

Rapid communication

Detection of contour continuity and closure in three-month-olds

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Abstract

The present study used an operant conditioning procedure and contour integration stimuli to test three-month-olds' sensitivity to both contour continuity and contour closure. The data demonstrate an immaturity of continuity detection and a lack of closure detection at that age, relative to a previous finding of a heightened sensitivity to closed contours in adult observers. This finding modifies the general view of infant visual perception that has been more focused on the quantitative development of various aspects of visual perception, including contrast sensitivity, binocular disparity processing, perceptual completion, and other perceptual skills. These results suggest qualitative change in terms of the organization of visual information during development, and implications of this finding for visual maturation of mechanisms suggested to underlie these detection abilities are discussed.

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1. Introduction

The process by which the human visual system distinguishes and delineates objects in a scene, often termed figure-ground segmentation, depends on the ability to detect continuous contours and closed regions in the visual field. The importance of “good continuation” and “closure” was first noted by the Gestalt school in the early part of the 20th century. More recently, good continuation and closure have been investigated in a contour integration procedure employing Gabor-based stimuli (see Fig. 1) appropriate for low-level cortical processing (Field, Hayes, & Hess, 1993; Kovács & Julesz, 1993, 1994; Pettet, McKee, & Grzywacz, 1998). Tests of adult human observers using these stimuli and a task involving the detection of a continuous path defined by orientation alignment against randomly oriented elements have shown that detection sensitivity is a factor of two greater for closed contours than for open contours (Kovács & Julesz, 1993; Pettet et al., 1998).

These findings show that closed contours are perceptually superior to open contours, substantiating the gestalt school theory that closed contours are not merely lines: closed contours appear to form a shape or surface area. This crucial step towards object-oriented processing appears to be initiated at an early cortical processing level by the intricate interactions of orientation-selective neurons in the primary visual cortex (V1) (Burkhalter, Bernardo, & Charles, 1993; Gilbert, Das, Ito, Kapadia, & Westheimer, 1996; Gilbert & Wiesel, 1983; Polat & Sagi, 1993; White, Coppola, & Fitzpatrick, 2001).

The specific connectivity pattern within the visual cortex responsible for enhancing continuous contours in the field of view has been investigated in psychophysical (Field et al., 1993; Kovács & Julesz, 1993, 1994; Pettet et al., 1998; Polat & Sagi, 1993), neurophysiological and neuroanatomical (Burkhalter et al., 1993; Gilbert et al., 1996; Gilbert & Wiesel, 1983; White et al., 2001), and imaging (Altmann, Bulthoff, & Kourtzi, 2003; Kourtzi, Tolia, Altmann, Augath, & Logothetis, 2003) studies. The underlying network has been found to include horizontal connections between cells of similar orientation tuning that code for neighboring locations of the visual field, and to rely on the statistics of

