How crowding, masking, and contour interactions are related: A developmental approach

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Young children are characterized by poor visual performances. Visual crowding, lateral interactions, and contour detection are critical functions for visual perception, context effect, and recognition that develop over the years up to maturity. The age at which the maturation's onset of the functions can be observed and the functions' underlying neural basis remain unclear. Here we used a development approach to investigate the onset of the foveal visual functions in order to learn about their neuronal basis and their relationships. We measured lateral interactions, crowding, and contour integration in participants aged 3–15 years. The results show that very young children do not exhibit collinear facilitation; rather, their vision is dominated by suppression and a high degree of crowding. Our results show sequential changes in the visual functions in parallel with the development of facilitation—that is, a significant reduction in crowding and an improved contour detection threshold. Our data suggest that the correlation between the onset age of maturation of collinear facilitation with crowding reduction and improvement of contour integration has underlying mutual neuronal mechanisms.

Introduction

The human visual system is immature at birth at different levels. It is accepted that visual performance significantly develops over the years at the level of the retina, lateral geniculate nucleus, and visual cortex (Atkinson, 1984; Garey, 1984). Until recently, it was thought that most development appears during the first years of life (Kozma, Kovács, & Benedek, 2001;

Wright, 1995). The changes in visual functions are considered to be relatively fast and thus provide a basis for cognitive development. Hubel and Wiesel (1970) used the term "critical period"—that is, a period, during early life, when the visual system is plastic and is affected by environmental stimuli. The critical period is considered as varying regarding its onset and duration for different brain regions, functions, and layers (Daw, 1994). It has been established that the critical period starts with the onset of the visual functions and that it depends on the anatomical level of the system: Functions processed at higher anatomical levels have a later critical period than do functions processed at lower levels (Daw, 1994). However, one study suggested that higher visual areas have a shorter critical period (Ellemberg, Lewis, Maurer, Brar, & Brent, 2002), whereas another study suggested that these areas are at a greater risk for a longer critical period (Li, Young, Hoenig, & Levi, 2005). The critical period for visual functions is thought to end after 7 years and not later than the first decade of life (Greenwald & Parks, 1999; Prieto-Diaz, 2000; von Noorden, 1981). Studies indicate that the basic skills of visual development, such as spatial resolution, develop over the first 6 years, but that the development of more complex functions such as motion-defined letters (Giaschi & Regan, 1997) may extend over a longer period (Daw, 1998; LeVay, Wiesel, & Hubel, 1980). Some studies showed relationships during the critical period between visual experience and sensory functions (Daw, 1998; Li et al., 2005).

As will be explained below, we suggest that the most influential factor in visual perception is the maturation process underlying the basic visual func-

tions in the primary visual cortex (V1). It is suggested that some visual functions can have an extended maturational time (Daugman, 1983; Kovacs, Kozma, Feher, & Benedek, 1999; Kozma et al., 2001). A study showed differences between anatomical and neuronal maturation: Whereas most anatomical structures are mature before birth, the neuronal maturation of the visual cortex extends into childhood (Braun, 1999). It was also suggested that there is an increase in the number of cortical cells between birth and 6 years of age (Shankle, Landing, et al., 1998), which may indicate the structural maturation of the primary visual cortex (Shankle, Romney, Landing, & Hara, 1998). In addition, the primary visual cortex exhibits adult-like levels of synaptic density by the age of 4 years (Huttenlocher & Dabholkar, 1997). This extended development process in V1 was also shown by functional magnetic resonance imaging and positron emission tomography (Giedd et al., 1996; Sowell, Thompson, Holmes, Jernigan, & Toga, 1999).

Visual acuity

Visual acuity (VA) develops during the first 3 to 5 years of life, from less than 6/60 to nearly 6/6, according to measurements that exclude crowding effects (Daw, 1998). Various studies disagree about the age that VA reaches the adult level; some studies indicate the age of 5 to 6 years (Birch, Gwiazda, Bauer, Naegele, & Held, 1983; Daw, 1997; Dobson & Teller, 1978; Lewis & Maurer, 2005), whereas other studies that use subjective behavioral techniques indicate age variability (6–10 years). Studies with visual evoked potential (VEP) suggest a later age for full development (Leat, Yadav, & Irving, 2009).

Contrast sensitivity

Contrast sensitivity (CS) presents the contrast detection thresholds, as the sensitivity (1/threshold) to gratings with different spatial frequencies. Several studies support the idea that CS provides a more complete analysis of visual performance than does a VA test (Adams & Courage, 2002; Campbell & Robson, 1968). CS has been reported to increase with age for all spatial frequencies up to around the age of 8 when adult levels are reached (Adams & Courage, 2002; Ellemberg, Lewis, Liu, & Maurer, 1999) or that they reach mature levels in 9–12 years (Beazley, Illingworth, Jahn, & Greer, 1980). However, it was suggested that CS was found to mature fully between the ages of 8 and 19 years (for a review, see Leat et al., 2009).

Crowding

Crowding is described as a reduction in letter acuity when the letter appears in a line of other letters, as compared with its acuity in isolation (Stuart & Burian, 1962). Acuity reduction (or contour interaction) is affected by the distance of the flankers from the central target (Flom, Weymouth, & Kahneman, 1963). The underlying mechanism is still unclear, but there are a number of theories from low-level processes, suggesting that crowding occurs early in the visual cortex and is influenced by higher level effects, such as attention (for a review, see Levi, 2008; Whitney & Levi, 2011). Related to this study, a model based on abnormal development *in amblyopia* suggested that long-range spatial interactions provide the basis of crowding (Bonneh, Sagi, & Polat, 2007; Polat, Sagi, & Norcia, 1997). There is not enough knowledge about the developmental time course of crowding, but it was suggested that, in contrast to acuity, which is nearly adult-like at the age of 3 years, crowding may still cause poor performance even at the age of 5 years (Atkinson & Braddick, 1983). Hence, crowding decreases after basic acuity (grating and single-letter acuity) has matured (Daw, 1998).

