

## Evidence of spatial and temporal channels in the correlational structure of human spatiotemporal contrast sensitivity

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1. The statistical correlation of detection thresholds for pairs of stimuli should be higher for stimuli detected by the same mechanism than for stimuli detected by different mechanisms – a property that can be used to probe the visual mechanisms that underlie detection.
2. Correlation of contrast sensitivities for pairs of spatiotemporal stimuli is approximately a linear function of spatial or temporal frequency separation in octaves. Using the slope of this function as an index of neural processing gave results consistent with: more spatial mechanisms than temporal; more spatial mechanisms at low temporal frequencies than at high; and at least two temporal mechanisms active at spatial frequencies up to  $22.6 \text{ cycles deg}^{-1}$ .
3. This method of analysing sensitivity data is insensitive to experimental conditions and applicable to any sensory detection task mediated by tuned channels. In addition to being applicable to psychophysical sensitivity measurements, it may also be useful in analysing some kinds of electrophysiological measurements that pool the responses from many active mechanisms (such as evoked potentials).

There is a broad consensus that the sensitivity of the human visual system to contrast is mediated by a number of tuned mechanisms in the visual cortex. Detection of spatial contrast is believed to be mediated by a relatively moderate number (about 7 at any given orientation) of overlapping spatial frequency channels, each with a bandwidth of 0.8–2.5 octaves (Blakemore & Campbell, 1969; Stromeyer & Julesz, 1972; Watson, 1983; Wilson, MacFarlane & Phillips, 1983). A similar range of bandwidths (0.5–3.0 octaves) has been found for cells in the striate cortex of macaques (De Valois, Albrecht & Thorell, 1982; Foster, Gaska, Nagler & Pollen, 1985). Conversely, detection of temporal variation is suspected to be mediated by a smaller number (2–4) of broadly tuned mechanisms (King-Smith & Kulikowski, 1975; Richards, 1979; Watson & Robson, 1981; Mandler & Makous, 1984; Moulden, Renshaw & Mather, 1984; Hess & Snowden, 1992). The tuning of these mechanisms is sufficiently broad that at least two temporal mechanisms seem to be active at all but the highest spatial frequencies (Burr, 1991; Smith, 1991). The broad tuning of these channels is consistent with the broad temporal bandwidths of cortical cells (Albrecht, 1978).

A variety of non-invasive methods has been developed to probe the functioning of visual mechanisms in humans. These methods include adaptation, masking, discrimination, and subthreshold summation. All of these methods are model dependent, and properties of the derived channels depend somewhat on the method employed (Graham, 1989; Tyler, Barghout & Kontsevich, 1993). It would be desirable if more straightforward experimental methods, such as the simple estimation of contrast thresholds, could be made to yield information about visual mechanisms.

Sekuler, Wilson & Owsley (1984) found that the variance/covariance structure of contrast sensitivity data is rich in information about the underlying channels. Because sensitivity is mediated by overlapping tuned channels, thresholds for similar spatial frequencies are highly correlated, while thresholds for stimuli several octaves apart are poorly correlated (Owsley, Sekuler & Siemsen, 1983). Sekuler *et al.* (1984) used these facts to derive plausible spatial channels from a factor analysis of the correlation matrix of their contrast sensitivity data. In this paper, we extend knowledge of the correlational structure of contrast sensitivity data to a broad range of

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Table 1. Pearson product correlations\* of contrast sensitivities for various spatial frequencies modulated at 0.25 Hz

Cycles deg <sup>-1</sup>	0.50	0.70	1.0	1.4	2.0	2.8	4.0	5.7	8.0	11.3	16.0	22.6
0.70	0.64											
1.0	0.68	0.87										
1.4	0.66	0.74	0.86									
2.0	0.58	0.61	0.76	0.82								
2.8	0.48	0.49	0.66	0.61	0.76							
4.0	0.40	0.31	0.44	0.65	0.69	0.54						
5.7	0.35	0.42	0.47	0.44	0.42	0.38	0.57					
8.0	0.16	0.09	0.10	0.16	0.25	0.16	0.57	0.52				
11.3	0.19	0.18	0.19	0.26	0.29	0.29	0.58	0.55	0.81			
16.0	0.07	0.01	0.10	0.13	0.20	0.17	0.48	0.52	0.73	0.70		
22.6	0.16	0.26	0.21	0.32	0.27	0.26	0.52	0.42	0.63	0.79	0.65	
32.0	0.09	0.15	0.03	0.17	0.22	0.18	0.49	0.16	0.72	0.70	0.68	0.86

\*  $r_{\text{crit}}(1, 38)$  (the value of the correlation coefficient for 38 deg of freedom) = 0.31,  $P = 0.05$ ;

$r_{\text{crit}}(1, 38) = 0.40$ ,  $P = 0.01$ .

spatiotemporal frequencies and we introduce a new methodology for studying this structure. We find that correlation between contrast sensitivities is approximately a linear function of the spatial/temporal frequency separation (in octaves) of the stimulus pair. Following the logic of Sekuler *et al.* (1984), the slope of this correlation function should be related to the number and tuning of the channels underlying sensitivity. We explore the consequences of these findings, specifically for contrast sensitivity, and more generally for other visual and sensory systems, and suggest that the technique holds promise for exploiting the extensive database of sensory threshold data and for mass action electrophysiological data such as evoked potentials.

