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SPATIAL FREQUENCY CHANNELS IN THE HUMAN VISUAL SYSTEM: EFFECTS OF LUMINANCE AND PATTERN DRIFT RATE[1]

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INTRODUCTION

RECENT psychophysical evidence suggests that there are multiple channels or analyzers in the human visual system with different channels sensitive to different ranges of spatial frequency. One phenomenon that indicates the existence of such channels is a frequency-specific adaptation effect: after an observer has looked at a grating of one spatial frequency, his contrast thresholds for gratings of similar spatial frequencies are raised but his contrast thresholds for gratings of very different frequencies are not affected (PANTLE and SEKULER, 1968; BLAKEMORE and CAMPBELL, 1969). Other evidence indicates that the outputs of these channels are detected independently (CAMPBELL and ROBSON, 1964, 1968; GRAHAM and NACHMIAS, 1971; SACHS, NACHMIAS and ROBSON, 1971) and that these channels are involved in the perception of supra-threshold gratings (BLAKEMORE and SUTTON, 1969; BLAKEMORE, NACHMIAS and SUTTON, 1970).

Prediction from neurophysiological results

Consider an array of retinal ganglion cells whose receptive fields are all of the same size and overlap extensively. Define the response of such an array to a sinusoidal grating as the difference between the firing rate of the cells responding most (those responding to the brightest parts of the grating) and that of the cells responding least (those responding to the dimmest part of the grating). Because of the antagonistic center–surround organization of these cells' receptive fields, the response of the retinal ganglion cell array is expected to be greatest when the sinusoidal grating is of intermediate frequency. The array's responsiveness to low frequencies is reduced by the inhibitory action of the surround mechanism. The array's responsiveness to high frequencies is reduced by summation within the center of the receptive field. Further, different arrays, where each array is composed of cells having the same size receptive fields and different arrays are characterized by different sizes of receptive fields, are expected to respond to different ranges of spatial frequency (ENROTH-CUGELL and ROBSON, 1966). Although such arrays cannot be the whole of the physiological

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[1] I am very grateful to JACOB NACHMIAS for his help and encouragement. The oscillator that produced the sine and cosine input signals to the synchro-resolver was designed and kindly provided by JOHN ROBSON.

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mechanism underlying psychophysically-measured spatial frequency channels, it is quite possible that they form the first stage.[2] If this is the case, one might expect the dependence of the psychophysically-measured channels on various stimulus parameters to mirror the dependence of retinal ganglion cell arrays on the same parameters.

Two conditions are known in which a retinal ganglion cell array is expected to change its frequency-selectivity, becoming equally sensitive to all low frequencies (and less sensitive to higher frequencies) rather than maximally sensitive to an intermediate frequency. These conditions are low luminance level and the presence of certain temporal variations in the stimulus patterns (patterns drifting quickly across the visual field for example). This change in frequency-selectivity is expected because the surround mechanism of the receptive field is ineffective in these two conditions (BARLOW, FITZHUGH and KUFFLER, 1957; ENROTH-CUGELL and ROBSON, 1966; MAFFEI, CERVETTO and FIORENTINI, 1970).

Hence, if a retinal ganglion cell array is indeed an important part of the mechanism for a spatial frequency channel, the frequency-selectivity of each channel may change as mean luminance is lowered or the drift rate of the patterns is increased. The channel should be maximally sensitive to an intermediate frequency when the patterns are stationary and of moderate mean luminance but be equally sensitive to all low frequencies (and less sensitive to higher frequencies) when the patterns either are drifting quickly across the field or have a low mean luminance.

Relevance to the psychophysical contrast sensitivity function

The change in the frequency-selectivity of individual channels predicted by retinal ganglion cell physiology would explain certain changes known to occur in the psychophysical contrast sensitivity function. If the sensitivity function of each individual channel loses its peak and flattens out at the low frequency end under some conditions, so will the predicted psychophysical contrast sensitivity function (assuming it to be the envelope of the functions of individual channels). This predicted flattening is illustrated in Fig. 1A. And, in fact, such flattening of the low-frequency end of the psychophysical contrast sensitivity function is reported to occur under precisely those conditions where flattening in the sensitivity functions of individual channels is predicted by retinal ganglion cell physiology (for gratings of low mean luminance, PATEL, 1966, and DAITCH and GREEN, 1969; for gratings of fast drift rate, VAN NESS, KOENDERINK, NAS and BOUMAN, 1967,[3] and VAN NESS, 1968; for two other varieties of temporal change—gratings flickering at a fast rate, ROBSON, 1966, and gratings exposed for a short duration, NACHMIAS, 1967).

The change in shape of the individual channels' functions shown in Fig. 1A is, of course, only one of many possible explanations within a multiple channels framework for the changes in the shape of the psychophysical contrast sensitivity function. Each channel may be maximally sensitive to an intermediate frequency at all mean luminances and drifts rates (due to the action of cells higher in the visual system than the retinal ganglion cells) but the peak sensitivities of different channels may change relative to one another. Such a situation is shown in Fig. 1B.

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[2] Thomas (see THOMAS, 1970, for a review) has proposed an interesting model very similar to the multiple channels model discussed here. In Thomas's model, each channel or detection system is a single retinal ganglion cell.

[3] VAN NESS *et al.* (1967) and VAN NESS (1968), measured two kinds of contrast thresholds. The kind they named "flicker fusion" is the kind measured in this study. To see the dependence of the psychophysical contrast sensitivity function on drift rate in VAN NESS *et al.* (1967) replot the results in their Fig. 3 in terms of spatial frequency.