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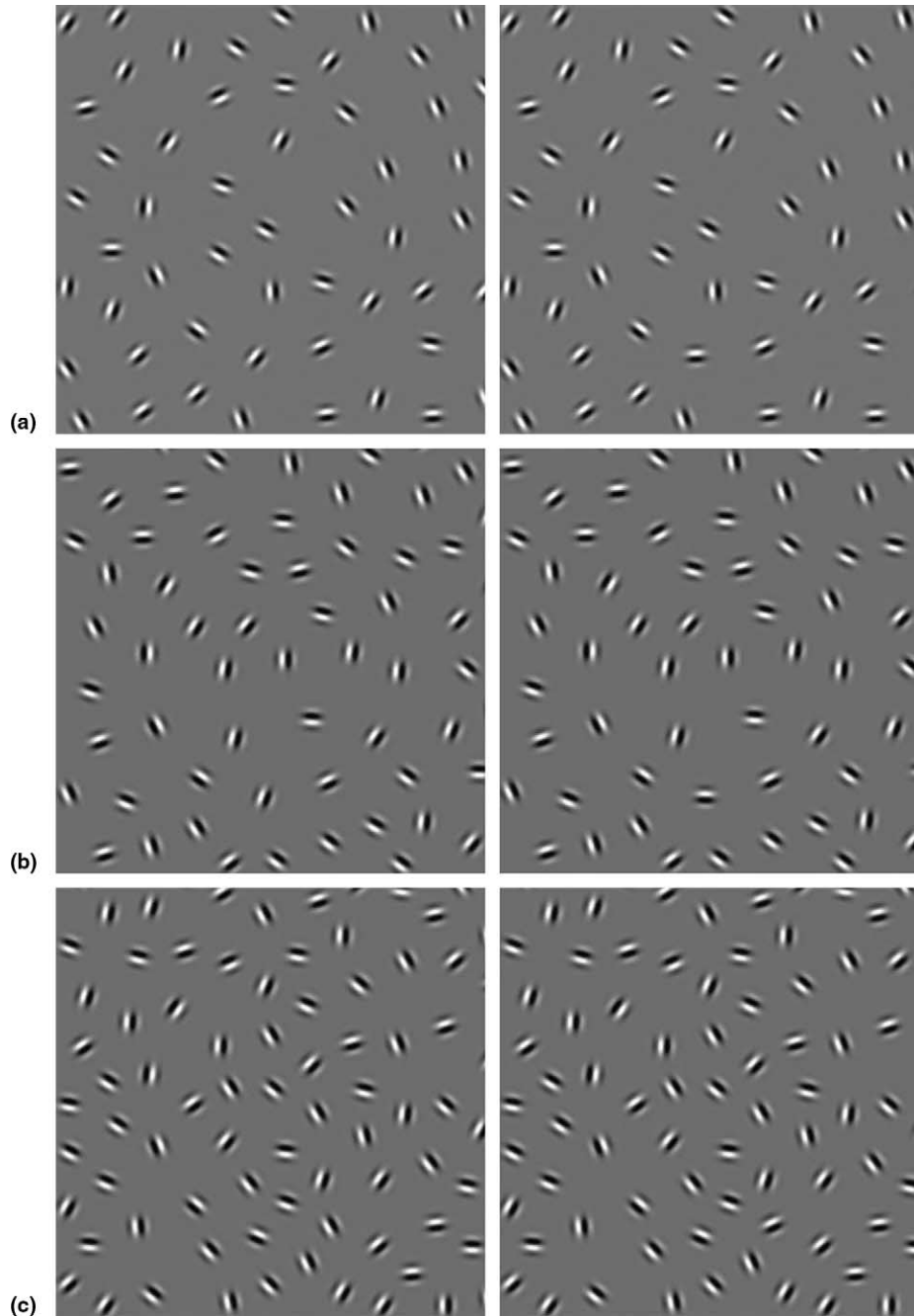


Fig. 1. Examples of contour integration stimuli, open (left panels) and closed (right panels), at all of the noise levels used in the experiment. (a) $D = 1.0$; (b) $D = 0.9$; (c) $D = 0.8$ ($D = \text{mean background spacing}/\text{contour spacing}$).

images encountered in the natural world (e.g., prevalence of long contours) during the fine-tuning of these connections (Olshausen & Field, 1996, 1997; Simoncelli & Olshausen, 2001). The plexus of long-range horizontal connections within layers of V1 is thought to be an important part of this network (Gilbert et al., 1996; Gilbert & Wiesel, 1983; White et al., 2001).

To what extent is the human infant's visual system equipped with this highly specific underlying network that gives rise to perception of well-defined (closed)

shapes? The maturation of horizontal connections in layer 2/3 of V1 seems to span several years in humans (Burkhalter et al., 1993). Burkhalter et al. reported that V1 neurons related to the processing of visual motion (layer 4B, 5, and 6) appear prenatally and begin to develop the mature "patchiness" characteristic of adults after about eight weeks of age, while connections in layers 2/3, generally associated with form perception, are not seen until after 16 weeks postnatal and do not appear to be neuroanatomically mature until well after

one year of age. These later-developing connections are suggested to be part of the physiological mechanism that instantiates good continuation and possibly closure detection in the visual system (see Kovács, 1996).

Neuroanatomical maturation does not necessarily translate to functional maturity, and research employing the contour integration procedure (Kovács & Julesz, 1993) has shown that contour integration ability is not adult-like in children 5–14 years of age (Kovács, Kozma, Feher, & Benedek, 1999), indicating that these neural circuits are likely experience-dependent and relatively slow to reach functional maturity. Psychophysical studies of the amblyopic human visual system emphasize the importance of normal visual input in building up these connections (Kovács, Polat, Norcia, Pennefather, & Chandna, 2000), and it has also been shown anatomically, in the ferret, that the full elaboration of both the local columnar circuits and the horizontal network in layer 2/3 requires the influence of normal visual experience (White et al., 2001).