## METHODS

### Apparatus and observers

We measured spatiotemporal contrast sensitivity in forty young observers (age 18–42 years) whose corrected acuity was at least 6/6. All observers gave informed consent and the study was approved by the Human Use Committee of the US Army Aeromedical Research Laboratory. Spatiotemporal stimuli were displayed on a Tektronix 608 monitor (P-31 phosphor) with a linearized Z-axis amplifier and additional corrections made in software. The luminance of the monitor orthogonal to the orientation of the grating is approximately (Robson, 1966):

$$L(x,t) = L_0[1 + M\cos(2\pi f_x x)\cos(2\pi f_t t)], \quad (1)$$

where  $x$  and  $t$  are the spatial and temporal variables,  $M$  is contrast, and  $L_0$ , the space-averaged luminance, was  $100 \text{ cd m}^{-2}$ . The monitor was surrounded by an illuminated screen of similar luminance and chromaticity. Subjects sat in a blackened cubicle, their heads supported by forehead and chin rests. Monitor and surround were viewed through a  $5 \times 5$  deg aperture in the cubicle that was filled by the monitor and its illuminated surround. Viewing was binocular, with natural pupils.

### Measurement of detection thresholds

Contrast detection thresholds were measured using a sixteen-trial yes/no staircase (Cornsweet, 1962), whose starting point was determined by the method of adjustment at the beginning of the session. Step size was 0.05 log units of contrast. Typically, a sixteen-trial staircase contained six to eight reversals. If there were fewer than four reversals, another eight trials were added to the staircase. Order of stimulus presentation was randomized. Temporal frequency of the stimuli ranged from 0.25 to 32 Hz, in steps of an octave, and spatial frequency ranged from 0.50 to 32 cycles  $\text{deg}^{-1}$ , in steps of 0.5 octave (a total of 104 combinations of spatial and temporal frequencies). Constraints on the size and grain of the display made it necessary to gather each observer's data in two sessions. One session, conducted at a viewing distance of 114 cm contained spatial frequencies of 0.5–4 cycles  $\text{deg}^{-1}$ , while the other session, conducted at a viewing distance of 342 cm, contained spatial frequencies of 4–32 cycles  $\text{deg}^{-1}$ . Each session lasted about 2.5 h. To correct for day, session and distance sensitivity shifts (Campbell & Robson, 1968; Graham, 1989), prior to computing the correlations for spatial frequencies in different sessions, contrast thresholds in the far session were adjusted so that sensitivity for the more distant 4 cycles  $\text{deg}^{-1}$  gratings coincided with sensitivity measured for 4 cycles  $\text{deg}^{-1}$  gratings in the near session. For some subjects, test–retest data were taken; results from multiple sessions were averaged. Many subjects could not see 32 cycles  $\text{deg}^{-1}$  gratings at high temporal frequencies, so the spatial correlation matrices modulated at temporal frequencies of 8 Hz and higher have a maximum spatial frequency of 22.6 cycles  $\text{deg}^{-1}$ .

To construct the correlation matrices, we held either spatial or temporal frequency constant. For example, the spatial frequency correlation matrix in Table 1 was constructed from contrast thresholds for spatial gratings modulated at 0.25 Hz. For each possible pair of spatial frequencies, the Pearson product correlation coefficient was computed from the logarithms of contrast thresholds of our forty observers (using logarithms of contrast sensitivity tends to equalize the variances across spatiotemporal frequencies;

**Table 2. Piecewise linear model fit to the structure of spatial frequency correlation matrices measured for various flicker rates**

Flicker rate (Hz)	Slope before breakpoint	Breakpoint (octaves)	Slope after breakpoint	Variance fit to model
0.25	$-0.188 \pm 0.012$	$3.38 \pm 0.20$	$-0.040 \pm 0.012$	0.990*
0.50	$-0.206 \pm 0.013$	$3.77 \pm 0.21$	$-0.024 \pm 0.015$	0.987
1.0	$-0.198 \pm 0.011$	$3.77 \pm 0.15$	$+0.045 \pm 0.019$	0.986
2.0	$-0.141 \pm 0.004$	$4.41 \pm 0.11$	$+0.007 \pm 0.012$	0.997
4.0	$-0.135 \pm 0.015$	$3.84 \pm 0.25$	$+0.048 \pm 0.025$	0.952
8.0	$-0.100 \pm 0.007$	—	—	0.962
16.0	$-0.097 \pm 0.013$	—	—	0.869
32.0	$-0.130 \pm 0.010$	—	—	0.945

Above 4 Hz, a single linear function suffices. Slope is in correlation units octave<sup>-1</sup>. Data for slope and breakpoint given as means  $\pm$  s.d. \* Model fit to correlation matrix in Table 1.

