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Investigating the interaction between low and intermediate levels of spatial vision at different periods of development

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Although much research has investigated the visual development of lower (local) and higher levels (global) of processing in isolation, less is known about the developmental interactions between mechanisms mediating early- and intermediate-level vision. The objective of this study was to evaluate the development of intermediate-level vision by assessing the ability to discriminate circular shapes (global) whose contour was defined by different local attributes: luminance and texture. School-aged children, adolescents, and adults were asked to discriminate a deformed circle (radial frequency patterns or RFP) from a circle. RFPs varied as a function of (a) number of bumps or curvatures (radial frequency of three, five, and 10) and (b) the physical attribute (luminance or texture) that defined the contour. Deformation thresholds were measured for each radial frequency and attribute condition. In general, results indicated that when compared to adolescents and adults children performed worse only when luminance-defined shapes had fewer curvatures (i.e., three and five), but for texture-defined shapes, children performed worse across all types of radial frequencies (three, five, and 10). This suggests that sensitivity to global shapes mediated by intermediate level vision is differentially affected by the type of local information defining the global shape at different periods of development.

Introduction

Visual object perception is the result of numerous levels of cortical processing that increase in complexity. For example, intermediate-level visual mechanisms

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underlying shape perception constitute a crucial step in the representation of complex visual objects, such as faces (van den Boomen, van der Smagt, & Kemner, 2012). The developmental trajectories of simple percepts or local attributes (e.g., lines) mediated by lower level visual cortical mechanisms, along with those of complex or global representations (e.g., faces or objects) mediated by higher level processes, are relatively well documented (Braddick & Atkinson, 2011; van den Boomen, van der Smagt, & Kemner, 2012). However, the relationship between lower and intermediate levels of perception has yet to be systematically assessed within a developmental context. This represents an important void in the literature since visual mechanisms operating at different levels within the visual hierarchy develop at different rates (Braddick & Atkinson, 2011), contingent on the type of the information each mechanism is most sensitive to (Braddick & Atkinson, 2011; Lewis & Maurer, 2005; van den Boomen, van der Smagt, & Kemner, 2012).

Visual mechanisms operating in V1, the earliest level of cortical processing, mediate simple information that is defined by changes in luminance (a first order characteristic; Baker, 1999; Baker & Mareschal, 2001; Ferster & Miller, 2000). When visual information is defined by nonluminance information, such as texture (second-order attributes, mediated by V2; Baker, 1999; Baker & Mareschal, 2001; Ferster & Miller, 2000; Nassi & Callaway, 2009) sensitivity is relatively decreased during local orientation (Lin & Wilson, 1996), local curvature (Wilson & Richards, 1992), and global shape (Bell & Badcock, 2008; Hess, Achtman, & Wang, 2001) perception tasks. This differential sensitivity is also reflected during development. For example, adult-like sensitivity to Landolt-C patterns defined by luminance occurs at approximately 10–12 years of age but goes beyond 12 years of age for those defined by texture (Bertone, Hanck, Guy, & Cornish, 2010), as does the ability to identify a global contour embedded in noise (Hadad, Maurer, & Lewis, 2010; Kovács, Kozma, Fehér, & Benedek, 1999). In general, the visual mechanisms responsible for processing simple, luminance-defined information seems to mature earlier than mechanisms underlying the integration of visual information into coherent forms (Bertone et al., 2010; Kovács, 2000; Parrish, Giaschi, Boden, & Dougherty, 2005).

While attributes or characteristics (e.g., luminance or texture) can define a contour, features of the contour describe a global shape. Among other global stimuli, the human visual system displays exquisite (hyperacuity) sensitivity to radial frequency patterns (RFP). RFPs are complex circular shapes whose contour can be manipulated by adding deformations deviating from a perfect geometrical circle (Wilkinson, Wilson, & Habak, 1998). Such shapes are processed by intermediate-level visual mechanisms (most likely in V4) that integrate local deformations or curvatures (local elements or features) into a complete global representation (global pooling) of its shape (Gallant, Shoup, & Mazer, 2000; Loffler, 2008; Pasupathy & Connor, 1999, 2001, 2002; Wilkinson et al., 2000).