These previous studies demonstrate that the contour integration system is not mature until well into childhood, if not later. The ontogenetic beginning of this process, however, is not well-understood. Three-month-old infants, lacking the horizontal interconnections in layers 2/3 (Burkhalter et al., 1993), should show poor performance, relative to the mature system, if these horizontal connections are indeed an integral part of the physiological mechanism that implements contour integration. If, in particular, these connections are needed to implement a closure detection mechanism, then infants at this age should show an approximately equal level of performance in detecting open as compared to closed contours. This would be in contrast to adults, for whom closure, as noted above, imparts a clear advantage to contour detection, with detection sensitivity a factor of two greater for closed contours than for open contours (Kovács & Julesz, 1993). The present experiment extends this test of detection thresholds downward to infants 3–4 months of age, and in doing so, provides evidence in support of the hypothesis that these connections play an integral role in contour integration and closure detection.

The contour-integration task employs orientation noise to estimate the efficiency of the integration of orientation information across the visual field; this task has been used extensively to study perceptual organization in normal adult observers (Field et al., 1993; Kovács, 1996; Kovács & Julesz, 1993, 1994; Kovács, Feher, & Julesz, 1999). To study the human developmental pattern of spatial integration, a card-test version of the contour detection task was constructed (Kovács, 1996; Kovács et al., 1999; Pennefather, Chandna, Kovács, Polat, & Norcia, 1999). Each card in this version displayed a closed chain of colinearly aligned Gabor signals (contour) similar to the stimuli illustrated in Fig. 1 (right

panels) in a background of randomly oriented and positioned Gabor signals (orientation noise—see Fig. 1). The task was to detect the contour. The orientation noise forces the observer to rely solely on long-range interactions between local filters while connecting the signals perceptually. To estimate the actual strength of long-range interactions in each observer, relative noise density is varied. Relative noise density (D) is defined as the ratio of average noise spacing over contour spacing. The current test of infants uses a variation of the stimuli displayed on these cards, adapted to infant visual acuity (see Section 2).

2. Methods

2.1. Subjects

Infants, recruited from birth announcements in local newspapers, were randomly assigned to conditions as they became available for study. The final sample included 63 infants with normal vision (no clinical diagnosis of a vision problem) ranging in age from 75 to 128 days (M age = 96.5 days, $SD = 13.1$). The infants were Hispanic ($N = 4$), African-American ($N = 2$), Asian-American ($N = 1$), Caucasian ($N = 55$), and 1 infant for whom ethnicity was not reported. Additional infants were dropped from the final sample for excessive crying, defined as crying for 2 min continuously ($n = 10$), scheduling changes/equipment problems ($n = 6$), failure to meet a preset learning criterion, defined as an increase of 1.5 above a specific infant's mean baseline for 2 out of any 3 min during acquisition ($n = 3$), and a clinically diagnosed vision problem ($n = 1$; infants with a clinically diagnosed condition were excluded from the sample). This level of loss is typical for an experimental design (see below) requiring three consecutive daily visits (Greco, Hayne, & Rovee-Collier, 1990).

2.2. Apparatus

The investigation employed an operant conditioning procedure in which an infant's foot was attached to a mobile using a ribbon (Rovee & Rovee, 1969; Rovee-Collier, 1999; Rovee-Collier & Gekoski, 1979). Each infant was placed in a standard infant sling seat (thus, seated reclining, but looking straight ahead) and a "mobile" of sorts was placed directly in the infant's line of sight, at a viewing distance of 20–25 cm, with three stimulus cards (each displaying the same stimulus pattern) presented orthogonal to the infant's line of sight (see Fig. 2). A trained observer, out of the infant's line of sight, recorded kicks during each minute of each session. A second observer, blind to the infant's condition, also recorded kicks on 45% of sessions, resulting in a mean correlation of 0.93 across these sessions.



Fig. 2. An infant in the apparatus.

