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Visuospatial interpolation in typically developing children and in people with Williams Syndrome

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ABSTRACT

Visuospatial interpolation is the estimation of object position or contour shape computed from known “anchor” positions. We characterized the developmental profile of interpolation by measuring positional thresholds as a function of inter-element separation without (Experiment 1) and with (Experiment 2) the context of illusory contours in typically developing children, typical adults and individuals with Williams Syndrome (WS), a genetic disorder that causes impaired global visuospatial abilities. We found that typically developing children and WS individuals had more difficulty integrating information across distant elements than typical adults. However, illusory contours improved thresholds in all participant groups in a similar way. Our results suggest that in WS individuals, and in typically developing children, the grouping mechanisms that enable long-range spatial integration are immature. We hypothesize that WS individuals and young children can use stimulus-driven grouping cues for bottom-up integration, but have immature mechanisms for top-down integration of spatial information.

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1. Introduction

In this paper, we examine the nature of visuospatial interpolation in typically developing children and people with WS, a rare genetic deficit that gives rise to an unusual pattern of severely impaired spatial cognition together with relatively strong language skills. Visuospatial interpolation is an especially useful tool to examine spatial development and patterns of deficit in cases such as WS for several reasons. First, many experimental procedures for measuring visual interpolation are well suited for testing children and atypical populations because they are easy to understand. One common interpolation task is the three-point Vernier alignment task, which is used to efficiently assess retinal and cortical impairments in children (Kim et al., 2000), older adults (Yebra-Pimentel Vilar et al., 1995) and clinical populations (Fang et al., 2000). In this task, observers are asked to judge the position of a central dot relative to flanking dots (see Fig. 2). Second, visuospatial interpolation is fundamental to our ability to judge the position of an object relative to other locations in space, and this supports various everyday skills such as object avoidance (e.g. parallel parking), and object tracking (e.g. following a caravan). Third, positional thresholds of

typical adults have been extensively studied using tasks of bisection (Levi, Klein, & Yap, 1987), separation discrimination (Westheimer & McKee, 1977) and alignment discrimination (Hess & Hayes, 1993). For these tasks, adult functions are well specified: they generally follow Weber's law as a function of inter-element separation. This function (positional threshold vs. inter-element separation) has a log-log slope of 1 for high contrast, long-duration, broadband stimuli (e.g. Hess & Hayes, 1993). That is, the Weber fraction for judging relative position is constant across inter-element separation. Deviation from this function would be indicative of a mechanism that operates differently from that of typical adults.

Since the time of Fechner in the mid-19th century, localization of an object relative to other objects has been found to proportionally depend on their inter-object separation in typical adults. However, very little is known about how judgment of relative location behaves in typical development, and whether it is susceptible to developmental damage. The present study is a *parametric* investigation of how relative position across multiple elements at different inter-element distances is judged (i.e., interpolated) by typical children and Williams Syndrome (WS) individuals. Since typically developing children (e.g. Carkeet, Levi, & Manny, 1997) and WS individuals (Farran & Jarrold, 2005; Landau & Hoffman, 2005) show some difficulty judging relative position, it is possible that they may have interpolation functions that are different from typical adults.

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1.1. Williams Syndrome

Williams Syndrome is a rare genetic disorder that occurs in 1 out of 20,000 live births, associated with a microdeletion of about 20+ genes on chromosomal region 7q11.23 (Lenhoff, Wang, Greenberg, & Bellugi, 1997). WS causes mild to moderate mental retardation, with an average IQ of 60, but is typically associated with relative aptitude in language abilities despite profound weakness in visuospatial abilities (Bellugi, Lichtenberger, Mills, Galaburda, & Korenberg, 1999). This uneven cognitive profile suggests that different cognitive systems might be linked to specific genetic deficits (see also Karmiloff-Smith, 2002; Karmiloff-Smith, 2007). In particular, the genes related to WS might target a suite of visuospatial functions. To date, however, our understanding of the mechanisms underlying the spatial impairment in WS is incomplete.