However, when the number of deformations along the circumference varies, processing can shift towards local or global integration (Bell & Badcock, 2008; Jeffrey, Wang, & Birch, 2002; Loffler, 2008; Poirier & Wilson, 2006). Deformation detection of a circular shape relies on local curvature, with integration over only a limited portion of the contour for a high number of curvatures (≥ 10). Precisely, with greater numbers of curvatures surrounding the contour of the shape, a sequential analysis is performed, whereby information along the contour of the shape is added sequentially, resulting in what is known as probability summation (Loffler, Wilson, & Wilkinson, 2003; Schmidtmann, Kennedy, Orbach, & Loffler, 2012; Wilkinson et al., 1998). On the other hand, for fewer than five-eight deformations, integration is global over the entire shape (Jeffrey, Wang, & Birch, 2002; Loffler, Wilson, & Wilkinson, 2003). In this case, an object-centered approach is used, whereby information surrounding the contour of the shape is integrated in reference to the center, an approach known as global pooling (Loffler, Wilson, & Wilkinson, 2003; Wilkinson et al., 1998).

In addition to manipulating the number of curvatures surrounding the contour of the RFP, the physical attributes defining the shape can be manipulated by having RFPs defined by either luminance- (first-order) or texture-defined (second-order) information (Bell & Badcock, 2008; Loffler, Wilson, & Wilkinson, 2003). The processing of texture information is more complex than for the processing of luminance information since larger receptive fields of neurons tuned for local orientation need to be integrated, a process that takes longer than for luminance information. Therefore, an extra processing stage is involved when processing this physical attribute as compared to when luminance information defines the shape (Habak, Wilkinson, & Wilson, 2009; Lin & Wilson, 1996). By assessing the detection of RFPs defined by luminance and texture information, it is possible to assess whether manipulating the complexity of the shape differently influences intermediate level perception in children compared to adolescents and adults, which to our knowledge has never been conducted before.

In sum, the aim of the present study was to assess development of the interplay between low and intermediate levels of processing, by manipulating the attributes defining the contour (luminance-texture) and the amount of deformation surrounding the shape (local-global). To accomplish this, we used radial frequency patterns (RFP) defined by either luminance or texture that varied in the number of deformations about the contour.

Methods

Participants

Forty-seven participants in total participated in the study and were placed into three age groups (a) 7–12 years, $n = 16$, seven girls and nine boys, mean chronological age (CA) = 9.93; (b) 13–17 years, $n = 15$, three girls and 12 boys, mean CA = 15.87; (c) 18–26 years, $n = 16$, two women and 14 men, mean CA = 22.18. Forty-three of these participants were recruited from the Clinique d'Évaluation des Troubles Envahissants du Développement (CETED), at Rivière-des-Prairies Hospital. The remaining participants were recruited from outside the hospital setting. A semi-structured interview was used to exclude participants with a history of psychiatric treatment or learning disabilities, a familial history (first degree) of mood disorders, autism, or schizophrenia, and defective vision or audition, as well as those who were taking medication. All participants had Wechsler IQ (i.e., WISC-IV or WASI) of 80 or higher and had normal or corrected-to-normal far and near vision, which was assessed using both near and far acuity charts (i.e., near point directional –E- and –C-cards, Snellen letter sequence-A-new Logmar).

Apparatus and stimuli

Stimulus construction, presentation, and data recordings were controlled using custom Matlab software, incorporating routines from the Psychophysics and Video Toolbox (Brainard, 1997; Pelli, 1997). Stimuli were presented on a gamma-corrected, 19-in. Viewsonic CRT G90fb monitor, driven by a Macbook Pro laptop, and a CS-100 Minolta Chromameter was used for luminance/color reading and monitor gamma correction. Mean luminance of the monitor was 30.00 cd/m^2 (u' = 0.1912, v' = 0.4456 in CIE color space) with minimum and maximum luminance levels of 0.5 and 59.5 cd/m^2, respectively.

