is that different types of experiments may lead to signifi-

cantly different values. Quite different estimates of channel bandwidth come from studies of subthreshold summation as opposed to masking experiments, for instance. Subthreshold summation studies typically produce very narrow bandwidth figures (e.g., Sachs, Nachmias, & Robson, 1971); masking experiments generally yield broader estimates (e.g., Legge & Foley, 1980). Does this mean that one set of estimates is right and others, wrong? That, of course, depends in part on one's model of spatial frequency channels. We would argue that different experimental techniques could simply be tapping different types of channels or different levels of interactions. Such differences should not be distressing unless one assumes that channels are fixed and immutable physiological entities, sculpted perhaps in dendrites, and unchanging, regardless of the conditions.

It is also possible (perhaps even likely) that the logic applied to some of the experimental paradigms is in error, and that the measurements therefore do not reflect channel bandwidth directly, but perhaps something like the bandwidth of inhibitory interactions, or probability summation. Such suggestions have been made by Dealy and Tolhurst (1977) concerning adaptation experiments, and by Graham et al., (1978) with respect to grating summation experiments. One should thus be cautious about interpreting such experiments.

With these caveats in mind, it is of interest to look at the bandwidth estimates derived from different types of psychophysical experiments, and to compare these with the physiological data. In Table 6.1 are summarized the full bandwidths at half amplitude of the spatial frequency channels as estimated from a selection of various types of experiments. It can be seen that with the exception of the subthreshold summation experiment, most of the studies come to a rough agreement on a spatial frequency bandwidth of about 1 to 1.4 octaves. With the sensitivity of each channel falling to half amplitude about 0.6 octaves to either side of its peak, stimuli about 1 octave away to either side would be almost totally ineffective.

Shown also in Table 6.1 are results from a physiological study of macaque striate cortical cells (R.L. De Valois, Albrecht, & Thorell, 1982). It can be seen that the mean bandwidth of striate cells, both simple and complex, is somewhat larger than the psychophysical estimates of channel bandwidths, reflecting perhaps the inclusion of the considerable proportion of cortical cells with rather geniculate-like spatial frequency tuning (and often little or no orientation tuning). Since the bandwidth distributions are skewed, the medians give a better estimate of the central tendency, but they are also slightly larger than the psychophysical estimates. However, the cortical population (see Figure 4.12) includes a sizable proportion of cells that are tuned as narrowly as, or more narrowly than, the psychophysical estimates.

Single-unit recording and 2-DG studies in the striate cortex can provide very powerful evidence as to the total population of cell properties to be found, e.g., the total range and distribution of spatial frequency and orientation bandwidths. This sets distinct limits to plausible psychophysical models: theories postulating cells extremely narrowly tuned for orientation or spatial frequency would be untenable (at least at the level of the striate cortex), as would theories postulating

TABLE 6.1. Channel bandwidth estimates (in octaves)

Technique	Psychophysical Measures	
	Study	Bandwidth
Adaptation	Blakemore & Campbell (1969)	1.3
	K. K. De Valois (1977b)	0.7
Masking: high-contrast gratings	Pantle (1974)	2.4
	Legge & Foley (1980)	1.8
	Wilson, McFarlane, & Phillips (1983)	1.2 to 2.4 (frequency dependent)
Masking: low-contrast gratings	Sachs, Nachmias & Robson (1971)	0.4
	Legge & Foley (1980)	0.5
	Watson (1982)	0.5
Masking: noise	Stromeyer & Julesz (1972)	1.0 to 1.5

Animal	Electrophysiology: Bandwidths of striate cortex cells	
	Study	Bandwidth
Macaque	De Valois, Albrecht, & Thorell (1982)	1.4 (0.5 to 3.0)
Macaque	Foster, Gaska, & Pollen (1983)	(0.7 to 2.8)
Cat	Movshon, Thompson, & Tolhurst (1978c)	1.3 (0.7 to 3.2)

a single very broadly tuned cell type whose sensitivity approximated the behavioral CSF. What the physiological evidence cannot do as well, however, is to tell us which cells within this overall population are involved in a particular task—e.g., those being tapped in the psychophysical studies discussed earlier in this chapter. Indeed, one cannot even say with confidence whether a particular behavioral response reflects the activity of one, or thousands, of cortical cells. What we can say, however, is that there is clearly no contradiction between the psychophysical and physiological data in indicating the presence of multiple mechanisms with spatial frequency bandwidths of about 1 octave tuned to each of many spatial frequencies across the spatial spectrum.