Contour integration

Contour detection is defined as the ability to distinguish chains of Gabor elements embedded in random Gabor element backgrounds (Field, Hayes, & Hess, 1993; Kovacs & Julesz, 1994). It was suggested that the detection of oriented elements in a contour should be considered as global neuronal integration due to the contribution of long-range interactions rather than as an output of local individual neurons (Polat & Bonneh, 2000). Abnormalities in contour detection thresholds were first reported in amblyopic subjects (Kovacs, Polat, & Norcia, 1996) and later in genetically neurodevelopmental disorders, such as Williams Syndrome (Gervan, Gombos, & Kovacs, 2012), and in visual agnosia (Lev et al., 2014). Contour integration becomes apparent at 3–4 years, but the greatest improvement seems to appear between ages 5 and 7 years. At an older age there is increased progress in performance, with a tendency for slight improvement, after adolescence (Braun, 1999; Kovacs, 2000). These data are also consistent with experiments involving monkeys (Kiorpes & Bassin, 2003); the development of contour integration was compared to grating acuity in macaque monkeys and was shown to develop recognition substantially later than acuity. It was suggested that the mechanism underlying contour detection may be mediated by the V1 function (Kiorpes & Bassin, 2003). However, there is no agreement regarding the relation-

Age (years)	n	M	SE
3	7	3.49	0.13
4	8	4.49	0.11
5	5	5.22	0.13
6	3	6.20	0.24
7	3	7.27	0.18
8	3	8.30	0.25
9	4	9.40	0.17
10	2	10.60	0.42
11	2	11.35	0.49
12	3	12.37	0.15
13	2	13.20	0.28
14	3	14.53	0.29
15	1	15.00	0.00

Table 1. Distribution of subjects.

ships between lateral interactions at an early level of the visual processing and contour integration.

Lateral interactions

The visibility of a small, foveally viewed Gabor patch (GP) is either enhanced or suppressed by laterally placed GPs of similar orientation and spatial frequency (Polat, 1999; Polat & Norcia, 1996; Polat & Sagi, 1993). The sign of this effect—enhancement or suppression— depends on target and flank separation and on the relative orientation of the target and its flanks. It has been shown that the visibility of a local target improves when it is presented between two collinear flankers, mainly with small target-mask spatial separations (Polat & Sagi, 1993). Facilitation of the contrast detection threshold occurs mainly for collinear configurations (Polat & Sagi, 1993, 1994). The patterns of the long-range interactions are related to a later maturity stage and depend on the hierarchical development (Burkhalter, 1993; Polat & Sagi, 1994). An anatomical study (Burkhalter et al., 1993) of human cortex found that the horizontal connections exist at birth but change progressively up to 15 months after birth. Psychophysical studies suggest that the development of these connections in humans lasts longer than the development of other primary functions (i.e., motor areas; Gervan, Berencsi, & Kovacs, 2011) in infancy possibly until around school age (Sireteanu & Rieth, 1992). It was suggested that children exhibit poor visual integration performance compared with adults owing to perceptual immaturity (Kovacs et al., 1999). A few studies have demonstrated the presence of suppressive interactions in infants (Hou, Pettet, Sampath, Candy, & Norcia, 2003; Sokol, Zemon, & Moskowitz, 1992), but maturation of facilitation interaction is not yet clear. Recently, in a study on infant macaques, it was reported that the development of lateral spatial interactions show

a different trend of development between suppression and facilitation (Li, Hagan, & Kiorpes, 2013). These results indicate that suppressive interactions are present from early in life without changes over the years, whereas facilitation develops slowly during the first year. Until now, most studies of visual development have focused on the progress of a specific visual function (e.g., VA, CS, and spatial integration), but there is no combined information during the entire maturation process. Here we used the development approach to investigate the onset of the visual functions in order to learn about their neuronal basis and the mutual relationships between them. Our hypothesis is that the development of lateral interactions (facilitation) may lead to reduction of crowding, followed by improved abilities of contour integration. The results indicate a pronounced cascade of development of these visual functions, which may suggest a common neuronal basis.

Methods

Subjects

Forty-six subjects aged 3–15 years with normal vision participated in the study (see Table 1). All subjects' VAs were tested by an optometrist; in addition, in order to ensure that there were no visual impairments, children aged 3–10 years were also examined by an ophthalmologist using eye dilation. All the participants were tested using two standard clinical tests that serve as baseline measures: (a) Distance VA was measured according to its best visual correction at a distance of 3 m, using a modified Bailey–Lovie (LogMAR) chart (ETDRS) for the older children (Bailey & Lovie, 1976) or LEA/Landolt C charts for the younger children (Hyvarinen, Nasanen, & Laurinen (1980; Ruamviboonsuk, Tiensuwan, Kunawut, & Masayaanon, 2003). To avoid crowding, VA was measured using a "window" (paper aperture) allowing exposure of a single letter at a time. (b) A Randot Stereo test, which tests the ability to identify geometric forms from a random dot background using polarized glasses, was used. All parents were informed of the nature of the procedures and informed concern was obtained. They signed a consent form that was approved by the Helsinki Committee.