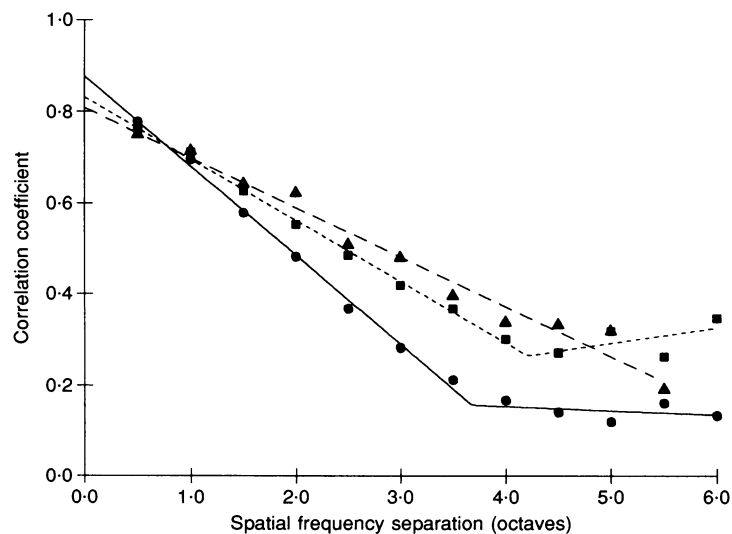
see Peterzell, Werner & Kaplan, 1991 for additional comments). This process was repeated for each of the seventy-eight non-redundant, non-diagonal spatial frequency pairs, for each spatial frequency correlation matrix (Table 1) and for each of the twenty-eight non-redundant, non-diagonal temporal frequency pairs in each temporal frequency correlation matrix (Tables 3 and 4).

## RESULTS

### Correlations in spatial contrast sensitivity

Table 1 shows the Pearson product correlation matrix for spatial sine wave gratings modulated at 0.25 Hz. The structure of the matrix is quite similar to that found by

Owsley *et al.* (1983). Nearby spatial frequencies are highly correlated; the correlation becomes smaller as the separation increases. Similar relationships hold for data taken at higher temporal frequencies. We quantified this relationship by averaging all correlations along each diagonal of the correlation matrix (e.g. averaging all the correlations for 0.5 octaves of frequency separation, 1 octave, and so on). To avoid statistical bias in averaging correlation coefficients (which are not normally distributed), correlations were Fisher Z-transformed, averaged, then backtransformed (Kendall & Stuart, 1979). We found that correlation drops off linearly for several octaves before



**Figure 1. Piecewise linear models fitted to the correlational structure of spatial contrast sensitivity data**

Correlational structure of spatial data falls into roughly three groups (see Table 2). The structure for low temporal frequencies (●, average of 0.25–1 Hz) has an initial slope of  $-0.196 \pm 0.007$  correlation units octave<sup>-1</sup>. The medium temporal frequency group (■, 2–4 Hz) has an initial slope of  $-0.135 \pm 0.007$  units octave<sup>-1</sup>. The high temporal frequency group (▲, 8–32 Hz) has a slope of  $-0.109 \pm 0.006$  units octave<sup>-1</sup>, throughout its range.

**Table 3. Correlations in contrast sensitivity for various temporal frequencies (spatial frequency of gratings set to 0.50 cycles deg<sup>-1</sup>)**

Cycles s <sup>-1</sup>	0.25	0.50	1.0	2.0	4.0	8.0	16.0
0.5	0.72						
1.0	0.67	0.81					
2.0	0.68	0.68	0.79				
4.0	0.32	0.48	0.57	0.66			
8.0	0.51	0.62	0.54	0.63	0.71		
16.0	0.35	0.48	0.42	0.39	0.49	0.60	
32.0	0.20	0.38	0.47	0.59	0.67	0.55	0.39

beginning to level off. We quantified this with a piecewise linear model, using MINSQ (MicroMath, Salt Lake City, Utah, USA), a non-linear least-squares model estimation algorithm. The results of these fits are listed in Table 2. As inspection of Table 2 shows, the initial slope of these functions tends to be greater for low temporal frequencies than for high. Data for 8–32 Hz were well fitted by a single linear function. The data in Table 2 are clustered into roughly three groups. For illustrative purposes, the correlational functions in Fig. 1 were produced by pooling similarly behaved data into the three groupings noticed in Table 2 (low, moderate and high temporal frequencies).