Stimuli consisted of radial frequency patterns (RFP), which resemble deformed circular contours and are defined by a sinusoidal modulation to a circle's radius according to the following equation:

$$r(\theta) = r_o\Big(1 + A\sin(\omega\theta + \phi)\Big), \qquad (1)$$

where r and θ are the polar coordinates of the contour and r_o is the mean or average radius (that of the base circle). The shape's geometry is controlled by the remaining parameters: ω is the radial frequency, which represents the integer number of sinusoidal modulation cycles around the circumference (number of curvatures or bumps and dips), is the angular phase, which controls the overall orientation of the shape, and A is the amplitude of the modulation and represents the depth of the bumps and dips as a proportion change in radius (Wilkinson et al., 1998). In addition, stimuli were defined either by luminance (first-order) or texture (second-order) information. Luminance-defined RFPs (first order; Figure 1, top) were constructed using a fourth derivative of a Gaussian (D4) with a peak spatial frequency of 4 c/° (bandwidth = 1.24 cycles) and a luminance contrast of 90% (see Wilkinson, Wilson, & Habak, 1998). Texture-defined RFPs (second order; Figure 1, bottom) were created by multiplying a radially modulated Gaussian Window by a radial carrier grating with a spatial frequency of 4 c/° and a luminance of 90% (see Habak, Wilkinson, & Wilson, 2006). For the pattern defined by second-order characteristics, we chose a texture that consisted of a sinusoidal carrier so that spatial frequency could be matched exactly to that of the first-order RFP, whereas a noise carrier (or other) would contain higher spatial frequencies and confound any differential effects of development on stimulus characteristics with spatial frequency sensitivity. In order to encourage participants to perceive the patterns globally, the position of all patterns was slightly jittered and presentation time was set at 200 ms. Radial frequencies of three, five, and 10 cycles per circumference were presented in separate runs (see Figure 1). Based on pilot testing, six different levels of amplitude modulation were chosen (0.001, 0.002, 0.004, 0.008, 0.016, and 0.032) for each RFP. Non-RFP (nontarget) stimuli were perfect circular shapes (amplitude = 0).

Procedure

Thresholds for the minimal deformation (or amplitude) needed to detect the deformed circle (the RFP) were measured. The method of constant stimuli was used in a two-interval forced choice paradigm (2-IFC), where participants indicated which of the two intervals contained the deformed circle or RFP (amplitude > 0); the other interval contained a perfect circle (amplitude $= 0$). Each stimulus was presented for 200 ms with a 400 ms interstimulus interval, during which the mean-gray background was maintained. Thresholds were measured for RFPs of varying radial frequency (three, five, & 10 RF) with contours defined by either luminance or texture, for a total of six experimental conditions. In each block, a single combination of radial frequency and contour definition was shown. Within each block,

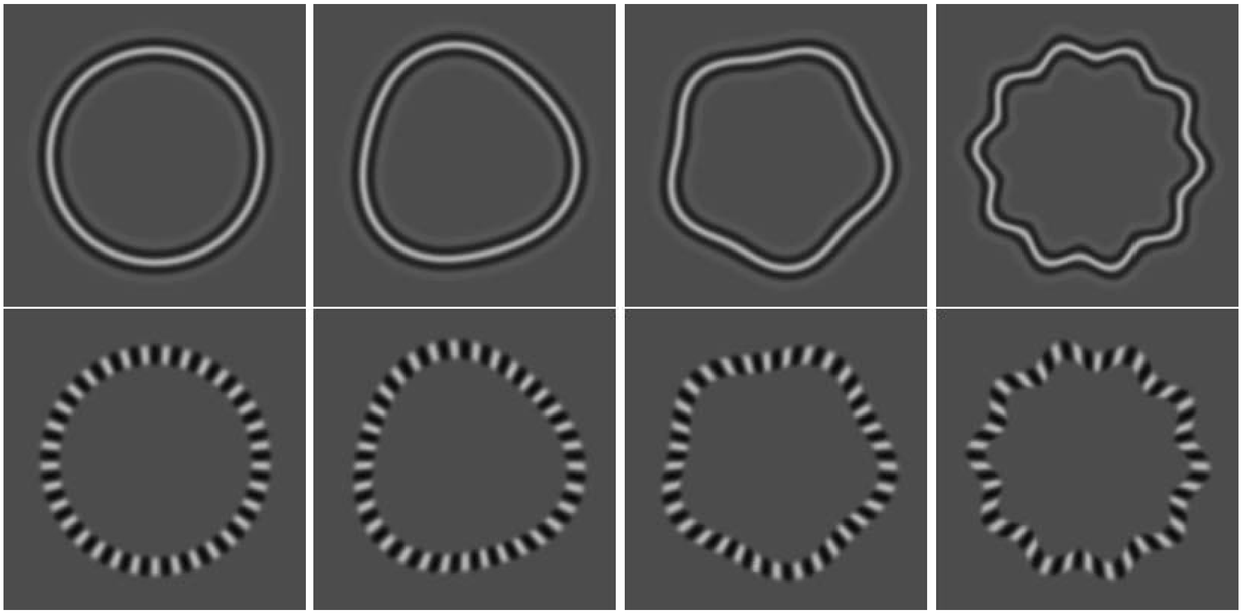

Figure 1. The stimuli located at the top row of the image are luminance-defined RFPs of zero, three, five, and 10 radial frequencies. Located at the bottom row of the image are texture-defined RFPs of zero, three, five, and 10 radial frequencies.