Apparatus

Stimuli were presented on a Philips 107P color monitor (Philips, Amsterdam, The Netherlands), using a PC (1024 × 768 pixels at a 100 Hz refresh rate; gamma correction was applied). The effective size of the monitor screen was 32 × 23 cm, which, at a viewing

Figure 1. Stimuli: E test and the crowding paradigm. (A) Single E. (B) Multi E = crowding.

Figure 2. Stimuli: CS task with different frequencies.

distance of 1.5 m, subtends a visual angle of 9° × 12°. The experiments were conducted in a dark environment, in which the only ambient light came from the monitor (except for the VA and contour detection tests, which were conducted in a full-light environment).

Experimental procedures

All tests were adapted for children and designed so that the attentional bias could be neutralized as much as possible. All were static presentations of the stimuli. Negative feedback (audio) was given for incorrect answers, but positive rewards were given at the end or sometime during the experiment. When necessary (particularly with very young children), the researcher (the first author) sat with his back to the monitor, thus avoiding bias, and pressed the keyboard according to the child's answers. In all experiments, viewing was direct and binocular. Since young children (3–6 years) have poorer CS (in particular, for higher spatial frequencies) than do older participants (7–15 years), we measured the middle frequency level (6 and 9 cycles per degree [cpd]) only for the psychophysical tasks.

VA and crowding

The Tumbling-E patterns (TeVA) test paradigm was used (Bonneh, Sagi, & Polat, 2004). The stimulus consisted of black E patterns on a white background, which corresponds to a subset of the LogMar chart, with a baseline (TeVA = 0) pattern size corresponding to the baseline (i.e., 6/6 vision) of the LogMar chart. The viewing distance was 300 cm. Children were asked to detect the direction of the central E—one of four directions (see Figure 1A). A staircase with pattern size and spacing modified by 0.1 log unit in each step was used to determine the size for 50% correct (the chance is 25%). The performance when the central E was presented alone (TeVA single) was measured separately. Crowding (see Figure 1B) is given by TeVA elevation = crowded − single (difference on a log

scale)—that is, normalizing the crowded condition by the acuity of a single letter.

Contrast Sensitivity

The contrast detection task paradigm was used (Katz et al., 2010; Lahav, Levkovitch-Verbin, Belkin, Glovinsky, & Polat, 2011). Stimuli consisted of GPs— that is, vertically oriented sinusoidal gray-level gratings with spatial frequencies of 6 and 9 cpd, using a static presentation at one of the four locations on the screen: up, down, right, and left (see Figure 2). Response was required in each trial—using the keyboard's arrows. Thresholds were measured utilizing a 3:1 down staircase approach, which estimates the stimulus strength at a 79% accuracy level (Levitt, 1971). The viewing distance was 150 cm. CS was defined as a 100/contrast threshold.

Contour integration

Cards for testing the contour detection and the method were replicated from the study of Chandna, Pennefather, Kovacs, and Norcia (2001), as described below. Each card was 17.5 × 24 cm, consisting of a smoothly aligned, closed path of 13 Gabor signals embedded in a randomly oriented array of Gabor elements having identical spatial frequency (5 cpd) at a test distance of 50 cm. Interelement spacing along the contour was fixed at seven wavelengths of the carrier, center to center (1.4°). The angular difference between adjacent contour segments was assigned within a range of 0° to 30°. Contour visibility was varied by varying the average density of the background Gabor elements, while maintaining the contour. Contour detection thresholds were determined by the ratio of background elements to contour element spacing. The ratio varied between 1.2 and 0.50 in steps of 0.05 over a set of 15 cards. Each card was presented for around 30–60 s in a staircase paradigm that required a correct answer to at least two of three presentations of the same card. Subjects were asked to trace the contour with their finger (see Figure 3). Only a full response (the subject had to trace the entire contour) was counted as correct;
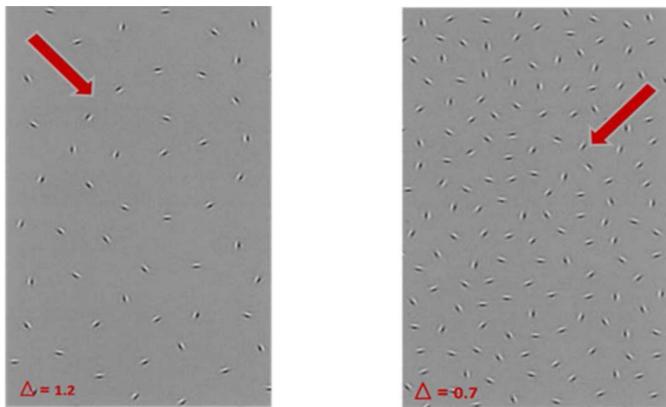
Figure 3. Contour cards. Paths of high-contrast Gabor signals embedded in a random background of Gabor signals.

otherwise it was counted as incorrect. When an incorrect response was reported, a more difficult card was presented to validate that the mistake is not random. Then, after two consecutive mistakes, the order of the difficulty level was reversed, and one card with an easier difficulty level was presented until the participant correctly identified the stimulus. This procedure was repeated three times. The threshold was calculated as the average of the three reversals.