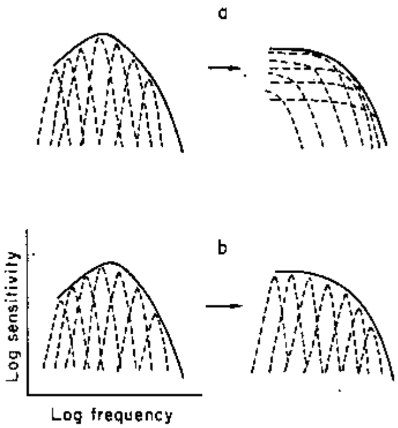

FIG. 1. Two ways in which changes in the sensitivity functions of individual channels may cause changes in the psychophysical contrast sensitivity function. In both left-hand drawings, the individual channels' sensitivity functions (dashed curves) are peaked and are arranged relative to each other in such a way that the psychophysical contrast sensitivity function (solid curve) is peaked at an intermediate frequency. In the right-hand drawing of A, the individual channels' functions have flattened out at low spatial frequencies (as suggested by retinal ganglion cell physiology for conditions of low mean luminance and fast drift rate). In the right-hand drawing of B, the peak sensitivities of individual channels have changed relative to each other but the shape of each channel's sensitivity function has not changed. Either change, A or B, would cause the psychophysical contrast sensitivity function to flatten out at low spatial frequencies.

This study

This study is intended to discover whether the shape of the sensitivity functions of individual channels, as measured psychophysically, changes as the mean luminance or drift rate of gratings changes. In particular, does the shape change in the way suggested by retinal ganglion cell physiology? The experimental measure used was the adaptation effect studied by BLAKEMORE and CAMPBELL (1969)—elevation of the contrast thresholds of sinusoidal gratings after adaptation to sinusoidal gratings of similar frequency. The first half of this study explored the effect of mean luminance by using stationary adapting and test gratings at several mean luminance levels; the second half explored the effect of drift rate by using gratings of moderate mean luminance drifting at several rates.

METHODS

Apparatus and procedures

Vertical sinusoidal gratings were generated on the face of a cathode-ray tube (CAMPBELL and GREEN, 1965). The spatial frequency and contrast of the gratings was varied (keeping the mean luminance constant) by changing the temporal frequency and amplitude of the sinusoidal signals that triggered the CRT's electron beam and modulated the electron beam's intensity. The mean luminance of the pattern was varied by mounting neutral density filters in front of the observer's eyes. Gratings were made to drift across the screen at various rates by means of a synchro-resolver which continuously varied the phase between the triggering and modulating signals (ENROTH-CUGELL and ROBSON, 1966).

In all experiments, the CRT contained a P31 phospher which appeared a desaturated yellow-green to the observer. (For the first half of the experiments, a Tektronix 503 oscilloscope was used with the CRT intensity adjusted to a mean luminance of 3 ft-L. For the second half, a Tektronix 502A was used at a mean luminance of 1 ft-L.) The CRT was viewed through a square hole (subtending 4 × 4 deg of visual angle at the viewing distance of 114 cm) in an illuminated circular surround (its diameter subtending 17 deg of visual angle). The visible surround—a cardboard screen illuminated through coloured plastic by a hidden circular fluorescent bulb—was matched to the CRT face in hue, saturation, and brightness.

The observer sat in a small darkened room in which some objects other than the display were dimly visible. He stabilized his head in a chin rest and viewed the grating with both eyes. When the gratings were stationary, the observer was instructed to allow his gaze to roam over an area the size of a 25-cent piece (which has a diameter subtending 1·25 deg at that viewing distance) in the center of the pattern. This procedure prevents after-images from forming. When the gratings drifted, the observer was instructed to fixate a small dark dot (a square one-tenth of a degree on a side in the middle of the screen).

Contrast thresholds were determined by the method of adjustment. The observer varied the contrast by pushing one button wired to a Grayson–Stadler Recording Attenuator in order to increase the contrast and one to decrease the contrast; as long as the observer held a button down, the contrast of the grating changed at the rate of four-tenths of a log unit per second. The observer was instructed to adjust the contrast to that point at which he could just discriminate the pattern from a completely homogeneous field containing neither temporal nor spatial fluctuations. The observers all approached threshold by increasing the contrast (if necessary) until they could see the pattern distinctly and then decreasing the contrast to threshold (Observers JK and GH used this approach spontaneously. DS was instructed to do so.)

Experiments

In each of ten experimental conditions, the contrast thresholds for gratings of several test frequencies were determined before and after adaptation to gratings of a number of adapting frequencies. In each condition, the test and adapting gratings were all at the same mean luminance and were all drifting at the same rate. The contrast of the adapting gratings was always 80 per cent (where contrast is one-half the difference between the maximum and minimum luminance divided by the mean luminance). Table 1 summarizes the other conditions of these experiments. As can be seen in the left three columns of Table 1, in the first five experimental conditions (designed to investigate the effect of mean luminance) stationary gratings were used at mean luminances of 3·0, 0·1 and 0·01 ft-L with observer JK, 0·3 ft-L with DS, and 3·0 ft-L with GH. In the second five conditions (designed to investigate the effect of drift rate) gratings at 1 ft-L were used, drifting at 2, 12 and 18 Hz with observer DS and 2 and 12 Hz with GH. In each half-hour session, thresholds for several test frequencies (see column 5 of Table 1) were determined before and after adaptation (see columns 7 and 8 for numbers of determinations) to one adapting frequency. The number of adapting frequencies (column 4) and the number of sessions each was used in (column 6) varied from condition to condition.

