The Development of Basic Mechanisms of Pattern Vision: Spatial Frequency Channels

MARTIN S. BANKS

University of California, Berkeley

BENJAMIN R. STEPHENS

Williams College

AND

E. EUGENIE HARTMANN

University of New Orleans

The mature visual system possesses mechanisms that analyze visual inputs into bands of spatial frequency. This analysis appears to be important to several visual capabilities. We have investigated the development of these spatial-frequency channels in young infants. Experiment I used a masking paradigm to test 6week-olds, 12-week-olds, and adults. The detectability of sine wave gratings of different spatial frequencies was measured in the presence and the absence of a narrowband noise masker. The 12-week data showed that at least two spatial-frequency channels with adult-like specificity are present at 12 weeks. The 6week data did not reveal the presence of narrowband spatial-frequency channels. Experiment 2 used a different paradigm to investigate the same issue. The detectability of gratings composed of two sine wave components was measured in 6-week-olds and adults. The results were entirely consistent with those of experiment 1. The 12-week and adult data indicated the presence of narrowband spatial-frequency channels. The 6-week data did not. The results of these experiments suggest that the manner in which pattern information is processed changes fundamentally between 6 and 12 weeks of age. C 1985 Academic Press, Inc.

Like a camera, the visual system gathers and encodes environmental information. The analogy breaks down, however, when one considers how environmental information is represented in the two devices. The representation in a camera is simply a one-to-one mapping of intensity values onto a two-dimensional surface. The visual system, in contrast, transforms environmental information and represents it symbolically. We now know quite a bit about the early stages of transformation and representation in the adult visual system. We know little, however, about the operation of these stages in early infancy and about how they develop thereafter. This paper and its companion paper (Stephens & Banks, 1985) consider aspects of how pattern information is transformed and represented early in the visual system during the first 3 months of life.

Some of the ways in which pattern information is transformed and represented in the mature visual system are revealed by electrophysiological studies of cats and monkey and by psychophysical investigations of humans. The mature visual system clearly possesses many parallel pathways (or channels) each specialized to carry information about particular types of stimuli. Electrophysiological investigations have shown that different sorts of information from the same location in the visual field are signaled by different neurons. For example, different neurons in the visual cortex respond selectively to bars or edges of different orientations (Hubel & Wiesel, 1962, 1968). More recent evidence suggests that the stimulus preferences of cortical neurons can be well described in spatial frequency terms; that is, the

preference of each neuron is limited to a range of orientations and a band of spatial frequencies.[1] So one cell might respond maximally to contours that are vertical and low in spatial frequency and another to contours that are horizontal and high in frequency (Albrecht, De Valois, & Thorell, 1980; Campbell, Cooper, & Enroth-Cugell, 1969; Movshon, Thompson, & Tolhurst, 1978). This evidence implies that the responses of single cortical neurons convey orientation and spatial frequency information from a particular region in the visual field. Some investigators have equated these neurons with the feature analyzers proposed by some pattern recognition models (e.g., Selfridge, 1959; Uhr, Vossler, & Uleman, 1962).

A large number of psychophysical experiments in human adults has demonstrated that pattern information is processed in parallel by "channels" analogous to the cortical cells mentioned above. Different channels appear to be tuned to different orientations and spatial frequency bands (Blakemore & Campbell, 1969; Braddick, Campbell, & Atkinson, 1978; Campbell & Robson, 1968; Graham & Nachmias, 1971). The evidence for spatial-frequency selectivity among these channels lies in the fact that spatial frequencies interact in detection, adaptation, and masking experiments, but only if they lie within about 1 octave (a factor of 2) of each other.[2]

Figure 1 demonstrates how spatial frequencies interact in a masking experiment. The figure shows that one band of spatial frequencies can mask (decrease the visibility of) another, but only if they are similar in frequency. Figure IA shows a 0.5 (c/deg) sine wave grating presented on the right side of the display. The contrast of the grating is fairly high, so it is quite visible. Figure IB is the same as A except that now visual noise has been added to the whole field. The noise is a field of vertical bars whose position and width change over time. It has been filtered such that its spatial frequency content is clustered around 0.5 c/deg. Notice that the 0.5 c/deg sine wave grating (Fig. IA) is now quite difficult to discern; in other words, the noise masks the low-frequency sine wave gratings. Figure IC is similar to A, but the sine wave grating has a spatial frequency of 2 c/deg rather than 0.5. Figure ID is the same as C except that visual noise centered at 0.5 c/deg has been added to the whole field as it was in Fig. I B. The 2 c/deg sine wave grating remains quite visible; the noise does not mask the high-frequency grating. The fact that noise clustered around 0.5 c/deg masks a 0.5 c/deg grating, but not a 2 c/deg grating, is, evidence that at least two mechanisms, tuned to different spatial frequencies, are operating. One mechanism—the one that detects a 0.5 c/deg grating-is clearly influenced by the addition of noise centered at 0.5 c/deg. The other mechanism—the one that detects a 2 c/deg grating-is not influenced by 0.5 c/deg noise.

---

[1] Spatial frequency and related terms are described fully by Cornsweet (1970) and Banks and Salapatek (1981). We will describe them very briefly here. The contrast sensitivity function (CSF) has become a standard index of the visual system's sensitivity to pattern information of various sorts. The CSF is determined by measuring an observer's sensitivity to sine wave gratings of different spatial frequencies. A sine wave grating is a pattern composed of regularly spaced light and dark stripes. Sine wave gratings are specified by three parameters: (1) spatial frequency, the number of light stripes per degree of visual angle; (2) orientation; and (3) contrast. The reason sine wave gratings are used derives from Fourier's theorem and linear systems analysis. Fourier's theorem implies that any two-dimensional pattern can be exactly described by combining a set of sine wave gratings of various spatial frequencies, orientations, and contrasts. Linear systems analysis allows one, in principle, to predict the visibility of any pattern if the observer's CSF is known. Examples of the use of this technique are provided by Cornsweet (1970) and Banks and Salapatek (1981). One simple way to describe spatial-frequency information is in terms of the coarseness of pattern information. Low spatial frequencies correspond to coarse pattern information such as the outline shape of large objects. High spatial frequencies, on the other hand, correspond to fine pattern information such as the texture of a surface. This distinction is illustrated by Fig. 2.

[2] Throughout the text we describe these "channels" as spatial-frequency-selective mechanisms. By using this terminology, we do not mean to imply that these mechanisms are spatial-frequency analyzers per se. In other words, we do not mean that they respond to the presence of a specific spatial frequency at any location in the visual field. In fact, the mechanisms appear to respond to a I- or 2-octave range of spatial frequencies in a limited region of the visual field (Braddick et al., 1978). Thus, we use the phrase "spatial-frequency selectivity" to convey the band-limited nature of these mechanisms.
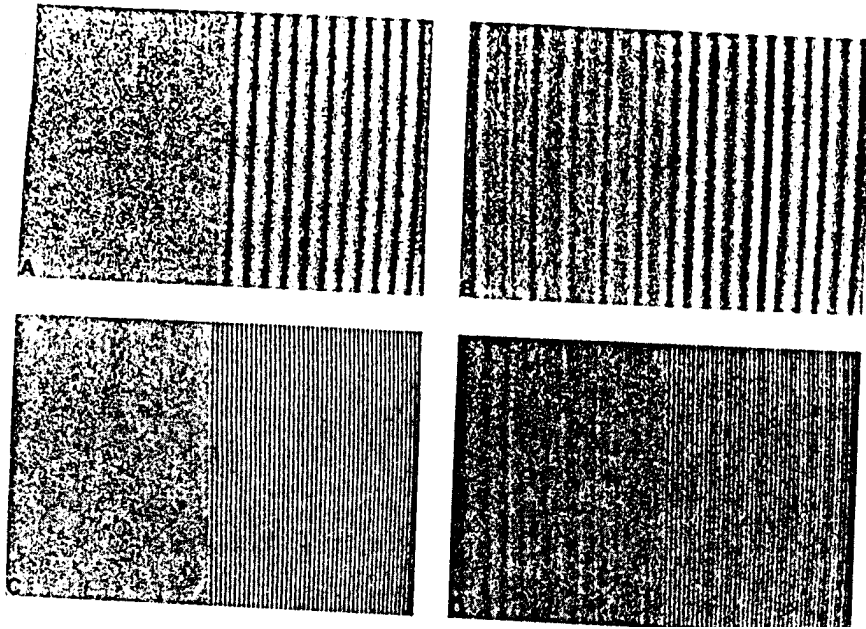
FIG.1 Demonstration of a spatial-frequency-specific masking effect. (A) A 0.5 c/deg sine wave grating on the right and a uniform field on the left. (B) The same grating as in A, but now a narrowband visual noise has been added to the entire screen. The center frequency of the noise is 0.5 c/deg. Notice that the noise decreases the visibility of the low-frequency grating significantly, (C) A 2 c/deg grating on the right. (D) The same grating as in C but with the 0.5 c/deg noise added. Notice that the noise has little effect on the visibility of the high-frequency grating. This figure should be viewed at a distance of 8 cm. for the spatial frequencies to be as stated.