Lateral interactions

The lateral interaction tasks, using GPs, were similar to those described by Polat and Sagi (1993, 1994). Stimuli were vertically oriented GPs, at 6 and 9 cpd, consisting of a low-contrast target and two high-contrast collinear flankers (masks). In each session only one configuration (spatial frequency) was tested. Contrast thresholds were measured utilizing a staircase method, which was shown to converge to 79% correct (Levitt, 1971). In this method, the target contrast was increased by 0.1 log units (26%) after an erroneous response, and it decreased by the same amount after three consecutive correct responses. About 40 trials were needed to estimate the threshold in each block. The subjects were asked to detect the target (displayed on the right side or the left side of the screen), in
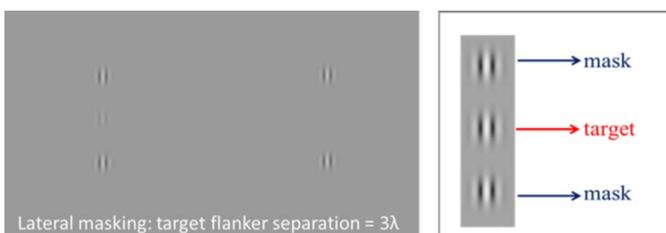

Figure 4. Stimuli: Lateral masking. Target in the presence of flankers (right side) and flankers without the target (left side).
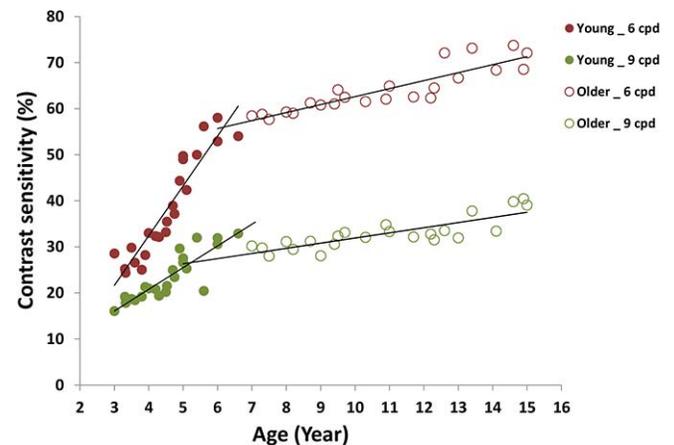

Figure 5. Progress of the CS versus age at 6 and 9 cpd. CS (*y*-axis) is presented as a function of age (*x*-axis). Each datum represents one participant. The solid line represents straight-line fits.

differing target-flanker separations of two, three, and four wavelengths (lambda, λ, see Figure 4). Response was required in each trial—using two alternative spatial forced-choices with the keyboard's arrows. Threshold elevation was determined by measuring the contrast detection of a localized target in the presence of a mask minus the target condition (target alone): Orthogonal flankers were positioned at a distance of 15 λ above and below the target (Amiaz, Zomet, & Polat, 2011; Zomet, Amiaz, Grunhaus, & Polat, 2008). The viewing distance was 150 cm.

Results

Contrast sensitivity

The subjects were divided into two age groups: the younger group, ages 3–7 years (6 years and 11 months) and the older group, ages 7–15. Contrast thresholds were measured at 6 and 9 cpd. Figure 5 shows CS functions for all subjects as a function of age. There is a systematic increase in CS for the two spatial frequencies with age, 6 cpd: $R = 0.95$, $F(1, 44) = 411.97$, $p < 0.001$, $n = 46$; 9 cpd: $R = 0.907$, $F(1, 44) = 204.31$, $p < 0.001$, $n = 46$. The sensitivity of the younger group was lower (6 cpd: 38.56% ± 2.3%; 9 cpd: 23.44% ± 1.07% [$M \pm SE$]) than for the older group (6 cpd: 64.15% ± 1.03%; 9 cpd: 32.9% ± 0.72%) in both spatial frequencies ($p < 0.001$, $df = 44$; *t* test, two-sample equal variance, two-tailed distribution). These results are consistent with early studies (Norcia, Tyler, & Hamer, 1990; for a review, see Leat et al., 2009). The results show that in the early years there is a rapid increase in CS, as measured for the two frequencies (6 and 9 cpd). Sensitivity also rises after
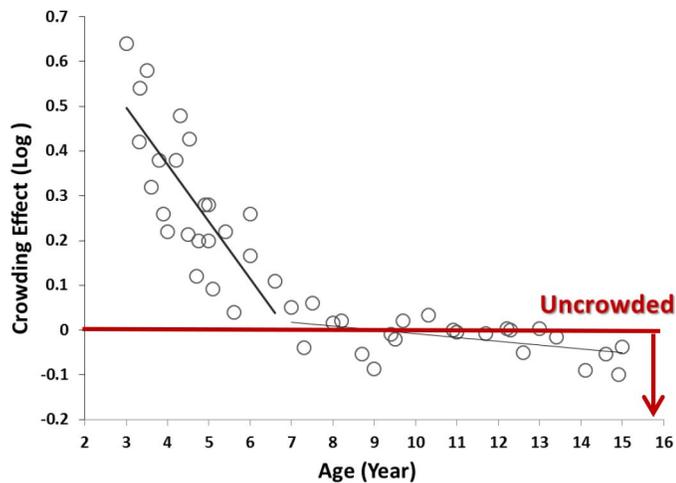
Figure 6. Crowding performance versus age. The crowding effect (*y*-axis) is presented as a function of age (*x*-axis). Each datum (open circle) represents one participant. The solid line represents regression. The results show that crowding was reduced dramatically up to 6–7 years.

Figure 7. Contour integration performance versus age. Contour detection threshold (*y*-axis) is presented as a function of age (*x*-axis). Each datum (open circle) represents one participant. The solid line represents regression. The results show improvement of the contour detection thresholds with age.

entering adolescence but at a more moderate rate. Apparently, the rate of development changes near age 7 years, when it nearly approaches the adult level.

