



Infant Contrast Detectors are Selective for Direction of Motion

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In order to investigate the presence of directionally selective mechanisms in 3-month-old infants, we employed a summation-near-threshold paradigm previously developed for studies of adult vision (Levinson & Sekuler, 1975 *Journal of Physiology (London)*, 250, 347–366); Watson, Thompson, Murphy & Nachmias, 1980 *Vision Research*, 20, 341–347). The degree of contrast summation occurring between two sinusoidal gratings moving in opposite directions was determined by comparing the contrast threshold for a compound stimulus (a counterphase-reversing grating) with the contrast threshold for one of its components (a single moving grating). Using the forced-choice preferential looking (FPL) technique, contrast thresholds were obtained for both counterphase and single moving gratings within individual infant subjects. Data were collected at several speeds, ranging from 2.8 to 66.8°/sec (temporal frequency range: 0.7–16.7 Hz). At slow speeds, infants' thresholds were approximately equal for counterphase and moving gratings, indicating that non-directional mechanisms were responsible for detection. At an intermediate speed (22.3°/sec), thresholds were nearly twice as high for counterphase gratings as for single moving gratings, indicating the existence of directionally selective mechanisms at detection threshold for this speed. For faster speeds, relative thresholds for the two types of stimuli fell between the two extremes; a model incorporating probability summation between directionally selective mechanisms was sufficient to account for the data. These results demonstrate that, at speeds greater than or equal to 22.3°/sec (t.f. = 5.6 Hz), 3-month-old infants possess directionally selective mechanisms at threshold.

Visual development Motion Directional selectivity Speed Temporal contrast sensitivity function
 Probability summation

INTRODUCTION

The ability to perceive visual motion is one of the most fundamental and essential facets of vision. While much has been learned over the years about motion processing in adults, little is known about its development in infants. Several studies have demonstrated that infants can discriminate a moving from a static pattern, by virtue of the fact that they prefer to stare at the former (e.g. Volkman & Dobson, 1976; Kaufmann, Stucki & Kaufmann-Hayoz, 1985; Freedland & Dannemiller, 1987; Aslin, Shea & Gallipeau, 1988; Dannemiller & Freedland, 1989; Aslin & Shea, 1990; Dannemiller & Freedland, 1993). With rare exception, however, few studies have directly addressed whether infants can encode *direction of motion*. The best evidence that infants possess some mechanism for encoding direction of

motion is that they exhibit optokinetic nystagmus (OKN) and other directionally appropriate eye movements in response to moving stimuli (e.g. Dayton, Jones, Aiu, Rawson, Steele & Rose, 1964; Kremenitzer, Vaughan, Kutzberg & Dowling, 1979; Atkinson & Braddick, 1981; Hainline, Lemerise, Abramov & Turkel, 1984; Roy, Lachapelle & Leporé, 1989; Shea & Aslin, 1990). In addition to this line of evidence, more recent experiments have demonstrated that infants can detect "relative" (Dannemiller & Freedland, 1991; Wattam-Bell, 1992, 1993) or "shearing" (Bertenthal & Bradbury, 1992) motion, providing further proof that infants can discriminate direction of motion.

Despite the fact that infants appear to differentiate direction of motion, the existence of *directionally selective mechanisms*—i.e. mechanisms that respond to motion in one direction but not another—has not yet been firmly established for infants. In adults, several psychophysical paradigms have been described that provide conclusive evidence for the existence of multiple detectors that are directionally selective (see Graham, 1989 for a review). One of these paradigms, *summation-near-threshold*, has been well established in the adult domain, and is particularly feasible for infant psychophysical experiments. These summation experiments in-

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volve determining the degree of *contrast summation* occurring at detection threshold between two gratings that move in opposite directions (Levinson & Sekuler, 1975; Watson *et al.*, 1980).

Summation experiments take advantage of the fact that a counterphase-reversing grating of contrast C is physically identical to the sum of two gratings of contrast $C/2$ that move in opposite directions, as described in the following equation:

$$C \cos 2\pi f_x X \cos 2\pi f_t T = C/2 \cos 2\pi (f_x X + f_t T) + C/2 \cos 2\pi (f_x X - f_t T),$$

where C is contrast, f_x and f_t are spatial and temporal frequencies, X is distance and T is time.

If the two oppositely-moving gratings provide input to the same detector, they are expected to sum their individual contrasts. If, on the other hand, the two oppositely-moving gratings provide input to independent detectors tuned for direction of motion (i.e. directionally selective mechanisms), no summation is expected to occur. This theoretical argument is schematized in Fig. 1. For example, suppose that a directionally selective mechanism requires a contrast C_D in order

to reach detection threshold (Fig. 1, left panel). An individual directionally selective detector will respond when a single grating of contrast C_D moves in its preferred direction. When presented with a counterphase grating, however, a directionally selective detector will require a contrast of $2C_D$, since only the component moving in its preferred direction (i.e. of contrast C_D) can elicit a response. By contrast, a non-directionally selective detector requiring a contrast of C_N to reach threshold (Fig. 1, right panel) will respond if either a single moving grating of contrast C_N , or a counterphase grating of contrast C_N , is presented. It is important to point out, however, that while *both* directional and non-directional mechanisms might exist, only the most sensitive of the two, i.e. the one with the lowest contrast threshold, will be activated in a psychophysical threshold experiment.

In sum, if the mechanism responsible for detection, i.e. the most sensitive mechanism, is directionally selective, no summation should occur and the psychophysical contrast threshold for counterphase gratings should be twice that for single moving gratings. Conversely, if the most sensitive mechanism is not directionally selective, the contrasts of the component gratings should sum

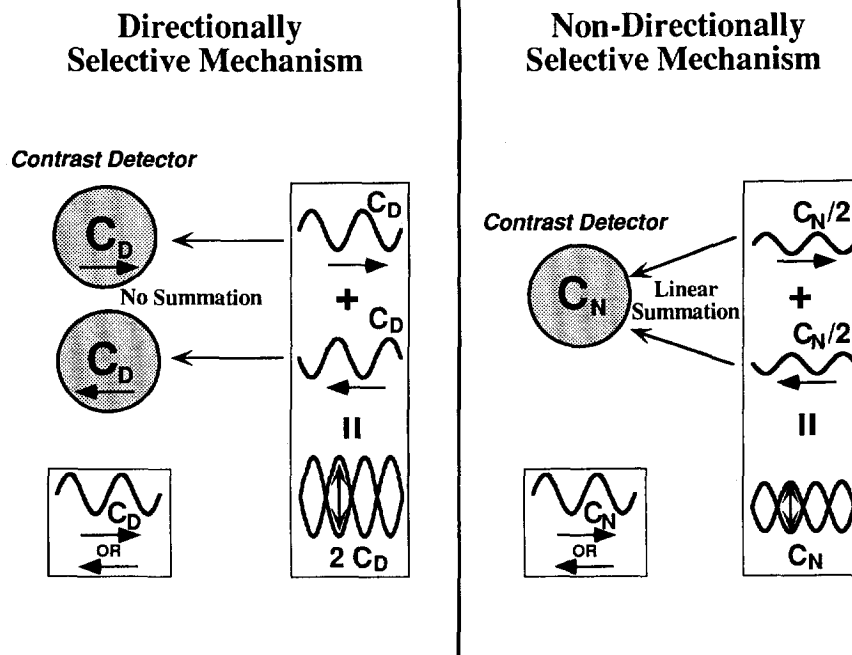


FIGURE 1. Schematic depiction of directionally selective and non-directionally selective contrast detectors presented with either single moving or counterphase-reversing gratings. On the left are shown two directionally selective contrast detectors, one which responds exclusively to rightward motion, and the other exclusively to leftward motion. Each detector requires a contrast of C_D in order to reach a threshold response. Thus, if either a leftward or a rightward moving grating is presented in *isolation*, it would need to be of contrast C_D in order for one of the two detectors to respond. However, if a counterphase grating is presented, however, a contrast of $2C_D$ would be required, since an individual detector will respond only when the component of the counterphase grating moving in its preferred direction is of contrast C_D . If probability summation occurs between the two detectors, a slight advantage will exist for the counterphase grating, which will reduce the required contrast somewhat below $2C_D$ (see text for details). On the right, a non-directionally selective contrast detector requires a contrast of C_N in order to reach a threshold response. If either a leftward or a rightward moving grating is presented in *isolation*, it would need to be of contrast C_N in order for this detector to respond. However, if a leftward *and* a rightward moving grating are presented simultaneously, which is equivalent to a counterphase grating, each component grating would only need to be of contrast $C_N/2$, if the mechanism sums the contrasts linearly. For this mechanism, therefore, a counterphase grating of contrast C_N would also be sufficient. In sum, whereas a directional mechanism requires twice as much contrast in a counterphase grating compared to a single moving grating, a non-directional mechanism should be equally sensitive to both types of stimuli.

together and the detection threshold for counterphase and moving gratings will be the same.

