

Development of Sensitivity to Texture and Contour Information in the Human Infant

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Abstract

■ Texture discrimination and bounding contour extraction are essential parts of the object segmentation and shape discrimination process. As such, successful texture and contour processing are key components underlying the development of the perception of both objects and surfaces. By recording visual-evoked potentials, we investigate whether young infants can detect orientation-defined textures and contours. We measured responses to an organized texture comprised of many Gabor patches of the same orientation, alternated with images containing the same number of patches, but all of random orientation. These responses were compared with a control condition consisting of the alternation between two independently random configurations. Significant difference

potentials were found as early as 2–5 months, as were significant odd harmonics in the test conditions. Responses were also measured to Gabor patches organized either as circles (all patches tangent to an imaginary circular path) alternated with pinwheels (all patches having a fixed orientation offset from the path). Infants between 6 and 13 months also showed sensitivity to the global organization of the elements along contours. Differential responses to our texture and contour stimuli and their controls could only have been generated by mechanisms that are capable of comparing the relative orientation of 2 or more patches, as no local information at a single patch distinguished the random and organized textures or the circle and pinwheel configurations. ■

INTRODUCTION

Texture and bounding contour discrimination are essential parts of the object segmentation and shape discrimination process. Textures are spatially homogeneous and typically contain repeated structures, often with some random variation (e.g., random positions, orientations, or colors). Textures are deformed systematically by the volumetric shape of an object or by the layout of a surface. These deformations thus provide powerful cues for segmenting objects from their backgrounds and for shape recognition. In addition, the outline silhouette of an object provides supplementary information about its shape.

The perception of texture-defined forms is limited by the ability to extract the appropriate image statistics, to integrate these statistics across scales, and to resolve or segment the shape that is represented. To evaluate the developmental preconditions for texture-defined form processing, we tapped into the most primitive level of texture sensitivity—the extraction of a difference in orientation statistics. Specifically, we studied the development of brain responses to textures composed of Gabor patches of a single spatial scale that were defined

by differences in their orientation statistics. Because the spatial uniformity of the Gabors restricts the scale of local processing mechanisms, the rather wide spacing between the patches in our stimuli forces integration spanning a range well beyond the scale that is optimal for local processing. These textures allowed us to isolate the integration of local, single-scale orientation measurements into a global organization. We compared infants' ability to integrate orientation information in textures to their ability to detect Gabor-defined contours, a task that requires specific integration of orientation information along the orientation axis of the patches, rather than over a region.

Previous texture visual-evoked potential (VEP) studies in adults have all used broadband stimuli such as isodipole textures (Victor & Conte, 1989, 1991; Victor & Zemon, 1985) or orientation-defined forms based on random-line stimuli (Fahle, Quenzer, Braun, & Spang, 2003; Romani, Callieco, Tavazzi, & Cosi, 2003; Bach, Schmitt, Quenzer, Meigen, & Fahle, 2000; Caputo & Casco, 1999; Caputo, Romani, Callieco, Gaspari, & Cosi, 1999; Romani, Caputo, Callieco, Schintone, & Cosi, 1999; Lamme, van Dijk, & Spekreijse, 1993; Meigen & Bach, 1993; Bach & Meigen, 1992, 1997, 1998; Lamme, Van Dijk, & Spekreijse, 1992). In the studies of isodipole textures, the textures were constructed by the introduction of specific higher order correlations between the

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pixels of binary images (Diaconis & Freedman, 1981; Julesz, Gilbert, & Victor, 1978). The construction rule is such that each exemplar of an isodipole texture has same spatial frequency spectrum (second-order or “dipole” statistics) and is thus indiscriminable to mechanisms that only compute local measures of spatial frequency, orientation, and phase. Isodipole textures activate human striate cortex (Beason-Held et al., 2000; Levine et al., 2000; Beason-Held, Purpura, Krasuski, Maisog, et al., 1998; Beason-Held, Purpura, Van Meter, et al., 1998; Purpura, Victor, & Katz, 1994), although the activation is stronger over a range of extrastriate visual areas, including both dorsal areas and areas on the ventral surface. Isodipole textures also activate the striate cortex of macaque (Purpura et al., 1994).

The second main line of texture VEP research has used texture- or orientation-defined forms that are made up of regions that differ in image statistics. These stimuli typically lead to a percept of a figure against a background and potentially activate shape and figure/ground mechanisms, in addition to texture mechanisms. Texture-defined forms activate the striate cortex of macaque (Rossi, Desimone, & Ungerleider, 2001; Lamme, Rodriguez-Rodriguez, & Spekreijse, 1999; Lamme, Zipser, & Spekreijse, 1998; Lamme, 1995; Lamme et al., 1992, 1993; Lee, Mumford, Romero, & Lamme, 1998), but have been found to activate extrastriate, rather than striate cortex in human (Kastner, De Weerd, & Ungerleider, 2000). There have been no previous VEP studies of contour integration, but Oka, van Tonder, and Ejima (2001) have used related targets to study symmetry processing.