Each session began with varying amounts of dark adaptation (from 8 min for the dimmest condition, 0·01 ft-L, to none for the brightest, 3 ft-L) followed by 2 min of adaptation to a homogeneous field at the mean luminance for that session. Thresholds for the test frequencies to be used in that session were then determined prior to any adaptation to gratings, with 15 sec of looking at an unpatterned field preceding each adjustment. The set of test frequencies was presented in random order, and the initial value of contrast for each adjustment was chosen randomly from a set spanning 1·5 log units around the estimated threshold of that test frequency prior to adaptation. Next, the observer looked for 2 min at the adapting grating, the contrast of which was 80 per cent and the frequency of which was constant within a session. Adapting frequencies were randomized across sessions. Thresholds were then re-determined for the test frequencies, with 15 sec of re-adaptation preceding each adjustment. An initial adaptation period of 2 min with re-adaptation periods of 15 sec is sufficient to maintain adaptation at a maximum level (BLAKEMORE and CAMPBELL, 1969).[4]

A minimum of 1 hr was allowed to elapse between sessions with the same subject in order to permit adaptation effects to dissipate. There was never any evidence of adaptation after the 1 hr recess.

In addition to the results from the conditions summarized in Table 1, two other sets of results were collected. The first was from a series of short sessions (only one test frequency per session) at various mean luminances using observer DS. The second was from a number of sessions in which contrast sensitivity functions at various mean luminances and drift rates were collected. The procedures were identical to those described above (with the obvious changes to allow for only one test frequency per session or no adaptation to gratings in a session). The particular mean luminances, drift rates, and spatial frequencies that were used will be given with the results.

Subjects

JK was an undergraduate who worked as a paid subject; GH and DS were graduate students in psychology. JK and DS were relatively naive about the current hypotheses and results in the study of pattern vision; GH was not. All three had good visual acuity (for GH, achieved only with corrective lenses).

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[4] The sessions in the condition of 3 ft-L for subject JK (top row Table 1) were somewhat different. A series of increasing contrast levels was used, and the test thresholds were re-determined twice after adaptation to each contrast level. Most of these results are not reported in this paper. The four determinations after adaptation that are reported here include two after adaptation to 80 per cent contrast and two after adaptation to 65 per cent contrast. This irregularity of using 65 per cent contrast will continue to be ignored in the text and 80 per cent will always be the percentage named. However, whenever the level of adapting contrast was used in any calculation, the correct amount—65 per cent—was used for the irregular determinations.

TABLE 1. SUMMARY OF CONDITIONS

Subjects	Mean luminance (ft-L)	Drift rate (Hz)	Number of adapt frequencies*	Number of test frequencies†	Number of sessions at each adapt frequency	n‡ before	n‡ after
JK	0·01	0	8	4	4	2	4
JK	0·10	0	8	7	1	1	3
JK	3·0	0	11	4	1	2	4
DS	0·30	0	10	5	2	3	3
GH	3·0	0	11	5	1	2	4
DS	1·0	2	9	5	2	3	3
DS	1·0	12	9	5	2	3	3
DS	1·0	18	8	5	2	3	3
GH	1·0	2	9	5	1	3	3
GH	1·0	12	9	5	1	3	3

* For the first (second) set of five conditions, the set of 11 (9) adapting frequencies included frequencies from 1 to 18 c/deg (17 c/deg) spaced equally apart on a logarithmic frequency scale with 8 steps per log unit (2 steps per octave). When fewer than 11 (9) adapting frequencies were used, the highest frequencies were the ones omitted.

† The values of the test frequencies are given in Table 2.

‡ n is the number of determinations per session of each test frequency's threshold either before (column 7) or after (column 8) adaptation.

RESULTS

Relative adaptation curves

Figure 2 shows the results at mean luminance 3 ft-L for observer JK (the experimental condition summarized in row 1 of Table 1). Adapting frequency A is plotted on the horizontal axis, and the logarithm of the threshold after adaptation minus the logarithm of the threshold before adaptation is plotted on the vertical axis.[5] The results with the four test frequencies are represented by different symbols and the points for each test frequency are connected. It is apparent that the greatest effect of adaptation occurred when the adapting frequency equalled the test frequency and that the effect decreased as the difference between the adapting and test frequencies increased. Further, the peak adaptation effect was larger for higher than for lower test frequencies.

In order to show the relative effects of adapting to different frequencies, a *relative adaptation curve* was computed for each test frequency from the results of Fig. 2. This computation amounted to normalizing the curve for each test frequency in Fig. 2 by dividing it by its height at the peak (where the adapting frequency equals the test frequency). To write this definition in symbols, let $\theta(T;A,c)$ be the contrast threshold for a test grating of frequency T after adaptation to a grating of frequency A containing contrast c; in this study, c was either zero (that is, there had actually been no adaptation to gratings in which case A

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[5] Thresholds before adaptation were collected in every session, whereas only one adapting frequency was used per session. Consequently, for each test frequency, many more thresholds before adaptation were collected than thresholds after adaptation to any one adapting frequency. The average of *all* the thresholds before adaptation (for that test frequency, observer, mean luminance, and drift rate) was used for the $\theta(T;0,0)$ term in this computation and in all computations of the relative adaptation curves and of adaptabilities. Throughout this study, all averages are taken over the *logarithms* of the contrasts resulting from individual threshold determinations.

was also written as zero) or 80 per cent. Then, the relative adaptation curve for a given test frequency T takes on the value

$$\frac{\log \theta(T;A,80\%) - \log \theta(T;0,0)}{\log \theta(T;T,80\%) - \log \theta(T;0,0)} \tag{1}$$

at each adapting frequency A. The relative adaptation curves computed from the results of Fig. 2 are plotted in Fig. 3 on a log (adapting frequency/test frequency) axis. Using log (adapting frequency/test frequency) as abscissa shifts the curves from different test frequencies so that their centers coincide.