Following this logic, Levinson and Sekuler (1975) tested adult subjects and found that the contrast threshold for a counterphase grating was twice that for a moving grating, a result which has since been corroborated by other investigators (Stromeyer, Madsen, Klein & Zeevi, 1978; Kelly, 1979; Murray, MacCana & Kulikowski, 1983). Thus these results demonstrate a lack of summation for gratings moving in opposite directions, providing strong evidence for the existence of directionally selective mechanisms at threshold. Extending these original experiments, Watson *et al.* (1980) addressed the issue of *probability summation* between directionally selective mechanisms that are independently perturbed by noise. They argued that in the directionally selective case (i.e. Fig. 1, left panel), probability summation between the two independent detectors tuned for opposite directions of motion should reduce the contrast threshold for the counterphase grating below $2C_D$, by an amount that depends on the slope of the psychometric function. Performing nearly identical experiments to those of Levinson and Sekuler, Watson *et al.* replicated the finding of independent directionally selective mechanisms at threshold, provided probability summation was taken into account.

Watson *et al.* also varied the spatial and temporal frequency of their stimuli, and found more summation at low temporal and high spatial frequencies than at high temporal and low spatial frequencies. Since spatiotemporal frequency can be directly converted into speed values, these effects of spatial and temporal frequency suggested that directionally selective mechanisms exist at threshold for fast, but not slow, speeds. Based on cumulative results from several summation-near-threshold studies employing different combinations of spatial and temporal frequency (see Graham, 1989), it appears that stimuli moving faster than approximately $1^\circ/\text{sec}$ are detected by directionally selective mechanisms, while stimuli moving slower than this speed are detected by non-directionally selective mechanisms.

In infants, contrast thresholds have been obtained using moving gratings (e.g. Atkinson, Braddick & Braddick, 1974; Atkinson, Braddick & Moar, 1977a, b) and counterphase-reversing gratings (e.g. Lasky, 1980; Swanson & Birch, 1990; Hartmann & Banks, 1992), however, thresholds for both types of stimuli have not been assessed within an individual experiment or within an individual infant subject. In the present experiment, we used a summation-near-threshold paradigm to investigate the existence of directionally selective mechanisms in infants. A *within-subjects* design was employed, in which contrast thresholds for the detection of counterphase and single moving gratings were determined within individual infant subjects. To investigate whether the presence of directionally selective mechanisms depends on speed, as is the case for adults, infants were tested at five different speeds. Data obtained at different speeds had the added benefit of providing us with

temporal contrast sensitivity functions (tCSFs) for both moving and counterphase gratings.

For comparison, data were also collected from adult subjects. Results obtained from both our infant and adult groups were compared to predicted values based on probability summation, in order to determine the extent to which such effects could account for our findings.

METHODS

Subjects

Infants. A total of 48 infants took part in this study. All infants were born within 14 days of their due date. The average age on the first day of testing was 88.2 days (SD = 1.8 days). Infants were brought in for 3–5 days within a 1-week time period, and each daily session lasted approximately 45 min. Except for one, all infants had normal, uncomplicated births: one infant had a seizure at the time of birth, but quickly recovered from the trauma and was determined by a pediatrician to be developing normally. His data were therefore included in our analysis. Data from 45 infants contributed to the results presented here. Three infants failed to meet the minimum trials criterion ($N \geq 180$) due to fussiness and were therefore not included in the analysis.

Adults. Four adult subjects were tested under stimulus conditions nearly identical to those employed in our infant paradigm. The first author (KRD) and three naive viewers, aged 18–30, participated in these experiments. All had normal or corrected-to-normal vision.

Visual stimulation

Apparatus. Stimuli were generated on a high resolution RGB monitor (19" Barco CDCT 6451, 67 Hz, non-interlaced, 640×480 pixels), driven by a Mac II computer. The 8-bit video board in the computer allowed for 256 discrete levels of luminance. The mean chromaticity of the monitor was calibrated to equal energy white (C.I.E. chromaticity coordinates = 0.333, 0.333), and the voltage/luminance relationship was linearized independently for each of the three guns in the display (Cowan, 1983).

Adult apparatus. In order to produce the low luminance contrasts required to span adult contrast thresholds, adult subjects were tested using an auxiliary field in the following manner: a second monitor (No. 2), which displayed a homogeneous equal energy white field, was placed orthogonally to the main stimulus monitor (No. 1). A piece of glass (36×28 cm) was placed between the two monitors at a 45° diagonal, 41 cm from the center of each monitor. Direct viewing of monitor No. 2 through the glass allowed 90% transmittance of light from monitor No. 2 and 10% reflection of light from monitor No. 1. The average luminances on the two monitors (14 and 32 cd/m^2 for monitors No. 1 and No. 2, respectively) were set such that the mean luminance of the combined display was 30 cd/m^2 . Sinusoidal gratings

presented on monitor No. 1 were thus reduced in contrast by 95%.

Stimuli. All stimuli were horizontally-oriented, luminance-defined (black/white) sinusoidal gratings. Spatial frequency was set at 0.25 cyc/deg, which is near the peak of the contrast sensitivity function for infants 3 months of age (Atkinson *et al.*, 1977a, b; Banks & Salapatek, 1978). The mean luminance of the gratings and the background field was set at 30 cd/m². Luminance contrast in the gratings was defined as the Michelson contrast: $(L_{\max} - L_{\min}) / (L_{\max} + L_{\min})$, which ranged from 1.25 to 80% for infant experiments, and from 0.1 to 1.2% for adult experiments.

For infants, who viewed the 53° by 40° monitor from a distance of 38 cm, stimuli subtended 16° × 16° of visual angle (4 total cycles) and were centered 13° to the left or right of the center of the video display. For adults, who viewed the stimulus monitor from a distance of 76 cm, visual stimuli subtended 8° × 8°, and were centered 6.5° from the center.

Moving stimuli were of the "apparent motion" type, i.e. movement was achieved by spatial phase offset at regular intervals occurring in synchrony with the vertical refresh of the video monitor (i.e. at multiples of 15 msec). The angular displacement of this spatial offset in combination with the frame duration determined the apparent speed of the grating. For these experiments, spatial offset varied from 0.08° to 1.0° visual angle (7.5°–90° phase shift). Frame duration was set at 15 msec for the three fastest speeds tested and at 30 msec for the two slowest speeds. These discrete combinations of spatial and temporal offsets are known to be within the range that renders a clear percept of smooth motion in adult subjects (Burr, Ross & Morrone, 1986; Watson, Ahumada & Farrell, 1986). Vertical motion was employed in order to reduce the potential for optokinetic eye movements, or OKN (Hainline *et al.*, 1984; Hainline & Abramov, 1985). As would be expected by the use of relatively small stimulus fields in conjunction with vertical motion, tracking or OKN eye movements were never observed in our subjects.

Counterphase-reversing stimuli were constructed using sinusoidal temporal modulation. A complete temporal cycle was created using the same number of discrete frames as required to cycle through a period of the moving stimulus. This ensured that the two types of stimuli (i.e. moving and counterphase) were equally sampled in time and space. In order to stay within the convention of previous infant contrast sensitivity studies, we describe the luminance contrast of the counterphase grating in terms of its "full" contrast (e.g. Levinson & Sekuler, 1975; Kelly, 1979), rather than by the contrast of its moving components (e.g. Watson *et al.*, 1980).