six levels of deformation (amplitudes of 0.001, 0.002, 0.004, 0.008, 0.016, and 0.032) were presented 20 times in pseudorandom order, for a total of 120 trials per condition.

Prior to data collection, participants completed a brief practice session, with the same 2-IFC procedure as the experimental conditions. However, in order to facilitate comprehension of the task, radial frequency patterns were presented from easiest to hardest (amplitude of 0.062, 0.032, 0.016, 0.008, 0.004, 0.002, and 0.001). Throughout the entire testing session, participants were reminded to fixate the center of a uniform screen. In order to avoid participant fatigue, short breaks were provided after each condition. The experimenter entered the participants' response (first or second interval) by pressing a key on the computer's keyboard. Conditions were counterbalanced across all subjects. The entire testing session took approximately 1½ to 2 hours. This study was carried out in accordance with the Declaration of Helsinki as well as was approved by the ethics committee at Rivière-des-Prairies Hospital. All participants provided informed consent and were given financial compensation for their time.

Data analysis

Data from each block were fit with a Weibull function (Weibull, 1951) using maximum likelihood estimation, and thresholds were estimated at 75% correct responses. Two separate mixed analyses of variance (ANOVAs) were conducted, one for first-order RFPs and the other for second-order RFPs. After analyzing the data for basic assumptions, two participants were identified as having extreme scores (i.e., two standard deviations above the mean) on all conditions. These participants (one child and one adult) were therefore removed from all analyses. The final sample size was 45, with 15 participants being included in each of the three age groups. All other basic assumptions were met except for that of sphericity. Since multiple analyses were performed and the basic assumption of sphericity was not met, the Greenhouse-Geisser estimated F value and an alpha level of 0.01 were used (Tabachnick & Fidell, 2007). Finally, minimal deformation thresholds were logged transformed; all analyses were performed on log-transformed thresholds.

Results

The first analysis (Groups [between] × RFP [within]) was conducted to evaluate differences between age groups for luminance-defined RFPs of varying number of curvatures (three, five, 10 RFs). From this analysis, a significant Group × RFP interaction was firstly identified, $F(2.76, 57.99) = 4.70$, $p = 0.006$, $\eta^2_{partial} = 0.18$ (see Figure 2). This interaction indicated that age group differences vary for differing number of RFPs. Simple main effects tests, conducted to evaluate group differences for three, five, 10 RFPs, revealed group differences for RFPs of three, $F(2, 42) = 11.41$, $p < 0.001$, $\eta^2_{partial} =$

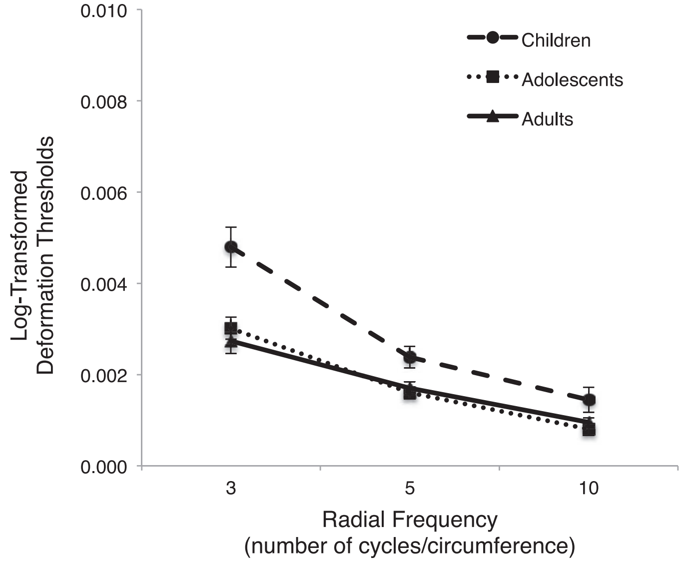

Figure 2. Mean deformation thresholds (arc min) (+*SE*) for children (circles), adolescents (square), and adults (triangle) as a function of luminance-defined RFPs.