Given that texture processing reflects integration at multiple levels of the cortical hierarchy, developmentalists have begun to use responses to these stimuli as probes of global integrative mechanisms. Orientation-based figure/ground segmentation has been studied in infants using the preferential-looking technique and line-orientation-defined segmentation. Rieth and Sireteanu (1994) and Sireteanu and Rieth (1992) have found that segmentation of forms based on line-orientation emerges only at 9–12 months, becoming adult-like around school age, whereas Atkinson and Braddick (1992) showed that discrimination is present as early as 14–18 weeks. The range of onset ages between the 2 studies is considerable and we were interested in the age at which electrophysiological selectivity could first be demonstrated, because the task demands for VEP recording are considerably less than those involved in organizing a behavioral response. There have been no studies in human infants using Gabor-defined contours, although it has been shown using a contour in noise paradigm, that adult performance is achieved only in late childhood (Kovacs, Kozma, Feher, & Benedek, 1999). Contours in noise activate V1 and V2, but produce their greatest activation in lateral occipital areas (Altmann, Bulthoff, & Kourtzi, 2003; Kourtzi, Tolia, Altmann, Augath, & Logothetis, 2003).

In our experiments, we found differential responsiveness to organized versus random textures emerges no later than 2–5 months of age. Responsiveness to orientation-defined contours emerges no later than 6–13 months.

RESULTS

Texture-related Responses

We recorded responses to displays that randomized the global orientation of the organized state on every image update, so that both locally and globally, all orientations are presented equally often in both the organized and random images. The stimuli for this experiment are illustrated schematically in Figure 1.

The adult response waveforms and difference potentials are shown in Figure 2. The thin lines correspond to the control condition (a random configuration for the first 500 msec followed by another random configuration during the second 500 msec) whereas the thick lines show the test condition (an organized texture during the first 500 msec followed by a random configuration during the second 500 msec). The ordering of the channels runs from the 6-cm right derivation on the top to the 6-cm left derivation at the bottom, with Oz in the middle. The response in the control condition is composed of a multiphasic potential, with a positive peak at 100 msec, a negative peak at 180 msec, and a positive peak at 220 msec. The response to the organized/random alternation on the lateral channels is identical to that of the random/random alternation up to 170 msec, after which it stays relatively negative until approximately 300 msec. At Oz, a significant difference was also detected at 120 msec. The difference potential is shown on the

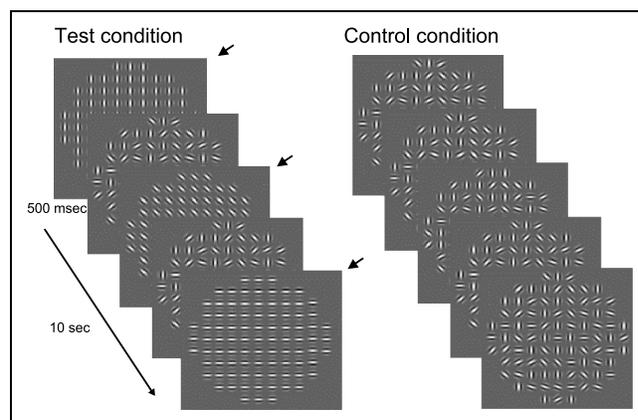


Figure 1. Texture stimuli. Textures made of globally aligned Gabor patches were alternated with textures made of randomly aligned patches. Each image was presented for 500 msec and new exemplars of both the aligned (random global orientation) and the random patterns were drawn for each update. The control condition comprised a series of random texture interchanges.

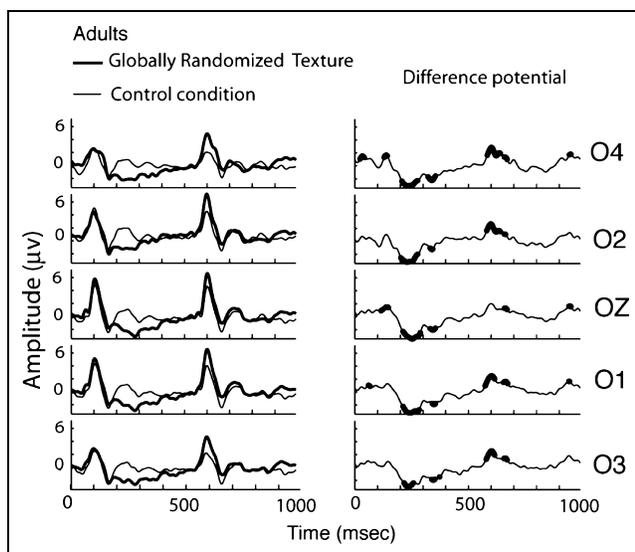


Figure 2. Left: Adult response waveforms for alternation between uniform and random patterns (thick lines) compared with random/random alternations (thin lines). The uniform patterns were presented between 0 and 500 msec in the test condition. Right: Difference potential. Significant differences (indicated by dots in difference potential) are found on both transitions, from random to organized (0–500 msec) and from organized to random (500–1000 msec).

right-hand side of Figure 2. The difference potential is maximal at 220 msec after the transition from random to organized. The difference potential after the transition between the organized and random states is significant as early as 80 msec versus approximately 120 msec at the earliest, for the transition between random and organized. The dots on the difference potential indicate significant differences by permutation testing (Blair & Karniski, 1993).