2.3. Procedure

The mobile conjugate reinforcement procedure (Hartshorn et al., 1998) was used to train and test infants. This procedure, which typically takes place in the infant's home, provides preverbal infants with a behavioral response that can be used to test visual perceptual capacities (Rovee-Collier & Gerhardstein, 1997). The procedure included two 15-min training sessions and a 15-min testing session occurring over three consecutive days (the training and test mobiles typically differ across experimental conditions, but there is always a control condition in which no change occurs between training and test).

Each session began with a 3-min period of non-reinforced exposure to the stimuli (the ribbon was not attached to the mobile during this period), followed by a 9-min period of reinforced exposure during which infants' kicks caused the mobile to move and sway slightly, and caused the bells to jingle. Stronger kicks produced larger amounts of reinforcement (movement and sound). Each session ended with a 3-min period of non-reinforced exposure.

The first 3-min period on Day 1 is labeled the Baseline phase, and provides an assessment of the infant's operant, or unlearned, kicking level. The final 3-min period of Day 2 is labeled the immediate retention test (IRT), and serves as an indication of the infant's kicking level immediately following training. The initial 3-min period of Day 3 serves as the discrimination test (DT). Note that all three phases, Baseline, IRT, and DT, are non-reinforcement phases; the infant has no opportunity for new learning during these phases.

The mean Baseline and mean IRT for a group establish a range on which the infants' performance during the discrimination test phase can be evaluated. Responding during the DT-phase at or near the group's Baseline indicates complete discrimination (the test stimulus has failed to cue the trained response), while

responding during DT-phase at or near the mean IRT for a group indicates a failure of discrimination, or generalization (the test stimulus was successful in cuing the trained response). An intermediate response would indicate near-threshold performance. Thus, when analyzing the raw data using an ANOVA, an interaction of group and phase would indicate that one group likely discriminated while another did not; a follow-up test on DT data alone is used to further support this assertion. Note that a main effect of phase is generally taken to indicate that the infants, across group, showed learning; this conclusion is made as part of an assertion that the IRT mean (across groups) is significantly higher than the Baseline mean.

2.4. Stimuli

The mobiles used in the experiment contained three 5 in. cards, each displaying a stimulus consisting of a set of Gabor patches (small sinusoid gratings with blurred edges) rendered with a spatial frequency of 2.95 cpd (Gabor wavelength = 0.34 deg, with an envelope size equal to the wavelength) and maximal contrast, viewed under natural daylight (see Figs. 1 and 2). The stimulus pattern and the overall number of patches on a stimulus card varied by condition (see Section 2.5, and Fig. 1).

2.5. Design

2.5.1. Initial test groups

Infants were trained and tested in one of two initial groups ($N = 8$ per group; M age = 92.2 days, $SD = 11.5$ days) to determine whether or not they could detect a pattern rendered using Gabor patches. A *no-change group* was trained and tested with a set of cards displaying either randomly oriented Gabor patches ($N = 2$) or cards in which all of the Gabor patches were arranged into a pattern (a spiral; $N = 3$, or a starburst pattern; $N = 3$). Infants in a *pattern-change group* were trained with cards displaying one pattern and were then tested with the untrained pattern (training/test pattern was counterbalanced across infants). The spiral and starburst patterns had the same number of elements, and element locations were also the same. Therefore, the patterns could only be discriminated if the observer was able to employ the orientation information provided by the Gabor patches.

2.5.2. Contour type and density manipulation

Following this initial test, six additional groups of randomly assigned infants ($N = 8$ per group; M age = 97.7 days, $SD = 13.0$ days) were trained with cards displaying randomly oriented Gabor patches. These infants were tested (on Day 3) with cards displaying either an open contour (one element was rotated out of align-

ment with the path of the closed contour of Fig. 1, left panels) or a closed contour (Fig. 1, right panels). Contours (closed and open) were rendered by aligning Gabor patches in a field of visual noise consisting of randomly oriented Gabor patches. The contours were rendered with a contour density (D) of 1.0, 0.9, or 0.8 (D = mean background spacing/contour spacing).