To interpret the data, we note that correlation for detection thresholds of a pair of spatial frequencies is expected to be high if both frequencies are detected by the same channel (Sekuler *et al.* 1984). Correlation should be lower if two or more overlapping channels each contribute to detection. Correlation would be very low (chance) if each stimulus was detected by separate non-overlapping and non-interacting channels. (Correlations would also be uniformly low if the data were very noisy, or if the range over which the data were taken was unduly restricted.) If there were only one spatial frequency channel mediating detection, then correlation coefficients would be expected to be close (within experimental error) to unity, and the slope of the correlational function would be zero (see Discussion for an

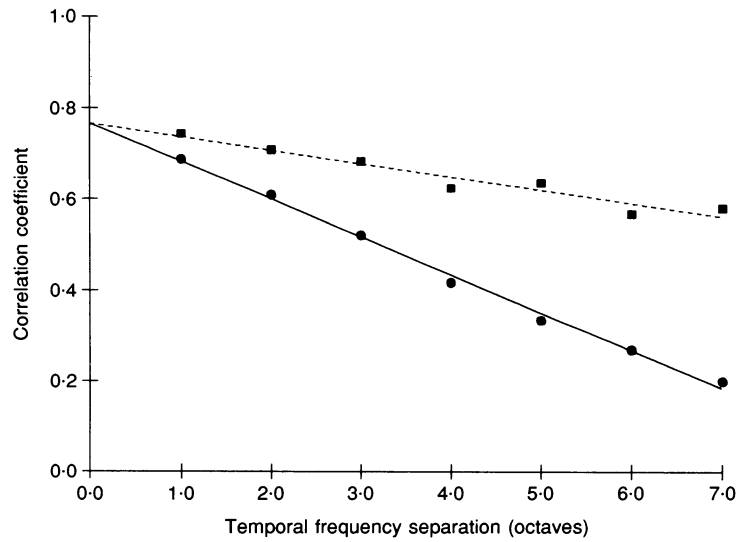
exception). If every stimulus was detected by its own channel and no other, correlation would approach zero, and the slope of the correlation function would approach infinity (see Discussion for an exception). The overall structure of our correlation matrices – high correlations for stimuli with similar spatial frequencies, lower correlations for stimuli with different spatial frequencies – is consistent with multiple overlapping spatial frequency channels. The linearity of the correlation functions suggests that the slope of the correlational function could be used as an index of neural processing. High slopes are consistent with many relatively narrow channels. Lower slopes are consistent with relatively fewer broadband channels. The shallower slopes of the spatial correlation functions for higher temporal frequencies are consistent with psychophysical and electrophysiological reports that the spatial frequency channels active at high temporal frequencies are smaller in number or broader in bandwidth, or both, compared with spatial frequency mechanisms active at low temporal frequencies (Watson & Robson, 1981; Wilson *et al.* 1983).

#### Correlations in temporal contrast sensitivity

Similar calculations were done for temporal frequency contrast sensitivity data with spatial frequency held constant. For example, Tables 3 and 4 show correlation matrices for 0.50 and 11 cycles deg<sup>-1</sup> gratings modulated at various temporal frequencies. Linear functions were fitted

**Table 4. Correlations in contrast sensitivity for various temporal frequencies (spatial frequency of gratings set to 11 cycles deg<sup>-1</sup>)**

Cycles s <sup>-1</sup>	0.25	0.50	1.0	2.0	4.0	8.0	16.0
0.5	0.83						
1.0	0.63	0.79					
2.0	0.66	0.70	0.64				
4.0	0.56	0.58	0.69	0.69			
8.0	0.68	0.72	0.79	0.64	0.76		
16.0	0.53	0.60	0.64	0.52	0.69	0.80	
32.0	0.60	0.71	0.72	0.66	0.72	0.75	0.68



**Figure 2. Linear models fitted to correlational structure of temporal contrast sensitivity data**

Correlational structure of temporal data fall into roughly two groups (see Table 5). For spatial frequencies below 8 cycles deg<sup>-1</sup> (0.5–5.7 cycles deg<sup>-1</sup>, ●), the slope of the pooled temporal data is  $-0.083 \pm 0.003$  correlation units octave<sup>-1</sup>. For higher spatial frequencies (8–23 cycles deg<sup>-1</sup>, ■), the slope of the pooled temporal data is a much shallower  $-0.029 \pm 0.004$  units octave<sup>-1</sup>.

to temporal correlation data for various spatial frequencies. These temporal correlation functions are similar to the spatial functions, although slopes for temporal correlations are shallower than for spatial correlations and are linear throughout the entire 7-octave range of temporal frequencies (Table 5). For illustrative purposes, the correlational functions in Fig. 2 were produced by pooling similarly behaved data into two groups – low spatial frequencies (slope of  $-0.083 \pm 0.003$  correlation units octave<sup>-1</sup>) and high spatial frequencies (slope of  $-0.029 \pm 0.004$ ). Two

simple inferences are possible. First, by the reasoning of the previous section, the shallower slopes of the temporal correlation data (compared with the higher initial slopes of the spatial data) are indicative of fewer temporal mechanisms than spatial mechanisms mediating the detection of contrast. This inference has considerable support in the literature (see Graham, 1989, for a review). Second, the different and non-zero slopes of the temporal correlation functions (Fig. 2) for low and high spatial frequencies may have implications for studies that find