Figures 3 and 4 show response waveforms for 2- to 5-month-olds ($n = 10$) and 6- to 8-month-olds ($n = 11$), respectively. The infant response waveforms have a very different structure than those of adults. Both infant groups show bifid positivities at Oz after each image update (latencies of 100–200 msec) in the control condition. The infant difference potential is dominated by a sinusoid with a period equal to that of the full image sequence (first harmonic). The adult difference potential was, by contrast, comprised of brisker transients occurring after the transition from random to organized and organized to random. The difference potential from the youngest infants is similar in waveform to that of the older infants, but is less robust statistically.

Because the difference potential is nearly sinusoidal and because of the periodic stimulation protocol we used, the data are well suited to analysis in the frequency domain, because all stimulus-related activities are forced to occur at exact integer multiples of the stimulus

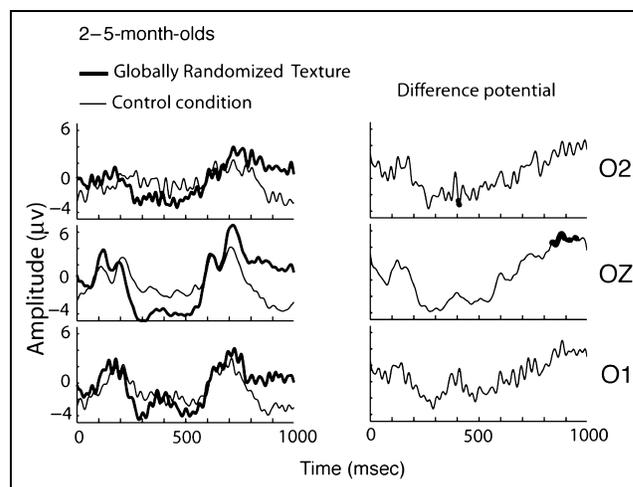


Figure 3. Left: Infant (2- to 5-month-old) response waveforms for alternation between uniform and random patterns (thick lines) compared with random/random alternations (thin lines). The uniform patterns were presented between 0 and 500 msec in the test condition. Right: Difference potential. Significant differences are present, but only for the latest time-points.

frequency. Moreover, all activities that differ for the 2 transitions will project onto the odd harmonics (1, 3, 5, 7 Hz, etc.), whereas all activity that is common to the 2 transitions will project onto the even harmonics (2, 4, 6, 8 Hz, etc.). Spectrum analysis of periodic responses provides a substantial improvement in the signal-to-noise ratio of the relevant response components compared with that available from time averages. Each point on the time average is contaminated with noise

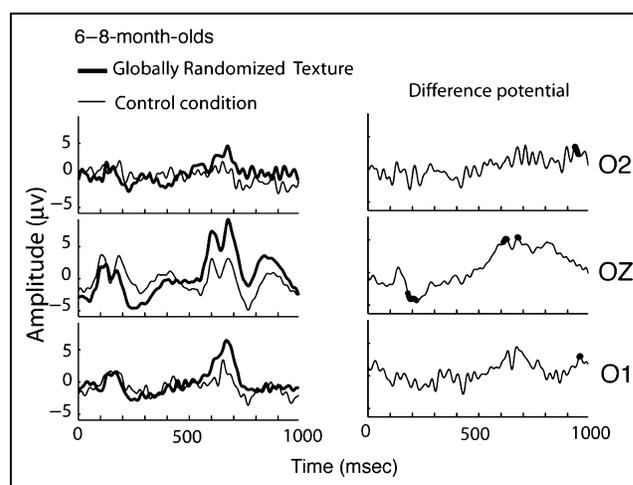


Figure 4. Left: Infant (6–8 months old) response waveforms for alternation between uniform and random patterns (thick lines) compared with random/random alternations (thin lines). The uniform patterns were presented between 0 and 500 msec in the test condition. Right: Difference potential. Significant differences are present after both types of stimulus transition.

over the entire bandwidth of the recording, whereas the noise in the frequency analysis is restricted to a limited (0.5-Hz) band centered on each frequency of interest.