Crowding

The results (Figure 6) show a reduced pattern regarding the crowding effect with increasing age. High levels of crowding are present at a younger age (3–5 years) and approach the adult level near the age of 6–7 years, younger: $R = 0.754$, $F(1, 21) = 27.711$, $p < 0.001$, $n = 23$; older: $R = 0.5$; $F(1, 21) = 7.542$, $p = 0.01$, $n = 23$). These results are consistent with previous studies (for a review, see Atkinson, 1991).

Contour integration

Our results (Figure 7) show a linear improvement in the contour thresholds with increasing age, $R = 0.956$, $F(1, 44) = 476.78$, $p < 0.001$, $n = 46$. The thresholds at the age of 3 years were very high and improved with age. The data indicate that the pattern of development progressively continues into the teen years. These results are consistent with previous studies (Kovacs, 2000; Kovacs et al., 1999).

Lateral interactions

We measured lateral interactions for collinear configuration as a function of age. Our results indicate that the typical pattern of lateral interactions is absent
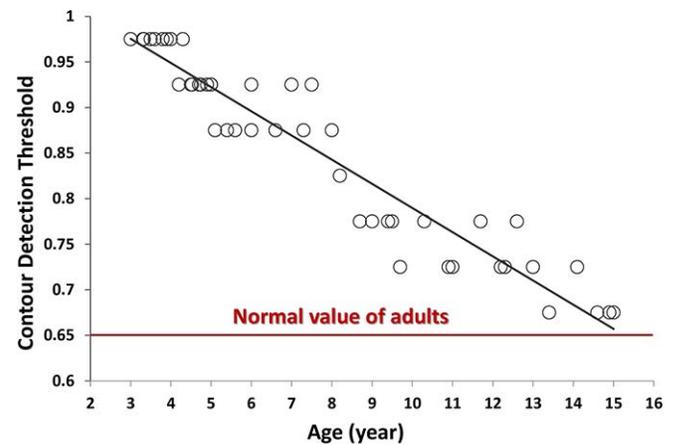
at a younger age but appear at a later age (Figure 8A, B). This pattern behaves similarly at both spatial frequencies (6 and 9 cpd). Participants aged 6–15 years (the older group) exhibit a normal effect of lateral interactions (Adini, Sagi, & Tsodyks, 1997; Bonneh & Sagi, 1998; Levi & Carney, 2011; Polat & Sagi, 1993, 1994). Suppression was demonstrated at a small target-flank distance (2 λ) and facilitation was demonstrated at larger target-flank distances (3λ and 4λ). This group did not exhibit significant changes in the facilitation effect as a function of age, 6 cpd: $R = 0.437$, $F(1, 21) = 4.9$, $p = 0.036$, $n = 23$; 9 cpd: $R = 0.002$, $F(1, 21) = 0.000166$, $p = 0.98$, $n = 23$—that is, the results show that when facilitation appears, it is stable and similar to an adult's amplitude. In contrast, children aged 3–5 years (the younger group) present only suppression at all target-flanker distances. Both young children and adolescents exhibit similar trends regarding suppression (at 2 λ) across all age ranges, 6 cpd: $R = 0.098$, $F(1, 44) = 0.313$, $p = 0.57$, $n = 46$; 9 cpd: $R = 0.176$, $F(1, 44) = 1.40$, $p = 0.24$, $n = 46$—that is, there was no significant change in the level of suppression with age. Interestingly, for target-flanker separations larger than 2 λ, the results suggest that there is a sharp shift between suppression and facilitation effects from 5 to 6 years. However, Figure 8A may suggest that for a spatial frequency of 6 cpd, the turning point between suppression and facilitation ($y = 0$) appears for 4 λ slightly before 3 λ—that is, facilitation appears at 6 years for 4 λ and slightly later, at 6.5 years, for 3 λ (3 λ: $R = 0.875$; 4 λ: $R = 0.8788$). This may hint at maturation of facilitation for larger target-flanker separations before the smaller ones, an effect that is being scrutinized in our laboratory.
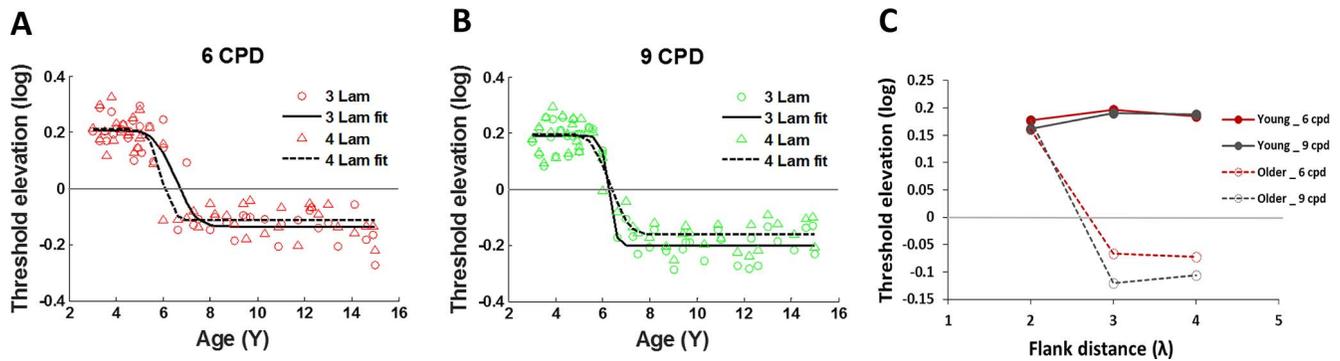
Figure 8. Threshold elevation (normalized to the target alone) as a function of age for different target-flanker separations. (A) 6 cpd for 3 and 4 λ separations. Red circles denote threshold elevation at 3 λ. Red triangles denote threshold elevation at 4 λ. (B) 9 cpd for 3 and 4 λ. Green circles denote threshold elevation at 3 λ. Green triangles denote threshold elevation at 4 λ. Threshold elevation (y-axis) is presented as a function of age (x-axis). Each datum represents one participant. Facilitation is indicated by values below zero, and suppression by values above zero. The black solid and dashed lines denote inverse cumulative Gaussian fit curves; they show the development of facilitation over the years. (C) The average threshold elevation at ages 3–5 years (younger) and 6–15 years (older) versus flanker distance. Filled symbols denote the effect of spatial interactions for young children. Open symbols denote the effect of spatial interactions for the older group. Red circles denote threshold elevation at 6 cpd and green triangles denote threshold elevation at 9 cpd.

