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Individual Differences in Contrast Sensitivity Functions: The Lowest Spatial Frequency Channels

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The number and nature of spatial channels tuned to low spatial frequencies in photopic vision was examined by measuring individual differences in the contrast sensitivity functions (CSFs) of seven visually normal adults. Stationary, 51 cd/m^2, low spatial frequency sinusoidal gratings between 0.27 and 2.16 c/deg were used as stimuli. Correlational and factor analyses revealed that the set of CSFs contained only one statistical source of individual variability at spatial frequencies below 1 c/deg (tuned to a peak of about 0.8 c/deg), and a second source above 1 c/deg (tuned to about 1.4 c/deg). The sources ("factor-channels") mapped well onto the two coarsest spatial frequency channels from some existing computational models. The analysis was applied also to earlier data from 4-, 6- and 8-month-old infants, in which two sources of variability have been found below 1 c/deg [Peterzell, D. H., Werner, J. S. & Kaplan, P. S. (1995). *Vision Research, 35,* 961–980]. The combined results are consistent with the hypothesis that in photopic vision of the neonate, there are two channels with peak sensitivities below 1 c/deg, and that these channels shift their tuning from lower to higher spatial frequencies by about a factor of four during development. Copyright © 1996 Elsevier Science Ltd.

Contrast sensitivity Factor analysis Individual differences Spatial frequency Spatial vision Visual development Covariance structure analysis

INTRODUCTION

The processes underlying the detection of spatial contrast are well established. It is widely believed that visual images are processed by a set of spatial channels each tuned for a different range of spatial frequencies and orientations (Blakemore & Campbell, 1969; Campbell & Robson, 1968; for reviews, see De Valois & De Valois, 1988; Graham, 1989; Wilson *et al.*, 1990). Classical evidence for these channels comes from a variety of psychophysical paradigms, primarily masking, adaptation and summation at threshold (De Valois & De Valois, 1988).

Coarsest spatial channels

There is some evidence from adaptation studies that for the detection of stationary gratings, the lowest frequency channel has its peak sensitivity near 1 c/deg (Greenlee *et al.*, 1988; Tolhurst, 1973). For adapting gratings above 1 c/deg, "on-peak" adaptation effects occur; i.e. the peaks of threshold elevation functions match the spatial frequency of the adapting grating. For adapting gratings below 1 c/deg, the peaks of the threshold elevation functions remain at or near 1 c/deg.

This "lowest adaptable channel" is a specific feature of the detection of stationary gratings; with moving or flickering gratings, on-peak adaptation can occur for much lower spatial frequencies (Greenlee *et al.*, 1988). Moreover, it can be argued that even for stationary gratings, multiple channels may exist at frequencies lower than 1 c/deg. On-peak effects have been found well below 1 c/deg in some experiments, using adaptation, masking, summation paradigms, luminance dependence, or suprathreshold frequency discrimination (Furchner *et al.*, 1977; Green *et al.*, 1981; Hess & Nordby, 1986; Hess & Howell, 1988; Kranda & Kulikowski, 1976; Stromeyer *et al.*, 1982; Watson & Robson, 1981). However, Greenlee *et al.* (1988) suggest that the results of some of these studies may reflect either differences between threshold and suprathreshold effects of adaptation, or artifacts due to scaling procedures. Others suggest that channels tuned to very low spatial frequencies differ from

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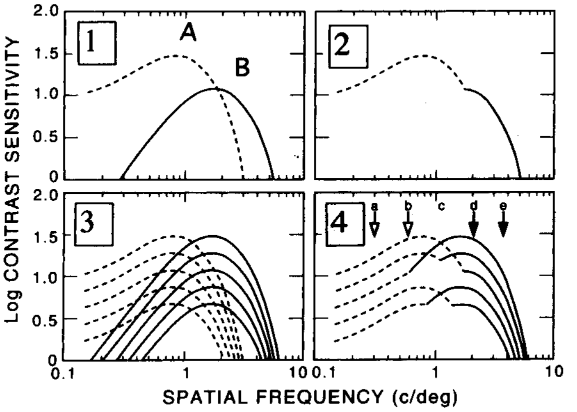

FIGURE 1. Schematic of one possible model of individual differences in CSFs. It is assumed that the two independent spatial frequency channels (panel 1) determine the overall CSF (panel 2) for any individual observer. Individual differences in the sensitivity of each spatial frequency channel (panel 3) are assumed to determine individual variability in the overall shapes of individual CSFs (panel 4). See text for details (adapted from Peterzell *et al.*, 1995).

their higher-frequency counterparts (e.g. they may be unadaptable, or sensitive at scotopic light levels only), or that their neural bases differ from those of higher-frequency channels (Hess & Howell, 1988; Stromeyer *et al.*, 1982). In sum, the number and nature of channels tuned to very low spatial frequencies — i.e. channels with peaks below 1 c/deg — remains unclear. Different paradigms provide different answers.