3. Results

3.1. Initial test groups

One infant was dropped from the no-change group following data collection due to a post-testing diagnosis of astigmatism. Infants in the *no-change* group responded slightly more strongly during the discrimination test than at the end of training, indicating that they recognized the test stimulus, while infants in the *pattern change* group did not; their discrimination test

rates were almost identical to their pre-training baseline rates. An analysis of variance on kick rates, using factors of phase (Baseline, IRT, and DT) and group (no-change, pattern-change) confirmed this interpretation: The main effects of group and phase were both significant, and the interaction of group and phase was reliable, $F(2, 26) = 12.68$, $p < 0.001$. A significant main effect of phase shows that the infants' training was effective. The presence of a reliable interaction shows that the pattern of responding across phases differed between the two groups (see Fig. 3). This result suggests that infants could discriminate between the two patterns, and therefore, could detect the Gabor patches used to render each pattern. A follow-up ANOVA on the same factors, but including only baseline and IRT phases, revealed only a main effect of phase, $F(1, 13) = 33.96$, $p < 0.0001$. There was no effect of group and no interaction, indicating that the interaction found in the overall analysis was due to differences in phase DT. A planned comparison between the two groups at test (DT-phase;

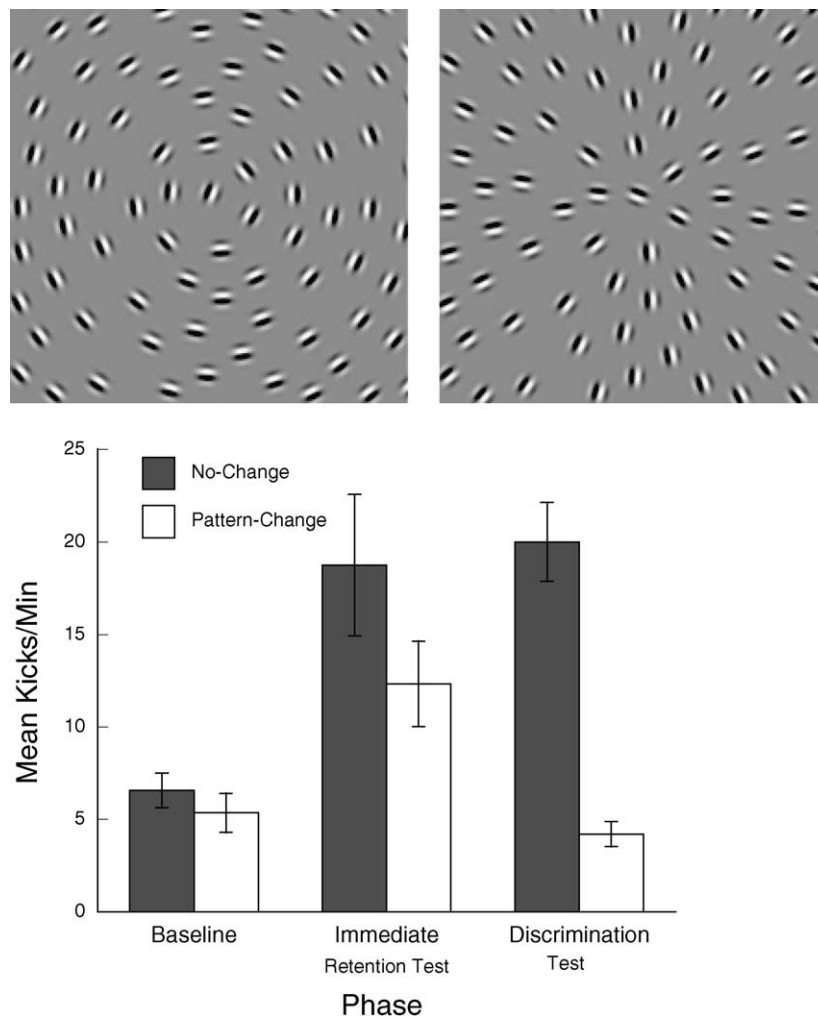


Fig. 3. Top: Stimuli for the initial test of infants. Bottom: Results of the initial test of infants with either no change between training and test, or a pattern change between training and test. Error bars indicate ± 1 standard error of the mean.