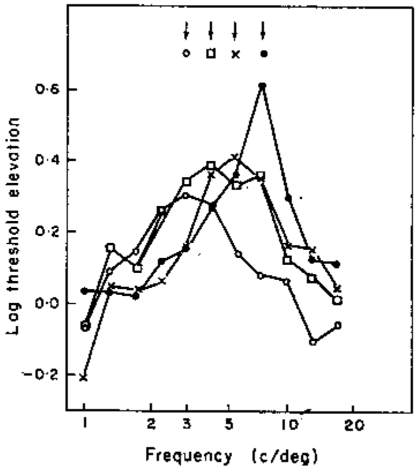

FIG. 2. The logarithm of the threshold after adaptation minus the logarithm of the threshold before adaptation for four test frequencies (3, 4, 5·5, and 7·5 c/deg) as a function of adapting frequency. Along the top of the figure each symbol is shown with an arrow to indicate the test frequency represented by the symbol. The results are for stationary gratings at a mean luminance of 3 ft-L with observer JK.

The relative adaptation curve has two nice properties. First, as was shown in an earlier study (GRAHAM, 1970), the curve at a given test frequency is approximately independent of the contrast level used in the adapting gratings,[6] at least for conditions of 3 ft-L mean luminance and stationary gratings where the effect of adapting contrast has been investigated. In other words, if results using adapting gratings at a contrast other than 80 per cent had been measured, the relative adaptation curves would have been approximately the same as those reported here.

Second, as can be seen in Fig. 3, the relative adaptation curves for different test frequencies (at the same mean luminance and drift rate) are very similar. This approximate independence of test frequency was found in all the conditions of the present study where the relative

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[6] BLAKEMORE and CAMPBELL (1969) used a transformation of the data different from that used here, and they showed that it also is roughly independent of adapting contrast. At first, their analysis seemed quite unlike the one presented here, but an investigation of what each implied for the functions relating test threshold after adaptation to adapting contrast suggests the two analyses are similar (GRAHAM, 1970).

adaptation curves for individual test frequencies could be measured accurately (in mean luminance and drift rate conditions where the threshold elevations were large enough). There were systematic differences but they were small.

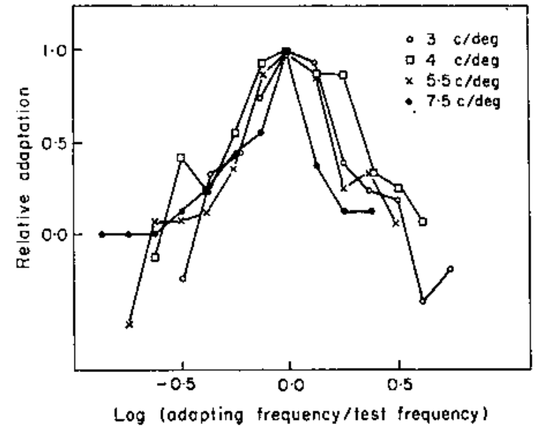

FIG. 3. The relative adaptation curves for four test frequencies (symbols same as Fig. 2) computed from the results of Fig. 2. 3 ft-L. Observer JK.

The relative adaptation curve's independence of test frequency justified condensing the results at each mean luminance or drift rate by averaging the relative adaptation curves from different test frequencies. For example, the results at mean luminance 3 ft-L with observer JK were condensed by averaging together the four curves of Fig. 3—that is, at each value of log (adapting frequency/test frequency) the four relative adaptation values, one from each curve, were averaged together. The resulting "averaged relative adaptation curve" is shown in the upper left corner of Fig. 4 (as filled circles).

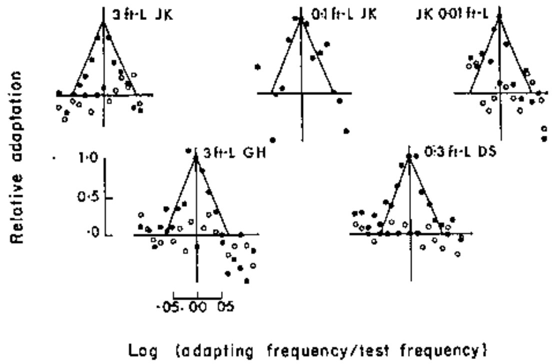

FIG. 4. Relative adaptation curves (filled circles) averaged over test frequency for different mean luminances and observers. The dispersion of the unfilled circles around the zero horizontal line indicates the variability in the results (see text).

In Fig. 4 also are shown relative adaptation curves averaged over test frequency for the four other experimental conditions where mean luminance was the variable of interest. Figure 5 shows the averaged relative adaptation curves for the five conditions where drift rate was the variable of interest (as filled circles).

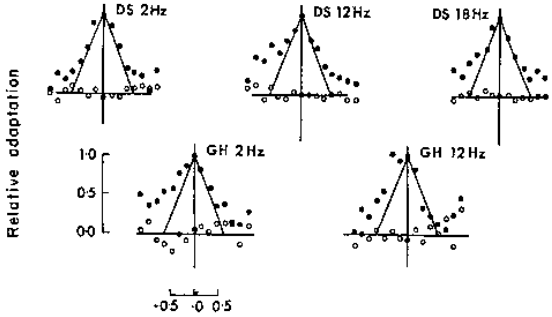

FIG. 5. Relative adaptation curves (filled circles) averaged over test frequency for different drift rates and observers. The dispersion of the unfilled circles around the zero horizontal line indicates the variability in the results (see text).

The variability in these relative adaptation curves is considerable, especially for the low mean luminances. This is an inevitable result of the small size of the maximum adapting effect, especially for low mean luminances (see Table 2), and of the large variability in the threshold adjustments. The standard deviation of a population of adjustments made under the same stimulus conditions ranged from 0·125 to 0·175 log units for the three observers. To give an idea of the variability in the averaged relative adaptation curves, "averaged baseline curves" were computed and are shown as unfilled circles in Figs. 4 and 5 (except for JK at 0·1 ft-L where there was not sufficient data). The baseline curve gives the deviation of the average of appropriate subsets of the before-adaptation thresholds from the average of all the before adaptation thresholds.[7] If there were no variability, the baseline curve would equal zero everywhere and the unfilled circles would all lie on the horizontal line through zero.