Although the physiological and psychophysical evidence for the existence of orientation-selective and spatial -frequency-selective channels is very persuasive, there is still considerable debate about the role these channels serve for visual perception. Rather than present an exhaustive list of the existing hypotheses, we have chosen to describe three that have been rather influential.

Pollen, Lee, and Taylor (1971) hypothesized that these channels provide something like a Fourier representation of visual stimuli. That is, they proposed that the visual cortex provides a representation of the spatial frequency, amplitude, orientation, and phase of all Fourier components in a visual stimulus. They also proposed that pattern recognition and identification are actually performed in the Fourier domain. This hypothesis is now considered by many visual scientists to be too extreme. The orientation and spatial frequency bandwidths of cortical neurons (and of psychophysical channels) are not nearly narrow enough to allow an accurate representation of Fourier components (Robson, 1975). Furthermore, it is not clear why pattern recognition and identification would be any easier in the Fourier domain than in the spatial domain (Duda & Hart, 1973; Schwartz, 1980).

A less extreme hypothesis has been offered by Marr and his colleagues (for a review, see Marr, 1982). They ascribe a relatively peripheral role to orientation- selective and spatial-frequency-selective channels. They propose that such channels are used to segregate pattern information early in visual processing in a way that will be useful upstream. For example, one problem encountered in visual scene analysis is how to distinguish intensity differences in the scene that are caused by shadows or highlights from intensity differences caused by true object boundaries. This is often a vexing problem. Marr (1982) and his colleague's have shown, however, that comparison of low-spatial-frequency (low pass) and high-spatial-frequency (high pass) representations of a scene may allow the visual system to distinguish contours caused by shadows and highlights from those created by object boundaries or discontinuities. Figure 2 illustrates this phenomenon. Three versions of a photograph are shown. The first (Fig. 2A) is the original, unfiltered picture of the face. The second (Fig. 2B) is a low-pass version: medium and high spatial frequencies have been filtered out so only frequencies from 0.8 to 3.2 c/deg remain. The third (Fig. 2C) is a high-pass version: only frequencies from 6.4 to 25.6 c/deg are represented. Note that distinct object boundaries (like the contour formed by the cheek and the background) appear in all three images whereas intensity gradients due to shadows (e.g., the region between the woman's right eye and her nose) and highlights (e.g., the bright spot on the chin) appear in only the original and low-pass images. Marr and

colleagues hypothesized that the visual system may correlate such filtered representations to distinguish intensity gradients due to object boundaries or discontinuities from those due to lighting conditions.

Another view of the function of spatial-frequency channels has been proposed by Georgeson and Sullivan (1975). This hypothesis is considered in detail in the accompanying paper (Stephens & Banks, 1985). Suffice it to say here that this hypothesis states that spatial-frequency channels are used to selectively enhance high-spatial-frequency information, much as is done in computer-enhanced imaging, to compensate for the defocusing effects of the eye's optics.

The development of spatial-frequency channels has only recently been investigated. This is unfortunate because the development of feature analyzers has played a central role in theories of perceptual development. Hebb (1949) proposed that "cell assemblies," which are essentially simple feature analyzers, are undifferentiated at birth and that they acquire greater specificity with sensorimotor experience. The Russian motor copy theorists (e.g., Zaporozhets, 1965) held a similar position. These points of view have been challenged by Minsky and Papert (1969) who argued that nontrivial feature analyzers could not develop from undifferentiated structures. Feature analysis is also a critical component of Gibson's (1969) differentiation theory of perceptual development, but she did n 's specify how basic feature analyzers, like those tuned to contours of a certain spatial frequency and orientation, develop.
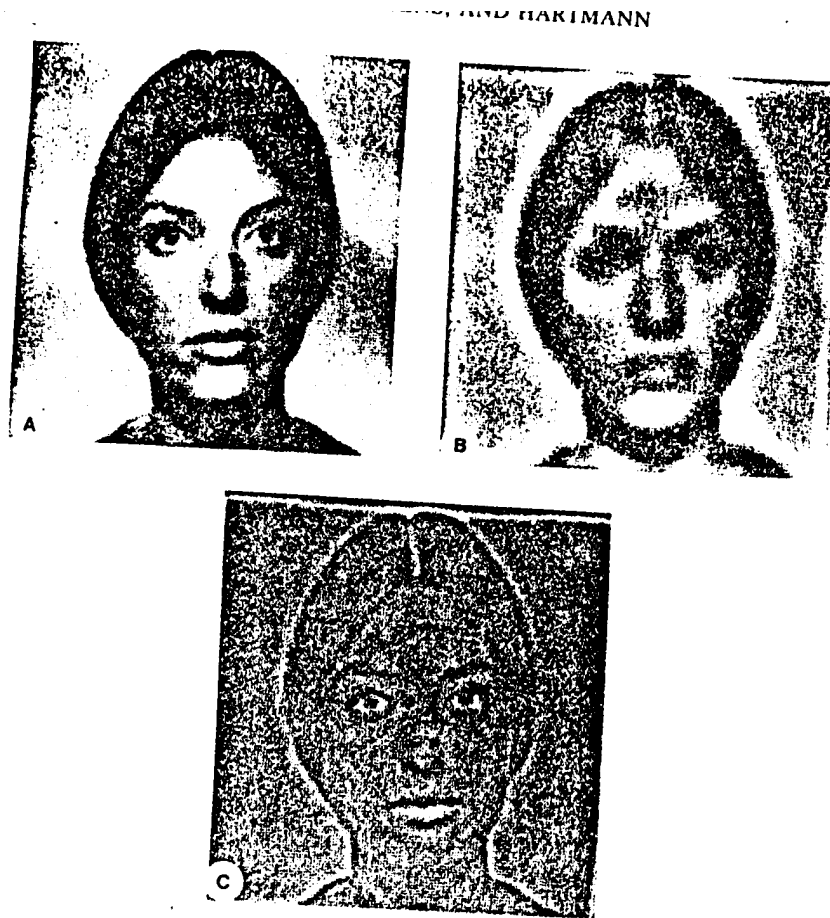
FIG. 2. Three photographs of a face. For the numbers in the text to be appropriate, please view this figure at a distance of 57 cm. (A) The original, unfiltered photograph of the face. (B) A filtered photograph of the same face. Medium and high spatial frequencies have been filtered out so only frequencies from 0.8 to 3.2 c/deg remain. (C) Another filtered photograph of the face. Low frequencies have been filtered out so only frequencies from 6.4 to 25.6 c/deg remain. (Adapted from Ginsburg, 1978).

Bronson (1974) and Salapatek (1975) have proposed that the feature analysis characteristic of mature visual processing develops postnatally. In particular, they proposed that visual behavior before 2 months of age is mediated primarily by subcortical mechanisms, such as the superior colliculus, and that visual behavior after 2 or 3 months is mediated to an increasing extent by cortical mechanisms. Since feature analysis, as we have described it, is a hallmark of cortical processing, it follows that Bronson and

Salapatek would predict that feature analysis develops, in at least a rudimentary fashion, during the first few months of life.

There is now an extensive literature on the development of feature-selective responding in the visual cortex of kittens and monkey. The vast majority of this literature, however, concerns orientation selectivity (reviewed by Banks, 1983, and Movshon & Van Sluyters, 1981). Only one report exists on the development of spatial-frequency selectivity. Derrington and Fuchs (198 1) examined single neurons in the visual cortex of kittens from 2 to 12 weeks of age. They found that most neurons in the younger kittens were unselective for spatial frequency and that selectivity did not approach adult values until 5-7 weeks.

There is only one report on the development of spatial-frequency selectivity in human infants. Fiorentini, Pirchio, and Spinelli (1983) used the visual-evoked potential (VEP) to assess the development of spatial-frequency channels in infants 6 and 14 weeks of age. They measured VEP amplitude to a sine wave grating presented alone and in conjunction with a masking sine wave grating of a different spatial frequency. They observed significant masking effects at 6 and 14 weeks, but only if the target grating and masking grating were within about 1.5 octaves of one another. They concluded that spatial-frequency channels with reasonably narrow tuning are present at both ages. This conclusion may be unjustified for the following reason. A close examination of their infant data reveals that only one 6-week-old and one 14-week-old provided data that suggest the presence of narrowband mechanisms. The other infants did not provide evidence for or against the presence of multiple, narrowband mechanisms. Therefore, there are currently no conclusive data concerning the development of spatial-frequency channels in human infants.