Bandwidths at Different Spatial Frequencies

Blakemore and Campbell (1969) estimated channel bandwidths by adapting to each of a number of spatial frequencies and measuring the resulting loss of contrast sensitivity. They concluded that bandwidths were somewhat narrower at high than at low spatial frequencies. Interpretation of this result is difficult, since with the small overall size of their stimulus pattern (1.5°), the bandwidth of the stimulus would be broader at low spatial frequencies (since only a few cycles of the stimulus would be present across the small oscilloscope face). It is a finding that would be worth examining with better experimental techniques. It is of interest, however, that physiological data from units in monkey striate (R.L. De Valois, Albrecht, & Thorell, 1982) confirm a narrowing of the tuning with
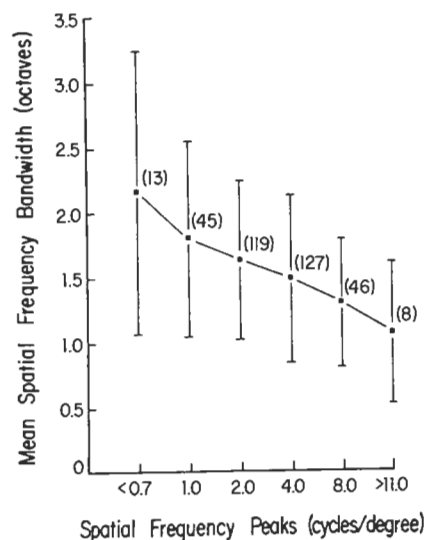
FIG. 6.11   Bandwidth distribution of macaque striate cortical cells as a function of their peak spatial frequencies. Plotted are the means (± 1 SD) of the spatial frequency bandwidths of a large group of cells. The numbers in parentheses show the number of cells in each group (from R.L. De Valois, Albrecht, & Thorell, 1982, *Vision Res., 22,* 545–559. Copyright 1982, Pergamon Journals, Inc. Reprinted by permission).

increasing spatial frequency (see Figure 6.11). Cells tuned to the very highest spatial frequencies are almost twice as narrowly tuned (on an octave scale) as those tuned to the lowest spatial frequencies. (Similar bandwidth narrowing at high spatial frequency has been found in cat striate cells by Kulikowski & Bishop, 1981.) However, it should be remembered that the bandwidths in Figure 6.11 are plotted on an octave, or logarithmic, scale. On a linear scale of spatial frequency, cells tuned to low spatial frequencies would be much more narrowly tuned than those with high spatial frequency peaks. Thus a cell with peak sensitivity to 0.5 c/deg and a 2-octave bandwidth would respond to gratings from about 0.25 to 1.0 c/deg, a 0.75-cycle linear range. A cell peaking at 10 c/deg and with only a 1-octave bandwidth would respond from 7 to 14 cycles, a 7.0-cycle linear range, almost 10 times as large as the lower frequency cell, which had double the octave bandwidth.

SPATIAL FREQUENCY OR SIZE?

We have been assuming throughout this chapter that the spatial dimension along which the visual system filters spatial information is (local) spatial fre-

quency, but some of the experiments discussed above could be interpreted as providing evidence for local size-tuned channels rather than spatial frequency channels. We will consider psychophysical, physiological, and anatomical experiments that bear directly on the issue of whether size or spatial frequency is the better description of the relevant visual spatial dimension. The infinity of possible spatial functions would seem to preclude the possibility of ever making an absolute determination of the most critical single spatial variable, but certainly it is possible to compare two reasonably well-defined variables.

A grating may be considered not as a pattern of a particular spatial frequency, but rather as a series of bars of some particular specifiable width, of some edge-to-edge distance. The adaptation experiments of Blakemore and Campbell (1969), for instance, could then be interpreted as showing the existence of size-tuned channels, mechanisms tuned to respond to bars of a particular width, rather than to particular spatial frequencies. Experiments can be, and have been, done to discriminate between these two possibilities. If a grating is considered as a series of bars of a particular width, the adaptational loss in contrast sensitivity produced by adapting to a single bar moved back and forth across the field should be equivalent in spatial tuning (though probably not in amplitude) to that produced by adapting to a drifting grating. From the point of view of its Fourier spectrum, however, a bar is quite different from a grating, particularly from a sinusoidal grating. A single bar has an extremely broad spectrum, with power at nearly all visible spatial frequencies (see Figure 6.12). If the visual system analyzes spatial patterns in terms of spatial frequencies, then, a single bar should excite virtually all the spatial frequency channels of the appropriate orientation and retinal locus, and adaptation to a single bar should reduce contrast
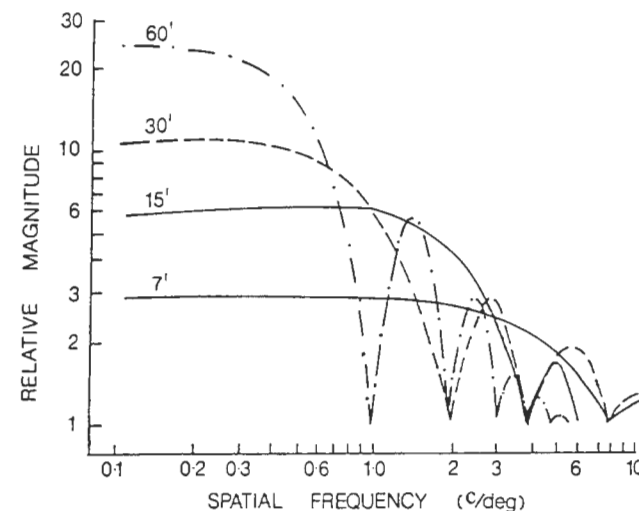