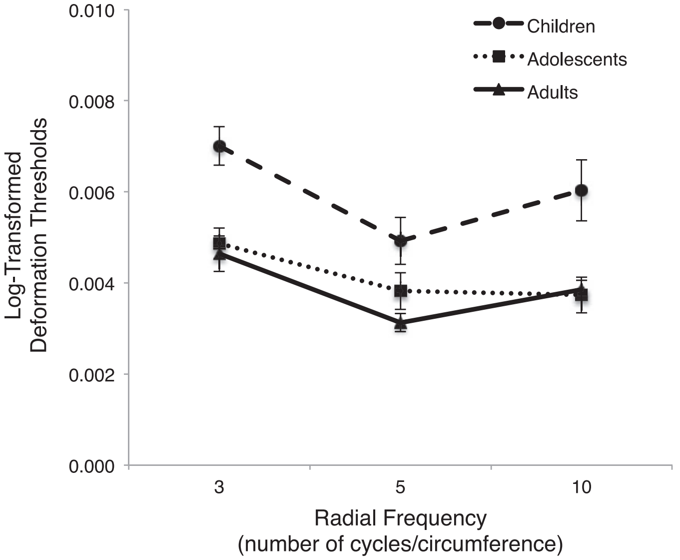

Figure 3. Mean deformation thresholds (arc min) (+*SE*) for children (circles), adolescents (square), and adults (triangle) as a function of texture-defined RFPs.

0.35, and five, $F(2, 42) = 5.60$, $p = 0.007$, $\eta^2_{partial} = 0.21$, radial frequencies. No group difference was noticed for RFPs of ten radial frequencies, $F(2, 42) = 3.43$, $p = 0.042$, $\eta^2_{partial} = 0.14$. Tukey post hoc tests were performed to evaluate group differences for RFPs of three and five radial frequencies. For both types of RFPs, children performed worse compared to adolescents (three RFP: $p < 0.001$; five RFP: $p = 0.004$) and adults (three RFP: $p < 0.001$; five RFP: $p = 0.01$); however, adolescents and adults performed similarly. These results are also evidenced when analyzing Figure 2, which demonstrates that thresholds decreased systematically as the number of curvatures surrounding the contour of the RFP increased suggesting that global processing (required for three or five radial frequencies—Jeffrey, Wang, & Birch, 2002; Loffler, Wilson, & Wilkinson, 2003) is more difficult than local processing (required for ten radial frequencies—Jeffrey et al., 2002; Loffler et al., 2003). The identified interaction revealed that children performed worse for first-order RFPs when a global processing strategy is required. Finally, a significant main effect of group, $F(2, 42) = 12.44$, $p < 0.001$, $\eta^2_{partial} = 0.37$, with Tukey post hoc tests revealing that children performed overall worse compared to adolescents ($p < 0.001$) and adults ($p < 0.001$). No significant difference between adolescents and adults was evidenced. There was also a significant main effect of RFP, $F(1.38, 57.99) = 114.63$, $p < 0.001$, $\eta^2_{partial} = 0.73$. Tukey post hoc tests, calculated by hand using an alpha level at 0.01, revealed that it is more difficult to discriminate RFPs of three radial frequencies compared to five ($p < 0.01$) and 10 ($p < 0.01$) radial frequencies, and it is more difficult to discriminate RFPs of five radial frequencies compared to 10 radial frequencies ($p < 0.01$). These main effects will not be discussed further, since a significant Group × RFP interaction was evidenced.

A second analysis (Groups [between] × RFP [within]) was conducted to evaluate differences between age groups for texture-defined RFPs of varying number of curvatures (three, five, 10 RFPs). From this analysis, no significant Group × RFPs interaction was noticed, $F(3.96, 83,15) = 1.03$, $p = 0.40$, $\eta^2_{partial} = 0.05$. However, a significant main effect of group was evidenced, $F(2, 42) = 13.27$, $p < 0.001$, $\eta^2_{partial} = 0.39$. Tukey post hoc tests revealed that children performed worse compared to adolescents ($p < 0.001$) and adults ($p < 0.001$). No significant difference between adolescents and adults was evidenced. This result signifies that for texture-defined RFPs children performed worse for both global and local visual processing. There was also a significant main effect of RFP, $F(1.98, 83.15) = 16.87$, $p < 0.001$, $\eta^2_{partial} = 0.29$. Tukey post hoc tests, calculated by hand using an alpha level at 0.01, revealed that it is more difficult to discriminate RFPs of three radial frequencies compared to five ($p < 0.01$) and 10 ($p < 0.01$) radial frequencies, but similar discrimination thresholds were identified for RFPs of five and ten radial frequencies. These results are evidenced on Figure 3, which demonstrates that children's performance thresholds is poorer as compared to adolescents and adults, suggesting that global and local visual processing is more difficult when stimuli are defined by texture-defined information.