In order to make comparison of the curves easier, the same isoceles triangle has been drawn on each of the averaged relative adaptation curves in Figs. 4 and 5. The height of the triangle is one and its base covers four octaves on the logarithmic frequency scale. Figure 4 shows that the relative adaptation curves at different mean luminances are all reasonably well fitted by this same triangle. There is perhaps some indication in the results for JK at 0·01 ft-L and for DS at 0·3 ft-L that adapting frequencies lower than the test frequency produce greater threshold elevation than do adapting frequencies higher than

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[7] The averaged baseline curve for each condition was computed by treating a subset of the thresholds for T before adaptation (the subset that had been collected in those sessions in which adapting frequency A was used) just as the set of thresholds for T after adaptation to A had been treated in computing the averaged relative adaptation curve. Remember (see footnote 5) that the average of *all* the thresholds for T before adaptation (not the average of the subset collected in those sessions involving adapting frequency A) was used for the $\theta(T;0,0)$ term in expression (1).

For JK at 3 ft-L and at 0·01 ft-L and for GH at 3 ft-L, the variability in the averaged baseline curve is expected to be somewhat larger than that in the averaged relative adaptation curve because in each session fewer determinations were made of the thresholds before adaptation than of the thresholds after adaptation.

the test frequency. These trends, however, do not appear convincing when the fluctuations in the baseline curve are also considered. Of course, any number of small differences among the functions might be hidden by the variability in the data.

On the other hand, from Fig. 5, it can be seen that the averaged relative adaptation curves for DS at 12 and 18 Hz are broader than those for DS at 2 Hz or with stationary gratings (see Fig. 4 for the latter). This broadening is especially evident toward the base of the triangle where the adapting frequency is somewhat removed from the test frequency. For GH, the averaged functions at both 2 and 12 Hz are broader than the one for stationary gratings.

It is clear from both Figs. 4 and 5 that, under all conditions, the relative adaptation curve is strongly peaked at the center—in other words, the greatest adaptation effect always occurred when the adapting frequency was the same as or close to the test frequency, and the adaptation effect decreased for adapting frequencies either higher or lower than the test frequency.

Adaptabilities

The second way in which the experimental results were summarized was to compute the "adaptability" of different frequencies. Loosely speaking, adaptability is the magnitude of adaptation per unit of above-threshold adapting contrast. Precisely, the adaptability of a frequency is the magnitude of adaptation (the logarithm of the threshold elevation) when both adapting and test gratings are of the given frequency divided by how far above threshold (in logarithmic units) the 80 per cent contrast used in the adapting grating is for that frequency, or

$$\frac{\log \theta(T;T,80\%) - \log \theta(T;0,0).}{\log 80\% - \log \theta(T;0,0)} \qquad (2)$$

The adaptabilities are plotted in Figs. 6 and 7.

The numerator in expression (2) for adaptability is the magnitude at the center of a curve like those in Fig. 2, or equivalently, it is the normalization factor used in computing the relative adaptation curve [the denominator in expression (1)]. For reference, these magnitudes of threshold elevation—the values of the numerator in expression (2) or the denominator in expression (1)—are given in Table 2 for all test frequencies and all conditions of this experiment. The denominator in expression (2) for adaptability—the amount of above-threshold adapting contrast—varied from one to three log units over the conditions of this study.

Computing adaptabilities revealed several regularities in the results.

First, as in the case of the relative adaptation curve, the adaptability at a given test frequency is approximately independent of adapting contrast (at least for stationary gratings of 3 ft-L mean luminance, the condition where different adapting contrasts were investigated; Graham, 1970).

Second, as is apparent in Figs. 6 and 7, at each mean luminance and drift rate the adaptability is constant for spatial frequencies lower than about 5 c/deg and then, for higher frequencies, the adaptability increases with increasing frequency. Adaptability is certainly not independent of test frequency, but varies with test frequency in a regular fashion.

Third, when mean luminance was varied, the adaptability at a given test frequency did

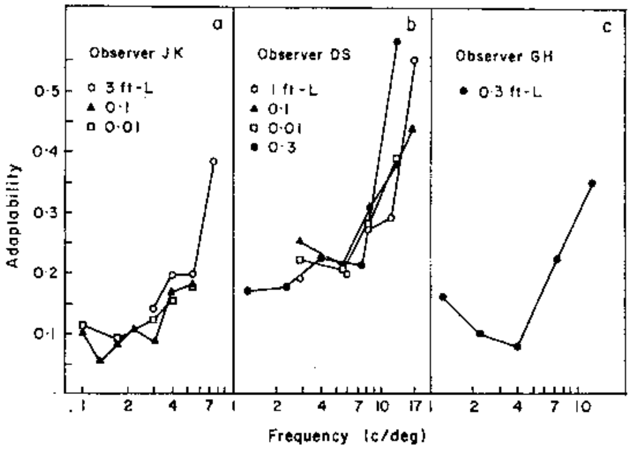

FIG. 6. Adaptability as a function of frequency at different mean luminances. (a) Observer JK. (b) Observer DS. (c) Observer GH.