FIG. 6.12   Relative amplitude spectra for bars of different widths (in arc minutes).

sensitivity to a broad range of spatial frequencies (although that effect would presumably be rather small, since the absolute amplitude in any one restricted frequency region would be small). By the same argument, a sinusoidal grating patch, which has a much more restricted power spectrum, would be expected to produce adaptation only in a similarly restricted spatial frequency range.

Sullivan, Georgeson, and Oatley (1972) measured the effect of adapting to gratings on the detection of bars and vice versa. Adaptation to a grating of 5 c/deg produced a small decrease in contrast sensitivity for bars of a wide range of widths, not just bars of a width equivalent to one half cycle of a 5-c/deg grating. In addition, adaptation to bars of any of a wide variety of widths produced a small loss in contrast sensitivity to gratings of 5 c/deg. In other words, there was much less selectivity when a bar was used as either test or adaptation stimulus than when gratings were used for both. This result is readily predicted from a consideration of the spatial frequency spectra of bars and gratings, but not from a consideration of bar width and the equivalent bar widths of gratings. It suggests that the channels are not size channels, but spatial frequency channels, as we have been referring to them.

The same comparison between bars and gratings can be made at the physiological level. If cortical cells are bar detectors, analyzing complex patterns into bars of various widths, they should be very selective for bar width. If a grating is treated as a series of bars, then cells should show similar selectivity for bars and gratings. On the other hand, if cortical cells are analyzing the (local) visual scene into its spatial frequency components, one would expect them to be very selective for gratings but quite unselective for single bars, given the broad spatial frequency spectrum of bars, as discussed above.

R.L. De Valois et al. (1978) and Albrecht, R.L. De Valois, and Thorell (1980) directly compared the narrowness of tuning of the same cortical cells for sinusoidal gratings of various spatial frequencies and for bars of various widths, matched in contrast. Both simple and complex cells showed considerably nar-
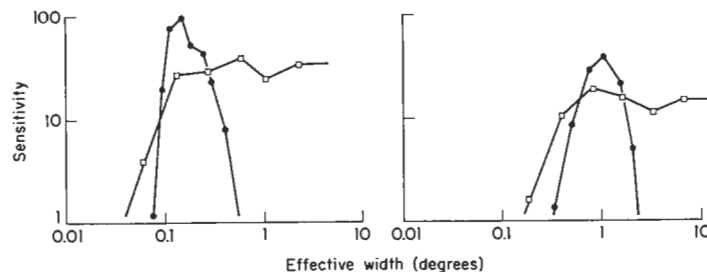

FIG. 6.13   Tuning functions for two representative striate cortex cells. Plotted are the sensitivity functions for bars of various widths (squares) and sinusoidal gratings of various spatial frequencies (circles). Note that both cells are much more narrowly tuned for grating frequency than for bar width (from Albrecht et al., 1980, *Science*, *207*, 88–90. Copyright 1980, AAAS. Reprinted by permission).

rower tuning for sinusoidal gratings than for bars of various widths; not a single cell was found that was less selective for gratings than for bars (see Figure 6.13). Similar results were also reported by Schiller et al. (1976c) in comparing selectivity for sine versus square wave gratings.

The physiological data, then, agree with the psychophysical results that a grating is best considered *not* just as a series of bars of a particular width, being detected by cells tuned to a particular bar width. Rather, cells are more selective along the dimension of spatial frequency, and the responses of cells to bars (as well as to other stimuli) can be predicted to a first approximation from the local Fourier spectra of the patterns and the contrast sensitivity of the cell.

DO CELLS RESPOND TO SPATIAL FREQUENCY COMPONENTS?