Psychophysical paradigm

Infant procedure. Infant contrast thresholds were estimated using the forced-choice preferential looking (FPL) technique (Teller, 1979) with the method of constant stimuli. An adult observer/experimenter (first

author KRD or an assistant, JDS) held the infant 38 cm away from the front of the stimulus monitor, and a video camera was aimed at the infant's face. The experimenter was unable to see the stimulus display (an occluder obstructed the view), but could see the infant's face in a camera monitor suspended above the apparatus. Each trial began with the presentation of a computer-generated fixation target (which consisted of one of 40 moving or stationary pictures) in the center of the video screen. When the infant was judged to be looking centrally at this fixation target, the grating stimulus appeared abruptly on the left, or right side of the video monitor (centered 13° from the middle of the screen) at one of five luminance contrasts (contrast range = 1.2 log units). Trials containing counterphase vs moving gratings were randomly interspersed throughout the experiment and the moving stimuli were balanced for upward and downward motion. The experimenter used cues such as the infant's head turning and gazing behavior to judge the left vs right location of the stimulus. The parent of the infant recorded the experimenter's verbal response by pressing one of two keys on the computer keyboard, and computer beeps provided feedback.

Our goal was to obtain approximately 200 total trials per infant. If we were able to obtain more than 200 trials, we did so, since the accuracy of threshold estimates increases with the total number of trials (e.g. McKee, Klein & Teller, 1985). The total number of trials collected from each infant ranged from 180 to 280, which corresponds to 18 and 28 trials for each of five luminance contrasts tested under each of the two stimulus conditions (i.e. moving vs counterphase gratings). On the average, 235 trials were obtained per infant.

Effects of speed. In order to determine whether speed influences the degree of contrast summation, each infant subject was tested at one of five speeds; 2.8, 8.4, 22.3, 44.5 or 66.8°/sec. Since spatial frequency was held constant at 0.25 cyc/deg, temporal frequency necessarily covaried with speed. Corresponding temporal frequencies were 0.7, 2.1, 5.6, 11.1 and 16.7 Hz, respectively.

For each of the five speeds, nine infants were tested with both counterphase and moving stimuli (45 total subjects). Speed groups were balanced to include an approximately equal number of girls and boys.

Adult procedure. Adult subjects viewed the stimulus display from a distance of 76 cm. Sinusoidal gratings were of the same spatial frequency, and spanned the same range of speeds and temporal frequencies, as in the infant experiments. Adults provided self reports by pressing key pads to signal the appearance of the stimulus on the left or right, and each adult subject was tested at all five stimulus speeds. As was the case for our infant procedure, eye position in our adult subjects was unrestricted, and stimuli remained present on the screen until a decision was made.

Data analysis

Contrast thresholds and sensitivity estimates. Psychometric curves were fit to the data using Weibull functions

(Weibull, 1951; Quick, 1974) and “maximum likelihood” analysis (Watson, 1979). For infants, upper asymptotes were fixed at 95% correct performance, a value that reflects those observed in our data set, and which has been previously demonstrated to produce consistent and accurate threshold estimates (Teller, Mar & Preston, 1992). For adults, an upper asymptote of 100% was employed. Using these parameters, all infant and adult data sets were well fit by Weibull functions.

The Weibull analysis provided a *contrast threshold* (defined as the luminance contrast yielding 75% correct performance) and a *slope estimate* (or β , defined as the steepness of the psychometric function; see Nachmias, 1981 and Graham, 1989). *Sensitivity* was determined by taking the inverse of the contrast threshold value (sensitivity = 1/threshold).

Sensitivity ratios. For each subject, a *sensitivity ratio* (SR) was calculated in order to compare the relative sensitivity for single moving (SM) vs counterphase (CP) gratings ($SR = Sens_{SM}/Sens_{CP}$). The advantage of using a within-subject design with interleaved trials is that the effects of extraneous variables such as attention and motivation, as well as individual differences in overall sensitivity, are factored out of the sensitivity ratio. Whereas comparison of absolute threshold values between subjects (e.g. between adults and infants) is likely to be confounded by such extraneous effects, comparison of sensitivity ratios is expected to be more directly interpretable.

A sensitivity ratio of 2.0 indicates a complete lack of summation of gratings moving in opposite directions, which is evidence for the existence of directionally selective mechanisms at threshold. By contrast, a sensitivity ratio of 1.0 indicates linear summation, which is evidence for the existence of non-directional mechanisms at threshold. Sensitivity ratios between 1.0 and 2.0 may also be evidence for independent directionally selective mechanisms, provided that probability summation between such mechanisms is taken into account.

Sensitivity ratio predictions based on probability summation. Probability summation predicts an advantage for detecting the counterphase stimulus, simply because it is composed of *two*, rather than a *single*, moving components (e.g. Watson, 1979; Watson *et al.*, 1980; Nachmias, 1981). Thus, even if a counterphase stimulus is detected by two independent analyzers for direction of motion, if the analyzers are independently affected by noise, sensitivity ratios are predicted to fall below 2.0 by an amount that depends on the slope of the psychometric function. The theory behind this concept, which is described in Appendix A, results in the following formula:

$$\text{Predicted Sensitivity Ratio} = \frac{2}{2^{1/\beta}}$$

where β represents the slope of the psychometric function generated by the single moving grating condition.

In order to determine whether probability summation within directionally selective mechanisms could account for the sensitivity ratios observed in our subjects, we

calculated predicted sensitivity ratios using the slope values obtained from the Weibull analysis. Predicted sensitivity ratios were determined using group mean slope values, separately for each speed tested. This produced *mean* predicted sensitivity ratios, which were then directly compared to those obtained from actual ratios of sensitivities (i.e. where $SR = Sens_{SM}/Sens_{CP}$).

RESULTS

Contrast sensitivities were obtained for each of 45 infants tested with both counterphase and single moving gratings at one of five speeds: 2.8, 8.4, 22.3, 44.5 or 66.8°/sec (corresponding to temporal frequencies of 0.7, 2.1, 5.6, 11.1 and 16.7 Hz, respectively). For each infant, we obtained a sensitivity ratio by dividing the sensitivity for single moving gratings by the sensitivity for counterphase gratings.

Representative results from two 3-month-old infant subjects are shown in Fig. 2. For one infant (left panel), moving and counterphase stimuli were presented at 5.6 Hz, which produced a speed of 22.3°/sec for the moving stimulus. The detection threshold for the moving stimulus was approximately half of that observed for the counterphase stimulus, resulting in a sensitivity ratio of 2.16 and indicating the presence of directionally selective mechanisms at threshold. For another infant (right panel), moving and counterphase stimuli were presented at 0.7 Hz, which produced a speed of 2.8°/sec for the moving stimulus. At this speed, thresholds for moving and counterphase gratings were approximately equal, resulting in a sensitivity ratio of 1.17. This ratio is close to that predicted by linear summation of gratings moving in opposite directions, suggesting that the stimulus was detected by a non-directional mechanism.

Infant sensitivity ratios. The distribution of sensitivity ratios for individual infant subjects is shown in Fig. 3. With the exception of one subject tested at 8.4°/sec (2.1 Hz), all of the sensitivity ratios fell between 0.6 and 2.5. This infant’s sensitivity ratio (4.22) was determined to be an outlying data point; it was clearly outside the range observed at any speed tested, and a test of “standardized residuals” demonstrated a value of 8 standard deviations away from the mean. This resulted mostly from an extremely high sensitivity to the moving stimulus (7.7 SDs away from the mean). Furthermore, we found that for the four other speeds tested, medians and means were nearly identical. This was clearly not the case for the 8.4°/sec speed condition when the outlying data point was included. For this reason, we have excluded this infant’s data point from our analysis.