Early work on WS suggested that reconstruction of global structure of visual stimuli was impaired, which led to the hypothesis that visuospatial integration, which is the combination or coordination of separate elements into a unified group, was the root of WS spatial deficits (Bellugi et al., 1999). WS individuals draw local elements of Navon stimuli well, but often miscopy their global configurations (Bihrlé, Bellugi, Delis, & Marks, 1989). Moreover, WS individuals often fail to recreate the global configuration in block construction tasks (Hoffman, Landau, & Pagani, 2003). However, the severe deficits in these visual-spatial construction tasks are not observed in perception tasks using the same stimuli. Farran and Jarrold (2003) reported that the global configurations of Navon stimuli were drawn poorly by WS individuals (see also Georgopoulos, Georgopoulos, Kurz, & Landau, 2004), but were perceptually identified well relative to controls. This suggests that the integration difficulty experienced by people with WS may not extend to strictly perceptual processes.

Evidence on this issue is mixed. WS individuals can use grouping properties to accelerate visual search (Pani, Mervis, & Robinson, 1999), and are susceptible to visual illusions (Palomares, Ogbonna, Landau, & Egeth, 2008). However, Gestalt grouping by shape, orientation and proximity is perceived poorly by WS individuals, while grouping by luminance, closure and alignment is perceived normally relative to controls, suggesting that not all global configurations are perceived in a typical manner (Farran, 2005). It has also been reported that detection of contours composed of collinear gratings is impaired in WS (Kovacs, Lukacs, Feher, Racsmany, & Pleh, 2001).

1.2. Weber's law and predictions

In typical adults, interpolation of high contrast, broadband stimuli generally scales with inter-element separation (Hess & Hayes, 1993; Hess & Hayes, 1994; Levi et al., 1987). That is, typical adult observers have constant Weber fractions for judging relative position across near and far elements. Here, we asked whether the interpolation function of typical children and WS individuals scale with separation as in typical adults (Fig. 1a), or whether it deviates from scaling (Fig. 1b).

Fig. 1 shows two possible outcomes for our study (see Appendix for details). The dashed lines represent the interpolation functions of typical adults, which have log-log slopes of 1. Farran and Jarrold (2005) found that judgment of relative position is less precise in WS individuals than in typical adults. One possibility is that this imprecision is a constant proportion of inter-element separation. This case would be depicted by a vertical translation of the WS interpolation function relative to the typical adult function. That is, these results would indicate that although the Weber fractions for judging relative position are different for WS individuals compared to typical adults, the Weber fractions are constant across inter-element separation in both WS individuals and typical adults (Fig. 1a).

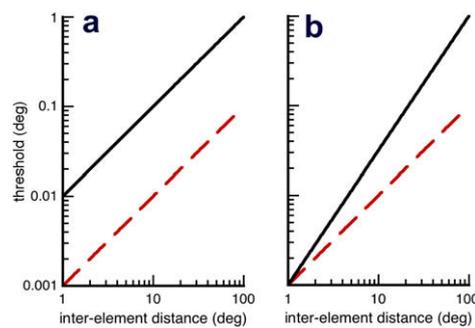


Fig. 1. Predictions for three-point Vernier tasks. (a) Vertical translation of interpolation function without a change in slope. (b) Change in the slope of the interpolation function. Solid lines represent thresholds of WS and dashed lines represent thresholds of normal adults. See text and Appendix A for details.

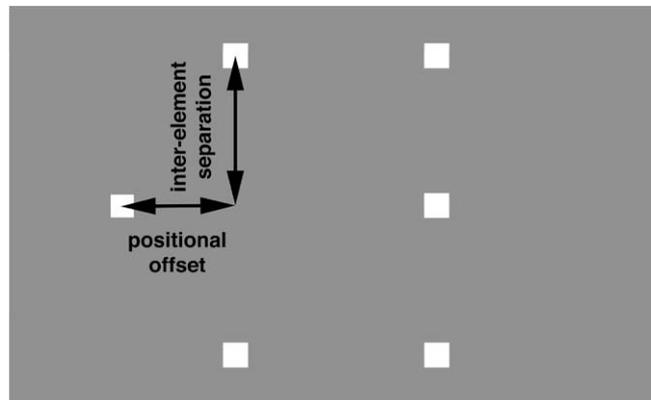


Fig. 2. Schematic of stimuli in Experiment 1. Observers were asked which group of squares, left or right, was misaligned. We measured positional offset thresholds as a function of inter-element separation (1.5, 3.0, 4.5, 6.0 and 11.5 deg).