The estimation of channel characteristics is complicated further by recent challenges to channels theory. Although masking and adaptation paradigms have been invaluable to our developing understanding of the channels underlying CSFs, concerns exist about these paradigms' validity in estimating quantitative characteristics of spatial channels. It has been argued (Barghout-Stein & Tyler, 1994, 1995; Tyler *et al.*, 1993, 1994) that the oft-made assumption that threshold elevation functions resemble the shapes of underlying channels may be incorrect. Rather, each threshold elevation function may well be controlled by multiple adjacent channels and thus give little information about the tuning of any single channel. Another assumption — that on-peak tuning curves indicate the existence of channels tuned along a continuum of spatial frequencies — also appears to be incorrect. Rather, Tyler *et al.* have shown that a discrete-channels model can lead to on-peak masking or adaptation. Consequently, previous estimates of the number, nature (discrete vs continuous) and tuning of channels need further validation.

Individual differences

A paradigm that may avoid the aforementioned limitations is based on the analysis of individual differences (Sekuler *et al.*, 1984; MacLeod & Webster, 1988; Webster & MacLeod, 1988). The individual differences paradigm has been used recently to quantify the number of spatiotemporal channels and to measure the spatial and temporal frequency tuning of these channels in adults and infants (Owsley *et al.*, 1983; Sekuler *et al.*, 1984; Peterzell *et al.*, 1990, 1991, 1993, 1995, 1996; Strasburger *et al.*, 1993; Mayer *et al.*, 1995; Billock & Harding, 1996; Peterzell & Kelly, 1996). The individual differences paradigm uses simple detection data to assess the unadapted, unmasked visual system. This paradigm, unlike others, requires little by way of complex assumptions or theoretical structure to estimate channels and thus provides relatively direct estimates of channel tuning (Sekuler *et al.*, 1984; MacLeod & Webster, 1988; Webster & MacLeod, 1988; Peterzell *et al.*, 1991; 1993; 1995).

Figure 1 contains a schematic model of individual differences underlying CSFs. It illustrates the rationale for and assumptions of the paradigm.

Assumption 1: Multiple spatial channels exist. Panel 1 shows the sensitivities of two hypothetical channels that could exist in a subject. For purposes of illustration, the model consists of only two channels. This subject's first channel (A, dashed line) is more sensitive than the second (B, solid line).

Assumption 2: Channels determine CSF shape. As shown in panel 2, Channel A determines the CSF at low frequencies, Channel B at higher frequencies. For simplicity of illustration, the CSF is deemed free of measurement error and a winner-take-all summation rule has been applied.

Assumption 3: Channel sensitivities vary independently across individuals. Peak sensitivity of each channel is regularly distributed across subjects and independent of the sensitivity of other channels

Panel 3 shows the Channels A and B, each at five different sensitivity levels. The subject in panel 1 has a highly sensitive Channel A and a Channel B of average sensitivity, based on the selection available in panel 3.

Implication 1: Individual variability in channel sensitivities causes measurable individual variability in CSFs. This implication is illustrated in Panel 4, which shows CSFs for five hypothetical subjects. The five contrast sensitivities measured at spatial frequency *a* fall within a statistically regular (possibly normal) distribution. The five sensitivities measured at frequency *b* also fall within a statistically regular distribution, mappable, *with rank retention*, onto the distribution for *a*. This rank retention is due to the shared underlying channel (A). Likewise, the five sensitivities measured at frequency *d* fall within a distribution that is mappable, with rank retention, onto the distribution for frequency *e*, as Channel B controls sensitivity at these frequencies. However, rank is not retained *across* the two distributions (*a*, *b* vs *d*, *e*) because different channels control sensitivity. Frequency *c* represents the boundary region at which the two channels overlap, and is not fully determined by either channel.

Thus each subject retains his rank across the range of frequencies controlled by any one channel; the five sensitivities at one frequency correlate with those at nearby but not distant frequencies. For instance, the five sensitivities at frequency *a* correlate strongly with the five at frequency *b*, weakly with those at *c* and not at all with those at *d* and *e*. This selective correlational structure is akin to selectivity for narrow ranges of spatial frequency.