To obtain mean sensitivity ratios, individual sensitivity ratio values were averaged across infants tested at the same speed (temporal frequency). Mean sensitivity ratios and standard errors are plotted as a function of both speed and temporal frequency in Fig. 4A (■). The highest mean sensitivity ratio (1.86) was observed at 22.3°/sec (5.6 Hz), with the sensitivity ratio decreasing at higher and lower speeds. At this peak in the curve, the mean sensitivity ratio approached a value of 2.0, consist-

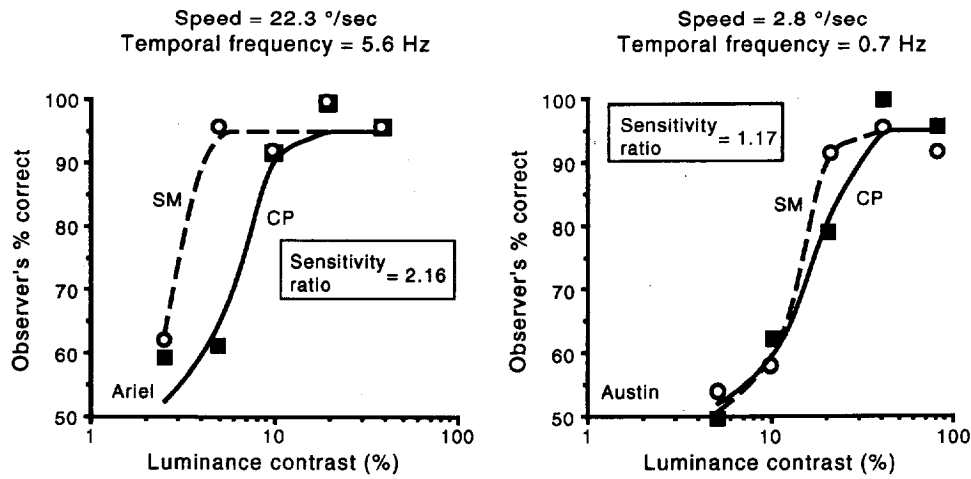


FIGURE 2. Data obtained from two 3-month-old infants tested with both single moving (SM, ○) and counterphase (CP, ■) 0.25 cyc/deg gratings. The adult observer's percent correct is plotted as a function of luminance contrast. Solid and dashed lines are best-fitting Weibull functions. The infant on the left, tested at 22.3°/sec (5.6 Hz), exhibited a higher threshold for counterphase than for moving gratings, with a sensitivity ratio (SR = Sens_{SM}/Sens_{CP}) of 2.16. The infant on the right, tested at 2.8°/sec (0.7 Hz), exhibited approximately equal thresholds for counterphase and moving gratings, with a sensitivity ratio of 1.17.

ent with the hypothesis that the mechanism responsible for detection is directionally selective. By contrast, at 8.4°/sec (2.1 Hz), the mean sensitivity ratio was indistinguishable from 1.0, consistent with the hypothesis that the detection mechanism is non-directional. To examine the effects of speed on the sensitivity ratio, we conducted a single-factor ANOVA. The main effect of speed was found to be significant [$F(4,39) = 3.14, P < 0.025$].

Probability summation predictions. In order to determine whether the observed sensitivity ratios could be accounted for by probability summation between directionally selective mechanisms, we used mean slope values

(β , computed from the Weibull functions for single moving gratings) to calculate predicted mean sensitivity ratios and standard errors, separately for each speed (see Appendix B). We expected that probability summation could be responsible for the intermediate mean sensitivity ratios (1.38, 1.36 and 1.30) observed at three of the five speeds tested (2.8, 44.5 and 66.8°/sec, respectively).

Predicted sensitivity ratios based on probability summation are shown in Fig. 4A (□) and can be directly compared to actual mean sensitivity ratios (Fig. 4A, ■). At a relatively slow speed of 8.4°/sec, the mean sensitivity ratio fell significantly below the probability summation prediction, supporting the previous assertion that the most sensitive mechanism is not directional at this speed. At 2.8°/sec, the mean sensitivity ratio was greater than 1.0, yet below the probability summation prediction, again suggesting a lack of directional mechanisms at threshold for slow speeds.

At the two fastest speeds (44.5 and 66.8°/sec), mean sensitivity ratios and standard errors completely overlapped with the predicted values, consistent with the existence of probability summation between directional mechanisms at these speeds. For the 22.3°/sec condition, the mean sensitivity ratio fell clearly above that predicted by probability summation, supporting the previous assertion that the most sensitive mechanisms are directionally selective at this speed. Moreover, the fact that the mean sensitivity ratio was significantly higher than that predicted by probability summation suggests the existence of some sort of inhibition between detectors tuned for opposite directions, such that the effects of probability summation are diminished (e.g. Levinson & Sekuler, 1975).

In sum, all speeds greater than or equal to 22.3°/sec (5.6 Hz) yielded mean sensitivity ratios that were consistent with, or fell significantly above, those predicted by probability summation between directionally selective

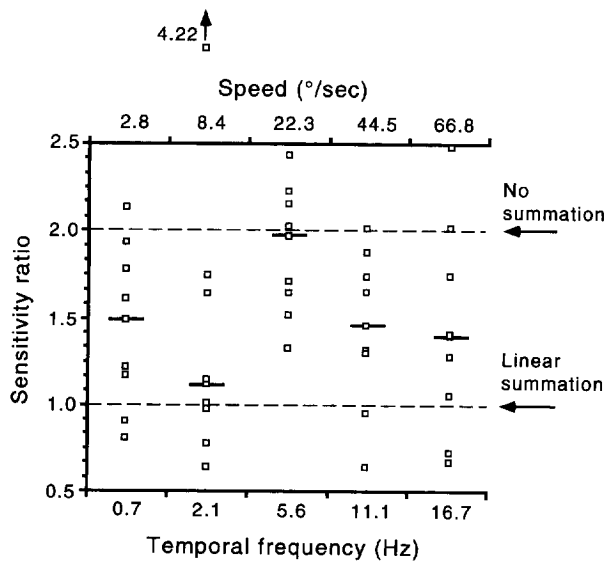


FIGURE 3. Distribution of sensitivity ratios for 45 infant subjects. With the exception of one subject who exhibited a sensitivity ratio of 4.22, all of the calculated sensitivity ratio values fell between 0.6 and 2.5. The dashed line at 2.0 represents the lack of summation at threshold. Conversely, the dashed line at 1.0 represents linear summation at threshold. Solid horizontal lines correspond to the medians of the sensitivity ratios for each speed group.

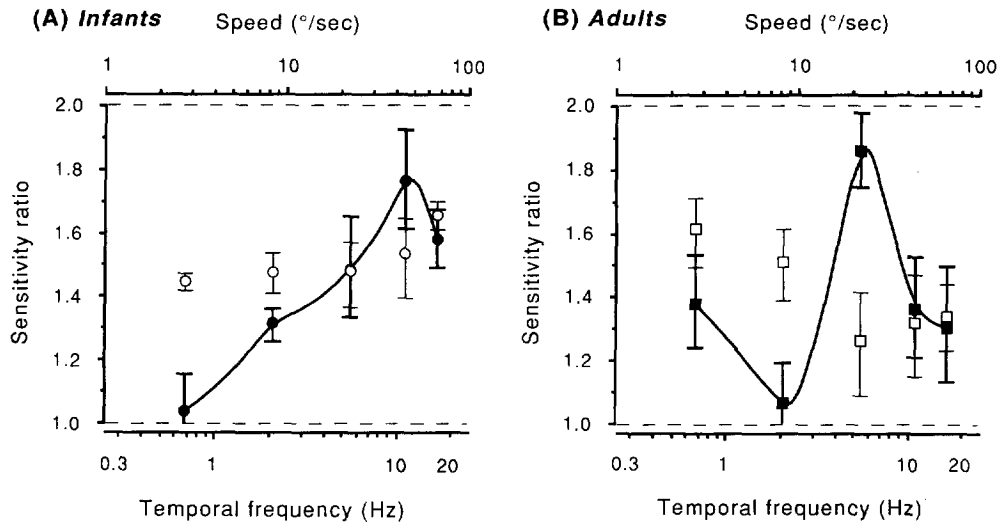


FIGURE 4. Infant and adult group mean sensitivity ratios plotted as a function of temporal frequency and speed. (A) Infant data (■). Open squares represent mean sensitivity ratios predicted by probability summation (see text for details). Error bars denote standard errors of the means for data (—) and predictions (—). The dashed line at 2.0 represents the lack of summation at threshold. Conversely, the dashed line at 1.0 represents linear summation at threshold. Mean sensitivity ratios in infants vary with the speed of the stimulus, ranging from 1.07 (at 8.4°/sec, 2.1 Hz) to 1.86 (at 22.3°/sec, 5.6 Hz). At 2.8 and 8.4°/sec, the mean sensitivity ratios are below the probability summation predictions, indicating detection by non-directional mechanisms. At speeds greater than or equal to 22.3°/sec (5.6 Hz), mean sensitivity ratios are consistent with, or fall significantly above, those predicted by probability summation between directionally selective mechanisms. At relatively high speeds/temporal frequencies, therefore, infants appear to possess directionally selective mechanisms at threshold. (B) Adult data (●) and probability summation predictions (○). Similar to infants, mean sensitivity ratios for adults range from 1.04 (at 2.8°/sec, 0.7 Hz) to 1.77 (at 44.5°/sec, 11.1 Hz). Furthermore, the overall pattern for the two groups is quite similar: both infants and adults exhibit non-directional mechanisms at threshold for slow speeds/temporal frequencies, and directionally selective mechanisms at threshold for higher speeds/temporal frequencies.

mechanisms. We can therefore say with certainty that, at least for relatively high speeds/temporal frequencies, infants possess directionally selective mechanisms at threshold.