Figure 5 plots amplitude as a function of the first 6 harmonics of the stimulus frequency for the data sets shown in Figures 2–4. The first harmonic amplitudes in all age groups from the globally organized texture stimulus (dark bars) are significantly different from zero, whereas the first harmonic amplitudes from the random/random stimulus are not significant. The first harmonic component dominates the infant difference potential, whereas the adult difference potential also contains measurable odd-harmonic components at higher frequencies. The overall pattern of even harmonic content differs between adults and infants, with the second harmonic being the largest component in the adults and the fourth harmonic being largest in the infants. The adults also show elevated second harmonic amplitudes in the organized/random condi-

tion, an effect not seen in the infants or at any of the other higher order even harmonics in adults.

Contour-related Responses

In the next experiment, we asked whether the infant visual system is capable of detecting collinearity along Gabor-defined contours. Contour integration involves specific pooling of elements along their orientation axis: Iso-orientation is not a sufficient cue (Field, Hayes, & Hess, 1993) as it is for textures. The stimuli consisted of Gabor patches whose centers were arranged along imaginary circles. In the test condition, cocircular arrangements were alternated with “pinwheel” configurations. The control condition consisted of an alternation between 2 symmetrically offset pinwheels undergoing the same angle of local rotation as in the test condition. The distribution of local orientations was the same across conditions, as was the