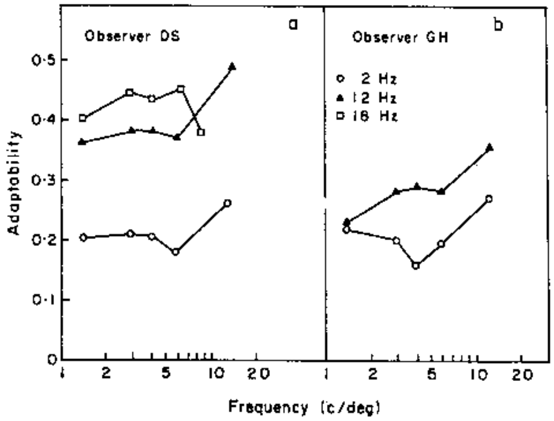

FIG. 7. Adaptability as a function of frequency at different drift rates. (a) Observer DS. (b) Observer GH.

not change. Figure 6a displays the invariance in the adaptabilities calculated from JK's results at three mean luminances. To verify this result, an additional series of short sessions at each of three mean luminances (1·0, 0·1, 0·01 ft-L) was run with observer DS. In each session only one value of test and one value of adapting frequency (and the test frequency was the same as the adapting frequency) were investigated. The thresholds before and after adaptation were each determined four times. The adaptabilities calculated from these short sessions are shown in Fig. 6b, along with the adaptabilities calculated from the longer sessions at 0·3 ft-L. For DS also, the adaptability of each test frequency is independent of mean luminance.

TABLE 2. LOG $\theta(T;T,80\%)$ − LOG $\theta(T;0,0)$, THE LOG THRESHOLD ELEVATION WHEN TEST AND ADAPTING FREQUENCIES ARE EQUAL

Condition	Frequency in c/deg								
	1·0	1·3	1·7	2·25	3·0	4·0	5·5	7·5	13·0
JK 0·01 ft-L	0·14	—	0·12	—	0·14	0·16	—	—	—
JK 0·10 ft-L	0·16	0·09	0·14	0·19	0·14	0·24	0·19	0·08	—
JK 3·0 ft-L	—	—	—	—	0·30	0·39	0·42	0·60	—
DS 0·30 ft-L	—	0·39	—	0·38	—	0·50	—	0·38	0·65
GH 3·0 ft-L	—	0·40	—	0·25	—	0·19	—	0·44	0·50

	Frequency in c/deg					
	1·4	2·9	4·1	5·9	8·4	12·0
DS 2 Hz	0·56	0·58	0·57	0·47	—	0·56
DS 12 Hz	0·87	0·86	0·86	0·74	—	0·66
DS 18 Hz	0·73	0·76	0·68	0·62	0·44	—
GH 2 Hz	0·67	0·56	0·43	0·50	—	0·50
GH 12 Hz	0·50	0·56	0·53	0·47	0·43	—

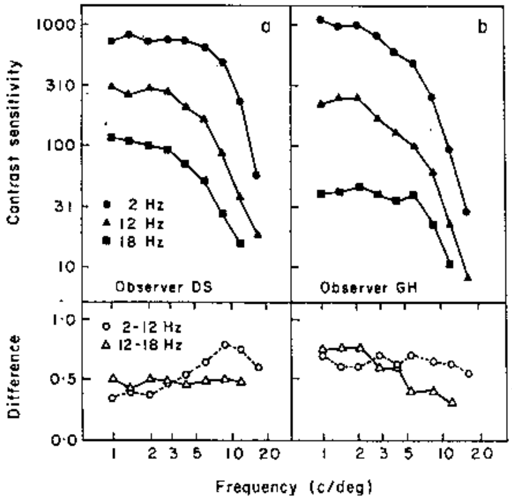

FIG. 8. Top: Contrast sensitivity functions at different drift rates. All gratings at a mean luminance of 1 ft-L. Contrast sensitivity is the reciprocal of the contrast threshold where the contrast threshold is expressed as a fraction. Bottom: Log contrast sensitivity at 2 Hz minus log contrast sensitivity at 12 Hz (circles). Log contrast sensitivity at 12 Hz minus log contrast sensitivity at 18 Hz (×'s). These differences are equivalent to the logarithms of the ratios of the sensitivities at two different drift rates. Observer DS's results are on the left; observer GH's results are on the right.

When drift rate was varied, however, the adaptability of a given test frequency increased as the drift rate increased. This is shown in Fig. 7. The change between 2 and 12 Hz is more marked for DS than for GH (as was the broadening of the averaged relative adaptation curves between 2 and 12 Hz more marked for DS than for GH).

Psychophysical contrast sensitivity functions

Contrast sensitivity functions were measured for all three observers with stationary gratings at several mean luminances (ranging from 3 to 0·01 ft-L). As has been reported in previous studies (PATEL, 1966; VAN NESS *et al.*, 1967; DAITCH and GREEN, 1969), the functions at the high mean luminances (1–3 ft-L) were peaked at intermediate frequencies but the functions at the lowest mean luminance (0·1 ft-L) were constant for a range of low frequencies before decreasing for higher frequencies.

Contrast sensitivity functions were also measured with gratings of mean luminance 1 ft-L that were drifting at several rates (2, 12, 18 Hz) for two observers, GH and DS. These functions are shown in the top of Fig. 8. As with variations of mean luminance, variations of drift rate definitely affected the shape of the contrast sensitivity function. To show the effect of drift rate more clearly, the differences between the functions at different drift rates (the log sensitivity at one drift rate minus the log sensitivity at another drift rate) are displayed in the bottom of Fig. 8. If the contrast sensitivity functions at all drift rates had the same shape on the logarithmic plot (that is, if they differed from each other only by a multiplicative factor) the difference functions would all be constant as frequency increased. There are definite inconsistancies in the results of both observers.[8]

As has been reported by other investigators (VAN NESS *et al.*, 1967; VAN NESS, 1968), the contrast sensitivity functions at 18 Hz are constant for a range of low spatial frequencies rather than being peaked at an intermediate frequency. However, in this study, unlike the other studies, the functions at 2 Hz are not peaked. This discrepancy between the results of Van Ness' observer and those of GH and DS, as well as other differences among observers, may reflect differences in the eye movements or in the criteria for threshold used by different observers. Or the differences may actually reflect properties of different observers' multiple channels.