Adult sensitivity ratios. As was performed for infant data, sensitivity ratios were calculated for each adult subject. Group means and standard errors are plotted as a function of speed and temporal frequency in Fig. 4B (●). Similar to the infant data, mean sensitivity ratios for adults ranged from 1.04 to 1.77, and the effect of speed was found to be statistically significant [ANOVA, $F(4,15) = 3.99, P < 0.02$]. Mean sensitivity ratios predicted by probability summation were computed using adult mean slope values, separately for each speed. Predicted values are shown in Fig. 4B (○).

For the three fastest speeds tested (i.e. 22.3, 44.5 and 66.8°/sec), mean sensitivity ratios overlapped with the probability summation prediction, suggesting detection by directionally selective mechanisms. At the peak of the adult curve (occurring at 44.5°/sec), the mean sensitivity ratio was higher than that predicted by probability summation. Similar to the interpretation of our infant results, this elevated sensitivity ratio suggests the existence of inhibition between mechanisms tuned for opposite directions of motion. For the two slowest speeds (i.e. 2.8 and 8.4°/sec), mean sensitivity ratios fell significantly below the predicted values, a result that is inconsistent with detection by directional mechanisms.

In order to facilitate comparison between the patterns of sensitivity ratios for infant and adult subjects, infant

and adult data are plotted together in Fig. 5. Although both infants and adults exhibit sensitivity ratios that vary with speed, the two groups appear to exhibit peaks at different speeds (22°/sec and 45°/sec for infants and adults, respectively), which are also the respective speeds that produce sensitivity ratios substantially above the probability summation prediction. This difference

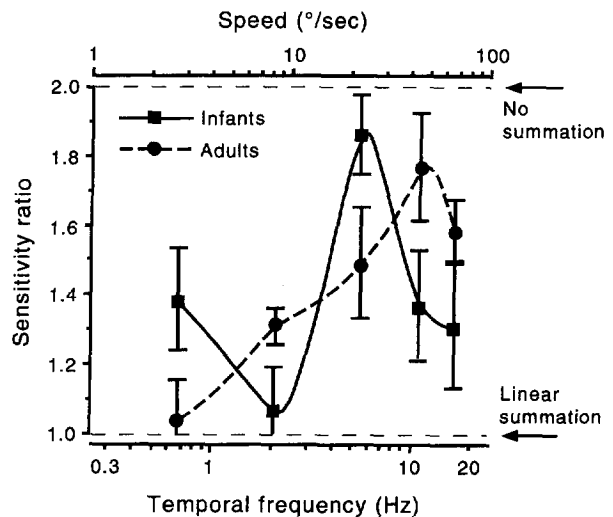


FIGURE 5. Comparison of sensitivity ratios in infants (■) and adults (●). While the overall pattern is quite similar for both groups, the most robust demonstration of directional mechanisms at threshold is found at a slower speed/temporal frequency for infants (22.3°/sec, 5.6 Hz) compared to adults (44.5°/sec, 11.1 Hz).

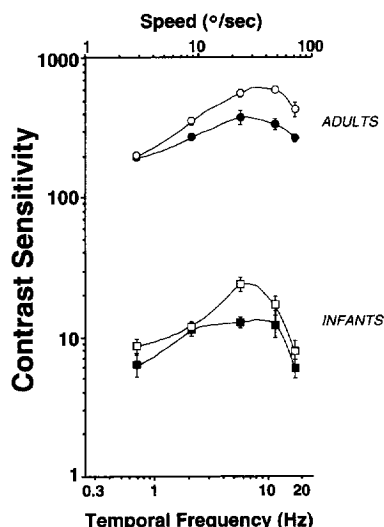


FIGURE 6. Infant and adult temporal contrast sensitivity functions (tCSFs) for both counterphase gratings (●, ■) and moving gratings (○, □). Error bars denote standard errors of the means. For infants, the peak sensitivity is near 5 Hz, which is also the temporal frequency that yields the largest and most significant difference between moving and counterphase sensitivity. Adults also exhibit a peak sensitivity near 5–10 Hz, although they are more than a log unit more sensitive than infants at all speeds/temporal frequencies tested.

suggests that the best speed for eliciting directional mechanisms in infants may be somewhat shifted to slower speeds/temporal frequencies, compared to adults.

Nonetheless, the overall pattern for the two groups is quite similar: both infants and adults exhibit non-directional mechanisms at threshold for slow speeds/temporal frequencies, and directionally selective mechanisms at threshold for higher speeds/temporal frequencies.

Infant temporal contrast sensitivity functions. In addition to providing information about directional mechanisms *per se*, data collected at different temporal frequencies allowed us to look at the effects of speed/temporal frequency on *absolute* contrast sensitivity, for both moving and counterphase gratings. In order to obtain an estimate of the mean sensitivity for counterphase and moving gratings, contrast sensitivities were averaged across infants tested at the same speed (temporal frequency). Group means and standard errors are shown in Fig. 6 (□, ■). Plotted in this way, these data provide us with *temporal contrast sensitivity functions* (tCSFs), like those previously described for adults (e.g. Robson, 1966; Kelly, 1971) and infants (Swanson & Birch, 1990; Hartmann & Banks, 1992; Teller, Lindsey, Mar, Succop & Mahal, 1992). In accordance with previous infant experiments employing counterphase stimuli (Hartmann & Banks, 1992), the data in Fig. 6 show a peak contrast sensitivity near 5 Hz, for both counterphase and moving gratings.

In order to investigate statistically the effects of stimulus type, speed and the interaction between the two, a two-factor ANOVA was performed. The results from this analysis revealed that infants were significantly more sensitive to moving than to counterphase gratings [$F(1) = 36.36$, $P < 0.0001$]. Furthermore, we found a

significant effect of speed [$F(4) = 7.52$, $P < 0.0001$], as well as a significant interaction between speed and stimulus type [$F(1,4) = 2.87$, $P < 0.05$]. *Post-hoc* analysis, using a “*t*-test” for correlated means with a Bonferroni adjustment, revealed a significant difference in moving vs counterphase sensitivity only for the 22.3°/sec (5.6 Hz) condition ($P < 0.005$, 1-tail). Therefore, although infants were overall more sensitive to moving vs counterphase stimuli, the largest and most significant difference between the two measures was found at 5.6 Hz (22.3°/sec). This difference is approximately a factor of two, as would be expected if the detecting mechanism is directionally selective.

Adult temporal contrast sensitivity functions. As was performed for infant data, adult mean contrast sensitivities were computed separately at each speed/temporal frequency. Adult group mean contrast sensitivities for both counterphase and single moving gratings are plotted along with the infant data in Fig. 6 (○, ●). The peak contrast sensitivity for adults occurred between 5 and 10 Hz, in accordance with previous results obtained using low spatial frequency counterphase gratings (Robson, 1966; Levinson & Sekuler, 1975; Kelly, 1979) and moving gratings (Levinson & Sekuler, 1975; Kelly, 1979; Burr & Ross, 1982; Anderson & Burr, 1985). As expected from previous studies (e.g. Banks & Salapatek, 1976; Atkinson, Braddick & Moar, 1977a, b; Banks & Salapatek, 1978, 1981; Hartmann & Banks, 1992), adults were found to be greater than a log unit more sensitive than 3-month-old infants.