Alternatively, the imprecision for judging relative position may not be a constant proportion of inter-element separation. A difference in slope with no difference in intercept (Fig. 1b) would indicate that the interpolation function of WS individuals does not scale with separation, unlike the interpolation function of typical adults. That is, in WS individuals, the Weber fraction for judging relative position may vary with inter-element separation (Fig. 1b). The pattern of results depicted in Fig. 1b would suggest that mechanisms underlying visuospatial integration in WS are atypical compared to those of typical adults.

2. Experiment 1: Interpolation of three squares

In this study, we used a two-alternative forced choice version of the three-point Vernier alignment task over a wide range of inter-element spacing (Fig. 2) to determine how positional precision varied over distance and whether it differed for normally developing children and WS individuals compared to typical adults.

2.1. Methods

2.1.1. Participants

Sixty observers with normal or corrected-to-normal vision participated in this experiment. There were five participant groups each with 12 observers. These included individuals with WS (mean

age = 18 years; minimum age = 11 years 4 months; maximum age = 24 years 5 months), typical adults (mean age = 23 years 2 months), typically developing children aged 3–4 years (mean age = 4 years 2 months), 5–6 years (mean age = 5 years 8 months) and 7–9 years (mean age = 8 years 7 months). Our study tracked typical development of visuospatial interpolation, which allowed us to compare performance of WS to performance of typical observers at different ages.

All WS observers were positively diagnosed by a geneticist for the WS genetic marker with a fluorescent *in situ* hybridization test. WS observers were given the Kaufman Brief Intelligence Tests version 2 (KBIT2), an intelligence test that measures vocabulary (verbal) and non-verbal analytical skills (matrices), as well as the block construction subtest of the Differential Abilities Scales (DAS; Elliot, 1990). The WS group had mean raw scores of 54 (range of 35–77) for verbal and 23 for matrices (range of 15–32) components of the KBIT2. The KBIT2 verbal scores fell below the 18th percentile for chronological age, while the matrices scores fell below the 32nd percentile. These correspond to scores of typical 9- to 10-year olds (verbal) and 7- to 8-year olds (matrices) at the 50th percentile. The mean full IQ of the WS group was 68 (range of 40–88). The mean of the DAS block construction scores was 104 (range of 40–126), which fell below the 7th percentile for chronological age. These correspond to scores of typical 6- to 7-year olds at the 50th percentile.

2.1.2. Stimuli, design and procedure

This experiment was executed on an Apple iMac G3 computer attached to a 19" NEC monitor using MATLAB software with the VideoToolbox (Pelli, 1997) and Psychophysics Toolbox extensions (Brainard, 1997). The gray background luminance was set to the middle of the monitor range, about 18 cd/m². The stimuli were two groups of three white squares (Fig. 2), one group 8.0 deg left and the other 8.0 deg right from the center of the monitor (i.e., stimulus groups were 16 deg apart). The squares in each group were 1.0 deg × 1.0 deg in size, and were aligned vertically. Each group had vertical inter-element separations of 1.5, 3.0, 4.5, 6.0 or 11.5 deg (measured from the center of the squares) that varied across experimental blocks. Observers sat 48 cm away from the monitor.

In each trial, one group of squares was perfectly aligned, while the other was misaligned due to a horizontal positional offset of a middle square. Observers were instructed to point to which group of squares, the left or right, was misaligned. The experimenter noted the observers' choice by typing "1" for left and "2" for right using the number pad on the keyboard. The stimuli remained on the screen until response, and observers were allowed to freely make eye movements. On 25% of randomly chosen correct trials, the computer played a verbal recording of "Good job", or "Excellent" as feedback. No feedback was given on incorrect trials.

Positional alignment thresholds were measured using an adaptive staircase method. The horizontal positional offset progressively decreased until the observer makes an error, after which the offset increased. For each experimental block, the initial horizontal positional offset (at Trial 1) was 30% of the inter-element separation (e.g. the initial offset was 0.45 deg at 1.5 deg inter-element distance). After a correct trial, the subsequent trial was made more difficult by reducing the current horizontal positional offset by 30%. After an incorrect trial, the subsequent trial was made easier by increasing the offset by 60%. For example if an observer chose the correct answer in a trial with a 0.5-deg offset, the subsequent trial would have an offset of 0.35 deg. Alternatively, an incorrect trial would result in an offset of 0.8 deg in the subsequent trial. The positional threshold was the average of the last three positional offsets at which observers made errors. The number of trials was fixed at 25 for WS individuals and typical 3- to 4-year

old children, 35 for typical 5- to 6- and 7- to 9-year-old children, and either 40 or 45 for typical adults.¹ Accuracies for each block converged to about 70% correct.