We have tested 6week-olds, 12-week-olds, and adults in two experiments designed to measure spatial-frequency selectivity. The two experiments used entirely different techniques yet yielded the same results. The results from Experiment I have previously appeared in a brief report (Banks, 1982).

EXPERIMENT 1

Methods

Subjects. Infants were recruited by letter and phone. Five 6week-olds (three females) and five 12-week-olds (three females) completed the entire experiment. Typically this required four to six 45-min sessions. The data from these infants is referred to below as the within-subjects data. The longest time between the first and last sessions for these infants was 12 days, and the average was 8 days. Another eleven 6week-olds (four females) and thirteen 12-week-olds (seven females) completed one-third or two-thirds of the experiment. This generally required one to four 45min sessions. Data from these infants are referred to as the between-subjects data. The attrition rate was high because of the need for multiple sessions in a short period of time. Twenty-four 6week-olds and twenty-one 12-week-olds did not complete one-third or more of the entire experiment due to fussiness, sleepiness, equipment malfunction, experimenter error, or failure to return for a subsequent session.

Apparatus and stimuli. The stimuli were generated on a large-screen CRT (Hewlett-Packard 1317A with P31 phosphor) using the method of Campbell and Green (1965). Viewing distance was always 40 cm because young infants are most likely to accommodate accurately to this distance (Banks, 1980; Haynes, White, & Held, 1965). At this distance the display subtended 48 X 37'. Space-average luminance was 10.6 cd/m^2 for all stimuli regardless of condition. Testing was conducted in a dark room and the surround of the display was dark.

In the first experiment, we used a masking paradigm similar to one used in an adult psychophysical experiment by Stromeyer and Julesz (1972). The paradigm is demonstrated in Fig. 1 and schematized in Fig. 3. Contrast thresholds (the minimum contrast required for detection) were measured for sine wave gratings of three different spatial frequencies under two conditions: in the presence of the masking noise and in the absence of the noise. Thus, six threshold measurements were required for the entire experiment. The spatial frequencies of the sine wave gratings were chosen such that the lowest frequency (F) was at the peak of the contrast sensitivity function (CSF) for that age group (Atkinson, Braddick, & Moar, 1977; Banks & Salapatek, 1978, 1981). For 6week-olds, the frequencies of F, 2F, and 4F were 0.3, 0.6, and 1.2 c/deg, respectively. For 12-week-olds, they were 0.5, 1, and 2 c/deg.
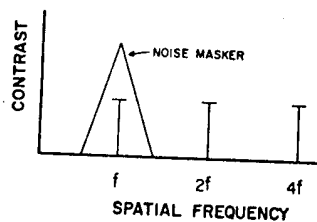
FIG. 3. Schematic of the paradigm used in Experiment 1. The contrast of various stimuli is plotted as a function of spatial frequency. Each vertical bar represents a different sinewave grating. Notice that the center frequency of the noise masker was the same as the spatial frequency of the sine wave grating *F*. Two other sine waves were presented that were either two or four times higher in frequency than *F*. Each of the three sine wave gratings was presented with the noise present and with the noise absent.

The masking noise was produced by bandpass filtering broadband (white) noise. The center frequency of the filtered noise was set to F (0.3 c/deg for 6-week-olds and 0.5 c/deg for 12-week-olds). Its energy decreased at a rate of 48 dB/octave on both the low- and high-frequency skirts. The noise was dynamic; that is, its appearance changed from instant to instant. We conducted a pilot study to ensure that it was visible to both age groups: contrast thresholds were measured for detection of the noise masker alone. Using those data, we set the contrast of the noise to v9lues that were roughly 0.2 log units above threshold. (The noise level used for the 6-week-olds had the same rms voltage as a sine wave grating with a contrast of 0.30. The noise level for the 12-week-olds had the same rms voltage as a grating with a contrast of 0.19. Two levels were used for adults: 0.19 and 0.09).

Procedure. The entire experiment required six contrast threshold measurements-one with noise and one without noise-for each of three spatial frequencies. We will refer to contrast thresholds obtained with noise as masked thresholds and to contrast thresholds obtained without noise as unmasked thresholds. To estimate contrast thresholds, we used the forced-choice preferential looking procedure (Teller, 1979). The parent held the infant in front of the display either in the lap or over the shoulder. The parent's view of the display was occluded by a curtain. An adult observer, positioned behind the display so he could not see it, viewed the infant through a 3-cm slot above the display.

In the unmasked (noise absent) condition, the display was unpatterned before a trial was initiated. To attract the infant's fixation to midline, the observer lowered a noise-making toy to the middle of the screen. Once the observer judged that the infant was fixating centrally, he lifted the toy from view and initiated a trial with a button press. A sine wave grating appeared on either the left or right half of the screen (see Fig. IA and Q. Simultaneous presentation of the grating on half the display and a uniform field on the other was accomplished by splitting the screen electronically at midline. The grating and uniform fields were identical in space-average luminance, spectral composition, and size. Unless the infant simply did not attend to the display, the observer judged which side of the display contained the sine wave grating based on the infant's eye and head movements. When the observer responded, a trial was terminated and the grating was replaced by an unpatterned field. The observer was then given feedback and the sequence began once again.

In the masked (noise present) condition, the display was filled with the noise masker before initiation of a trial. Again the observer presented a noise-making toy to attract the infant's fixation to midline. Once the observer judged that fixation was central, he lifted the toy from view and initiated a trial. A sine wave grating was then added to the noise on either the left or right half of the screen (see Figs. I B and D). Again the observer used the infant's eye and head movements to judge the location of the grating. When the observer responded, the grating, but not the noise, was extinguished and feedback was provided.

In both the masked and unmasked conditions, animated toys were employed in an attempt to reinforce the infants for fixating the grating. The reinforcement procedure we used has been described fully by Mayer and Dobson (1980). Whenever the observer correctly judged the position of the grating, which implies that the infant fixated the grating, a toy was illuminated and set into motion for 2 s on the side of the display on which the grating had appeared. Whenever the observer was incorrect, which implies that the infant did not preferentially fixate the grating, no toys were illuminated or set into motion. We did not attempt to assess whether the infants actually learned the association between the grating's position and the reinforcement.

The contrast of the sine wave grating was varied according to the method of constant stimuli in both experimental conditions.[3] The laboratory computer randomly selected the contrast to be presented. The observer was always unaware of the value selected. A block of 5 trials was completed at a given contrast before a new value was chosen. Twenty trials were presented at each of the three or four contrasts for each threshold determination. Representative data are shown in Fig. 4. We used probit analysis (Finney, 1971), a standard statistical technique in psychophysical work, to locate the contrast threshold from these psychometric data. Probit analysis finds the cumulative normal distribution (ogive) that fits the psychometric data most accurately. We used the contrast associated with 70% correct response on the best fitting ogive as the estimate of contrast at threshold. All of the results from Experiment 1 are based on this estimate of contrast threshold.

Contrast threshold estimates were completed sequentially; that is, one spatial frequency and masking condition was completed before beginning another. Generally, one or two measurements were completed in each session for the infants who finished the entire experiment.
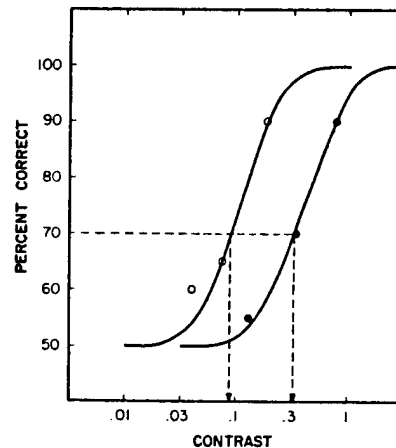

FIG. 4. Representative psychometric data. Observer's percentage correct is plotted as a function of the stimulus contrast presented to the infant. Open symbols represent data from the unmasked threshold condition and filled symbols represent data from the masked threshold condition. The solid lines represent the ogives that best fit the data points. The broken lines show how contrast thresholds were determined from our estimates of the 70% correct point.

One adult, with 20/20 vision uncorrected, was also tested using the same apparatus and the method of constant stimuli. He viewed the display binocularly with natural pupils. The adult initiated trials and responded himself. As with the infants, six contrast thresholds were measured, three without noise (one each at F, 2F, and 4F) and three with noise. The adult was tested in three experimental sessions. In one session, the spatial frequencies of F, 2F, and 4F were 3, 6, and 12 c/deg, and the center frequency of the noise was 3 c/deg. The viewing, distance was 180 cm in this session, so the display subtended 11 X 8°. In a second session, the frequencies of F, 2F, and 4F were 0.5, 1, and 2 c/deg and the center frequency of the noise was 0.5 c/deg. The viewing distance in this session was 40 cm, so those conditions were identical to the ones presented to the 12-week-olds. In a third session, the frequencies of F, 2F, and 4F were 0.3, 0.6, and 1.2 c/deg and the center frequency of the noise was 0.3 c/deg. Thus, those conditions were the same as the ones presented to the 6-week-olds.