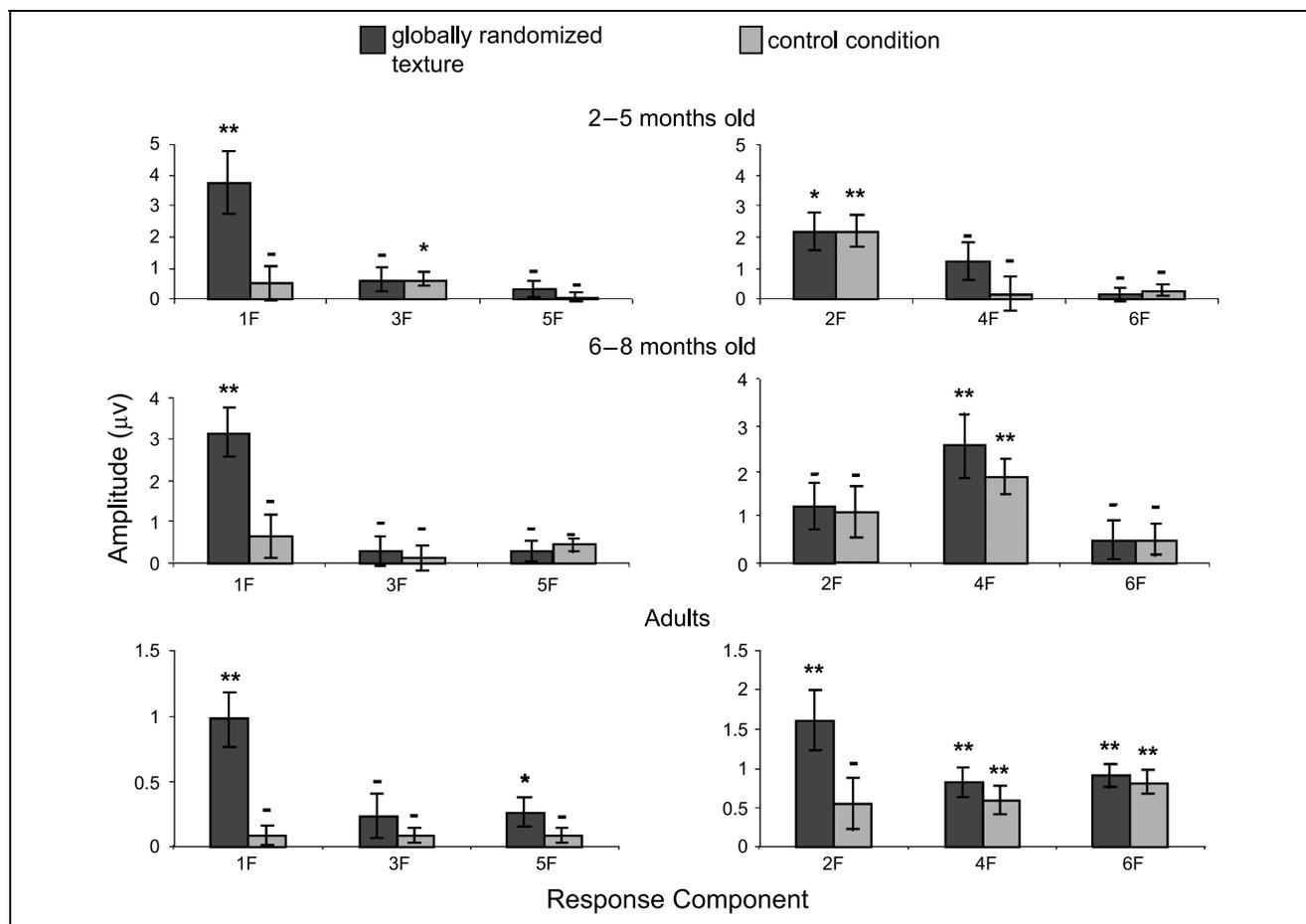


Figure 5. Spectral analysis of the responses shown in Figures 2–4. Top: Infant (2–5 months old) response spectra for the randomized global orientation alternation (dark bars) compared with random/random alternations (light bars). Middle: Infant (6–8 months old) spectra, as in the top panel. Bottom: Adult response spectra, as above. Errors are 1 SE of the vector mean amplitude. Significant odd-harmonic components are only present in response to the texture alternations containing global structure. Significance levels for the odd harmonics in the test and control condition: $\bar{p} > .10$, $*p < .05$, $**p < .01$.

amount of local motion, only the relative orientations of neighboring patches served to differentiate the 2 conditions. The stimuli are illustrated schematically in Figure 6.

The adult response to the pinwheel/pinwheel display (the control condition for the contour experiment) is similar to that seen with the control textures—consisting of a sharp positivity at around 100 msec, followed by a negativity at 170 msec (Figure 7). The adult peak-to-peak response amplitudes for the contour control condition are smaller than those for the texture control condition by a factor of almost 2. The difference potential for the contour response (pinwheel/circle minus pinwheel/pinwheel) is maximal at 100 msec after the transition to the circle state from the pinwheel state (600 msec on the time axis) rather than at around 200 msec for the texture response (Figure 2).

In the infants, the response in the pinwheel/pinwheel control condition was similar in amplitude and waveform to that measured in the texture control condition (compare Figure 4 with Figure 8), with peak-to-peak amplitudes of 7 and 8 μV , respectively. Consistent with this, the amplitudes of the first 3 even harmonics are very similar in the contour and texture control conditions (compare Figure 5 with Figure 9). In contrast to the texture case, the infant difference potential did not reach statistical significance.

Spectrum analysis however indicated the presence of significant first and third harmonics in the pinwheel/circle condition for the infant group (Figure 9). In adults, the contour condition elicited significant configuration

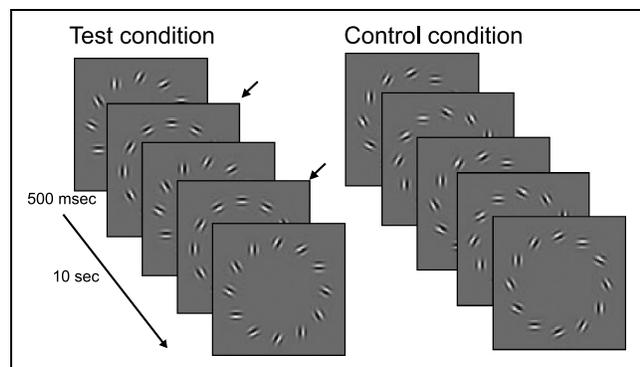


Figure 6. Contour stimuli. Gabor patches ($n = 12$) were located on an imaginary circular contour, with the individual patches separated by 3 wavelengths of the Gabor carrier frequency. There were a total of 11 circular contours arranged on a hexagonal lattice covering the display area, with at least 8 fully complete contours present. In the test condition, the patches were rotated on their centers through an angle of 60° . In the initial state ($t = 0$), all patches were offset by 60° to the local tangent. At 500 msec, the patches were all locally tangent to the imaginary circle. In the control condition, patches at the same locations were also rotated on their centers through an angle of 60° . In the initial state, the patches were all offset by -30° from the local tangent and at 500 msec, the patches were all offset by 30° from the local tangent.

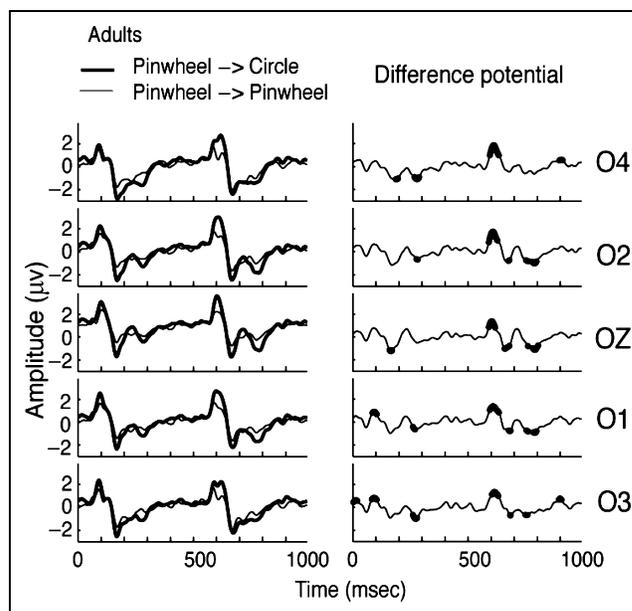


Figure 7. Left: Adult response waveforms for pinwheel/circle alternations (thick lines) compared with pinwheel/pinwheel alternations (thin lines). Note that the transition to the more collinear global organization occurs at 500 msec for the contour stimuli and at 0 msec for the textures. Right: Difference potentials were significant at the time-points indicated by the circles on the waveforms.