Implication 2: Spatial channel characteristics can be inferred from individual differences in CSFs. Having assumed that individual variation in underlying channels contributes to individual variation in empirical CSFs, one can use individual differences in CSFs to test and generate models of spatial channels. The methods for doing so are described below, and in greater detail in earlier papers (Sekuler *et al.*, 1984; Peterzell *et al.*, 1991, 1993, 1995).

The individual differences paradigm proceeds as follows. First, contrast thresholds are measured at many spatial frequencies in a set of N individual subjects. Then, a correlation matrix is calculated across the N subjects for each spatial frequency against each other spatial frequency. Regions of high intercorrelations among sets of adjacent spatial frequencies suggest the existence of sets of spatial frequencies that are detected by the same underlying channel, while correlations near zero among more widely separated spatial frequencies suggest detection by different channels; intermediate correlations suggest transition zones. Factor-analytic statistics (e.g. principal component analysis, structural equation modeling), which derive variability sources (or *factors*) from the data, are then used to indicate the nature of the spatial channels (Sekuler *et al.*, 1984; Peterzell *et al.*, 1991, 1993, 1995). Because these tools can provide estimates of how many significant factors a data set contains, they can estimate the minimum number of spatial channels required to model the CSFs. Factor loadings (which describe correlations between a variable and a factor) can then be used to estimate the tuning of the channels. We here introduce the term "factor-channels" to refer to the spatial frequency channels estimated from such analyses. The factor-channels can be compared to the number and spatial frequency tuning of the channels predicted from existing models.

The goal of the present study was to apply individual differences methodology to the question of the number and tuning of spatial frequency channels near and below 1 c/deg. In particular, we wished to test the hypothesis that the coarsest spatial channel underlying adult contrast sensitivity functions (CSFs) for stationary gratings is maximally sensitive to spatial frequencies near 1 c/deg, and that this channel controls sensitivities at all frequencies below 1 c/deg. To that end, we have made detailed measurements of CSFs at low spatial frequencies in seven adult subjects and analyzed the data using individual differences methods. The resulting factor-channels were compared to the coarsest spatial channels from existing computational models (Wilson & Gelb, 1984; Barghout-Stein & Tyler, 1994). Finally, the approach was extended to the developmental data of Peterzell *et al.* (1995), and to Wilson's (1988, 1993) model of the development of spatial channels.

A brief report of the adult data reported here has been presented previously (Peterzell & Teller, 1995).

EXPERIMENTAL METHODS

Human subjects

Seven adults participated, including the two authors. Each had normal or corrected-to-normal vision, and was between 20 and 56 yr. The presbyopic subject (DT) was tested with appropriate correction for the test distance. The experiment was undertaken with the understanding and written consent of each subject.

Apparatus

Two 19″ high-resolution RGB (Barco CDCT 6451) monitors (screens A and B), controlled by a Macintosh computer, were combined with a beam splitter. Grating stimuli appeared on screen A, while screen B contained a uniform auxiliary field designed to allow presentation of very low contrast gratings while minimizing quantization problems.

The beam splitter reflected 13% of the light from screen A and transmitted 87% from screen B. The mean luminances of the two screens were set such that the mean luminance of the display was 51 cd/m^2. Screen A had 8 bit resolution per gun, with 256 luminance levels simultaneously displayable. The voltage/luminance relationship was linearized independently for each of the three guns in the display, using calibration files (Cowan, 1983). The maximum output for each monitor was calibrated to equal energy white (C.I.E. chromaticity coordinates = 0.333, 0.333), using a Minolta colorimeter. The available contrasts of the combined field ranged from 0.3 to 8.8%. At 38 cm the display subtended 53×40 deg, large enough to present 12 cycles per grating for spatial frequencies as low as 0.27 c/deg.