Results

The adult's contrast sensitivity values (the reciprocal of contrast thresholds) for masked and unmasked conditions are shown in Fig. 5. For simplicity, we have presented the results of only two of the three experimental sessions; one in which F was 0.5 c/deg and one in which F was 3 c/deg. Notice that contrast sensitivity was always higher (contrast threshold was lower) for the unmasked (noise absent) condition than for the masked (noise present) condition. In other words, the narrowband noise masked the gratings. The most important aspect of these data, however, is the fact that the magnitude of masking depended strongly on the difference between the spatial frequencies of the grating and the noise. The

---

[3] Contrast was defined in the conventional way $-(L_{max} - L_{min})/(L_{max} + L_{min})$ where L_{max} refers to the maximum luminance of the grating and L_{min} refers to the minimum luminance. The contrast of every stimulus presented in these experiments was measured in situ using a Photoresearch Spot Meter.

masked/unmasked threshold difference was roughly tenfold when the grating was similar in frequency to the noise, but was only two- to threefold when the grating was two octaves (a factor of four) higher than the noise. These statements were true whether the center frequency of the noise was 0.3, 0.5, or 3 c/deg, so the differential masking effect was robust. The fact that masking was much greater when the frequencies of the noise and grating were similar than when they were dissimilar is evidence that at least two mechanisms, tuned to different spatial frequencies, were operating in each of the adult experiments.
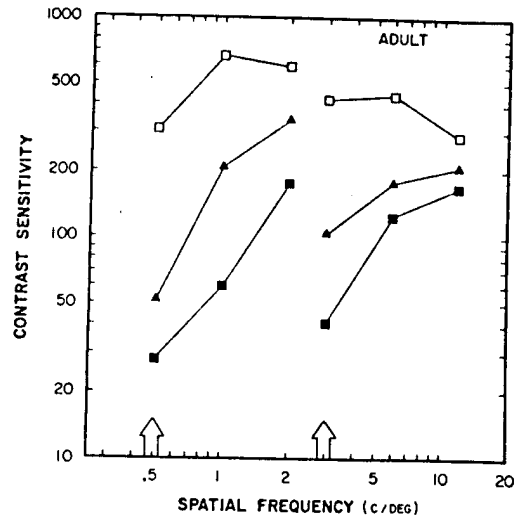

FIG. 5 Masked and unmasked thresholds from the adult subject. Contrast sensitivity, the reciprocal of contrast at threshold, is plotted as a function of spatial frequency. The open arrows indicate the center frequency of the noise masker in two different experiments. On the left are masked and unmasked thresholds when the center frequency of the noise was 0.5 c/deg. On the right are thresholds when the center frequency of the noise was 3 c/deg. Open symbols represent unmasked thresholds and filled symbols represent masked thresholds for two different levels of noise.

We used these data to estimate the specificity or bandwidth of the masking effect, and by inference, the selectivity of the underlying mechanisms. The conventional definition of bandwidth is the ratio of frequencies of the noise and grating that produces half of the maximum masking effect. Of course, the maximum masking effect occurred when the grating's spatial frequency was the same as the center frequency of the noise. Our estimates indicate that the magnitude of masking fell to one-half of this maximum when the grating and noise differed by about I octave. The precise estimates of bandwidth were 1.3 octaves when F was 0.3 c/deg, 1.1 octaves when F was 0.5 c/deg, and 1.3 octaves when F was 3 c/deg. These bandwidths are similar to those reported in other adult masking experiments (reviewed by Braddick et al., 1978) but are broader than those obtained using other techniques.[4]

Individual data from the 10 infants who completed the entire experiment are shown in Fig. 6. Group average results for these same infants are displayed in Fig. 7. Consider the ' 12-week results first. For every infant, masking was greatest when the spatial frequency of the grating was at the center frequency of the masking noise. Furthermore, there appeared to be no masking when the noise and grating differed by 2 octaves; stated another way, the contrast sensitivity values for a 2 c/deg grating were essentially the same for masked and unmasked conditions. One might argue that the similarity of masked and unmasked sensitivity values at 2 c/deg was due to a floor effect. This is not the case because each of these points were computed from psychometric data (see Fig. 4) that were not constrained by floor or ceiling effects.[5]

---

[4] The reasons for discrepancies between the bandwidth estimates from different psychophysical paradigms are beyond the scope of this paper. The interested reader should consult Braddick et al. (1978) or Graham (1980).

[5] The fact that the masked and unmasked thresholds at 2 c/deg were essentially the same is important. It shows that the 12-week-olds were responding well to the addition of the grating in the masked condition, even though pattern information was present on both sides of the screen. We should also point out that the difference in the size of the masking effect at 2 octaves between adults and 12-week-olds is probably not meaningful. Adults' contrast sensitivity is much higher than infants' so the noise masker should have been much further above threshold for the adult. Consequently, masking should have been greater at all spatial frequencies for the adult.
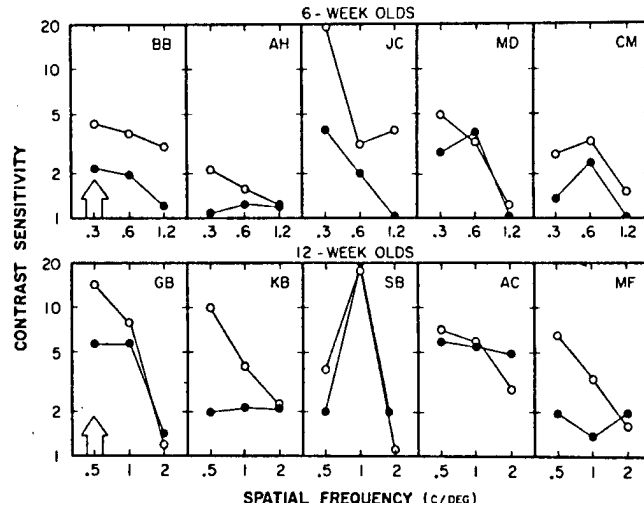
FIG. 6. Individual data for 6-week-olds and 12-week-olds. Again contrast sensitivity is plotted as a function of spatial frequency. The open arrows indicate the center frequency of the noise.
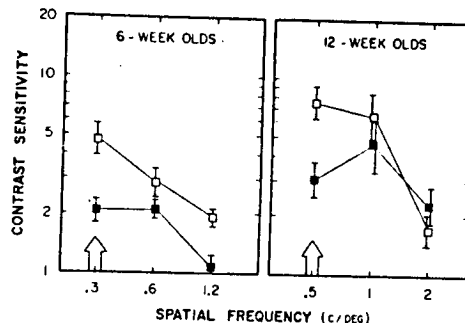

FIG. 7. Group average data for the 6-week-olds and 12-week-olds who completed the entire experiment. Axes and symbols are the same as in Fig. 6. Error bars represent *SEM* once overall differences in sensitivity are partialled out.

The 12-week results in Figs. 6 and 7 were confirmed by the between-subjects data. The center frequency of the noise was always 0.5 c/deg for these infants but different infants were tested with different grating frequencies. Six of them gave a masked and an unmasked threshold at 0.5 c/deg, another five at I c/deg, and another six at 2 c/deg. These data were quite similar to the within-subject results: masking was much larger when the frequencies of the noise and grating were similar than when they differed by 2 octaves.

Both sets of data are strong evidence that at least two mechanisms, tuned to different spatial frequencies, were operating at 12 weeks. We used the within-subject data to estimate the bandwidth of the masking effect. Surprisingly, it was 1.3 octaves, a value within measurement error of the adult value.

Now consider the within-subjects data of the 6-week-olds in Figs. 6 and 7. Two of these infants (AH and MD) exhibited a pattern of results similar to the 12-week-olds. Specifically, more masking was observed at 0.3 c/deg than at 0.6 or 1.2 c/deg. The other three infants (BB, JC, and CM) behaved differently: the magnitude of masking was roughly equal at all three spatial frequencies. The group average data on Fig. 7 were similar to the individual results from the latter three infants. We were concerned, however, that the pattern of results exhibited by AH and NID (the pattern consistent with the 12-week data) was more typical of 6-week-olds and that our group average data were unrepresentative. Therefore, we obtained partial data from a larger number of 6-weekolds. The center frequency of the noise was always 0.3 c/deg for these infants. Seven infants contributed a masked threshold and an unmasked threshold at 0.3 c/deg, one at 0.6 c/deg, and four at 1.2 c/deg. These between-subjects data also showed that masking was about equal in magnitude from 0.3 to 1.2 c/deg. This finding is inconsistent with the adult and 12-week results and implies that multiple, narrowband mechanisms are not generally present at 6 weeks.