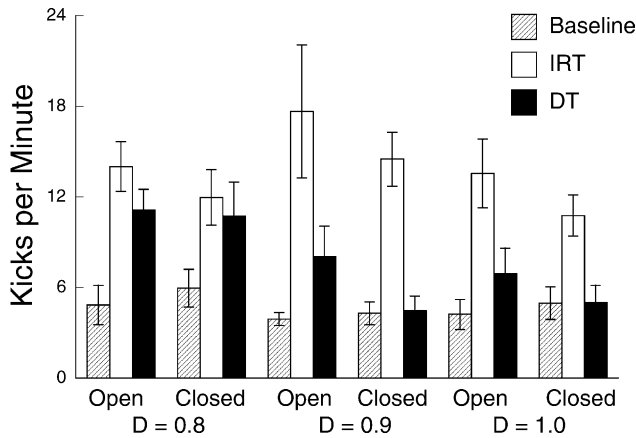


Fig. 4. Infants' responses in all three phases of the experiment. The three bars show data from baseline, prior to training (striped bar), the immediate retention test (IRT-white bar) following training at the end of day 2 and before the introduction of a test stimulus, and the discrimination test (DT-black bar) on day 3 with a new stimulus present. Error bars represent ± 1 standard error of the mean.

no-change $M = 19.99$, pattern-change $M = 4.20$), $t(13) = 7.5$, $p < 0.001$, confirmed this interpretation, showing that infants' performance across groups differed specifically during phase DT (see Fig. 3).

3.2. Contour type and density manipulation

Infants tested at $D = 0.8$ (with both open and closed contours) showed significantly greater levels of responding at discrimination test relative to baseline than infants tested at higher levels (see Fig. 4). An analysis of variance over mean kicks per minute, on the factors of phase (baseline, IRT, and discrimination test), density (D : 1.0, 0.9, 0.8) and contour type (open, closed) confirmed this conclusion; there was an interaction of phase and density, $F(4, 82) = 4.43$, $p < 0.003$. The only other significant effect was a main effect of phase, which demonstrates that the infants' training was effective. A follow-up ANOVA conducted on the same factors, but including only baseline and IRT phases, showed a main effect of phase, $F(1, 42) = 101.26$, $p < 0.0001$, but no other significant main effects or interactions, again demonstrating that training was effective, and showing that the interaction detected by the overall analysis was due to differences in performance during the discrimination test (DT) phase.

Was there an effect of contour type (open or closed)? The initial test suggests that there was not, because there was no main effect of contour type and no interaction. A stronger test, however, would be a set of comparisons between performance of infants tested with open contours and infants tested with closed contours at each level of D . These tests (Tukey–Kramer posthocs) support the initial conclusion; there was no indication of a significant difference at any level of D (while planned comparisons are not really justified in this situation,

the outcome is the same if planned comparisons are conducted instead of posthoc tests).

What is the infants' threshold for contour detection (open or closed)? Follow-up ANOVAs on phase at each level of D , collapsing across contour type, showed reliable effects (all p 's < 0.0001). Bonferroni posthoc tests at $D = 1.0$ showed that responding at test (DT) was significantly lower than during IRT, but did not differ from baseline. This outcome shows that infants could detect the contour at this level of D . The same posthoc tests at $D = 0.8$ showed the reverse pattern; responding at test (DT) was not significantly lower than during IRT, but was significantly higher than baseline. Posthoc tests at $D = 0.9$ follow the same general pattern as 1.0 (DT significantly lower than IRT, no difference from baseline), but the DT-baseline comparison is significant ($p = 0.047$) before the Bonferroni correction is applied. This suggests that infant performance at $D = 0.9$ is only slightly above threshold. Overall, these follow-up tests show that the infants viewing the contours embedded in noise at $D = 0.8$ failed to discriminate between noise-only stimuli and contour-containing images, while infants at $D = 0.9$ did show discrimination, suggesting that the infants' threshold for the detection of a contour in noise is in the $D = 0.8$ – 0.9 range. The outcome actually suggests that the threshold is closer to 0.9, but a more precise threshold determination would require further testing.

This threshold, while imprecise, is considerably higher than previously reported adult thresholds of approximately $D = 0.65$ for closed contours (Kovács & Julesz, 1993). The lack of any significant difference between infants' performance on open and closed contours, in combination with their overall insensitive performance in detecting closed contours, suggests that the mechanism responsible for detecting closure, as compared to contour continuity in general, is weak or non-functional at this early stage in ontogeny.