Stimuli

Test stimuli were horizontal luminance-modulated gratings that varied from 0.27 to 2.16 c/deg (seven frequencies, equally spaced on log coordinates). They contained 12 cycles, including eight unattenuated sinusoidal cycles: the two cycles near the top and bottom edges were tapered using a Gaussian vignette to a uniform background of 51.4 cd/m^2. Each grating covered a square area. Horizontal and vertical extents were both equivalent to 12 cycles of the grating (or 8×12 including the unattenuated portion only). Thus, each stimulus covered, approximately, the ten-period functional summation area reported by Howell and Hess (1978). Contrast was defined by standard Michelson contrast. The five contrast levels for any test frequency included the mean threshold (log contrast) based on pilot data along with log contrasts of ± 0.25 and ± 0.5 log units from the mean. A 1 sec Gaussian temporal window ($\sigma = 0.32$ sec) was used to ramp each stimulus to its

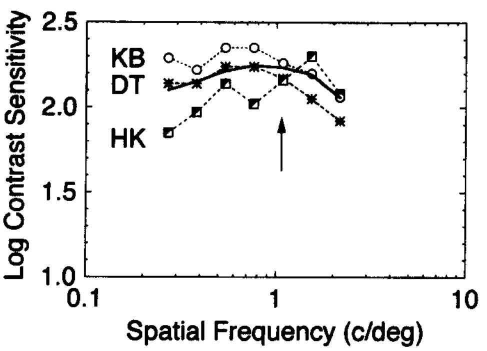

FIGURE 2. Log contrast sensitivity from three adult subjects, plotted as a function of spatial frequency. These data are selected from the population of seven subjects to illustrate the finding that sensitivity values at a particular spatial frequency are correlated with sensitivity values at neighboring, but not distant, spatial frequencies. Note the rank retention for individual subjects across spatial frequencies below 1 c/deg (left of arrow), and the retention of different ranks above 1 c/deg (right of arrow). The solid line shows the mean CSF for all seven subjects.

specified contrast and back to zero contrast during the display interval.

Procedure

Subjects sat 38 cm from the screens in an otherwise dark room, using a chin- and forehead-rest. A two-alternative temporal, forced-choice procedure was used in conjunction with the method of constant stimuli.

At the beginning of each trial, a dim fixation cross appeared in the center of the display (one observer had difficulty detecting the cross because it was near her contrast threshold). The observer fixated on the cross, and pressed a button to start each trial. First, a tone sounded and the fixation cross disappeared, followed by a 1 sec display interval during which the stimulus could be ramped on and off. Then, the cross reappeared for 500 msec, accompanied by two tones. Then, the cross disappeared, followed by a 1.3 sec display interval. (For the second interval, the additional 300 msec was added between the offset of the fixation cross and the onset of the test stimulus interval, due to a programming error. The additional 300 msec delay caused a slight but noticeable asymmetry in the timing of the first and second display intervals with respect to the fixation cross, but is not believed to have had serious consequences for the experiment.) A tone signalled the end of the trial. One of the two display intervals, chosen randomly, contained the stimulus, while the other was blank. Subjects judged which interval contained the stimulus. Immediate feedback (a tone) was provided for correct responses.

Two hours of testing were required to obtain a complete data set for each subject. Testing was divided into a series of blocks. All seven spatial frequencies appeared within a single block, each at the five different contrasts. Patterns appeared in random order. The resulting psychometric functions for each spatial frequency were based on at least 100 trials per function.

TABLE 1. Correlations (r) among spatial frequency variables (log contrast sensitivities for seven adults)

Spatial frequency (c/deg)	0.27	0.38	0.54	0.76	1.08	1.53
0.38	**0.82***					
0.54	**0.83**	**0.56**				
0.76	**0.93**	**0.86**	**0.75**			
1.08	**0.53**	**0.54**	0.33	**0.47**		
1.53	0.05	0.10	0.12	0.35	−0.14	
2.16	0.09	0.22	0.26	0.24	***0.52***†	***0.54***

*Bold text: frequencies *below* 1 c/deg are highly intercorrelated.
†Italicized, bold text: frequencies *above* 1 c/deg are highly intercorrelated.

Threshold was defined as the contrast that yielded 75% correct performance. Contrast sensitivity was taken as the inverse of contrast threshold.

RESULTS AND ANALYSIS

Figure 2 shows mean contrast sensitivity as a function of spatial frequency for all seven subjects, along with the individual CSFs for three subjects (KB, DT, HK) selected for illustration. These functions have the inverted-U shape common to most CSFs; the low frequency roll-off is slight, consistent with other studies in which stimuli with more than eight cycles per grating have been used (McCann *et al.*, 1978).

Systematic variability — fundamental to the theory of individual differences — is evident in Fig. 2. The ranking of KB, DT and HK is maintained at all spatial frequencies below 1 c/deg (e.g. the three contrast sensitivity scores at 0.27 *predict* or *are correlated with* the ranking of scores at 0.38, 0.54 and 0.76 c/deg). Above 1 c/deg, the rankings change; KB moves toward the mean CSF, DT drops below the mean, and HK improves to above-average sensitivity. The ranking of these three individuals again becomes consistent across the two highest spatial frequencies (1.53 and 2.16 c/deg). In other words, the three sensitivities measured at 1.53 c/deg fall within a distribution that is mappable, with rank retention, onto the distribution at 2.16 c/deg.