The statistical reliability of these data was assessed in two ways. First, a 3 (Spatial Frequency) x 2 (Condition) x 2 (Age) ANOVA was conducted on the within-subjects data. Spatial Frequency and Condition were within-subjects factors and Age was a between-subjects factor. The ANOVA revealed significant main effects for Spatial Frequency ($F(2, 16) = 8.14, p < .005$), Condition ($F(1, 8) = 12.53, p < .01$), and Age ($F(1, 8) = 6.01, p < .05$), and significant interactions for Age X Condition ($F(2, 16) = 18.55, p < .0001$) and Age X Condition X Spatial Frequency ($F(2, 16) = 11.04, p < .001$).

A more detailed analysis was conducted by considering the ratios of masked to unmasked thresholds separately for each spatial frequency. This allowed us to combine the between- and within-subjects data and thereby achieve greater statistical power. A ratio of 1.0 indicates no masking and a ratio greater than 1.0 indicates masking. Consider the 12week results first. The masked/unmasked threshold ratio was significantly greater than 1.0 at 0.5 c/deg ($t(10) = 2.28, p < .025$, one tailed), marginally greater than 1.0 at 1 c/deg ($t(9) = 1.78, p < .055$, one tailed), and not different from 1.0 at 2 c/deg ($t(10) = -1.21$, n.s.). Thus, a significant masking effect occurred when the grating's frequency corresponded to the center frequency of the noise, but not when the grating was 2 octaves higher. Now consider the 6-week results. At this age, the masked/unmasked threshold ratio was significantly greater than 1.0 for all grating frequencies. For 0.3 c/deg, $1(11) = 2.32, p < .025$, one tailed. For 0.6 c/deg, $t(5) = 2.45, p < .05$, one tailed. For 1.2 c/deg, $t(8) = 1.94, p < .05$, one tailed.

In summary, the adult and 12-week data from Experiment 1 were quite similar: narrowband noise masked gratings whose spatial frequency was similar. to the noise Much more than it masked gratings that were 2 octaves higher. The bandwidths of the masking effects for the adult and the older infants were roughly the same. Thus, it appears that multiple spatial-frequency channels with adult-like specificity are present by 12 weeks of age.

The 6-week data were generally dissimilar from the 12-wcek and adult data. For most of these infants, narrowband noise caused similar amounts of masking whether the spatial frequency of the grating was similar to or higher than the center frequency of the noise. There are two plausible interpretations of this result. The most obvious interpretation is that multiple spatial-frequency channels with narrow bandwidths are not present at 6 weeks of age. We will refer to this as the single-channel interpretation. Unfortunately, an alternative exists. Perhaps multiple, narrowband channels exist at this age, but our experiment did not detect their presence. An explanation of how this might have occurred requires some discussion of the procedure. In the unmasked condition, the screen was unpatterned between trials and, upon initiation of a trial, a sine wave grating appeared on one side. Thus, the infant was given a choice of' either a patterned or an unpatterned field. In the masked condition, the screen was filled with dynamic noise between trials. When a trial commenced, the only change was the addition of a grating to one side. In this situation the infant was given a choice between two patterned fields: one with dynamic noise and one with dynamic noise plus a static grating- Perhaps the 6week-olds could often detect the grating embedded in the noise but did not fixate it because they simply chose to fixate the patterning on the other side of the screen. If this occurred, one would expect a uniform elevation of masked thresholds relative to unmasked thresholds and this is exactly what we observed. We will refer to this as the multiple-channel interpretation. This interpretation is, of course, not relevant for the 12week data because those infants clearly responded well to the addition of the grating when the noise was present (see the *4F* thresholds in Figs. 7 and 8). Thus, one unattractive feature of the multiple-channel interpretation of the 6-week data is that it requires the assumption that 6week-olds respond qualitatively differently to the onset of a stimulus than do 12-week-olds. We conducted a second experiment in order to evaluate these two interpretations of the 6-week findings.

EXPERIMENT 2

The second experiment employed a paradigm that predicted different outcomes for single-channel and multiple-channel processing, yet did not require the use of a noise masker. Therefore, if the multiple-channel interpretation of the 6-week data from Experiment 1 is correct, the results in Experiment 2 should be consistent with the predictions of a multiple-channel model. If, on the other hand, the single-channel interpretation is correct, the results in Experiment 2 should agree with single-channel predictions. We also tested 12-week-olds in this experiment in an attempt to replicate the 12-week results of Experiment 1.

The paradigm of Experiment 2 was used originally in an adult experiment by Graham and Nachmias (1971). In our adaptation of the paradigm, four contrast thresholds were measured. The gratings used in

these measurements are schematized in Fig. 8. They are (1) a sine wave grating of medium spatial frequency (T), (2) a sine wave grating three times higher in frequency *(3f)* (3) a composite grating in which *F* and *3F* are added together in "peaks-subtract" phase (that is, the gratings are added in such a way that their peaks and troughs do not superimpose), and *(4)* a composite grating in which *F* and *3F* are added together in "peaks-add" phase (so that their peaks and troughs superimpose). Thresholds for *F* alone and for *3F* alone are used to adjust the relative amplitudes of these two components when they are added to form the composite gratings; this equates the visibility of the two components. Examples of the two composite gratings are displayed in Fig. 9. Graham and Nachmias originally pointed out that single-channel models make different predictions about the relative contrast thresholds for the two composite gratings. The multiple-channel model proposes that the visual system uses separate mechanisms to process the *F* and *3F* components of the composites. Thus, this model predicts that the contrast threshold for the peaks-add composite should be identical to the threshold for the peaks-subtract composite. Stated another way, the contrast threshold for a peaks-add grating divided by the contrast threshold for the peaks-subtract should be 1.0. The single-channel model proposes that the F and *3F* components are processed by the same mechanism. This model predicts a lower contrast threshold for the peaks-add composite than for the peaks-subtract because adding components in peaks-add phase produces a grating with higher contrast than does adding components in peaks-subtract phase (see Fig. 8). The single-channel model actually predicts that the contrast threshold for peaks-add divided by the contrast threshold for peaks-subtract should be 0.76 (Graham, 1980, discusses these predictions and potential complicating factors in more detail). Graham and Nachmias reported ratios very close to 1.0 in their adult experiments, so adults' thresholds were consistent with the multiple-channel model's predictions.

Methods

Subjects. Six-week and 12-week infants were recruited by letter and phone. This experiment was quite demanding in that it required (for reasons stated below) that four thresholds be obtained from each infant in only two experimental sessions. Six 6-week-olds and five 12-weekolds yielded the requisite number of thresholds. The longest time between the first and second session was 9 days, and the average was 4 days. Ten 6-week-old and twelve 12-week-old infants failed to complete all four threshold measurements. The high attrition rate was caused by our strict requirement that two thresholds be completed in Session 1 and two more in Session 2.

Apparatus and stimuli. The stimuli were generated on the Hewlett-Packard 1317A CRT. The viewing distance was 35 cm. Space-average luminance was the same as in Experiment 1. The two component gratings – *F* and 3F – were 0.3 and 0.9 c/deg for 6-week-olds and 0.5 and 1.5 c/deg for 12-week-olds. As in Experiment 1, these values are chosen so as to place *F* at the peak of the CSF for the appropriate age group. The two composite gratings – peaks-add and peaks-subtract – were composed of *F* and 3F added in either peaks-add or peaks-subtract phase. These gratings are schematized in Fig. 8 and displayed in Fig. 9.
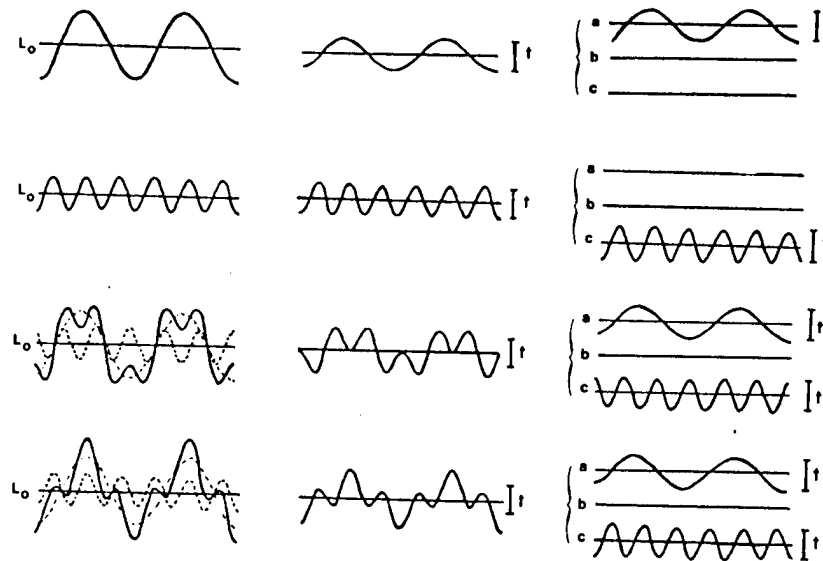
FIG. 8. A schematic of the stimuli used in Experiment 2 and the predictions of multiple and single-channel models. Four contrast thresholds were measured in Experiment 2, one for each of the gratings shown on the left: (1) a threshold for a sine wave grating of medium spatial frequency (F); (2) a threshold for a sine wave grating three times higher in frequency (3P); (3) a threshold for a composite grating in which *F* and *3F* were added together in a "peaks-subtract" phase; and (4) a threshold for a composite grating in which F and V were added in "peaks-add" phase. The middle and rightmost columns illustrate the predictions of a single-channel and multiple-channel model, respectively. Consider the single-channel predictions first. Since multiple channels do not exist according to this view, the *F* and 3F components of the composite gratings are assumed to be processed by the same channel. The middle column shows that the peaks-add composite actually has more contrast overall than the peaks-subtract composite. For this reason, the single-channel view holds that the peaks-add composite should be more detectable than the peaks-subtract. Now consider the multiple-channel predictions. According to this view, the *F* and *3F* components of the composite gratings are processed by different mechanisms. Consequently, the way in which they are added together should have no effect on their detectability. Reproduced by permission of the publisher, from Graham and Nachmias (1971).