2.2. Results

2.2.1. Comparing thresholds of Williams Syndrome individuals and typical adults

Positional thresholds were plotted as a function of inter-element separation. We compared thresholds of WS individuals with those of typical adults (Fig. 3a). We found that positional thresholds of typical adults had a log–log slope of 1.03 ($R = .703$). This shows that visuospatial interpolation scales (on a unit slope) as a function of inter-element separation, which replicates results of other studies on positional alignment (Hess & Hayes, 1993; Hess & Hayes, 1994; Levi et al., 1987). However, we found that thresholds of WS individuals did not scale with inter-element distance; log–log slope of 1.62 ($R = .773$). That is, they had a different Weber fraction for integrating near and far elements. Fig. 3a shows that thresholds of typical adults and WS individuals diverge at far separations and converge at near inter-element separations. A 5 (inter-element separation) × 2 (participant group) ANOVA on log thresholds shows significant effect of inter-element separation, $F(4,88) = 75.379$; $p < .001$, a significant difference between WS and typical adults, $F(1,22) = 31.372$; $p < .001$, and more importantly, a significant interaction between inter-element separation and participant group, $F(4,88) = 7.394$; $p < .001$. Tukey post-hoc analyses showed that thresholds of WS individuals were significantly higher than thresholds of typical adults at inter-element separations of 3.0 deg ($p < .001$), 4.5 deg ($p < .001$), 6.0 deg ($p = .011$) and 11.5 deg ($p < .001$), but not at 1.5 deg ($p = 1.000$).

Planned *t*-tests were also performed for the nearest (1.5 deg) and farthest (11.5 deg) inter-element separation. We found that the log thresholds of WS individuals and typical adults were not significantly different at the nearest separation, $t(22) = 0.079$; $p = .938$, but were significantly different at the farthest separation, $t(22) = 5.409$; $p < .001$. This pattern of results indicates that integration of positional information in WS is not a generalized impairment. WS individuals had difficulty in integrating positional over distant locations, but are within normal range in integrating information over near locations.

2.2.2. Thresholds of typically developing children

We also looked at how typical maturation affects visuospatial interpolation (Fig. 3b–d) to address the possibility that elevated positional thresholds of WS over distant locations might be due to arrest or retardation of visual functions. If this is the case, then interpolation functions of typical children should also have increased slopes relative to typical adults.

Indeed, interpolation functions of typical children had slopes that decrease over development: 1.61 for 3- to 4-year olds ($R = .805$), 1.40 for 5- to 6-year olds ($R = .839$), 1.29 for 7- to 9-year olds ($R = .829$) and 1.03 for typical adults ($R = .703$), indicating that interpolation functions of typical children do not scale with inter-element separation (i.e., slope $\neq 1.0$). This shows that typical children have different Weber fractions for close and far inter-element separations that become a single consistent Weber fraction over development.

¹ The number of trials was chosen based on an a priori assumption that WS individuals and normal children would be worse than normal adults on this task, which would necessitate more trials for normal adults. That is, WS individuals and normal children would reach threshold more quickly, with fewer trials than normal adults. Due to experimenter error in Experiment 1, different numbers of trials were used in the normal adult group: six normal adults had 40 trials and six normal adults had 45 trials across all conditions. In Experiment 2, all 12 normal adults had 40 trials for each condition.