The *rank retention* below 1 c/deg is due, in theory, to a shared underlying spatial channel that varies in sensitivity across individual subjects (see Fig. 1). Similarly, the rank retention above 1 c/deg occurs, in theory, because a second channel controls sensitivity at these frequencies. However, rank is not retained across the two distributions (0.27, 0.38, 0.54, 0.76 vs 1.53, 2.16 c/deg), in theory because different channels control sensitivity. The three sensitivities at 1.08 c/deg occur at the boundary region at which the two channels overlap, and are not determined fully by either channel.

To examine the systematic variability across all subjects, the correlation matrix was computed from the log contrast sensitivities contained within the seven (spatial frequencies) by seven (subjects) data set. This correlation matrix is shown in Table 1. Table 1 clearly indicates that there are two main sources of variability (or

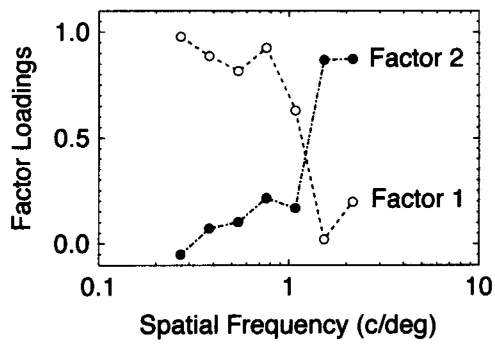

FIGURE 3. Factor loadings that relate the two statistically significant factors to the seven original variables, plotted as a function of spatial frequency. The first factor (open circles) accounts for individual differences in sensitivity at low spatial frequencies and the second factor (solid circles) accounts for individual differences in sensitivity at the higher spatial frequencies.

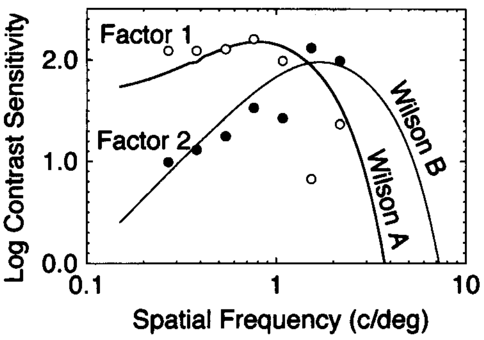

FIGURE 4. Estimates of the contrast sensitivity of the two coarsest "factor-channels", plotted as a function of spatial frequency. The symbols are the factor loadings in Fig. 3, converted to contrast sensitivity using equation (1) (see text). Smooth curves represent the spatial frequency channels A and B from Wilson and Gelb (1984).

factors) underlying the data. One factor (bold type) can largely account for sensitivities for frequencies lower than 1 c/deg because measures taken at these frequencies are intercorrelated. A second factor (bold, italicized type) can account for sensitivities for frequencies above 1 c/deg because measures taken at the highest frequencies are also intercorrelated. Factors 1 and 2 are largely independent, i.e. intercorrelations between the spatial frequencies controlled by the two separate factors are near zero in most cases.

A factor analysis was performed to investigate further the intuitive characteristics described above. This analysis used principal component analysis (PCA) to compute the two most significant factors (i.e. statistical sources of variability), and then rotated the orthogonal components to "simple structure" using the Varimax criterion (Gorsuch, 1983; Peterzell *et al.*, 1993, 1995). Figure 3 relates the seven original variables (i.e. seven spatial frequencies) to the two factors that emerged from the analysis; it shows factor loadings for the two factors as a function of spatial frequency. Each of the two factors shows clear spatial frequency tuning — their factor loadings vary systematically with spatial frequency. Moreover, a single factor accounts for nearly all of the variability below 1 c/deg.