4. Discussion

Our results show that three-month-old human infants are able to establish orientation correlations in the visual field, and lacking other visual cues, can rely solely on good continuation of contour elements. Their ability, however, is far from adult-like in terms of noise tolerance. We have suggested earlier that the pronounced noise sensitivity in children found using this paradigm might be related to the shorter spatial range of long-range spatial interactions relative to that of adults (Kovács, Kozma, et al., 1999). Anatomical findings (Burkhalter et al., 1993; White et al., 2001) and behavioral data (Hou, Pettet, Sampath, Candy, & Norcia, 2003) also suggest that normal maturation of V1 horizontal connections includes a stage where the axonal

connections are established, but are not yet specifically tuned. Recovery of the long and smooth contours occurring in the natural environment will be limited in either case, and the integration of orientation measurements by local neural elements is likely to be less efficient and more ambiguous.

The finding that three-month-old infants show no apparent closure-superiority effect also suggests that long-range connections in V1 are not operating at full power, although this result might also be attributed to the immaturity of feedback connections from higher cortical areas, as recent findings (Altmann et al., 2003; Kourtzi et al., 2003) have shown that both low-level (V1) and higher-level areas, such as the lateral occipital cortex (LOC) appear to be involved in contour integration. The lack of differential closure detection at three months of age might be a clue in explaining earlier developmental findings on object-related processing, where, for example, four-month-olds were not interested in static occlusion displays (Kellman & Spelke, 1983) or static displays more generally (Kellman, 1984). Sensitivity to closure means a general sensitivity to contextual influences, and so-called “global” image properties. More specifically, closure sensitivity should help in assigning surface areas and surface properties to contours, establishing boundary ownership, making decisions about occlusion relationships, and finally, segmenting objects in crowded scenes. The neural mechanism responsible for accomplishing these tasks is not clearly understood, but the mechanism probably relies on long-range orientation correlations at an early level, where closed chains of facilitatory interactions might enhance neural activity at important locations while suppressing spurious groupings of local elements elsewhere.

These conclusions regarding the lack of a closure superiority effect must be tempered by several cautionary notes. It is quite possible that the threshold for open contours is higher than that for closed, but that both are within the 0.9–0.8 range tested. This possibility would weaken, but not eliminate, the argument stated above, as the effect would be weaker than that of adults, and would again suggest the possibility of shorter (immature) long-range connections in the areas (layers 2/3) responsible for form perception in V1. Another issue might be the complexity of the stimuli, but the initial tests using the star and spiral patterns clearly demonstrate that the infants are capable of discriminating between two patterns, both rendered using Gabor patches.

The low-level visual system is considered to consist of banks of perceptual filters with small receptive fields, orientation and spatial frequency tuning, and interactions between filters of, for example, similar orientation tuning (Wilson & Wilkinson, 1997). The results show that the rough tuning of the filters might already be in place, because the infants were able to rely solely on orientation information when integrating the contours

(D at threshold < 1.0). Interactions between the filters, however, do not appear to be operating at full power. This immature system may provide the infants with a less detailed local edge map as compared to the mature system, and may contribute to an increase in ambiguity in determining boundary ownership, reduce the effectiveness of figure-ground segmentation, and increase errors in determining occlusion relationships, among other potential consequences of this impoverished input to the system at this early point in development.

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References

- Altmann, C. F., Bulthoff, H. H., & Kourtzi, Z. (2003). Perceptual organization of local elements into global shapes in the human visual cortex. *Current Biology*, *13*, 342–349.
- Burkhalter, A., Bernardo, K. L., & Charles, V. (1993). Development of local circuits in human visual cortex. *Journal of Neuroscience*, *13*, 1916–1931.
- Field, D. J., Hayes, A., & Hess, R. F. (1993). Contour integration by the human visual system: evidence for a local “association field”. *Vision Research*, *33*, 173–193.
- Gilbert, C. D., Das, A., Ito, M., Kapadia, M., & Westheimer, G. (1996). Spatial integration and cortical dynamics. *Proceedings of the National Academy of Sciences, USA*, *93*, 615–622.
- Gilbert, C. D., & Wiesel, T. N. (1983). Clustered intrinsic connections in cat visual cortex. *Journal of Neuroscience*, *3*, 1116–1133.
- Greco, C., Hayne, H., & Rovee-Collier, C. (1990). The roles of function, reminding, and variability in the categorization of 3-month-old infants. *Journal of Experimental Child Psychology*, *22*, 278–281.
- Hartshorn, K., Rovee-Collier, C., Gerhardstein, P., Bhatt, R. S., Wondolowski, T. L., Klein, P., et al. (1998). The ontogeny of learning and memory over the first year-and-a-half of life. *Developmental Psychobiology*, *32*, 69–89.
- Hou, C., Pettet, M. W., Sampath, V., Candy, T. R., & Norcia, A. M. (2003). Development of the spatial organization and dynamics of lateral interactions in the human visual system. *Journal of Neuroscience*, *23*, 8630–8640.
- Kellman, P. J. (1984). Perception of three-dimensional form by human infants. *Perception and Psychophysics*, *36*, 353–358.
- Kellman, P. J., & Spelke, E. (1983). Perception of partly occluded objects in infancy. *Cognitive Psychology*, *15*, 483–524.
- Kourtzi, Z., Tolia, A. S., Altmann, C. F., Augath, M., & Logothetis, N. K. (2003). Integration of local features into global shapes: monkey and human MRI studies. *Neuron*, *37*, 333–346.
- Kovács, I. (1996). Gestalten of today: early processing of visual contours and surfaces. *Behavioural Brain Research*, *82*, 1–11.
- Kovács, I., & Julesz, B. (1993). A closed curve is much more than an incomplete one: effect of closure in figure-ground segmentation. *Proceedings of the National Academy of Sciences, USA*, *92*, 7495–7497.