DISCUSSION

The effect of adaptation to gratings on the contrast thresholds of gratings was studied with stationary gratings at different mean luminances and with gratings at a mean luminance of 1 ft-L that drifted across the visual field at different rates. The results for each mean luminance and drift rate condition were summarized with two measures: the relative adaptation curve (which gives the threshold elevation at a test frequency caused by adapting to various frequencies, relative to the threshold elevation at that test frequency caused

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[8] The difference functions in Fig. 10 seem quite complicated particularly because the functions for the two observers are dissimilar. However, the apparent complexity is much reduced by the following interpretation. (1) The difference function between a "low" and a "medium" drift rate first increases and then decreases as spatial frequency increases; the difference function between a "medium" and a "high" drift rate decreases continually as spatial frequency increases; there are intermediate cases in which the difference function remains constant. This assumption is consistent with the results reported by VAN NESS *et al.* (1967), if, for their observer, 2 Hz is considered "low", 12 Hz "medium", and 18 Hz "high". (2) A particular drift rate is effectively a higher drift rate for GH than for DS, so that for GH 2 and 12 are "medium" and 18 Hz is "high" while for DS 2 Hz is "low" and 12 and 18 Hz are "medium". This assumption is consistent with the relative adaptation and adaptability results reported earlier.

by adapting to the test frequency itself) and the adaptability of various frequencies (the amount of threshold elevation per unit above-threshold adapting contrast when the test frequency itself is adapted to). Several regularities were found:

(a) Over the range of mean luminancies studied, from 3 to 0·01 ft-L, there was no measurable change in either the relative adaptation curve (which was always peaked at the center—in other words, adapting to the test frequency always caused greater threshold elevation than adapting to any other frequency) or the adaptabilities of different test frequencies.

(b) As drift rate was varied from 2 to 18 Hz, the relative adaptation curves broadened somewhat but remained peaked at the center, and the adaptabilities of all test frequencies increased markedly.

(c) At any mean luminance or drift rate, the adaptability was roughly constant for spatial frequencies lower than about 5 c/deg and then monotically increased at higher frequencies.

Sensitivity functions of individual channels

The experimental results summarized above were collected in order to find out whether the sensitivities of individual spatial frequency channels change when mean luminance or drift rate is changed. To deduce the sensitivities of individual channels from these experimental results, one must make assumptions about the properties of the channels. Making only two weak assumptions allows one to decide whether or not the sensitivity functions of individual channels change in the manner suggested by retinal ganglion cell physiology—that is, whether or not, when mean luminance is lowered or drift rate is raised, the sensitivity functions lose their peaks at intermediate frequencies and become constant for a range of low frequencies.

Assumption 1: Adaptation. The more sensitive a channel is to a grating, the more it will be affected (desensitized) by adapting to that grating. Precisely, if a channel's sensitivity for a grating of frequency x is greater than or equal to its sensitivity for a grating of frequency y, then the channel's sensitivity for an arbitrary frequency after adapting to x will be less than or equal to its sensitivity for the arbitrary frequency after adapting to y.

Assumption 2: Combination of channels to produce the psychophysical threshold. If in one state of adaptation-to-gratings (after adaptation to a particular grating, for example), every channels' sensitivity for some frequency z is less than or equal to its sensitivity for z when in a second state of adaptation, then the psychophysical sensitivity for frequency z in the first state of adaptation will be less than or equal to the psychophysical sensitivity for frequency z in the second state of adaptation (the psychophysical threshold in the first state will be greater than or equal to that in the second state).

Now consider what assumption 1 and 2 imply when the sensitivity function of every channel is constant for a range of low frequencies and then decreases for higher frequencies (as suggested by retinal ganglion cell physiology for conditions of low mean luminance or fast drift rate). Compare the effects on the psychophysical threshold for an arbitrary frequency z of adapting to two gratings, one of lower frequency (x) than the other (y). (The relationship of x and y to z is not fixed.) Since the channels' sensitivity functions are not peaked, every channel's sensitivity for the lower adapting frequency x is greater than or equal to its sensitivity for the higher adapting frequency y. By assumption 1, therefore, every channel's sensitivity for frequency z after adapting to frequency x will be less than or equal to its sensitivity for frequency z after adapting to frequency y. Consequently, by assumption 2, the psychophysical threshold for frequency z after adapting to x will be greater than or equal to the psychophysical threshold for frequency z after adapting to y. In short, whenever the sensitivity function of every channel is constant for a range of low frequencies and then decreases for higher frequencies (and as long as assumptions 1 and 2 are correct), viewing a grating of any frequency (x) will elevate the threshold for any frequency (z) at least as much as viewing a grating of a frequency higher than x will.

As can be seen in the results summarized in (a) and (b), in every condition of mean luminance and drift rate there were cases where viewing a grating of one frequency caused less threshold elevation than viewing a grating of a higher frequency. In particular, adapting to frequencies lower than the test frequency always caused less threshold elevation at the test frequency than adapting to the test frequency itself. Consequently, it seems safe to conclude that in no condition of this study were the sensitivity functions of individual channels constant for a range of low frequencies and then decreasing for higher frequencies; rather, they were always peaked at an intermediate frequency. In fact, the results summarized in (a) suggest that the selectivity of individual channels for spatial frequency is the same at all mean luminance levels. The results in (b) suggest that the individual channels may be sensitive to slightly broader ranges of frequency at fast drift rates than at slow. Of course, in the absence of a particular model relating the sensitivity functions of individual channels to the observed adaptation effects, these last suggestions must be treated cautiously.[9]