**Table 5. Linear model fit to the structure of temporal frequency correlation matrices**

Spatial frequency (cycles deg <sup>-1</sup> )	Slope	Variance fit to model
0.5	$-0.071 \pm 0.009$	0.924*
0.7	$-0.068 \pm 0.012$	0.863
1.0	$-0.070 \pm 0.007$	0.956
1.4	$-0.117 \pm 0.004$	0.993
2.0	$-0.075 \pm 0.005$	0.979
2.8	$-0.087 \pm 0.004$	0.990
4.0	$-0.094 \pm 0.006$	0.982
5.7	$-0.069 \pm 0.002$	0.994
8.0	$-0.033 \pm 0.009$	0.745
11.0	$-0.020 \pm 0.004$	0.853†
16.0	$-0.024 \pm 0.005$	0.813
22.6	$-0.040 \pm 0.006$	0.895

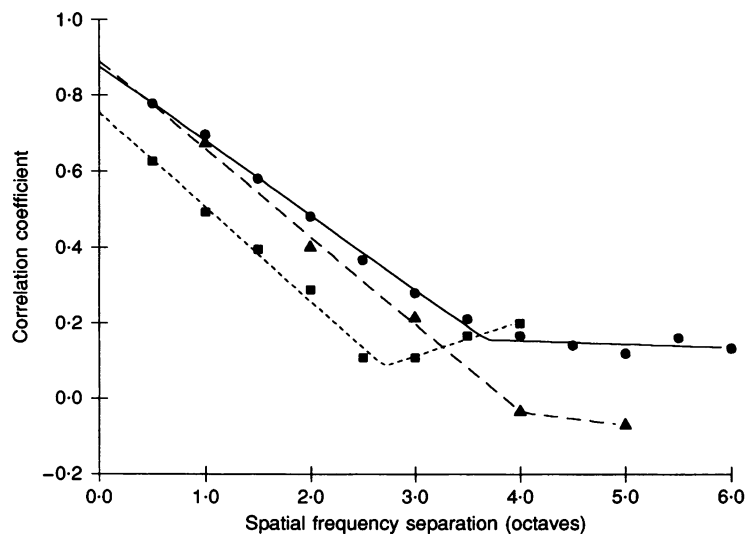
Slope is given in correlation units octave<sup>-1</sup>. \* Model fit to data in Table 3. † Model fit to data in Table 4.

either two (Watson & Robson, 1981; Moulden *et al.* 1984; Hammett & Smith, 1992) or three to four temporal mechanisms (Richards, 1979; Mandler & Makous, 1984; Hess & Plant, 1985; Hess & Snowden, 1992). At least two temporal mechanisms must be active at high spatial frequencies (up to 22.6 cycles  $\text{deg}^{-1}$ ), or else the slope would not be significantly steeper than zero ( $P < 0.01$ ). Similarly, since the slope of the temporal correlation function at low spatial frequencies is significantly greater than at high spatial frequencies ( $P < 0.01$ ), then either more than two temporal mechanisms are active at low spatial frequencies or their temporal tuning is different from the temporal tuning of the temporal mechanisms active at high spatial frequencies. Either way, the data imply a total of at least three temporal mechanisms (assuming spatiotemporal separability of individual temporal mechanisms, as Hess & Snowden (1992) found). It should be noted that at spatial frequencies higher than 22.6 cycles  $\text{deg}^{-1}$ , other results might be obtained. A number of studies show evidence for only one mechanism mediating detection of temporal modulation at spatial frequencies above 25 or 30 cycles  $\text{deg}^{-1}$ . As spatial frequency is increased above this range contrast reversals and spatial shifts are not detected, and abrupt presentations are seen as gradual (Kulikowski & Tolhurst, 1973; King-Smith & Kulikowski, 1975; Westheimer, 1980; Murray & Kulikowski, 1984); moving gratings appear stationary (Campbell & Maffei, 1979; Livingstone & Hubel,

1987). Visual-evoked potential data also show purely sustained responses in this range (Kulikowski, 1976; Russell, Murray & Kulikowski, 1987).

### Sensitivity to experimental conditions

The correlational structures reported here seem surprisingly robust with respect to differences in laboratories, subjects, and experimental conditions. We tested this by plotting data from two published spatial correlational studies with our data taken at low temporal frequencies (Fig. 3). One study was of ninety-one mostly elderly observers at 20  $\text{cd m}^{-2}$ , using the method of ascending contrast (Owsley *et al.* 1983). The other study was of a group of twenty-five 8-month-old infants, using preferential looking at 27  $\text{cd m}^{-2}$  gratings (Peterzell, Werner & Kaplan, 1991). All three studies, despite differences in experimental conditions, show similar correlational structures, with initial slopes ranging from  $-0.196$  to  $-0.247$  correlation units octave $^{-1}$ . Although there are no published temporal correlation matrices to compare with our temporal data, P. E. King-Smith has provided unpublished full screen flicker sensitivity data for seventy-five observers of various ages (luminance of 50  $\text{cd m}^{-2}$ , 8-cycle modified QUEST yes/no staircase procedure). The slope of the temporal correlational function derived from King-Smith's data is  $-0.094 \pm 0.011$  correlation units octave $^{-1}$ , similar to our slope of  $-0.083 \pm 0.003$  correlation units octave $^{-1}$ , measured for low spatial frequencies.