In contrast to the large difference in absolute sensitivity, the peaks and shapes of the infant and adult sensitivity curves appear to be rather similar. For example, both the adult and infant data exhibit a 3-fold variation in sensitivity across the different speeds of the moving grating condition (infants = 3.1, adults = 3.0) and a 2-fold variation in sensitivity across the different speeds of the counterphase grating condition (infants = 2.2, adults = 2.0). Compared to adults, however, infants appear to exhibit a somewhat steeper high temporal frequency fall-off, as well as a peak in the moving grating curve that is shifted to lower speeds (temporal frequencies). Nonetheless, the overall similarity between the shapes of the infants and adult tCSFs suggests that temporal tuning is relatively mature by 3 months of age.

DISCUSSION

Employing a summation paradigm, we have demonstrated that 3-month-old infants possess directionally selective mechanisms. Whereas previous studies have demonstrated that infants are able to differentiate direction of motion for supra-threshold stimuli (e.g. Dayton *et al.*, 1964; Kremenitzer *et al.*, 1979; Atkinson & Braddick, 1981; Hainline *et al.*, 1984; Roy *et al.*, 1989; Shea & Aslin, 1990; Dannemiller & Freedland, 1991; Bertenthal & Bradbury, 1992; Wattam-Bell, 1992, 1993), our experiments are the first to demonstrate the presence of multiple analyzers for direction of motion *at detection threshold*.

Before proceeding with the discussion of the results and their significance, we will first evaluate potential confounding factors and attempt to discount the possibility that they have contributed to the observed effects.

Potential confounding factors

Effects of attention and motivation. As previously mentioned, our within-subject design and our use of interleaved trials virtually eliminates the possibility of differential attention or arousal between the moving and counterphase conditions. Differences in sensitivity ratios between speeds, and also between infants and adults, should therefore reflect differences in sensory processing, rather than differences in attention. In our experiments, the "sensory hypothesis" predicts sensitivity ratios near 1.0 or 2.0 (or intermediate values if probability summation is involved). In accordance with these predictions, we observed sensitivity ratio values ranging from 1.0 to 2.0, depending on the speed. By contrast, one would need a rather arbitrary "motivation hypothesis" to predict the observed values as well as the shape of the sensitivity ratio curve. For these reasons we feel it highly unlikely that motivation or differential attention can account for our findings.

Eye movements. As is the case in all infant experiments, we are unable to control the eye movements of our subjects, and must therefore discuss their potential for confounding our results. In the experiments reported herein, it was important to minimize the potential for optokinetic nystagmus (OKN) or tracking eye movements, since this cue could assist the adult experimenter in determining the position of the stimulus in the FPL judgments. The fact that this cue would exist for moving stimuli, but not for counterphase stimuli, would provide an unfair advantage for the moving stimuli. Thus sensitivity ratios would be artificially elevated. In order to minimize tracking eye movements in our experiments, we employed upward and downward motion since OKN elicited by vertical motion has been shown to be substantially less robust than OKN elicited by horizontal motion (Hainline *et al.*, 1984; Hainline & Abramov, 1985). Subsequently, in no experimental run were eye movements ever noticed and/or used as a cue by the adult experimenter (KRD or JDS). We therefore feel certain that differential use of an eye movement cue can not explain the observed increased sensitivity for moving vs counterphase stimuli.

Another potential confounding factor concerns the fact that natural drifting and saccadic eye movements can affect contrast sensitivity assessments (e.g. Kelly, 1977). Furthermore, it has been suggested that they may improve sensitivity for counterphase stimuli more than for moving stimuli (Kelly, 1979). In our experiments, this would have the effect of bringing the thresholds for moving and counterphase gratings closer together, thereby lowering the sensitivity ratios. From this, we can gather that sensitivity ratios are, if anything, actually *higher* than those we observed. Fortunately, this could only strengthen our assertion that the observed ratios

reflect the existence of directionally selective mechanisms in infants.

Infant directional mechanisms

In the present experiments, the mean sensitivity ratio for infants varied with the speed of the stimulus, ranging from 1.07 to 1.86 (see Fig. 4A). At 8.4°/sec, the mean sensitivity ratio was near 1.0 and clearly below the probability summation prediction, indicating detection by non-directional mechanisms at this speed. At 2.8°/sec, the mean sensitivity ratio was greater than 1.0, yet below the probability summation prediction. Taken together, these results suggest that the low-speed (or low-temporal frequency) cut-off for the existence of directional mechanisms at threshold is approximately 8°/sec (~ 2 Hz).

At speeds greater than or equal to 22.3°/sec (5.6 Hz), mean sensitivity ratios were consistent with, or fell significantly above, those predicted by probability summation between directionally selective mechanisms. At relatively high speeds/temporal frequencies, therefore, infants appear to possess directionally selective mechanisms at threshold.

Probability summation between directional mechanisms. As previously described, probability summation between directionally selective detectors should reduce the contrast threshold for the counterphase grating, and thereby produce sensitivity ratios below 2.0. Despite the added benefit probability summation is expected to confer on detection of the counterphase stimulus, several summation experiments have reported a sensitivity ratio of *exactly* 2.0 (Levinson & Sekuler, 1975; Stromeyer *et al.*, 1978; Kelly, 1979; Murray *et al.*, 1983). This finding suggests the existence of some sort of mutual inhibition between analyzers selective for opposite directions of motion. This inhibition, in essence, overrides the expected effects of probability summation. In our study, we found that the probability summation prediction fell below the actual mean sensitivity ratio for infants tested at 22.3°/sec (see Fig. 4A) and for adults tested at 44.5°/sec (see Fig. 4B), suggesting the existence of inhibitory mechanisms at these respective speeds. The fact that probability summation accounted for data obtained at some, but not all, speeds implies that inhibition is involved more at some speeds/temporal frequencies than at others. This could arise, for example, if directionally selective detectors were themselves selective for speed, and the degree of inhibition varied across the different speed-tuned populations.

Probability summation: contribution from non-directional mechanisms. The results from our probability summation analysis revealed that infant sensitivity ratios at 44.5 and 66.8°/sec could be accounted for by probability summation within a directional mechanism. The possibility remains, however, that probability summation occurs across populations of *non-directional*, as well as directional, mechanisms (Watson *et al.*, 1980). Although we can not rule out this possibility, the results from our analysis clearly demonstrate that probability summation between directionally selective mechanisms

is at least *sufficient* to account for the intermediate sensitivity ratios observed at the two fastest speeds.

Along a similar line, it is also possible that probability summation occurs *between* directional and non-directional mechanisms. Intermediate sensitivity ratios could therefore reflect joint contributions from both types of mechanisms to detection. This could occur, for example, if both directional and non-directional mechanisms exist and are approximately equally sensitive (e.g. when $C_D = C_N$, Fig. 1). Sensitivity ratios would be closer to 2.0 or 1.0, depending on the relative proportions of the two mechanism types. This sort of phenomenon would result in sensitivity ratios that can not be sufficiently accounted for by probability summation in either a directional or a non-directional mechanism alone, as is seen in the adult data of Watson *et al.* (1980).

Effects of speed: relation to previous infant studies. In a related infant study, Bertenthal and Bradbury (1992) investigated the effects of speed on infants' ability to discriminate "shearing" from "unidirectional" motion. This task requires the ability to distinguish upward from downward motion, which implies the existence of directional mechanisms. Using random dot patterns at suprathreshold levels of luminance contrast, Bertenthal and Bradbury reported that 13-week-old (~3-month-old) infants could distinguish shearing from unidirectional motion at speeds greater than 3.5°/sec. That their infants appeared to exhibit directionally selective mechanisms at lower speeds than we observed (our low-speed cut-off was 8.4°/sec) might be due to the use of suprathreshold stimuli in the Bertenthal and Bradbury study vs threshold stimuli in our study. In other words, infants might possess directional mechanisms for very slow speeds, but *not at detection threshold*. With regards to faster speeds, Bertenthal and Bradbury unfortunately did not obtain a high-speed cut-off and/or peak speed (since they tested only up to 5.6°/sec). We are therefore unable to make comparisons at the high speed range.