specific responses at the third and fifth harmonics and nonsignificant trends at the first and seventh harmonics ($p = .075$ and $.11$, respectively). These components were insignificant in the contour control condition for both infants and adults. In the infants, the second, fourth, and sixth harmonics are significantly larger than zero in both the contour present and contour control conditions and do not differ in amplitude across conditions.

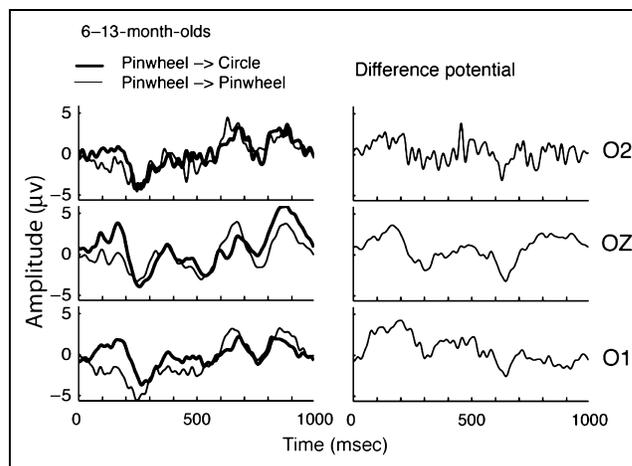


Figure 8. Left: Infant responses for pinwheel/circle alternations (thick lines) compared with pinwheel/pinwheel alternations (thin lines). No significant differences were detected.

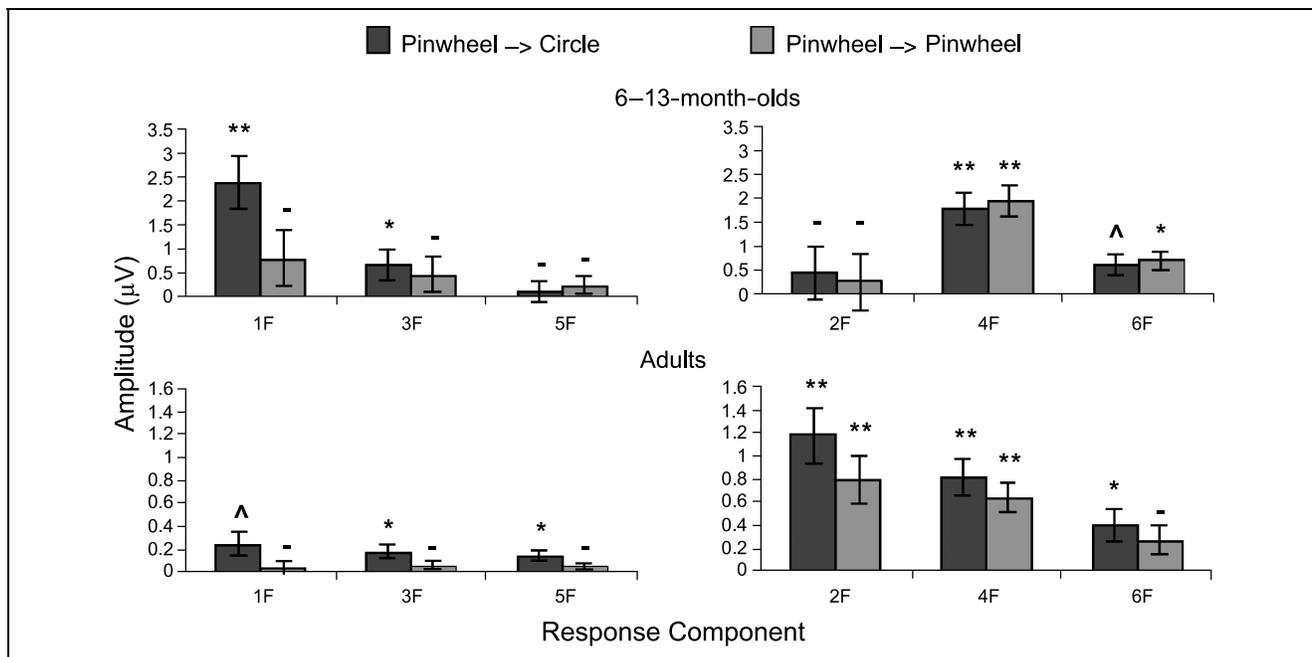


Figure 9. Spectral analysis of the responses shown in Figures 7 and 8. Top: Infant (6–13-month-olds) response spectra for the pinwheel/circle alternation (dark bars) compared with pinwheel/pinwheel alternations (light bars). Bottom: Adult response spectra, as above. Errors are 1 SE of the vector mean amplitude. Significant odd-harmonic components are only present in response to pinwheel/circle alternations. Significance levels for the odd harmonics in the test and control condition: $\bar{p} > .10$, $\hat{p} < .10$, $*p < .05$, $**p < .01$.