Figure 8C summarizes the average differences between the two groups: children aged 3–5 compared to the older group. This presentation of the threshold elevation as a function target-flank distance demonstrates well that the suppression effect is evident for both groups for both spatial frequencies at 2 λ. However, whereas the older group developed facilitation at 3 and 4 λ, the younger group did not exhibit facilitation; rather, it exhibited robust suppression at both 3 and 4 λ. These results are because the initial facilitation effect (as presented in Figure 8A, B) starts to become apparent from an age of about 6 years. The average of the younger group's results shows a slight rise in the suppression level for target-flanker separations of more than 2 λ compared with the 2 λ level ($p < 0.05$: 2 to 3 λ) and then it remains relatively stable ($p > 0.05$: 3 to 4 λ) at both 6 and 9 cpd. The older group shows an adult-like effect of facilitation at target-flanker separations of 3 and 4 λ.

Lateral interactions and crowding

We show here the relationships between masking (target-flanker separation at 6 cpd) and crowding. In order to directly test the correlation between the lateral interactions and crowding, the sum of the threshold elevation for 3 and 4 λ was calculated for each subject (2 λ was omitted from the analysis because it enables mutual data among the ages—that is, it shows a threshold elevation for younger and older ages, in contrast to 3 and 4 λ, whose behavior differs among the ages) and was presented against the crowding of the same subject. As shown in Figure 9, crowding is highly correlated with the masking condition, $R = 0.82$, $F(1, 44) = 96.356$, $p < 0.001$, $n = 46$. Children who exhibit stronger masking (suppression) exhibit a corresponding stronger crowding effect and vice versa. This spatial range pattern is related to progress with age.
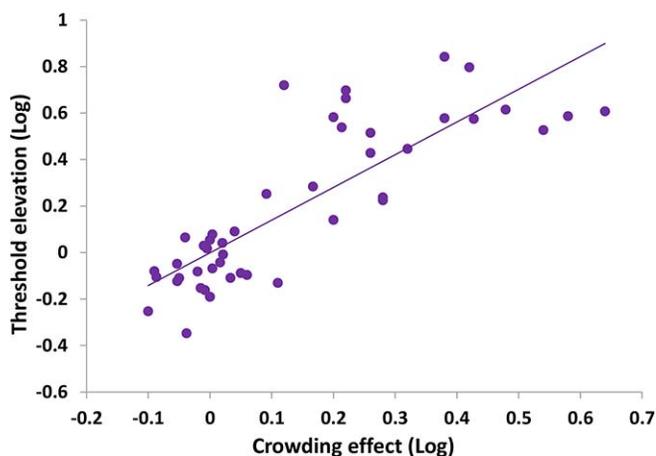
Figure 9. Correlation between masking and crowding: Each point represents the sum of the threshold elevation (one participant) for target-flanker separations of 3 and 4 λ for 6 cpd. The y-axis describes threshold elevation and the x-axis describes crowding.

Discussion

The visual system undergoes a development sequence of several functions and reaches maturation at different ages. It is known that lack of foveal maturation is the

main cause of low VA found in children. However, a VA of 6/6 is reached above the age of 3 years. VA maturation is also affected by the development of CS, which improves the overall quality of vision. Besides VA and CS, the visual system has high-recognition abilities that are reduced at a young age due to the high crowding effect. High crowding limits visual perception and the ability to recognize objects in clutter (Pelli, 2008; Pelli, Palomares, & Majaj, 2004; Whitney & Levi, 2011). In addition, contour integration is extremely important for identifying objects and for visual attention. As mentioned in the Introduction, young children cannot perform complex functions as adults do. Our experimental results suggest that the development of some visual processing can be explained by mutual changes in neuronal mechanisms. Initially, in young children, a strong crowding effect may limit or mask the appearance of facilitation. With increasing age, however, the crowding effect is reduced, reaching an adult's level at about the age of 6 years, which is the approximate age that the facilitation showed up in this study. Here we show a developmental sequence of visual functions over the maturation period, from early childhood up to an adult-like performance. During this period, the pattern of poor visual functions is developed and it reaches the adult level. This descriptive model can generally explain the shift from the high level of crowding, the high contour detection threshold, and lateral suppression, to a normal level of crowding and contour integration. This shift is paralleled by the sequential shift from a suppressive (abnormal) to a facilitative (normal) effect in collinear interactions in children approaching 6 years of age.