The tuning of factor-channels can be estimated by fitting the statistical factor loadings (Fig. 3) to the mean log contrast sensitivities (Fig. 2). To do so, we used the following equation from Peterzell *et al.* (1993):

$$\text{CHANNEL CONTRAST SENSITIVITY}_{in} = \frac{\text{MEAN LOG CONTRAST SENSITIVITY}_{n}}{(\text{abs}(1/\text{FACTOR LOADING}_{in})^{1/Q})} \qquad (1)$$

which determines the analyzer contrast sensitivity for factor i at spatial frequency n. Q is the exponent of an often-used probability summation equation (Quick, 1974). Q was set to 4 (i.e. between winner-take-all and Euclidean summation), consistent with existing channel theory (Wilson & Gelb, 1984), and following earlier work (Peterzell *et al.*, 1993; Sekuler *et al.*, 1984). For each of the two factors at each spatial frequency, equation (1) generates factor-channel sensitivity values that can range from near-zero (for factor loadings near zero) to the mean log contrast sensitivity (for factor loadings equal to one).

Figure 4 shows the estimated tuning functions (symbols) for the two coarsest factor-channels. Solid lines in Fig. 4 show the tuning functions of channels A and B from the computational model of Wilson and Gelb (1984), adjusted in sensitivity for the best fit to the mean CSF. There is excellent agreement in the figure between the two factor-channels from the empirical data and the model predictions of Wilson and Gelb (1984).

One point, however, falls below the predicted value (Factor 1, 1.53 c/deg). This deviation might be attributable to an unrepresentative, small statistical sample, or to the statistical factor rotation procedure chosen for our analysis (i.e. simple structure). Or, equally likely, it may be that the coarsest factor-channel is in fact tuned to a slightly lower spatial frequency than that predicted by the model of Wilson and Gelb (1984). (A shift of the coarsest channel toward lower spatial frequencies would be consistent with the new multiple channel model of Barghout-Stein & Tyler, 1994.) We do not, at present, have the statistical power to address these issues further.

DISCUSSION

The present experiment constitutes a re-investigation of the number of spatial channels that operate below 1 c/deg for stationary stimuli. Following earlier studies of individual variability in the CSFs of adults and infants, correlational and factor analyses were executed in order to determine the number and spatial frequency tuning of the spatial channels underlying contrast sensitivity in the low spatial frequency range.

The coarsest spatial channels

Below 1 c/deg, we found uniformly high (or equi-) correlational structure in the set of seven individual

CSFs. Moreover, the CSFs contained just one statistical factor at frequencies below 1 c/deg, and at least one additional factor above 1 c/deg. The results are consistent with masking and adaptation studies that indicate that at photopic levels the lowest frequency showing on-peak tuning is near 1 c/deg in adults (Greenlee *et al.*, 1988), and consistent with the multiple channel models of Wilson and Gelb (1984), and Barghout-Stein and Tyler (1994). The results also complement an earlier study of individual differences by Sekuler *et al.* (1984), in which a range of higher spatial frequencies was examined, and three additional frequency-tuned factors, consistent with the channels model of Wilson and Bergen (1979), were found. Our data and analysis thus provide independent yet converging support for the hypothesis that for stationary gratings at photopic levels, the coarsest spatial channel occurs near 1 c/deg.

How does one reconcile the results of the present experiment with prior evidence for multiple channels below 1 c/deg (e.g. Hess & Howell, 1988)? Several explanations are possible.

One possibility is that the foveal region is responsible for detection in our experiments (as discussed below). If so, then one might not expect to find channels tuned to very low spatial frequencies. Tyler *et al.* (1993) observed that while numerous investigators have found evidence for channels tuned to low spatial frequencies, they all adopted the strategem of using large test fields (greater than 2 deg) in order to do so. If detection in our experiments was determined by the foveal region (despite the large size of our stimuli), then this foveal detection might explain the absence of factor-channels below 1 c/deg.

A second possibility is that the factor-channel that detects spatial frequencies below 1 c/deg may in fact represent a combination of several spatial channels. We have assumed that variability within one channel is independent of variability in other channels, as shown in Fig. 1. However, channels below 1 c/deg could co-vary, unlike their higher frequency counterparts. As Hess (personal communication) suggests, the low-frequency channels may all be manufactured from common geniculate afferents since, at least for central vision, they appear first in the cortex. Thus, our coarsest factor-channel may represent a group of channels whose neural input is shared, and different than input to processes mediating higher spatial frequencies (consistent with Hess & Howell, 1988). As such, the coarsest factor-channel may represent a *group* of intercorrelated coarse spatial channels.