Procedure. Contrast thresholds were again measured using the forced choice preferential looking procedure. During testing, parents held their infant in front of the CRT screen in a dark room. The screen was uniformly illuminated between trials. The observer was positioned behind the screen, so he or she could not see the stimuli. The observer attracted the infant's fixation to midline with a toy and initiated a trial once central fixation was achieved. A grating then appeared on either the left or right half of the screen. The observer made a forced choice judgment of the grating's location based on the infant's behavior. Trial-by-trial feedback was provided.
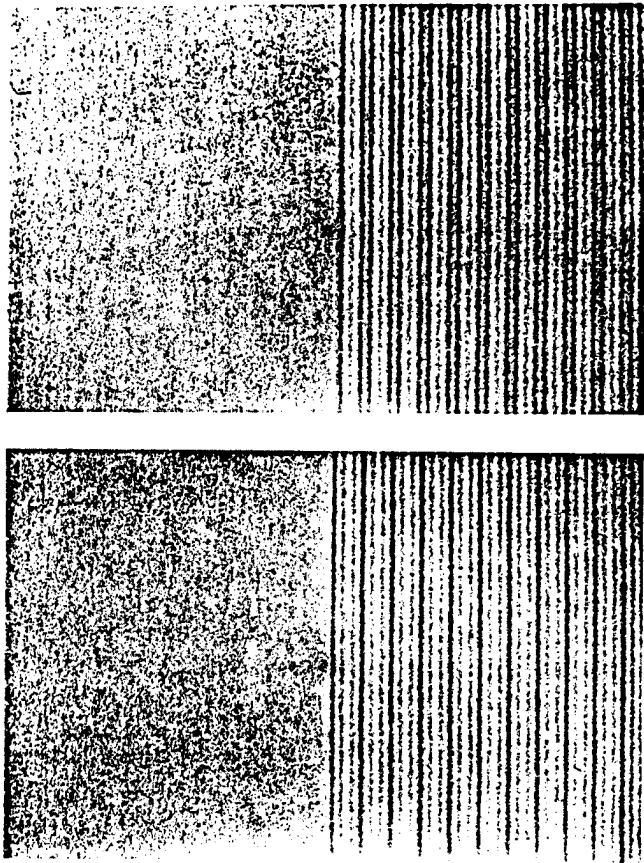
FIG. 9. Photographs of the peaks-subtract and peaks-add composite gratings used in Experiment 2.

As mentioned above, the experiment had to be completed in two 45-min sessions because it was very important to obtain accurate estimates of the F and 3F thresholds relative to one another as well as the peaks-add and peaks-subtract thresholds relative to one another. Therefore, we measured contrast thresholds for *F* alone and for *3F* alone in an interleaved fashion in the first session. Those data were then used to adjust the relative contrasts of the two components in the composite gratings used in the second session. In that session, thresholds for the peaks-add and the peaks-subtract composites were again measured in an interleaved fashion. Because the threshold measurements were interleaved, any fluctuations in behavioral state, or any other variable that might have affected performance, were equally distributed across the two measurements. Contrast was varied from trial to trial in both sessions according to ,ı two-down/one-up staircase procedure (Wetherill & . Levitt, 1965). Every time two trials in a row were correct contrast was reduced by 4 (M. Every time an incorrect response was made, contrast was increased by 4 dB. The staircase continued until the direction of contrast change had reversed 10 times. The average of the contrasts at the last 8 reversal points was taken as the estimate of threshold. Wetherill and Levitt have shown that this algorithm estimates the contrast associated with 71% correct performance.

We also tested two adults, one with 20/20 vision uncorrected and one with 20/20 vision corrected. The same apparatus and procedure were used except that the adults initiated trials and responded themselves. Three different experiments were conducted for the adults. In one, F was 2.5 and 3F was 7.5 c/deg in order to place F near the peak of the adult CSF. The viewing distance was 157 cm in this experiment. In another experiment, F was 0.5 and 3F was 1.5 c/deg. Viewing distance was 35 cm, so these stimulus conditions were identical to those experienced by the 12-week-old infants. In the final experiment, F was 0.3 and 3F was 0.9 c/deg, conditions identical to those presented to the 6-weekolds. We used interleaved, 18-reversal staircases to obtain thresholds for F alone and 3F alone first and then used those data to adjust the relative contrasts of the components in the peaks-add and peaks-subtract composite gratings. Thresholds for the composites were also measured in interleaved fashion.

Results

The important result in this experiment is the ratio of peaks-add and peaks-subtract thresholds. Recall that the multiple-channel model predicts a ratio of 1.0 and the single-channel model a ratio of 0.76. The average ratios for 6-week-olds, 12-week-olds, and adults are displayed in Fig. 10.

Consider the adult ratios first. Adults were tested with three different combinations of F and 3F. Notice that the ratios were generally closer to the multiple-channel prediction than to the single-channel prediction. The condition in which F was 2.5 c/deg is most similar to the conditions tested by Graham and Nachmias (1971), so our data at that frequency confirm their original observations. Graham and Nachmias did not present spatial frequencies below 0.9 c/deg, so our data at 0.3 and 0.5 c/deg extend the observation of multiple-channel processing with this paradigm to very low spatial frequencies.

The 6-week-olds were of primary interest in Experiment 2. The average peaks-add/peaks-subtract threshold ratio at 6 weeks was 0.71, a value close to the single-channel prediction of 0.76. Statistical tests supported the conclusion that the 6-week ratios were similar to the single-channel prediction (45) 1.09, n.s.) and were less than the multiple-channel prediction (t(5) 2.78, p < .025, one tailed). Thus, the 6-week data of Experiment 2 support the single-channel interpretation of the 6-weck findings from Experiment 1. in other words, Experiments 1 and 2 provided data at 6 weeks that were consistent with single-channel and not multiple-channel processing.
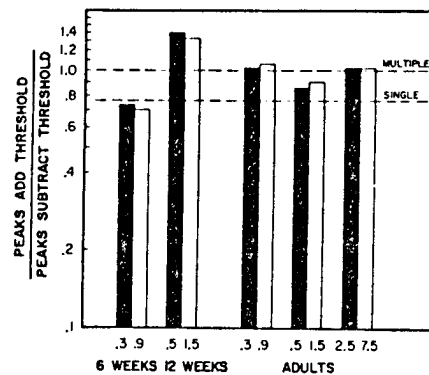

FIG. 10. Predictions and results of Experiment 2. The ratio of the contrast threshold for peaks-add divided by the contrast threshold for peaks-subtract is plotted for different age groups. Recall that the multiple-channel model predicts a ratio of 1.0 and the single-channel model predicts a ratio of 0.76. These are indicated by the broken lines. Tile histograms represent the average ratios for each age group. The open and closed bars represent two different ways of calculating the ratio. The open bars were calculated by dividing the contrast of the *3F* component when the peaks-add composite was at threshold by the contrast of the *3F* component when the peaks-subtract composite was at threshold. The closed bars were calculated using the F component.