The physiological and anatomical experiments discussed above address the general question of whether the essential machinery is present in the cortex for patterns to be filtered into multiple spatial frequency channels. The preponderance of the evidence, as we have indicated, supports this. What such physiological experiments do *not* answer, however, is the crucial question of whether the system functions sufficiently linearly to actually analyze patterns into their separate frequency components. This question was addressed at the psychophysical level by such experiments as those of Campbell and Robson (1968) and Graham and Nachmias (1971) discussed earlier. The question can also be posed—even more directly—at the physiological level. Such experiments have been carried out by K.K. De Valois et al. (1979); Maffei, Morrone, Pirchio, and Sandini (1979); and Pollen and Ronner (1982).

Consider a square-wave grating. The Fourier spectrum of a square wave (see Figure 1.3) consists of a fundamental with an amplitude of $4/\pi$ ($=1.27$), with respect to a sine wave of the same contrast, plus odd harmonics in decreasing amplitudes. If contrast were the crucial determinant of a cell's responses, sine and square wave gratings of optimal frequency and equal contrast should produce equal responses. On the other hand, if the cell were responding to the individual frequency components in the patterns, it should give 1.27 times as large a response to the square wave as to the sine wave. Another way to address the same question would be to compare responses to a square wave grating of a particular contrast and a sine wave grating of 1.27 times as high contrast; these have identical fundamental components. Pollen and Ronner (1982), recording the overall amplitudes of the responses of striate cells to such patterns, found that they behave as expected from the amplitudes of the Fourier fundamentals, not from the overall pattern contrasts.

We have confirmed the results of Pollen and Ronner. We have also examined the peristimulus time histogram for possible responses to higher harmonics of the square wave grating, as well. A square wave of one third the optimum spatial

frequency for a cell has a third harmonic which would be at the cell's optimum frequency. One would thus expect a simple cell to fire three times to each passage of such a low spatial frequency square wave grating across its RF (note that the cell would *not* respond to a sine wave grating of this frequency). This is what we found (see Figure 6.14). Similar results have also been reported by Maffei et al. (1979). Furthermore, the amplitudes of the responses to the third harmonic were

precisely those predicted from the amplitude of this Fourier component (i.e., one third as large as the response to the fundamental). Many narrowly tuned striate cells also respond to the fifth harmonic of a square wave grating (when the square wave is of such a low base frequency that its fifth harmonic is at the optimum spatial frequency for the cell); see Figure 6.14 bottom.

Such results are totally unpredictable from our phenomenological impression of a square wave—we can perceive no third or fifth harmonic lurking within the pattern. It is also not at all what one would predict from striate cells which are supposedly responsive to edges: there are not three—to say nothing of five— edges in one cycle of a square wave. But it is just what would be predicted if the striate network were indeed filtering patterns into their local spatial frequency components.
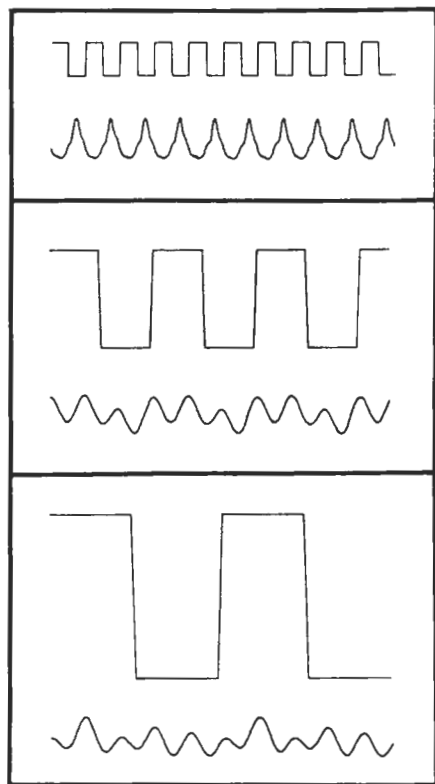

FIG. 6.14 Responses of a macaque striate cortex cell to square wave gratings of three different spatial frequencies drifted across its RF. The square wave in the upper box has its fundamental component at the cell's "best" spatial frequency. Note that the cell shows one response peak per stimulus cycle. In the middle box the square wave fundamental frequency is reduced by a factor of three. The third harmonic of the waveform is now in the cell's band-pass, and there are correspondingly three response peaks per cycle. In the lower box the stimulus fundamental is one fifth of the cell's "best" frequency. To this pattern the cell shows five response peaks which correspond to the fifth harmonic of the square wave—that component which is now the dominant stimulus for this cell. Note that the square wave amplitude has been systematically increased to keep the amplitude of the relevant stimulus component constant as its fundamental frequency varies.