A third possible explanation is that several spatial frequency channels may exist at very low spatial frequencies but may operate at scotopic luminances only (or, similarly, the peak of the channel might shift with low light levels, due, perhaps, to a reduction of influence of the surrounds of receptive fields). Hess and Howell (1988) have demonstrated that contrast sensitivity peaks near 0.2 c/deg when stimuli are presented at scotopic luminances. This low-frequency peak cannot be modeled using only a bandpass channel that peaks near 1 c/deg (e.g. the coarsest channel in Fig. 4). However, the coarse channel responsible for this 0.2 c/deg peak would not be expected to contribute greatly at photopic light levels.

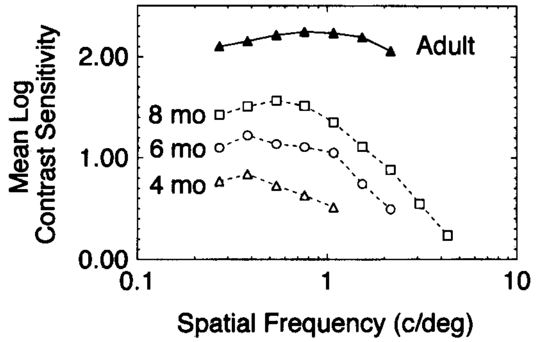

FIGURE 5. Mean log contrast sensitivity from 25 infants plotted as a function of spatial frequency at ages 4 (open triangles), 6 (open circles) and 8 months (open squares) (from Peterzell *et al.*, 1995). The solid line shows the mean adult data from Fig 2.

Relationship to developmental studies

Contrast sensitivity, like many other aspects of visual performance, increases during early development, and the peak contrast sensitivity shifts toward progressively higher spatial frequencies (Atkinson *et al.*, 1977; Banks & Salapatek, 1976; Norcia *et al.*, 1990; Peterzell *et al.*, 1991, 1995; *cf.* Boothe *et al.*, 1988). In general, sensitivity to low spatial frequencies matures earlier than does sensitivity to higher frequencies, with sensitivity values for low spatial frequencies reaching mature levels within the first year, and sensitivity values for higher spatial frequencies reaching mature levels by 8 yr (Bradley & Freeman, 1982).

Although multiple spatial channels have been shown (using masking and adaptation paradigms) to exist in infants above 3 months old (Fiorentini *et al.*, 1983; Banks *et al.*, 1985; Suter *et al.*, 1994), their development is not yet fully understood. A single spatial channel may exist at birth, with channels tuned to higher frequencies achieving measurable sensitivity only later (Banks & Ginsburg, 1985). Alternatively, multiple channels may exist at birth, shifting with age in *spatial scale* (i.e. along the spatial frequency axis toward higher frequencies) as well as in *sensitivity* (toward higher contrast sensitivity) (Brown *et al.*, 1987; Greenlee *et al.*, 1988; Wilson, 1988, 1993). Shifts in spatial scale by a factor of about four in central vision can be predicted from the known cone migration into the fovea during infancy (Yuodelis & Hendrickson, 1986), combined with changes in eye size (Brown *et al.*, 1987; Wilson, 1988). The infancy literature using masking and adaptation paradigms is ambiguous regarding possible shifts in spatial scale (Wilson, 1988; Banks & Crowell, 1993) and it is not obvious how classical methods could be employed to differentiate these hypotheses.

Possible shifts in spatial scale have been examined

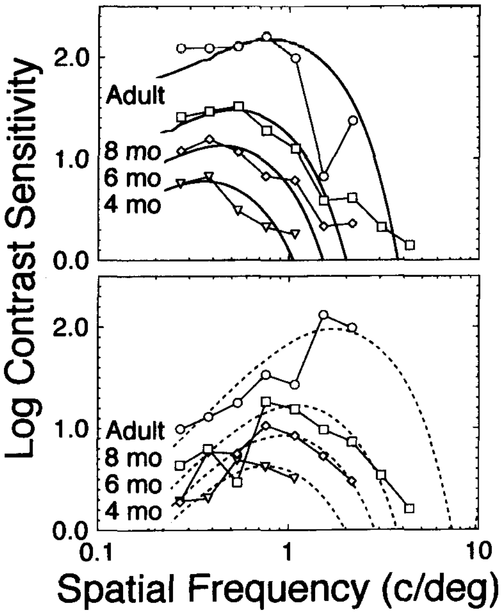

FIGURE 6. Estimates of the contrast sensitivity of the two coarsest factor-channels, plotted as a function of spatial frequency for 4-, 6- and 8-month-olds (Peterzell *et al.*, 1995) and for adults (present study). For infants, factor loadings from the 25 subjects were converted to contrast sensitivity using equation (1). For adults, the symbols are identical to those in Fig. 4. At all three ages, the first factor accounts for individual variability at the lower spatial frequencies and the second factor accounts for individual variability at the higher spatial frequencies. Both factors shift rightward to higher spatial frequencies with age, as predicted. Smooth curves represent the spatial channels A (solid lines) and B (dashed lines) of Wilson and Gelb (1984) and Wilson (1988) [shifted based on developmental changes in foveal cone spacing (Yuodelis & Hendrickson, 1986)].