The average threshold ratio among the older infants was 1.36, a value that was actually higher than the multiple-channel prediction. Inspection of the individual subject data revealed that one of these infants exhibited an unusually high ratio. The average ratio without this subject was 1.07, a value closer to the multiple-channel prediction. Statistical tests, with the anomalous subject included, support the conclusions that the 12-week data were similar to the multiple-channel prediction (f(4) = 1.09, p = n.s.) and were greater than the single-channel prediction (t(4) = 2.64, p < .05, one tailed). Furthermore, the 12-week ratio was significantly greater than the 6-week one (t(9) = 1.95, p < .05, one tailed).[6] The 12-week results from Experiment 2 were thus consistent with those from Experiment 1; once again, there was fairly clear evidence for multiple, narrowband channels at this age.

The paradigm used in Experiment 2 does not allow one to make a quantitative estimate of bandwidth. All that can be said is-that channels in 12-w-eek-olds and adults are narrow enough for F and 3F to not

---

[6] We also conducted statistical tests on the 12-week data with the anomalous subject excluded. In this case, the 12-week data were again similar to the multiple-channel prediction (0) = 0.40, n.s.) and were marginally greater than the 6-week data (t(8) = 1.82, p < .053, one tailed). However, the 12-week data with the anomalous subject excluded were not significantly greater than the single-channel prediction (1(3) = 1.52, n.s.). All of file 12-week-olds yielded ratios greater than the single-channel prediction, but when one of the five subjects was excluded, the statistical power was too low to reveal a significant difference. Thus. we can say with reasonable confidence that the 12-week data differed from the 6-weck data in the direction predicted by a shift front single- to multiple-channel processing whether the anomalous subject is included or not.

interact significantly. 3F is 1.6 octaves higher than F, so the 12-week bandwidths implied by Experiment 2 are 1.6 octaves or less.

DISCUSSION

These data from two different experimental paradigms imply that multiple spatial-frequency channels with narrow tuning develop between 6 and 12 weeks of age. Such channels do not appear to be operating at 6 weeks for spatial frequencies from 0.3 to 1.2 c/deg, a range that encompasses the peak of the CSF and frequencies 2 octaves higher. They appear to be operating at 12 weeks for spatial frequencies ranging from 0.5 to 2 c/deg, a range spanning the CSF peak at that age and frequencies 2 octaves higher. (We should emphasize the fact that multiple *broadband* mechanisms may be present at 6 weeks. Our experiments only rule out the presence of multiple *narrowband* mechanisms.)

Our 12-week results are consistent with the 14-week results reported by Fiorentini et al. (1983). Our findings with 6-week-olds, however, are inconsistent with their 6-week results: they found evidence of spatial-frequency-specific masking at 6 weeks and we did not. As mentioned earlier, only one of their 6-week-olds and one of their 14-week-olds contributed data relevant to this issue. We too observed some 6-week olds (AH and MD in Experiment 1) who exhibited spatial-frequency-specific masking, but our data as a whole suggest that this is not typical for that age. Thus, we believe our infant observations are better reflections of the development of spatial-frequency channels than are those of Fiorentini et al.

One might argue that the difference between the 6- and 12-week findings was the result of differences in the spatial frequencies used: perhaps multiple channels are simply never demonstrable at very low frequencies like those presented to the 6-week-olds, so the developmental shift we observed was caused by the change in frequencies presented. We do not believe that this is a valid argument for two reasons. First, the spatial frequencies were chosen to cover the span of most useful vision at each age tested; thus, our conclusions concern the mechanisms that are operating at spatial frequencies to which 6 and 12-week-olds are most sensitive. Second, the adults were tested with the same spatial frequencies presented to 6- and 12-week-olds and their data were always consistent with the multiple-channel view. Thus, it is not the case that multiple, narrowband mechanisms cannot be demonstrated at very low spatial frequencies.

Finally, one other plausible alternative explanation exists. Recall that the multiple-channel model holds that there are different mechanisms, tuned to different spatial frequencies, that process images on the same part of the retina. So, by this definition, a visual system with mechanisms tuned to higher frequencies near the fovea, medium frequencies in the parafovca, and low frequencies in the periphery is not a multiple-channel system. Our experiments do not allow us to reject the possibility that 12-week-olds possess this kind of visual system. To see why, consider our experimental setup. The stimulus field was quite large (48 x 37%), and, since the test gratings filled half the screen, they were quite large, too (24 x 370). For this reason, we cannot be certain what part of the retina the 12-week-olds were using to detect the stimulus from trial to trial. If they used high-frequency, foveal mechanisms to detect high frequency gratings and low-frequency, peripheral mechanisms to detect low frequencies, results very similar to those in Figs. 7 and 10 could have been obtained. Thus, strictly speaking, we have only demonstrated that multiple, narrowband mechanisms exist at 12 weeks; we have not shown that multiple mechanisms exist for each retinal region as is implied by the pure multiple-channel model. In order to differentiate these two types of multiple-channel visual systems, an experiment with spatially limited targets is required.

Our findings have several implications for theories of visual development. We will discuss three. The first concerns the development of neural structures subserving pattern vision. The second concerns the evaluation of theories of perceptual development. Finally, the third implication involves predictions of perceptual deficits that should accompany the absence of narrowband channels.

As we mentioned earlier, neurophysiological investigations have shown that narrowband mechanisms are not observed below the level of the visual cortex. Thus, retinal ganglion and lateral geniculate cells are generally responsive to a fairly broad range of spatial frequencies (Derrington & Fuchs, 1979; Enroth-Cugell & Robson, 1966). This conclusion has been confirmed indirectly by psychophysical studies of human adults. Blakemore, Nachmias, and Sutton (1970) have shown that the frequency-specific aftereffects associated with adaptation to a high-contrast grating transfer interocularly and are orientation specific. Since significant binocular interaction and orientation selectivity do not occur below the Visual cortex, these experiments must be revealing cortical (or higher) mechanisms.

Since the visual cortex seems to be the first site at which narrow band mechanisms are observed, the developmental shift we observed probably reflects cortical development. There is some indirect evidence

that bolsters this view. First, several pieces of evidence imply that the human Visual cortex undergoes marked development during the first 6 months of life. Conel (1939-1963) reported that individual neurons change dramatically after birth. For example, the number and arborization of dendrites increase greatly from birth to 6 months. It is also known that myelin, the sheath that insulates axons and dendrites, is still being formed in the visual cortex for months after birth (Yakovlev & LeCours, 1967). Second, electrophysiological studies of kittens have found that cortical neurons have poor contrast sensitivity and very broad bandwidths before 4 weeks (Derrington & Fuchs, 1981); it is only by 5-7 weeks that adult-like bandwidths are observed. (Unfortunately, there are currently no primate data on the development of frequency selectivity among cortical neurons.) For these reasons, our data probably reflect the development of cortical mechanisms. This is not to say that cortical neurons are inoperative at 6 Weeks -nor that they are completely adult-like at 12 weeks. The most likely situation is that the developmental change in tuning of spatial-frequency channels reflects changes in the selectivity of cortical neurons to different bands of spatial frequency.

Our findings also have implications for some theories of perceptual development. Two similar theories – Hebb's (1949) and Russian motor copy theory (Zaporozhets, 1965) – make fairly specific claims that feature analyzers are undifferentiated at birth and develop with visual experience. Moreover, Bronson (1974) and Salapatek (1975) imply that feature analyzers emerge at roughly 2 months of age. Our data are at least consistent with these theories in that they show that one aspect of feature analysis – spatial-frequency selectivity – develops postnatally. Further experimentation will be needed to determine if other important dimensions of feature analysis, such as orientation selectivity, also develop postnatally. It is unclear how our data bear on Gibson's (1969) differentiation theory of perceptual development; to our knowledge, she did not make any specific claims concerning the development of low-order feature analyzers like spatial frequency and orientation channels.

Finally, one should ask what the perceptual consequences of changes in spatial-frequency selectivity are. Specifically, what perceptual abilities should 12-week-olds and adults have that 6-week-olds do not? The answer to this question depends entirely on one's view of the perceptual function served by spatial-frequency channels, and, unfortunately, there is no consensus on this issue. Proponents of the view of Pollen ct al. (1971) (who claim that channels provide something like a Fourier representation of visual stimuli and that pattern recognition is accomplished in the Fourier domain) should predict that 6-week-olds would exhibit significant deficits in the ability to recognize suprathreshold stimuli relative to 12week-olds. On the other hand, proponents of the view of Marr and his colleagues, would predict that, among other things, 6-week-olds should have difficulty distinguishing intensity gradients caused by object boundaries or discontinuities from gradients caused by shadows and highlights. Finally, the view of Georgeson and Sullivan (1975) would lead one to predict that contrast constancy should not be observed at 6 weeks. This last prediction is, in fact, considered in the accompanying paper (Stephens & Banks, 1985).