- Kovács, I., & Julesz, B. (1994). Perceptual sensitivity maps within globally defined visual shapes. *Nature (London)*, *370*, 644–646.
- Kovács, I., Feher, A., & Julesz, B. (1999). Medial-point description of shape: A representation for action coding and its psychophysical correlates. *Vision Research*, *38*, 2323–2333.
- Kovács, I., Kozma, P., Feher, A., & Benedek, G. (1999). Late maturation of visual spatial integration in humans. *Proceedings of the National Academy of Sciences, USA*, *96*, 12204–12209.
- Kovács, I., Polat, U., Norcia, A. M., Pennefather, P. M., & Chandna, A. (2000). A new test of contour integration deficits in patients with a history of disrupted binocular experience during visual development. *Vision Research*, *40*, 1775–1783.
- Olshausen, B. A., & Field, D. J. (1996). Emergence of simple-cell receptive field properties by learning a sparse code for natural images. *Nature*, *381*, 607–609.
- Olshausen, B. A., & Field, D. J. (1997). Sparse coding with an overcomplete basis set: a strategy employed by V1? *Vision Research*, *37*, 3311–3325.
- Pennefather, P. M., Chandna, A., Kovács, I., Polat, U., & Norcia, A. M. (1999). Contour detection threshold: Repeatability and learning with 'contour cards'. *Spatial Vision*, *12*, 257–266.
- Pettet, M. W., McKee, S. P., & Grzywacz, N. M. (1998). Constraints on long range interactions mediating contour detection. *Vision Research*, *38*, 865–879.
- Polat, U., & Sagi, D. (1993). Lateral interactions between spatial channels: suppression and facilitation revealed by lateral masking experiments. *Vision Research*, *33*, 993–999.
- Rovee, C. K., & Rovee, D. T. (1969). Conjugate reinforcement of infant exploratory behavior. *Journal of Experimental Child Psychology*, *8*, 33–39.
- Rovee-Collier, C. (1999). The development of infant memory. *Current Directions in Psychological Science*, *8*, 80–85.
- Rovee-Collier, C., & Gekoski, M. J. (1979). The economics of infancy: a review of conjugate reinforcement. In H. W. Reese & L. P. Lipsitt (Eds.), *Advances in child development and behavior* (Vol. 13, pp. 195–255). New York: Academic.
- Rovee-Collier, C., & Gerhardstein, P. (1997). The development of infant memory. In N. Cohen (Ed.), *The development of memory in childhood* (pp. 5–40). Hove East Sussex: Psychology Press.
- Simoncelli, E. P., & Olshausen, B. A. (2001). Natural image statistics and neural representation. *Annual Review of Neuroscience*, *24*, 1193–1216.
- White, L. E., Coppola, D. M., & Fitzpatrick, D. (2001). The contribution of sensory experience to the maturation of orientation selectivity in ferret visual cortex. *Nature*, *411*, 1049–1052.
- Wilson, H. R., & Wilkinson, F. (1997). Evolving concepts of spatial channels in vision: from independence to nonlinear interactions. *Perception*, *26*, 939–960.