**Figure 3.** Comparison of three studies of human spatial vision

Studies shown are: ●, current study; ▲, Owsley *et al.* (1983); ■, Peterzell *et al.* (1991). Current study: low temporal frequency data (average of 0.25, 0.50 and 1 Hz), yes/no staircase, 40 observers (mean age of 26 years, 100  $\text{cd m}^{-2}$  display). Owsley *et al.* (1983): method of ascending contrast, 91 observers, mostly elderly, 20  $\text{cd m}^{-2}$  display. Peterzell *et al.* (1991): gradual onset gratings, preferential looking, 25 8-month-old observers, 27  $\text{cd m}^{-2}$  display. All three studies have similar correlational structures with initial slopes of  $-0.196 \pm 0.007$  (current study),  $-0.231 \pm 0.004$  (Owsley *et al.* 1983), and  $-0.247 \pm 0.006$  correlation units octave $^{-1}$  (Peterzell *et al.* 1991), respectively.

## DISCUSSION

### Assumptions and artifacts

In the analysis of our data, we assumed that the correlation structures we described arise from overlapping sensitivity of visual mechanisms to spatiotemporal stimuli. Specifically, we assume that thresholds for stimuli are correlated when they activate the same channel or channels. We do not assume complete statistical independence of channels – probability summation and other channel interactions are known to exist – however, structural modelling has shown that interchannel correlations are rather small (Sekuler *et al.* 1984; Peterzell, Werner & Kaplan, 1993). Below, we consider methods to take these interactions into account. Here, we draw attention to two more serious potential artifacts.

As discussed previously, correlational functions with non-zero slope are evidence for the operation of more than one mechanism. However, it is possible for a single channel model to give rise to a non-zero slope under some special circumstances. For example, suppose that each of our observers had a single channel which was low-pass in shape and that the variation in these observers was in the amplitude of the channel and its properties at high frequencies (e.g. slope, cut-off, etc.). Because the contrast sensitivity of low-pass channels is relatively constant over a wide range of low frequencies, there would be a trend for nearby spatial frequencies to give rise to highly correlated contrast thresholds in the pool of observers. More widely separated pairs of frequencies would tend to have one of the pair fall on the unchanging low frequency end of the contrast sensitivity function and the other stimulus of the pair fall on the rapidly changing high frequency end. These pairs would be less correlated in their sensitivities. Such a mechanism would cause correlation structures similar to those we report. While we cannot rule out this explanation as a factor, we can rule it out as an explanation for much of our data by examining the contrast sensitivity functions that our correlation matrices were calculated from. In general, the spatial contrast sensitivity functions of our observers are strongly bandpass (have peak sensitivities at moderate spatial frequencies at least 0.2 log units higher than sensitivity at 0.5 cycles deg<sup>-1</sup>) for temporal frequencies below 8 Hz. Similarly, the temporal contrast sensitivity functions of our observers are bandpass for spatial frequencies below 2 cycles deg<sup>-1</sup>. Since the linear correlation structures arise under conditions where contrast sensitivity functions are either lowpass or bandpass, the single channel lowpass model is insufficient to explain our data. We also noted that the steady decline of correlation over several octaves of spatial frequency is evidence for rather moderate spatial frequency bandwidths. If thresholds for each stimuli (which were spaced 0.5 octaves apart) had

been set by separate channels, then thresholds for similar stimuli would be poorly correlated, and the correlation function would have an extremely high slope. However, it is possible to have a large number of very narrowband filters results in correlation functions with moderate slopes if broadband internal noise, or other factors, lead to correlated sensitivity shifts in multiple channels. While we cannot rule out this possibility on the basis of our data, it does not seem likely. Electrophysiological studies show a broad range of bandwidths, with average bandwidths of more than an octave (1.2 octaves for cells with peak spatial frequencies of more than 11 cycles deg<sup>-1</sup>, larger bandwidths for mechanisms peaking at low spatial frequencies; De Valois *et al.* 1982). Early psychophysical evidence for very narrow channels are now thought to be artifacts of the methods used to analyse the data (for a review see Graham, 1989).