In the adults, the second and higher even-harmonic components are also significantly different from zero.

DISCUSSION

Differential responses to our texture and contour stimuli could only have been generated by mechanisms that are capable of comparing the relative orientation of 2 or more patches, as no local information at a single patch distinguished the random and organized textures or the circle and pinwheel configurations. Our measurements do not indicate the size or shape of the summation areas of these mechanisms, but are sufficient to say that a global mechanism exists for textures no later than 2–3 months age and for contours no later than 6–13 months.

Region versus Contour Integration

Integration of orientation cues along contours is best accomplished by specific pooling of similar orientations along their common orientation axis, whereas in the texture case, integration within a common orientation over any direction is equally relevant. Our results from the contour task indicate that infants possess a specific collinear integration mechanism operating over a range of at least 3 lambda. We found differential responsiveness to the pinwheel/circle configuration, compared with the pinwheel/pinwheel configuration. A region-based mechanism that was integrating based on orien-

tation similarity would not respond differentially to the pinwheel/circle and pinwheel/pinwheel configurations because they are equally regular and have the same relative orientation offsets between neighboring elements. Infants may in addition also have a region-based mechanism, although it would be possible to produce a differential response to our textures with only a collinear integration mechanism.

Previous psychophysical work has suggested that the adult visual system uses different mechanisms to process Gabor-defined textures and contours. Bonneh and Sagi (1998) have shown that uniform Gabor-defined textures are more salient than nonuniform (random) textures when both are presented at low contrast, but at high contrast, random textures are more salient (Bonneh & Sagi, 1999). The salience of collinear Gabor-defined contours relative to jagged ones is, on the other hand, independent of contrast (Bonneh & Sagi, 1999). The different way in which contrast effects the salience of texture and contour stimuli thus indicates that different mechanisms are being tapped by the two different tasks.

There is behavioral evidence that suggests that infant summation areas are larger than those of adults for both luminance and motion (Wattam-Bell, 1994; Hamer & Schneck, 1984). Moreover, using the VEP, we have previously found that infants integrate same-orientation information less selectively than do adults (Hou, Pettet, Sampath, Candy, & Norcia, 2003). Infants show relatively stronger lateral interactions between

oriented targets place side-by-side rather than end-to-end, compared with adults who show less interaction in the side-by-side case. Although we have demonstrated at least a rudimentary specificity for collinearity, immaturities in either the strength of collinear interaction or the shape of the interaction region may account for the extended developmental sequence for contours in noise observed behaviorally (Kovacs et al., 1999; Pennefather, Chandna, Kovacs, Polat, & Norcia, 1999).

Configuration Effects on the Second Harmonic of the Texture Response

Both texture and contour displays produced significant odd harmonics and their respective control conditions did not. We consider this to be an indication of configural sensitivity because it indicates that responses to transitions to and from the different global organizations produced different responses. In the case of the texture stimuli, the organized textures also produces a larger second harmonic than was measured in the control condition. This suggests the action of a process that is common to both transitions to and from the organized texture. It is possible that the adult observers implicitly adopted a different attentional set during the test condition than in the control condition. The test condition contained rapidly changing and unpredictable appearances of the global organization. This unpredictability is absent in the control condition. If the observers were attempting to attentively track the appearances of the global organization, this elevated level of attention or arousal in the texture condition could produce an overall enhancement of activity, relative to the control condition. Previous VEP (Schubo, Meinecke, & Schroger, 2001) and neuroimaging studies (Kastner et al., 2000) have found that texture segmentation proceeds at least partially in the absence of perceptual awareness. However, the texture segmentation VEP is enhanced by making the segmentation task relevant (Schubo et al., 2001). The contour stimuli were on the other hand, highly predictable in both test and control conditions and may not have elicited a differential attention/arousal effect. The second harmonic effect was not seen in another experiment in the same group of adults when the global organization of the texture was always presented at the same orientation (data not shown).