This relationship between the theory of channel function and predictions of perceptual capabilities leads to an important point. The developmental shift we have observed between 6 and 12 weeks of age provides a natural experiment that may ultimately be useful in evaluating theories of the function of channels. In other words, this may provide a situation in which infant data facilitate the evaluation of theories that concern adult phenomena. If a particular theory held that channels were necessary for it certain perceptual capability, then that capability should be deficient at 6, but not 12, weeks of age. If the capability was actually similar at 6 and 12 weeks, one might be able to reject the theory.

No matter what the specific role of spatial-frequency channels. is, the developmental shift we observed from broadband to narrowband processing has important implications. For one thing, the shift implies that the central nervous system's representation of any pattern would change from 6 to 12 weeks of age. Consequently, algorithms that 12-week-olds might use to recognize a pattern may differ from those used by 6-weekolds.

REFERENCES

Albrecht, D. G., De Valois, R. L., & Thorell, L. G. (1980). Visual cortical neurons: Are bars or gratings the optimal stimuli? *Science (Washington, D.C.), 207,* 88-90.

Atkinson, J., Braddick, 0., & Moar, K. (1977). Development of contrast sensitivity over the first 3 months of life. Vision *Research, 17, 1037-1044.*

Banks, M. S. (1980). The development of visual accommodation during early infancy. *Child Development, 51, 646-666.*

Banks, M. S. *(1982).* The development of spatial and temporal contrast sensitivity. *Current Eye Research, 2, 191-198.*

Banks, M. S., with Salapatek, P. *(1983).* Infant visual perception. In P. Mussen (Ed.). *Handbook of child psychology (Vol. 2).* New York: Wiley.

Banks, M. S., & Salapatek, P. *(1978).* Acuity and contrast sensitivity in 1-, 2-, and 3-month-old human infants. *Investigative Ophthalmology and Visual Science, 17, 361-365.*

Banks, M. S., & Salapatek, P. *(1981).* Infant pattern vision: A new approach based on the contrast sensitivity function. *Journal of Experimental Child Psychology, 31, 145.*

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.*

Blakemore, C., Nachmias, J., & Sutton, P. *(1970).* The perceived frequency shift: Evidence for frequency selective neurones in the human brain. *Journal of Physiology, 210, 727750.*

Braddick, 0., Campbell, *F. W., & Atkinson,* J. *(1978).* Channels in vision: Basic aspects. In R. Held, It. W. Leibowitz, & H.-L. Teuber (Eds.), *Handbook of sensory physiology (Vol. 8).* New York: Springer-Verlag.

Bronson, G. W. *(1974).* The postnatal growth of visual capacity. *Child Development. 45, 873-890.*

Campbell, F. W., Cooper, G. *F.,* & Enroth-Cugell, C. (1969). The spatial selectivity of the visual cells of the cat. *Journal of physiology. 203, 223-235.*

Campbell, F. W., & Green. D. G. *(1965).* Optical and retinal factors affecting visual resolution. *Journal of Physiology, 181, 576-593.*

Campbell, F. W., & Robson, J. 6 (1968). Application of Fourier analysis to the visibility of gratings. *Journal of Physiology, 197, 551-566.*

Conel, J. L. (1939-1963). *The postnatal development of the human cerebral cortex (Vols.* 1-7). Cambridge: Harvard Univ. Press.

Cornsweet, T. N. (1970). *Visual perception.* New York: Academic Press.

Derrington, A. M., & Fuchs, A. F. (1979). Spatial and temporal properties of X and Y cells in the cat lateral geniculate nucleus. *Journal of Physiology.* 293, 347-364.

Derrington, A. M., & Fuchs, A. F. (1981). The development of spatial-frequency selectivity in kitten striate cortex. *Journal* of *Physiology,* 316, 1-10.

Duda, P., & Hart, P. (1973). *Introduction to statistical pattern recognition.* New York: Wiley.

Enroth-Cugell, C., & Robson, J. G. (1966). The contrast sensitivity of retinal ganglion cells of the cat. *Journal of Physiology,* 187, 517-522.

Finney, D. J. (1971). *Probit analysis.* Cambridge: The Univ. Press.

Fiorentini, A., Pirchio, M., & Spinelli, D. (1983). Electrophysiological evidence for spatial frequency selective mechanisms in adults and infants. *Vision Research,* 23, 119-127.

Georgeson, X1. A., & Sullivan, G. D. (1975). Contrast constancy: Deblurring in human vision by spatial frequency channels. *Journal of Physiology,* 252, 627-656.

Gibson, E. J. (1969). *Principles of perceptual learning, and development.* New York: Appleton-Century-Crofts.

Ginsburg, A. P. (1978). *Visual information processing based on spatial-fillers constrained by biological data.* Doctoral dissertation, University of Cambridge.

Graham, N. (1980). Spatial-frequency channels in human vision: Detecting edges without edge detectors. In C. S. Harris (Ed.), *Visual coding and adaptability.* Hillsdale, NJ: Erlbaum.

Graham, N., & Nachmias, J. (1971). Detection of grating patterns containing two spatial frequencies: A comparison of single-channel and multiple-channel models. *Vision Research, 11,* 251-259.

Haynes, H., White, B. L., & field, R. (1965). Visual accommodation in human infants. *Science (Washington, D.C.), 148,* 528-530.

Hebb, D. 0. (1949). *Pie organization* of *behavior.* New York: Wiley.

Hubel, D. H., & Wiesel, T. N. (1962). Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. *Journal* of *Physiology,* 160, 106-154.

Hubel, 1). H., & Wiesel, T. N. (1968). Receptive fields and functional architecture of monkey striate cortex. *Journal* of *Physiology,* 195, 215-243.

Marr, D. (1982). *Vision: A computational investigation into the human representation and processing* of *visual information.* San Francisco: Freeman.

Mayer, D. L., & Dobson, V. (1980). Assessment of vision in young children. *Investigative Ophthalmology and Visual Science,* 19, 566-570.

Minsky, M., & Papert, S. (1069). *Perceptrons: An introduction to computational geometry.* Cambridge, MIT Press.

Movshon, J. A., Thompson, I. D., & Tolhurst, D. J. (1978). Spatial and temporal contrast sensitivity of neurones in areas 17 and 18 of the cat's visual cortex. *Journal of Physiology,* 283, 101-120.

Movshon, J. A., & Van Sluyters, R. C. (1981). Visual neural development. *Annual Review* of *Psychology,* 32, 477-522.

Pollen, D., Lee, J. R., & Taylor, J. H. (1971). How does the striate cortex begin the reconstruction of the visual world. *Science (Washington, D.C.),* 173, 74-77.

Robson, J. G. (1975). Receptive fields: Neural representation of the spatial and intensity attributes of the visual image. In E. C. Carterette & M. P. Friedman (Eds.), *Handbook of perception* (Vol. 5). New York: Academic Press.

Salapatek, P. (1975). Pattern perception in early infancy. In L. B. Cohen & P. Salapatek (Eds.). *Infant perception: From sensation to cognition. Basic Visual Processes. (Vol.* 1). New York: Academic Press.

Schwartz, E. (1980). Computational anatomy and functional architecture of striate cortex: A spatial mapping approach to perceptual coding. *Vision Research,* 20, 645-669.

Selfridge. 0. (1959). Pandemonium: A paradigm for learning. In D. V. Blake & A. M. Uttley (Eds.). *Symposium on the mechanization of thought processes.* London: H. M. Stationary Office.

Stephens. It. R.. & Banks, M. S. (1985). The development of contrast constancy. *Journal of Experimental Child Psychology, 40,* 528-547.

Stromeyer. C. F.. & Julesz, B. (1972). Spatial-frequency masking in vision: Critical bands and spread of masking. *Journal of the Optical Society. of America, 62.*

Teller. 1). Y. (1979). The forced-choice preferential looking procedure: A psychophysical technique for use with human infants. *Infant Behavior and Development, 2,* 135-153.

Uhr, L.. Vossler, C., & Uleman, J. (1962). Pattern recognition over distortions, by human still subjects and by a computer simulation of a model for human form perception. *Journal of Experimental Psychology, 63,* 227-234.

Welherill. G. B., & Levitt, ff. (1965). Sequential estimation of points on a psychometric function. *British Journal* of *Mathematical and Statistical Psychology.* 18, 1-10.

Yakovlev, 1). 1., & LeCours, A. (1967). The myelogenetic cycles of regional maturation of' the brain. In A. Minkowski (Ed.), *Regional development of the brain in early life*. Philadelphia: Davis.

Zaporozhets, A. V. (1965). The development of perception in the preschool child. In P. H. Mussen (Ed.), *European research in cognitive development.* Monographs of the Society for Research in Child Psychology, *30,* 82-101.