### Improvements to the method

There is at least one problem in fitting functions to correlational structure – correlations derived for stimuli with small frequency separations are the most precisely determined. For example, the correlation for frequencies separated by 0.5 octaves is based on the average of correlations for twelve spatial frequency pairs (e.g. the largest diagonal of Table 1). The correlation for frequencies separated by 3 octaves is based on the average of seven spatial frequency pairs. The correlation for frequencies separated by 6 octaves is based on only one pair (the correlation between thresholds for gratings of 0.5 and 32 cycles deg<sup>-1</sup>). It follows that for a piecewise linear model fit to this data, the slope for small frequency separations is better determined than the slope for large frequency separations, or the breakpoint between them. This was not a problem for our study, because the fit of the model to the data was excellent and because we placed little theoretical emphasis in interpreting the breakpoint or final slope. Also, by allowing correlations of data separated by several octaves to be fitted separately, the less precisely determined correlations had little effect on the determination of the slope for smaller frequency separations, on which theoretical emphasis has been placed. In this paper we sought for simplicity in our analysis and the present approach sufficed. Future work may involve data obtained from fewer observers, or may assign theoretical significance to the location of the breakpoint. In that case, it would be better to use a weighted fit (the weight proportional to the number of stimulus pairs from which the correlation was computed). Also, it ought to be noted that the linear model is not privileged. Other models may be motivated by theoretical considerations or may better fit the data. However, as shown by Tables 2 and 5, the linear model is adequate for our data.

### Applications and complications

There are several possible applications for this approach. The insensitivity of the method to differences in subjects or experimental method suggests that studies of correlational structure may be a useful way to compare data produced in different laboratories (or under different conditions) for similarity of neural processing. Substantial amounts of such data exist in clinical and human factors laboratories. For example, a clinical laboratory could compare correlational structure in normal subjects with subjects with visual pathologies, to see if fewer mechanisms in the latter group contribute to detection. It is also possible that the method could be used in place of, or as a supplement to, traditional confirmatory factor analysis techniques. Factor analysis of sensory data has proven useful (Sekuler *et al.* 1984; Webster & MacLeod, 1988; Peterzell *et al.* 1993; Mayer, Dougherty & Hu, 1995), however, to achieve stable results, factor analysis generally requires many observers, because the accuracy of each correlation coefficient is important to the analysis. By examining the overall structure of the correlation matrix, rather than each correlation coefficient, conclusions may be drawn from fewer observers. Specific models of tuned channels might be tested by generating correlation matrices from a population of simulated observers (Sekuler *et al.* 1984; Peterzell *et al.* 1993) and then comparing the slope of the resulting correlation function with that observed experimentally. These simulations are useful for taking into account the interactions between channels that are known to occur (such as probability summation and cross-channel inhibition; see Sekuler *et al.* 1984; Peterzell *et al.* 1993). Such simulations lie outside the scope of this paper, but will be the focus of later work. Finally, this approach is not limited to the analysis of contrast thresholds. Tuned channels are ubiquitous in the visual system, and in sensory systems in general. For example, one logical candidate for the study of correlational structure would be the photopic spectral sensitivity of dichromats, believed to be mediated by either one or two classes of photoreceptors. After eliminating observer differences due to preretinal absorptions, any significant variation from zero slope would indicate two active photoreceptor systems. The method should also be applicable to some kinds of electrophysiological measurements that pool the responses of multiple mechanisms, such as evoked potentials.

ALBRECHT, D. G. (1978). Analysis of Visual Form. PhD Dissertation, University of California, Berkeley, CA, USA.

BLAKEMORE, C. & CAMPBELL, F. W. (1969). On the existence of neurones in the human visual system selectively sensitive to the orientation and size of retinal images. *Journal of Physiology* **203**, 237–260.

BURR, D. C. (1991). Human sensitivity to flicker and motion. In *Limits of Vision*, vol. 5, *Vision and Visual Dysfunction*, ed. KULIKOWSKI, J. J., WALSH, V. & MURRAY, I. J., pp. 147–159. CRC Press, Boca Raton, FL, USA.

CAMPBELL, F. W. & MAFFEI, L. (1979). Stopped visual motion. *Nature* **278**, 55.

CAMPBELL, F. W. & ROBSON, J. G. (1968). Application of Fourier analysis to the visibility of gratings. *Journal of Physiology* **197**, 551–566.

CORNSWEET, T. N. (1962). The staircase method in psychophysics. *American Journal of Psychology* **75**, 485–491.

DE VALOIS, R. L., ALBRECHT, D. G. & THORELL, L. G. (1982). Spatial frequency selectivity of cells in macaque visual cortex. *Vision Research* **22**, 545–559.

FOSTER, K. H., GASKA, J. P., NAGLER, J. P. & POLLEN, D. A. (1985). Spatial and temporal frequency selectivity of neurons in visual cortical areas V1 and V2 of the macaque monkey. *Journal of Physiology* **365**, 331–363.

GRAHAM, N. V. S. (1989). *Visual Pattern Analyzers*. Oxford University Press, Oxford, UK.

HAMMETT, S. T. & SMITH, A. T. (1992). Two temporal channels or three? A re-evaluation. *Vision Research* **32**, 285–291.