In another related study conducted in infants, Wattam-Bell (1991) recorded visually evoked potentials (VEPs) elicited by moving random dot patterns that oscillated upward and downward. In 2.5-month-olds, motion-specific VEPs were found for stimuli moving at 5°/sec, but not at 20°/sec, suggesting that directional mechanisms existed only at the slower speed. By 3 months of age, infants exhibited VEPs in response to both speeds, although amplitudes were still larger for the 5°/sec, compared to the 20°/sec, stimulus. Taken together, these VEP results imply that directional mechanisms develop earlier for slower speeds than for faster speeds. By contrast, our summation paradigm revealed directional mechanisms at 22.3°/sec, but *not* at a slower speed of 8.4°/sec. While the discrepancy between the effects of speed in our study vs Wattam-Bell's study may be due to a variety of differences in experimental paradigm (e.g. behavioral vs VEP measurements) and stimulus parameters (e.g. gratings vs random dots, threshold vs suprathreshold stimuli, temporal frequency), further experiments are clearly needed to elucidate the issue.

Several other behavioral studies in infants have also investigated the effects of speed, although results have been somewhat equivocal. While some studies have reported that looking preferences for moving vs static stimuli in 3- to 4-month-old infants have a low-speed cut-off between 2.5 and 5°/sec (Aslin, *et al.*, 1988; Dannemiller & Freedland, 1989; Aslin & Shea, 1990; Dannemiller & Freedland, 1993), others have reported that these preferences are not simply determined by the speed of the stimulus (e.g. Freedland & Dannemiller, 1987; Skoczenski & Aslin, 1992). It is important to point out, however, that although a preference based on speed implies the existence of a *motion*-based system (e.g. Dannemiller & Freedland, 1993), experiments that measure preferences for moving vs static patterns do not tap into directional mechanisms *per se*, and are therefore not directly comparable to our study.

Infant directional mechanisms: comparison to adults. The results of our study demonstrate that infants, like adults, possess directionally selective mechanisms at threshold. With respect to differential effects of speed, however, we found the most robust demonstration of directional mechanisms at a slower speed for infants (22.3°/sec) compared to adults (44.5°/sec) (see Fig. 5). In accordance with previous suggestions (Aslin *et al.*, 1988; Dannemiller & Freedland, 1989; Aslin & Shea, 1990; Wattam-Bell, 1991; Bertenthal & Bradbury, 1992; Wattam-Bell, 1992; Dannemiller & Freedland, 1993), this result implies that 3- to 4-month-old infants possess relatively immature speed sensitivity.

There are several possible reasons why infant speed sensitivity might differ from that of adults. For example, differential speed sensitivity in infants vs adults may be due to differences in underlying spatial and/or temporal mechanisms that provide input to motion detectors. Models of motion processing propose that directionally selective motion detectors receive input from spatial-frequency-tuned units that are temporally phase-shifted from one another (e.g. Adelson & Bergen, 1985; van Santen & Sperling, 1985; Watson & Ahumada, 1985). Since the speed of a moving stimulus is directly related to its temporal and spatial frequencies, i.e. speed (deg/sec) = temporal frequency (cyc/sec) divided by spatial frequency (cyc/deg), one way to create a motion detector tuned for *slow* speeds is to have inputs that respond to *low* temporal and *high* spatial frequencies. If infants lack mechanisms tuned for high spatial frequencies, they might, consequently, lack motion detectors tuned for slow speeds. That infants do, in fact, lack high spatial frequency mechanisms has been well documented (e.g. Atkinson *et al.*, 1974; Banks & Salapatek, 1976, 1978; Dobson & Teller, 1978; Gwiazda, Brill, Monindra & Held, 1980; Teller, 1983; Norcia & Tyler, 1985; Brown, Dobson & Maier, 1987; Banks & Bennett, 1988; Hamer, Norcia, Tyler & Hsu, 1989; Allen, Bennett & Banks, 1992). In sum, depending on the differential spatial and temporal properties of units that provide input to motion detectors, speed is expected to affect motion sensitivity differentially in infants vs adults.

A second explanation for immature motion processing in infants is that retinal immaturities of the fovea limit and/or influence infants' motion sensitivity. For example, it is known that the foveal cone density (cones/mm) in infants is about a factor of two lower than that of adults (Hendrickson & Youdelis, 1984; Youdelis & Hendrickson, 1986). This difference is thought to contribute to the relative lack of high spatial frequency mechanisms in infants (e.g. Brown *et al.*, 1987; Banks & Bennett, 1988; Wilson, 1988), which, as described above, might limit infant motion sensitivity at slow speeds. In addition to this possibility, low photoreceptor density could also affect motion sensitivity in the following manner. The movement of an object through space results in a "flow" of activity across the retinal surface, with each photoreceptor responding to changes in the level of illumination it receives. Since infant foveal photoreceptors are spaced farther apart than those of adults, an object moving at a given speed would yield a lower number of activated photoreceptors per unit time for infants compared to adults. Such differences might result in a relative loss of motion sensitivity for infants, perhaps more at some speeds than at others.

On a final note, is it also possible that higher-level motion processing areas in infants are not yet fully developed. In the macaque monkey, whose visual system is quite similar to that of humans, cortical neurons selective for direction of motion are first found in layer 4B of striate cortex (area V1) (Dow, 1974). A particular directionally selective neuron might respond, for example, to upward motion but not to downward motion. Layer 4B projects directly (and indirectly, through area V2) to the middle temporal visual area (MT). Area MT contains a very high proportion of directionally selective neurons (e.g. Dubner & Zeki, 1971; Zeki, 1974; Maunsell & Van Essen, 1983; Albright, 1984), many of which are also tuned for speed (e.g. Maunsell & Van Essen, 1983; Rodman & Albright, 1987). A comparison between optimal speeds for MT vs V1 neurons reveals that neurons in area MT are tuned for higher speeds than are those in V1 (Maunsell & Van Essen, 1983; Van Essen, 1985; Mikami, Newsome & Wurtz, 1986).

The present study and earlier studies suggest that, compared to adults, infants exhibit directional mechanisms tuned for slower speeds (see Fig. 5 of the present study and Wattam-Bell, 1991). Our speculative suggestion to account for this difference is that in infants, the human analogue of area MT is not yet functioning at a mature level. Thus, infants may be forced to rely more heavily on area V1 directional mechanisms, which are tuned for slower speeds. Direct neurophysiological studies on the development of motion processing in primates will be required to address this hypothesis.

Infant temporal contrast sensitivity functions

Infant temporal contrast sensitivity functions (tCSF) have been described in three other studies, two of which employed counterphase-reversing stimuli (Swanson & Birch, 1990; Hartmann & Banks, 1992), and one which

employed homogeneous flickering fields (Teller *et al.*, 1992). Employing 0.1 cyc/deg counterphase gratings, Hartmann and Banks (1992) reported a peak in the 3-month-old tCSF curve at 5 Hz, a finding that is consistent with our own. Swanson and Birch (1990) also used counterphase gratings to obtain an infant tCSF. They used spatial frequencies of 0.35 and 1.0 cyc/deg, but only for the latter spatial frequency did they obtain a complete temporal contrast sensitivity curve. For their 0.35 cyc/deg condition, which more closely approximates the spatial frequency employed in our experiments, Swanson and Birch tested at two different temporal frequencies, 2 and 8 Hz. The results from this manipulation demonstrated that 4-month-olds were more sensitive at 8 than at 2 Hz.

To facilitate comparison, a summary graph of tCSFs obtained across infant studies is presented in Fig. 7. For the three studies employing sinusoidal gratings, there is relatively good agreement that the peak sensitivity for 3- to 4-month-old infants tested with low spatial frequency gratings is between 5 and 10 Hz. This peak temporal frequency is relatively fixed despite a 3-fold variation in *spatial frequency* across studies. This suggests that temporal frequency may be more important than the combination of temporal and spatial frequency, i.e. speed, for determining sensitivity. Indeed, evidence from adult studies strongly suggests that contrast sensitivity for moving gratings is determined exclusively by the temporal frequency, as opposed to the speed, of the stimulus (Kelly, 1979; Burr & Ross, 1982).