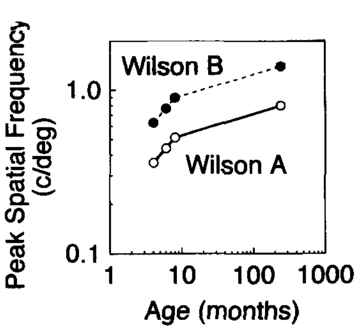

FIGURE 7. Peak sensitivity, as a function of age, of the two coarsest spatial channels from the model of Wilson (1988) (see also Peterzell *et al.*, 1995). Wilson's channels A and B are represented by open and solid symbols, respectively. As mean foveal cone spacing decreases and eye size increases with age (Yuodelis & Hendrickson, 1986), the peak sensitivity of each channel shifts from lower spatial frequencies to its adult value.

recently by applying individual-differences theory and methodology to the CSFs of human infants. In one experiment, CSFs were measured for 40 4-month-old infants (Peterzell *et al.*, 1993). In another, CSFs were measured longitudinally at 4, 6 and 8 months of age in 25 additional infants (Peterzell *et al.*, 1991; 1995).

Figure 5 shows the mean CSFs from the longitudinal study, along with the mean adult CSF from the present experiment. With development, the average CSF increases in overall sensitivity to contrast, shifts its peak toward higher frequencies and increases its high frequency cutoff.

Figure 6 shows, for all ages, the estimated tuning functions (symbols) for the two coarsest factor-channels. Adults' tuning functions are repeated from Fig. 4. Infants' functions were derived in the same manner as the adults' factor-channels in the present study; the factors from the analysis of Peterzell *et al.* (1995) were combined with the mean CSFs in Fig. 5 using equation (1). Estimates of infants' factor-channels are reported here for the first time.

With the factor-channels in Fig. 6 are plotted predictions for the two coarsest channels (A and B) from the developmental model of Wilson (1988). For adults, Channels A and B are identical to those of the model of Wilson and Gelb (1984), as plotted in Fig. 4. Wilson's channels for infants were generated by first shifting the channels to lower spatial frequencies, with the amount of spatial scale change at each age determined by anatomical data (Yuodelis & Hendrickson, 1986; for details see Peterzell *et al.*, 1993, 1995). By incorporating this change in spatial scale, the peaks of channels A and B change as a function of age, as shown in Fig. 7.

The shifted channels from Wilson's (1988) developmental model were then adjusted in sensitivity (vertically) to fit the mean CSF, as with the adult channels in the present study. (Note that this vertical shift is the only free parameter in this model.) The resulting predictions of this model are shown with the estimated factor-channels in Fig. 6. At each age, there is excellent agreement in the figure between the two factor-channels from the data of Peterzell *et al.* (1995) and the predictions of Wilson's (1988) shifting-channels model.

The analysis thus supports the conclusion that individual channels do not simply grow in sensitivity with age. Rather, as they grow in sensitivity, they also shift their spatial tuning to higher spatial frequencies. The results are consistent with the hypothesis that the growth of the eye and the migration of cones during development cause a change in spatial scale in the visual system, shifting the foveal CSF and its underlying channels to higher spatial frequencies.

This result suggests also that, throughout development, the foveal region of the retina is the most sensitive to spatial contrast, and determines contrast thresholds at all ages (at least for the conditions of our experiments). This conclusion follows because changes in photoreceptor packing are less salient in the periphery (Packer *et al.*, 1990; Hendrickson & Drucker, 1992; Hendrickson, 1993). If the periphery determines contrast sensitivity in infancy (*cf.* Brown *et al.*, 1987; Brown, 1990), a new explanation for the observed change in scale must be found.

In summary, we conclude that for stationary, photopic gratings, the peak of the coarsest spatial channel occurs near 1 c/deg in adults. Moreover, in infants, the coarsest channel is tuned to a frequency well below 1 c/deg.

During development, the peak spatial frequency of this channel shifts from lower to higher spatial frequencies by a factor of about four, becoming adult-like sometime after 8 months postnatal.

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