Some of the results we show here are consistent with previous studies, as described in the Introduction, showing an increase in CS with age. Moreover, here we also show that a sharp slope of improvement up to the age of 6 years precedes moderate progressive improvement. The contour detection threshold also decreases with age, but significant changes start to appear slightly before age 8 years. The most dominant factor regarding progression over the years is the sharp reduction in crowding. As the results indicate, the improvement in contour detection and crowding start at an early age (e.g., 3–5 years) during which time there was no evidence of a facilitative effect. At nearly 6 years, when the crowding effect diminishes to an adult's level, a facilitative effect "suddenly" appears. There is a parallel reduction in contour detection thresholds when an adult's level is reached. Carefully scrutinizing the results suggests that the suppressing zone in young children is large and may decrease with age. This possibility stems from the fact that the shift from suppression to facilitation appears slightly earlier for a distance of 4λ (6 years) than for 3λ (where suppression overcomes facilitation; see Figure 8A). This effect is

shown for 6 cpd but not for 9 cpd, consistent with the fact that at 6 cpd, maturation occurs earlier. It was suggested that the suppressive zone is indicative of a perceptive field size, and that this size is larger in the periphery (Lev & Polat, 2011). It was also shown that facilitation at the periphery is revealed from target-flanker distances larger than at the fovea. It was also suggested that visual functions of the fovea of children are reminiscent of these functions at the periphery and developed over the years. Thus, one can speculate that the absence of facilitation at 3 and 4λ in young subjects is due to late maturation of the fovea, and the size of the perceptive fields (suppression zone) is still larger than that of adults. Although this suggestion is not fully supported by the data shown here, this possibility seems to be supported by our ongoing investigation. According to this notion, between the ages of about 3 and 6 years, the reduction of crowding and the improvement of contour integration are caused by a gradual reduction in the size of the suppression zone with increasing age. From age 6 years onwards, further improvements in the contour integration task are due to the development of facilitation. We suggest that these changes are not incidental and are related. Older children display a profile similar to that of adults—that is, suppression for short target-flanker distances of 2λ. For larger target-flanker distances, the facilitation was found to reach a maximal facilitative effect at a distance of 3λ and it decreased with increasing target-flanker distances (4λ). These results correlate with the maturation of lateral interactions with age.

The underlying mechanisms of collinear interaction and the relationships among them and contour integration and crowding are still not widely agreed upon. Next, we will discuss how the existence of collinear facilitation may lead to reduced crowding and improved contour integration. We will also consider alternative views since we reached the conclusion that further experiments are needed to test this model and the causal relationship between the functions.

Collinear interactions

Target visibility can be improved when the target is presented with two collinear flankers (Polat & Sagi, 1993, 1994). This effect depends on target-flanker separation, their local orientations, contrast, and temporal order. The outcome is also dependent on the underlying perceptive field (depending on the location: fovea or periphery). The physiological basis of the observed lateral interactions may rely on the long-range connections in the primary visual cortex between similar orientation columns (Bolz & Gilbert, 1989; Gervan & Kovacs, 2010; Gilbert & Wiesel, 1985, 1989; Malonek, Tootell, & Grinvald, 1994; Ts'o, Gilbert, &

Wiesel, 1986). These connections extend for long distances and may convey contextual information (Fitzpatrick, 1996; Gilbert & Wiesel, 1983; Schmidt, Goebel, Lowel, & Singer, 1997). Collinear facilitation (interaction) is found in the early visual cortex (Crook, Engelmann, & Lowel, 2002; Kapadia, Ito, Gilbert, & Westheimer, 1995; Mizobe, Polat, Pettet, & Kasamatsu, 2001; Polat, Mizobe, Pettet, Kasamatsu, & Norcia, 1998), suggesting that early stages of visual processing are involved in mediating the effect. On the other hand, it was shown that facilitation benefits from focused attention by human observers (Freeman, Driver, Sagi, & Zhaoping, 2003; Freeman, Sagi, & Driver, 2001; Giorgi, Soong, Woods, & Peli, 2004) and monkeys (Ito & Gilbert, 1999), suggesting that higher levels of processing are involved in this process.

Relationships between masking and crowding

As mentioned before, the underlying mechanisms of crowding remain controversial, and several different models have been suggested, such as an optical source, a low-level receptive field, or high-level attention (Levi, 2008), and crowding might occur at different stages in the visual hierarchy (Whitney & Levi, 2011). The main classes of crowding models are masking, pooling, substituting, and grouping (Whitney & Levi, 2011). Some studies contend that grouping is involved with the crowding process and show that the crowding effect can be reduced by adding extra flankers that may group with the original flankers (Malania, Herzog, & Westheimer, 2007; Manassi, Sayim, & Herzog, 2012; Pelli et al., 2004). Data from our group show a correlation among masking, crowding, and collinear facilitation, suggesting that relationships exist among them in space and time. However, this study also suggests that crowding and masking may or may not be related, depending on the particular spatial-temporal parameters chosen in the study (Leve & Polat, Under revision). Therefore, our study's results support the suggestion that masking and crowding are related, at least at the fovea (Levi, Klein, & Hariharan, 2002; Polat & Sagi, 1993). Both crowding and lateral masking depend on the distance between the target and flankers, and their effect increases with increasing eccentricity. Moreover, recently it was suggested that crowding and masking may be similarly affected by the same lateral interactions (Lev & Polat, 2011). Overall, our results suggest that facilitation can balance and reduce the crowding. These results are also consistent with the relationships between lateral suppression (masking) and crowding, as shown by Polat and Sagi (1993), and suggest that the development of lateral facilitation can balance and reduce the suppressive effect of crowding. Studies also suggest that lateral interactions may mediate contour integration (Kovacs et

al., 1996; Polat & Bonneh, 2000; Polat & Sagi, 1994). In this regard, one can model the visual system of children, which is dominated by high levels of suppression; the crowding effect limits the appearance of facilitation, and when the crowding is reduced to the normal level, it enables the appearance of facilitation.