HESS, R. F. & PLANT, G. T. (1985). Temporal frequency discrimination in human vision: Evidence for an additional mechanism in the low spatial and high temporal frequency region. *Vision Research* **25**, 1493–1500.

HESS, R. F. & SNOWDEN, R. (1992). Temporal properties of human visual filters: Number, shapes and spatial covariation. *Vision Research* **32**, 47–59.

KENDALL, M. & STUART, A. (1979). *The Advanced Theory of Statistics*, vol. 1. Macmillan, New York, USA.

KING-SMITH, P. E. & KULIKOWSKI, J. J. (1975). Pattern and flicker detection analyzed by subthreshold summation. *Journal of Physiology* **249**, 519–548.

KULIKOWSKI, J. J. (1976). Methods for separating pattern and movement evoked potentials. *Journal of Physiology* **257**, 2–3P.

KULIKOWSKI, J. J. & TOLHURST, D. J. (1973). Psychophysical evidence for sustained and transient neurons in the human visual system. *Journal of Physiology* **414**, 223–243.

LIVINGSTONE, M. S. & HUBEL, D. H. (1987). Psychophysical evidence for separate channels in the perception of form, color, movement, and depth. *Journal of Neuroscience* **7**, 3416–3468.

MANDLER, M. B. & MAKOUS, W. (1984). A three channel model of temporal frequency perception. *Vision Research* **24**, 1881–1889.

MAYER, M. J., DOUGHERTY, R. F. & HU, L. (1995). A covariance structure analysis of flicker sensitivity. *Vision Research* **35**, 1575–1583.

MOULDEN, B., RENSHAW, J. & MATHER, G. (1984). Two channels for flicker in the human visual system. *Perception* **13**, 387–400.

MURRAY, I. J. & KULIKOWSKI, J. J. (1984). Movement detection and spatial phase. *Ophthalmic and Physiological Optics* **4**, 73–76.

OWSLEY, C., SEKULER, R. & SIEMSEN, D. (1983). Contrast sensitivity throughout adulthood. *Vision Research* **23**, 689–699.

PETERZELL, D. H., WERNER, J. S. & KAPLAN, P. S. (1991). Individual differences in contrast sensitivity functions of human adults and infants: A brief review. In *The Changing Visual System*, ed. BAGNOLI, P. & HODOS, W., pp. 391–396. Plenum Press, London.



- PETERZELL, D. H., WERNER, J. S. & KAPLAN, P. S. (1993). Individual differences in contrast sensitivity functions: The first four months of life in humans. *Vision Research* **33**, 381–396.
- RICHARDS, W. (1979). Quantifying sensory channels: Generalizing colorimetry to orientation and texture, touch and tones. *Sensory Processes* **3**, 207–229.
- ROBSON, J. G. (1966). Spatial and temporal contrast sensitivity functions of the visual system. *Journal of the Optical Society of America* **56**, 1141–1142.
- RUSSELL, M. H. A., MURRAY, I. J., KULIKOWSKI, J. J. (1987). Spatial frequency dependence of the human visual evoked potential. In *Evoked Potentials III*, ed. BARBER, C. & BLUM, T., pp. 231–239. Butterworths, Boston, MA, USA.
- SEKULER, R., WILSON, H. R. & OWSLEY, C. (1984). Structural modeling of spatial vision. *Vision Research* **24**, 689–700.
- SMITH, A. T. (1991). Limits of velocity perception. In *Limits of Vision*, vol. 5, *Vision and Visual Dysfunction*, ed. KULIKOWSKI, J. J., WALSH, V. & MURRAY, I. J., pp. 160–170. CRC Press, Boca Raton, FL, USA.
- STROMEYER, C. F. & JULEZ, B. (1972). Spatial-frequency masking in vision: Critical bands and spread of masking. *Journal of the Optical Society of America* **62**, 1221–1232.
- TYLER, C. W., BARGHOUT, L. & KONTSEVICH, L. L. (1993). Surprises in analyzing the mechanisms underlying threshold elevation functions. *Investigative Ophthalmology and Visual Science* **34**, suppl., 819.
- WATSON, A. B. (1983). Detection and recognition of simple spatial forms. In *Physical and Biological Processing of Images*, ed. BRADDICK, J. J. & SLEIGH, A. C., pp. 100–114. Springer Verlag, New York, USA.
- WATSON, A. B. & ROBSON, J. (1981). Discrimination at threshold: Labelled detectors in human vision. *Vision Research* **21**, 1115–1122.
- WEBSTER, M. A. & MACLEOD, D. I. A. (1988). Factors underlying individual differences in the color matches of normal observers. *Journal of the Optical Society of America* **5**, 1722–1735.
- WESTHEIMER, G. (1980). Spatial phase sensitivity for sinusoidal grating targets. *Vision Research* **20**, 443–452.
- WILSON, H. R., MACFARLANE, D. K. & PHILLIPS, G. C. (1983). Spatial frequency tuning of orientation selective units estimated by oblique masking. *Vision Research* **23**, 873–882.

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