The summary graph of Fig. 7 also plots the critical flicker frequency for 3-month-old infants, which has

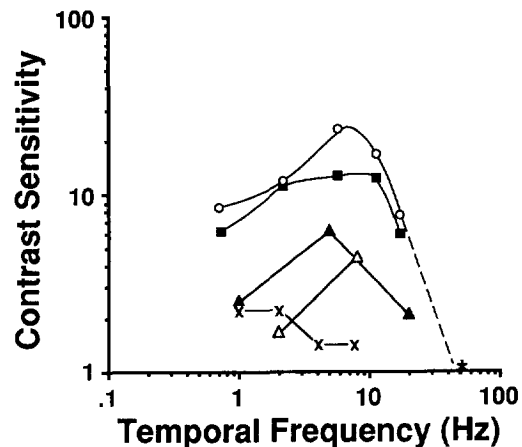


FIGURE 7. Summary of temporal contrast sensitivity functions (tCSFs) obtained in several infant studies. Infants participating in these studies ranged from 2 to 4 months of age. Stimuli consisted of either sinusoidal gratings or homogeneous flickering fields. For the three studies employing sinusoidal gratings, peak contrast sensitivity appears between 5 and 10 Hz. Furthermore, extrapolation (---) from the moving grating data of our study (○) is consistent with the 51 Hz critical flicker frequency (*) reported by Regal (1981). ■ Dobkins and Teller (1995), 0.25 c/deg, counterphase gratings (age = 3 mo); ○ Dobkins and Teller (1995), 0.25 c/deg, single moving gratings (age = 3 mo); ▲ Hartmann and Banks (1992), 0.10 c/deg, counterphase gratings (age = 3 mo); △ Swanson and Birch (1992), 0.35 c/deg, counterphase gratings (age = 4 mo); × Teller *et al.* (1992), homogeneous-field sinusoidal flicker (age = 2 mo); *Regal (1981), homogeneous-field square-wave flicker, cff (age = 3 mo).

been demonstrated to be near 51 Hz (Regal, 1981). Whereas previous infant studies had found it difficult to draw connections between low temporal frequency contrast sensitivity and critical flicker frequency (e.g. Teller *et al.*, 1992), the moving grating condition in our study produced sensitivities high enough to account for a critical flicker frequency near 51 Hz. The higher sensitivities obtained in our study compared to other studies are likely to be due to differences in stimulus parameters (e.g. spatial frequency, number of cycles, size, and eccentricity) or stimulus configurations (cf. Swanson & Birch, 1990).

Infant tCSFs: comparison to adults. For both the counterphase and moving grating condition, we found the peaks and shapes of the tCSFs to be quite similar for infants and adults, although adults were much more sensitive overall (see Fig. 6). This similarity suggests that the development of temporal contrast sensitivity from 3 months of age to adulthood involves mostly an increase in sensitivity (i.e. a vertical shift in Fig. 6), as opposed to a shift in temporal scale (i.e. a horizontal shift in Fig. 6). This stands in contrast to the development of *spatial* contrast sensitivity, which undergoes changes in both sensitivity and spatial scale (e.g. Banks & Salapatek, 1976, 1978, 1981; Wilson, 1988). Thus, while spatial tuning is quite immature at 3 months of age, temporal tuning appears relatively adult-like.

SUMMARY

In conclusion, the experiments reported herein demonstrate that temporal tuning and patterns of contrast summation in 3-month-old infants look quite similar to those of adults. Furthermore, these experiments contribute strongly to the mounting evidence for the existence of directionally selective mechanisms in 3-month-olds. The presence of directional mechanisms was found to be dependent on grating speed (temporal frequency), appearing at and above $22.3^\circ/\text{sec}$ (5.6 Hz). The fact that these directional mechanisms exist at *threshold* implies that, over a restricted speed (temporal frequency) range, the most sensitive contrast detectors in infants are directionally selective.

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APPENDIX A

In this appendix, we outline the equations underlying probability summation between detectors tuned for opposite directions of motion.

These equations have been taken from Watson *et al.* (1980) and Nachmias (1981), although the original descriptions can be found in Weibull (1951) and Quick (1974).

The probability that a mechanism selective for leftward motion will detect a leftwardly moving grating is described by the following equation:

$$P_L = 1 - \exp[-(m_L/\alpha_L)^\beta] \quad (\text{A1})$$

where m_L is the contrast of the leftwardly moving grating, α_L is the "contrast threshold" of the mechanism (the contrast at which the stimulus is detected 63% of the time), and β is the slope of the psychometric function plotted against log contrast, at the contrast threshold. [Note: When threshold is defined as the contrast yielding 75% detection, "2", rather than "e" is raised to the $[-(m_L/\alpha_L)^\beta]$ in equation (A1). See Graham, 1989.]

If leftward selective and rightward selective mechanisms are independent, then the probability of detecting a leftward (L) and a rightward (R) moving grating in *combination* is:

$$P_{(L+R)} = 1 - (1 - \gamma) (1 - P_L) (1 - P_R) \quad (\text{A2})$$

where γ is a guessing or false alarm parameter.

Combining equations (A1) and (A2):

$$P_{(L+R)} = 1 - (1 - \gamma) \exp[-R^\beta] \quad (\text{A3})$$

where

$$R = [(m_L/\alpha_L)^\beta + (m_R/\alpha_R)^\beta]^{1/\beta}. \quad (\text{A4})$$

If the leftward and rightward detecting mechanisms are equally sensitive (i.e. $m_L = m_R$), then the sensitivity to the compound stimulus (i.e. a counterphase grating) is:

$$\text{Sens}_{(L+R)} = \frac{2^{1/\beta}}{\alpha} \quad (\text{A5})$$

where α is the contrast threshold for either of the two component gratings (i.e. leftwardly or rightwardly moving grating).

The ratio of sensitivities to the compound vs the component stimulus is therefore simply:

$$\frac{\text{Sens compound}}{\text{Sens component}} = 2^{1/\beta}. \quad (\text{A6})$$

These equations refer to the contrast of the compound counterphase stimulus in terms of the contrast of the individual moving components. If, however, the contrast of the counterphase stimulus is described in terms of its "full" contrast (as is the case in the present study and

others, e.g. Levinson & Sekuler, 1975), then the ratio of sensitivities to the compound vs the component stimulus is:

$$\frac{\text{Sens compound}}{\text{Sens component}} = \frac{2^{1/\beta}}{2}. \quad (\text{A7})$$

Finally, the sensitivity ratio for the component stimulus (single moving grating) vs the compound stimulus (counterphase grating), as described in our study (i.e. $\text{SR} = \text{Sens}_{\text{SM}}/\text{Sens}_{\text{CP}}$), is the inverse of equation (A7):

$$\text{Sensitivity Ratio} = \frac{2}{2^{1/\beta}}. \quad (\text{A8})$$

In sum, the sensitivity ratio depends on the slope parameter of the psychometric function (β); as the steepness of the function increases (i.e. as β increases), the predicted sensitivity ratio gets larger.

APPENDIX B

In this appendix, we describe the method by which probability summation predictions were obtained. Predicting the sensitivity ratio that would arise from probability summation within a directional mechanism requires knowledge about the slope (β) of the psychometric function generated by the single moving grating condition. As is the case for threshold estimates, the relatively low number of trials we were able to obtain from each infant precludes the possibility of obtaining a very precise estimate of the slope. In order to obtain a more reliable slope estimate, we used the geometric group mean slope, computed separately for each speed. These mean slope values (β) were then inserted into equation (A8) to obtain mean predicted sensitivity ratios. Predicted values were determined separately for each speed, and separately for infant and adult data.

In addition to obtaining mean slope values, standard errors of the slopes were also determined. These standard error values were added and subtracted from the mean slope, in order to obtain the two slope values at the end of the standard error *range*. For each speed, the computed upper and lower slope range values were inserted into equation (A8), in order to determine the range of sensitivity ratios predicted by probability summation. Since these range values were obtained using the standard errors of the slopes, we refer to the error bars in Fig. 4 (plain lines) as the standard errors of the predicted means.

In order to further investigate predictions based on probability summation, we also determined sensitivity ratio values using the geometric mean of the slopes generated across *all* speeds, as well as *individual* slope values for each subject. Both methods produced results that were qualitatively the same as those reported in the text.