In general, school-aged children are less sensitive than adolescents and adults when RFPs are texture defined, regardless of radial frequency conditions (local or global). However, for luminance-defined RFPs, the performance of school-age children is similar to that of adults only when RFPs are discriminable using a local processing style (the 10 RF condition) but is inferior when RFPs require more global processing (three and five RF conditions).

Discussion

The principle objective of the present study was to evaluate the developmental interplay between intermediate and low-level vision by assessing the ability to discriminate circular shapes whose contour was characterized by differing stimulus attributes (luminance-texture) and number of deformations (local and global processing). Overall, our results demonstrated that the type of local information, whether the number of curvatures or the type of stimulus attributes, defining the contour of the shape, differentially influences visual processing in school-aged children.

For luminance-defined RFPs, children performed worse compared to adolescents and adults on shapes with fewer curvatures (three and five radial frequencies) but similarly on the RFP condition with the most radial frequencies (10). For school-aged children, the ability to discriminate luminance-defined shapes is adult like only when visual processing is biased towards local processing, which suggests that for such stimulus characteristic children's performance is reduced only when a global visual processing style is required. Past research has proposed that processing of RFPs is separate depending on the number of curvatures surrounding the contour of the shape (Bell, Badcock, Wilson, & Wilkinson, 2007; Jeffrey et al., 2002; Loffler et al., 2003). For RFPs with fewer numbers of curvatures, global pooling is solicited, whereas for RFPs with greater numbers of radial frequencies, probability summation is required (Bell et al., 2007; Jeffrey et al., 2002; Loffler et al., 2003; Wilkinson et al., 1998). Based on such evidence, it is likely that mechanisms underlying global pooling take longer to mature since our school-aged group was not adult-like for the processing of RFPs with fewer numbers of curvatures (i.e., three and five). However, school-aged children were adult-like for RFPs with greater numbers of curvatures, suggesting that mechanisms underlying probability summation mature faster, especially when stimuli are luminance defined.

A different pattern of results was observed for texture-defined RFPs. When texture information is added to the contour of the shape, targeting multiple visual mechanisms and is therefore more complex to visually process (Ashida, Lingnau, Wall, & Smith, 2007; Larsson, Landy, & Heeger, 2006), school-aged children's performance is worse as compared to adolescent and adult groups on all RFP conditions (three, five, and 10 radial frequencies). These results suggest that school-aged children's performance is affected for both global (RFP of three and five) and local (RFP of 10) shape processing when texture information defines the shape. Therefore, longer periods of development are not only identified for processes underlying global pooling but also for those underlying probability summation. The delayed maturation for both local and global processing of texture-defined RFPs might be a consequence of the fact that texture information is more complex to visually process since it requires an extra processing stage (Habak et al., 2009; Lin & Wilson, 1996). Visual mechanisms underlying the processing of texture information may therefore take longer to develop which may in turn generally affect the processing of RFPs in our school-aged group.

Altogether, the present results indicate that the timing of adult-like sensitivity depends on the type of local information (number of curvatures) and the physical attributes (luminance versus texture) defining the shape. Precisely, when luminance information defines the shape, adult-like sensitivity occurs earlier when visual processing is locally biased (before 12 years of age) than when it is globally oriented (after 12 years of age). On the other hand, adult-like sensitivity occurs later for both local and global visual processing (after 12 years of age) when texture information defines the shape. Therefore, timing of adult-like sensitivity is similar for both luminance- and texture-defined shapes when a global processing style is targeted. The difference in development occurs when a local processing strategy is advantaged, with adult-like sensitivity occurring earlier when patterns are luminance-defined than when texture-defined. Overall, this suggests that development of luminance-defined shapes is faster than for texture-defined shapes. Sensitivity to texture-defined RFPs does not only take longer to develop but also appears to deteriorate at a faster rate, with sensitivity being significantly reduced for older adults (i.e., 60–76 years old) than for younger adults (i.e., 20–30 years old) (Habak et al., 2009).