Implications for physiological correlates of the channels

If the dependence of the psychophysically measured channels on mean luminance and drift rate were determined by arrays of retinal ganglion cells, the sensitivity functions of individual channels should have lost their peaks, becoming constant for all low frequencies, under conditions of low mean luminance or fast drift rate. That they did not implies that neural cells higher in the visual system than the retina must make the range of each channel's sensitivity to spatial frequency narrower than the sensitivity at the retinal ganglion cell level, at least for patterns of low mean luminance and fast drift rate. (There is, of course, some chance that human retinal ganglion cells do not have the same properties as those of cat and monkey, or that the mean luminance at which the inhibitory surround becomes inactive and the drift rate at which the surround can no longer keep up are outside the ranges used in this study.) This result is consistent with two results of previous studies that have also implicated cells higher in the visual system than the retina; the psychophysically-measured channels are orientation sensitive (CAMPBELL and KULIKOWSKI, 1966) as are cortical neurons (HUBEL and WIESEL, 1968; CAMPBELL, CLELAND, COOPER and ENROTH-CUGELL, 1968, for example), and there is some binocular transfer of the adapting effect (BLAKEMORE and CAMPBELL, 1969). It would be interesting to know the temporal characteristics of cortical neurons and their properties in different states of light adaptation.

Implications for psychophysical contrast sensitivity functions

Since the sensitivity functions of individual channels remain peaked under all conditions, the flat low-frequency end of the psychophysical contrast sensitivity function at low mean luminance and fast drift rate (PATEL, 1966; VAN NESS *et al.*, 1967, for example) cannot be

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[9] A model, related to Stiles' model for color mechanisms, was tested by GRAHAM, 1970. It is conceptually simple and describes many aspects of the results. However, as it turned out, this model could not be used to deduce the sensitivities of individual channels under different conditions without collecting prohibitively large quantities of data.

explained by flat low-frequency ends of individual channels' sensitivity functions. Rather, the flattening and other changes in the shape of the psychophysical contrast sensitivity function must be explained by changes in the peak sensitivities of different channels relative to each other. Figure 1B, in short, illustrates more accurately than Fig. 1A the changes as mean luminance and drift rate are changed.

The question of why the relative peak sensitivities change from one condition of mean luminance and drift rate to another is probably not answerable apart from the question of why the peak sensitivities have the relationship they do (why the psychophysical contrast sensitivity function has the shape it does) for stationary gratings at moderate mean luminance. A multiple-channels model does not provide any easy explanation for the magnitudes of the peak sensitivities.

Adaptability of different channels

As summarized in (c), adaptability is different for different frequencies. As was shown by Watanabe, Mori, Nagata and Hiwatashi (1968), the rate of increase in perceived contrast with increasing physical contrast is also different for different frequencies. In fact, both adaptability and the rate of increase in perceived contrast vary approximately inversely with contrast sensitivity. This correspondence suggests that adaptability (the desensitization caused per unit of above-threshold adapting contrast) is greater for some channels than for others because the steepness of the stimulus-response function (the increase in perceived contrast per unit of above-threshold contrast) is greater for some channels than for others. Why the stimulus–response function varies, and, in particular, why it is steeper for channels responding to higher frequencies, is not clear.

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Abstract—Recent evidence indicates that the human visual system contains multiple channels, with each channel sensitive to a different narrow range of spatial frequency. In this study the sensitivity of these channels for patterns at low mean luminance or high drift rate is measured by the effect of adaptation to sinusoidal gratings on the contrast thresholds for sinusoidal gratings. The channels do not behave in the way expected from retinal ganglion cell physiology; rather, they remain selectively sensitive to narrow ranges of spatial frequency even when the luminance is low or the drift rate high.

Résumé—Des données récentes suggèrent plusieurs canaux de transmission dans le système visuel humain, chacun sensible à une étroite bande differente de fréquence spatiale. On mesure ici la sensibilité de ces canaux pour des figures à faible luminance moyenne ou à vitesse rapide de dérive, en étuduant l'effet de l'adaptation à des réseaux sinusoïdaux sur le seuil de contraste pour des rèseaux sinusoïdaux. Ces canaux ne se comportent pas comme on pourrait s'y attendre d'après la physiologie des cellules ganglionnaires de la rétine; ils restent au contraire sélectivement sensibles à des domaines étroits de fréquence spatible même si la luminance est faible ou la dérive rapide.

Zusammenfassung—Neue Erkenntnisse zeigen, daß das visuelle System des Menschen vielfache Kanäle umfaßt, wobei jeder Kanal auf einen verschieden engen Bereich von Ortsfrequenzen anspricht. In dieser Arbeit wird die Empfindlichkeit dieser Kanäle für Muster bei niederer durchschnittlicher Beleuchtung oder schnelle Bewegung gemessen mittels Adaptation an sinusoidale Gitter an der Kontrastschwelle für sinusoidale Gitter. Die Kanäle verhalten sich nicht so, wie von der Physiologie der Ganglienzellen der Retina erwartet, vielmehr bleiben sie selektiv empfindlich auf einem engen Bereich von Ortsfrequenzen, sogar wenn die Beleuchtung niedrig ist oder die Bewegung schnell.

Резюме — Последние данные указывают на то, что зрительная система содержит мдогие каналы, при чем каждый из этих каналов чувствителен к различным узким диапаэонам пространственной частоты. В предлагаемом исследовании чувствительность этих каналов по отношению к паттернам при средней низкой яркости или при большой скоростипредъявления (fast drift rate) была измерена по действию адаптация к синусоидалъным решеткам по контрастным порогам для синусоидальных решеток. Каналы ведут себя не так как это можно было предполагать по данным физиологии ганглиозных клеток сетчатки; скорее, они сохраняют свою избирательную чувствительность к узким диапазонам пространственной частоты, лаже в том случае, если яркость низкая или скоросмб предъявления большая.