Relationships between lateral interactions and crowding

In considering the models suggesting that masking and crowding are related, we will attempt to explain how collinear interactions may be related to crowding. However, we acknowledge that this view may contradict the view that masking and crowding are different. The type of lateral masking that we used here is thought to be mediated by lateral interactions (Polat & Sagi, 1993, 1994), since collinear interaction evokes effects of facilitation and suppression, depending on spatial-temporal parameters such as target-mask separation and contrast. The correlation between the lateral interactions and crowding is shown in Figure 9. Subjects with high crowding have no facilitation and exhibit increased suppression. The crowding effect is reduced with increasing age. This can lead to developing the ability to detect contours. It was suggested that crowding reflects the suppressive effect of masking (Polat & Sagi, 1993). In this regard, one can model the visual system of children as dominated by high suppression. Once the crowding effect reaches to normal level lateral facilitation appears.

Relationships among lateral interactions, contour integration, and crowding

The links between contour integration and crowding have been studied, revealing varied and complex explanations such as the integration field model (Chakravarthi & Pelli, 2011; May & Hess, 2007; Pelli et al., 2004) and the flanker facilitation model (Kovacs et al., 1996; Polat & Bonneh, 2000; Polat & Sagi, 1994). It was suggested that interactions between local processing needed for the task are modified by lateral facilitative and suppressive inputs from elements in the contour and background (Kovacs et al., 1999; Polat & Bonneh, 2000). The critical requirement that affects contour integration is the collinearity of the local orientation (Field et al., 1993; Kovacs, 1996; Pettet, McKee, & Grzywacz, 1998; Polat & Sagi, 1994), as well as the distance between the elements and closure (Kovacs, 1996; Kovacs & Julesz, 1993). Thus, contour integration is widely considered as integration of global neuronal activity rather than as the output of local and individual neurons (Polat & Bonneh, 2000). However, the collinear

facilitation model is also under debate; some studies claim that collinear facilitation does not exist in the periphery (Williams & Hess, 1998) or under dichoptic conditions (Huang, Chen, & Tyler, 2012; Huang, Hess, & Dakin, 2006) and therefore collinear facilitation is unlikely to underlie the mechanism governing contour detection, suggesting that these two phenomena have different cortical sites. Some models suggest that binding (i.e., grouping) has the same or a similar mechanism in crowding and contour interaction (Chakravarthi & Pelli, 2011; May & Hess, 2007). However, a recent study shows that collinear facilitation does exist in the periphery when proper target-flanker separation is used (Lev & Polat, 2011; Under revision), showing that there is no support for the claim that collinear facilitation at the fovea and periphery are different. Moreover, a recent study does show collinear facilitation under dichoptic conditions (Huang et al., 2012). Thus, recent studies do not support the claim that collinear facilitation is unlikely to underlie the mechanism governing contour detection. Moreover, our study focuses on foveal measurements, supporting the suggestion that masking and crowding are related (Levi et al., 2002; Polat & Sagi, 1993), that contour integration may rely on long-range interactions (Braun, 1999; Kovacs & Julesz, 1993), and that the existence of facilitation leads to reduced crowding and improved contour integration.

The developmental model

All of the above raises the possibility that collinear facilitation, reduced crowding, and improved contour integration have underlying mutual neuronal mechanisms affecting the development of maturation. This process occurs in parallel with the development of CS. Our new data regarding the pattern of the lateral interactions (facilitation/suppression) at a young age resembles that in the study of infant macaques (Li et al., 2013). That study described the lack of facilitation in macaque monkeys under one year of age, where it develops slowly over the first year after birth. Li et al. (2013) contended that a suppressive mechanism already exists at birth and that it is related to early maturation of the receptive fields in the visual cortex, whereas the origin of facilitation differs. In that study, the monkeys exhibited an increase in the amplitude of facilitation with age. Li et al. (2013) suggested that the early maturity of suppression is related to the maturity of the receptive field, whereas the late maturity of facilitation is due to late cognitive maturation. Our results show a similar profile regarding the lack of facilitation at a young age and with high suppression, presented at the age of three years. Studies have shown that the age (in weeks) of monkeys is approximately equivalent to months in humans (Lund, Boothe, & Lund 1977; Teller & Boothe,

1979). Thus, the age at which facilitation is present is similar for both humans and monkeys. Although there is agreement about the lack of facilitation at a young age, the underlying mechanism remains controversial, which suggests the possibility of different conclusions. Li and colleagues reported no difference in the suppression amplitude over the course of the development. Though it is not well established, our result hints that children aged 6 years exhibit facilitation at 4 λ, whereas facilitation at 3 λ appears around 6.5 years. Hence, it is possible that for the younger group (3–5 years), facilitation may exist at larger target-flanker separations that we did not test in this study. This may suggest different conclusions. Whereas Li and colleagues contend that the constant development of suppression and facilitation indicate that this late development is due to the top down process, we contend that suppression and facilitation at a young age may be affected by a gradual reduction in the size of the suppression zone with increasing age (as we proposed above). This idea is based on the suggestion that the fovea of children and strabismic amblyopies is like the periphery of normal adults (Levi & Carney, 2011; Levi & Klein, 1985). Our data in this study stimulated us to perform sequential studies in which we tested the development of the suppression zone using more target-flanker separations. Indeed, our accumulated data suggest that the suppression zone is larger in young children. At 3 years of age, like at the periphery, facilitation is found for large target-flankers separations of 5 λ, barely for 4.5–4 λ, and not for 3 λ. Thus, the size of the suppressive zone at 3 years of age is reminiscent of the size at 4° at the periphery in adults (Lev & Polat, Under revision). With increasing age, however, the suppression zone decreases, enabling the crowding to decrease and facilitation consequently appears.

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