Differential sensitivity to luminance- and texture-defined shapes throughout development was also identified by Bertone et al. (2010), who found that sensitivity to global Landolt-C patterns defined by texture (a second-order characteristic) reaches maturity later in development compared to those that are luminance defined. They proposed that the later development for forms defined by texture might be a consequence of the extensive recruitment of extrastriate visual areas, which are still immature in school-aged children (Bertone et al., 2010). Immature cortical networks might explain therefore why our school-aged children exhibit reduced sensitivity to texture-defined RFPs. It is worth noting however, that some controversy exists in the present literature. Sensitivity to texture-defined, band-pass gratings seems to reach adult-type levels before (5 years old) that of luminance-defined gratings (10 years old; Armstrong, Maurer, & Lewis, 2009; Bertone et al., 2008). According to these authors, less specialization might be required for early mechanisms responsible for the processing of second-order attributes and therefore would require a shorter developmental time course to reach adult levels compared to that of first-order attributes. Overall, sensitivity reflecting the relative maturation of texture-defined perception seems to depend on the stimuli and behavioral paradigm used, with findings of longer maturation associated with more complex types of visual information (i.e., forms, shapes) compared to more simple stimuli (i.e., gratings).

Past research and a recent review article have also described differential development for local and global visual processing: Local visual processing matures earlier than global visual analysis (see van den Boomen, van der Smagt, & Kemner, 2012, for review). Such delayed maturation for global visual processing is thought to be a consequence of restricted interactions between spatial cues at an earlier age (Kovács et al., 1999) as well as underdeveloped long-range connections (Gervan, Berencsi, & Kovács, 2011). Likewise, feedback and horizontal connections, which are useful for integrating contours, demonstrate delayed maturation (Lee, Birtles, Wattam-Bell, Atkinson, & Braddick, 2012). Along with delayed maturation, feedback pathways are also less synchronized at an early age, which might result from diminished myelination, maturation, and learning through repeated exposure (Werkle-Bergner, Shing, Müller, Li, & Lindenberger, 2009). Based on such accounts, children's overall inferior performance for RFPs that are processed globally in adults might be a consequence of inefficient visual integration, possibly mediated by immature feedback and horizontal connections underlying global form detection (Lamme, Supèr, & Spekreijse, 1998). However, the tuning of orientation-selective mechanisms operating locally in primary visual areas seem to be adult-like in our school-aged children since performances demonstrated to be equivalent across groups for luminance-defined RFPs with greater numbers of curvatures (10 radial frequencies), necessitating a local processing style (Jeffrey et al., 2002; Loffler et al., 2003).

The finding that school-aged children demonstrate inferior sensitivity to global RFP conditions for both luminance and texture conditions is similar to past studies that have investigated the development of mechanisms mediating the perception of faces, an ability that requires visual processing similar to that of RFPs (Loffler, 2008; Wilkinson et al., 2000). Behaviorally, it appears that at a young age, a local or featural (focusing on facial features) processing style is predominant. With age, the processing strategies used to represent faces becomes more configural or holistic (global). Being able to process faces globally is advantageous, as it allows for better identification and discrimination (Carey, Diamond, & Woods, 1980; Mondloch, Le Grand, & Maurer, 2002). Imaging studies have also identified delayed maturity for the facial processing areas. For example, physiological studies demonstrate that adult-like latencies when processing faces configurally are attained more progressively (Taylor, Edmonds, McCarthy, & Allisson, 2001; Taylor, McCarthy, Saliha, & DeGiovanni, 1999).

Conclusions

Overall, we have demonstrated that local information defining circular shapes interacts with the visual analysis of intermediate level (global) information, such as that preceding object and face perception, across different periods of development. This was evidenced by the finding that for luminance-defined RFPs, children performed worse than adolescents and adults when a global processing strategy was required, but for texture-defined RFPs, children performed worse compared to adolescents and adults across both local and global processing styles. The poorer performance in children compared to other age groups might be a consequence of poor visual integration between low and intermediate visual mechanisms and could be attributed to immature feedback and horizontal connections as well as underdeveloped visual cortical areas.

Keywords: spatial vision, typical development, low-level vision, intermediate vision

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