Comparison to Previous Developmental Studies of Global Integration

Our data suggest that at least a crude form of global form integration is present between 2 and 4 months of age. This is slightly earlier than seen by Atkinson and Braddick (1992) and substantially earlier than seen by Sireteanu and Rieth (1992) who studied texture segmen-

tation based on orientation cues. Sensitivity to the global organization of oriented line segments has been demonstrated at 4 months using visual habituation (Humphrey, Muir, Dodwell, & Humphery, 1988). By implication, extraction of the global orientation of textures or patterns indicates that the local orientation has been extracted as well. It is generally believed that orientation selectivity is present at birth (Atkinson, Hood, Wattam-Bell, Anker, & Tricklebank, 1988; Slater, Morison, & Somers, 1988) and that detection of dynamic changes in orientation emerges no later than 6 weeks (Braddick, Wattam-Bell, & Atkinson, 1986).

This is the first study of contour detection in human infants. Previous psychophysical studies have found that the majority of 3-year-olds can detect Gabor-defined contours in noise (Pennefather et al., 1999), but that adult levels of sensitivity are not reached until adolescence (Kovacs et al., 1999). It will be of interest to determine in future studies how the addition of noise affects infant sensitivity to contours.

Other developmental studies involving the detection of global patterns have been performed in the motion domain. Infants have been found to discriminate structure from motion random-dot displays by 7 months (Spitz, Stiles, & Siegel, 1993). At a more basic level of processing, the coherence threshold for the discrimination of a pattern made by moving dots is first measurable after approximately 3 months (Mason, Braddick, & Wattam-Bell, 2003; Banton, Dobkins, & Bertenthal, 2001; Banton, Bertenthal, & Seaks, 1999; Wattam-Bell, 1994). Fully adult performance appears to occur only in late childhood or early adolescence in both form and motion coherence tasks (Elleberg, Lewis, Maurer, Brar, & Brent, 2002; Gunn et al., 2002; Lewis et al., 2002; Atkinson, 2000; Giaschi & Regan, 1997) as well as texture segmentation (Sireteanu & Rieth, 1992). Thus, although basic competence can be demonstrated quite early in development, global integration mechanisms have an extended developmental sequence.

Mechanisms Underlying Global Integration

The Gabor patches we used to define our stimuli are spatially localized, as well as being of a single scale. Previous studies of the integration of orientation information using Gabor-based configurations have suggested that integration over 3 wavelengths is mediated, at least in part, by mechanisms that integrate the responses of small receptive field mechanisms that are similar in size to the patches themselves (Field et al., 1993; Kovacs & Julesz, 1993; Polat & Sagi, 1993). More recently, it has been found that the apparent receptive field size of V1 neurons is much larger when they are measured on a high-contrast textured background (Kapadia, Westheimer, & Gilbert, 1999). The full extent of the receptive field in early visual areas thus appears to be highly dependent on context and may well differ for textures

conductive gel (10–20, D. O. Weaver). In the adults, a row of 5 electrodes, each referenced to Cz was placed symmetrically at a level of Oz. The lateral electrodes were 3 and 6 cm to the right and left of Oz. For the infants, only the central 3 channels were used. Electrode impedance was between 3 and 10 k Ω . The EEG was amplified by a factor of 50,000 for the adults and 20,000 for the infants (Grass Model 12 amplifiers with analog filter settings of 0.3–100 Hz, measured at –6 dB points). The EEG was digitized to 16 bits accuracy at a sampling rate of 432 Hz.

Time-locked averaged waveforms were computed for each subject and grand averages were computed across subjects. The time averages were digitally filtered using an inverse discrete Fourier transform that computed a synthesis of the first 53 harmonics of the 1-Hz stimulus frequency. The epoch length for the transform was 2 sec and the EEG noise at the odd multiples of 0.5 Hz was excluded from the synthesis, because no driven activity occurred at these frequencies. Significance of the difference potentials was assessed using a permutation test based on that of (Blair & Karniski, 1993).

In addition, spectral analysis for single observer data was performed using an adaptive filter (Tang & Norcia, 1995), which provided better signal-to-noise performance than the discrete Fourier transform. The first 6–7 harmonics (1–7 Hz) were selected for quantitative analysis, because virtually all configuration-specific activity occurred below 6 Hz, although the transient response contained frequencies up to 25–30 Hz. For each subject and stimulus condition, the real and imaginary spectral coefficients were averaged separately across trials, and then the amplitude and phase were calculated from these “coherently” averaged coefficients. In a similar way, amplitudes and phases were calculated for each stimulus condition by coherently averaging the spectral data across subjects. Error statistics for the group averages were computed using the T_{circ}^2 statistic (Victor & Mast, 1991), a variant of Hotelling’s T^2 statistic that assumes equal variance and zero covariance between the real and imaginary spectral coefficients of a response. The T_{circ}^2 statistic is distributed as $F(2, 2n - 2)$, where n is the number of subjects. Significance levels reported in Figures 5 and 9 are probabilities of observing given coherent average amplitude equal to zero. Error bars in these figures are coherent standard errors, in which variance terms (and associated degrees of freedom) are the sum of squares of both the real and imaginary components from each subject. Coherent averaged amplitude goes to zero in the limit for EEG noise.

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