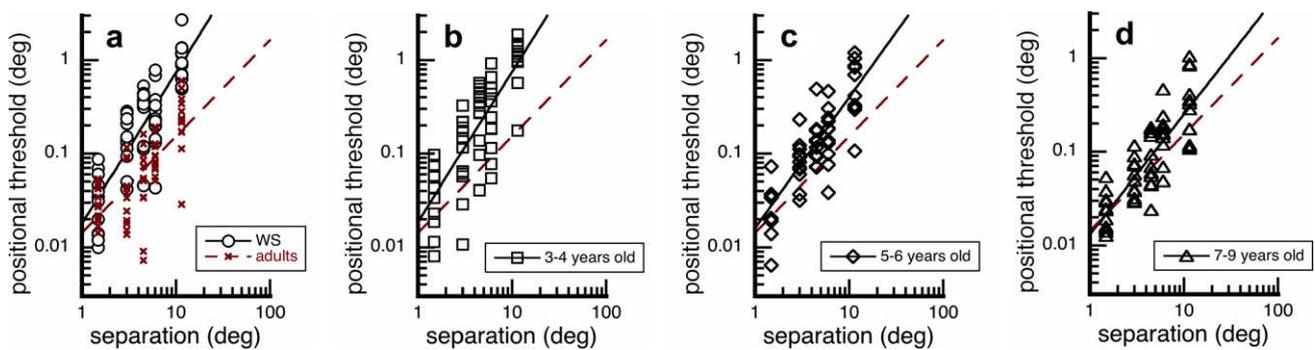


Fig. 3. Positional thresholds as a function of inter-element separation in Experiment 1. Solid lines represent threshold functions with slopes of (a) 1.62 for WS, (b) 1.61 for 3- to 4-year olds, (c) 1.40 for 5- to 6-year olds and (d) 1.29 for 7- to 9-year olds. Dashed lines in all panels represent threshold function for normal adults with a slope of 1.03. Thresholds of WS and normal 3- to 4-year olds are not significantly different. Thresholds of normal children improve with increasing age.

In other words, we found that age affected positional thresholds at more distant inter-element spacing, but not at nearer spacing (Fig. 3b–d). A more detailed assessment using a 5 (inter-element separation) \times 4 (participant group) ANOVA on log thresholds of typical children and adults indicated a significant effect of inter-element separation, $F(4,176) = 167.026$; $p < .001$, a significant effect of age group, $F(3,44) = 2.540$; $p < .001$, and a significant interaction between them, $F(12,176) = 2.887$; $p = .001$. Tukey's post-hoc analyses were conducted: at the nearest inter-element separation of 1.5 deg, positional thresholds did not vary across age (p values > 0.20). At 3.0 deg, thresholds of 3- to 4-year olds ($p = .008$) and 5- to 6-year olds ($p = .040$) were higher than thresholds of typical adults. At 4.5 deg, thresholds of 3- to 4-year olds ($p < .001$) and 5- to 6-year olds ($p = .007$) were higher than thresholds of typical adults. Thresholds of 3- to 4-year olds were also higher than thresholds of 7- to 9-year olds ($p = .002$). At 6.0 deg, thresholds of 3- to 4-year olds were higher than thresholds of typical adults. At 11.5 deg, thresholds of 3- to 4-year olds ($p < .001$) and 5- to 6-year olds ($p = .047$) were higher than thresholds of typical adults. Thresholds of 3- to 4-year olds were also higher than thresholds of 7- to 9-year olds ($p = .001$).

2.2.3. Comparing thresholds of typically developing children and WS

We also compared thresholds of WS individuals and typical children directly by conducting three separate 5 (inter-element separation) \times 2 (participant groups) ANOVAs. Thresholds of WS individuals and 3- to 4-year olds showed no main effect of group $F(1,22) = 0.011$, $p = .917$ and no interaction with distance $F(4,88) = 0.822$; $p = .515$. Thresholds of WS individuals and 5- to 6-year olds showed a significant main effect of group $F(1,22) = 5.658$, $p = .026$ but no interaction with distance $F(4,88) = 0.856$; $p = .493$. Thresholds of WS individuals and 7- to 9-year olds showed a significant main effect of group $F(1,22) = 22.430$, $p < .001$ and a significant interaction with distance $F(4,88) = 3.867$; $p = .008$. These results are consistent with the idea that interpolation abilities of WS individuals are immature, similar to the level of typical 3- to 4-year olds.

2.2.4. Correlations of WS scores

We computed correlations in order to determine whether our measures of visuospatial interpolation were related to scores of WS individuals on standardized tests. First, we evaluated whether our interpolation task was related to block construction by correlating positional thresholds with DAS block construction raw scores. Across all inter-element separations, we found no significant correlations with block construction (p values $> .20$). Second, we evaluated whether our interpolation task was related to lan-

guage abilities by correlating positional thresholds with the KBIT2 verbal raw scores. Across all inter-element separations, we found no significant correlations verbal scores (p values $> .15$). Third, we evaluated whether our interpolation task was related to non-verbal abilities by correlating positional thresholds with the KBIT2 matrices raw scores. Across all inter-element separations, we found no significant correlations with non-verbal scores (p values $> .20$). In addition, all possible correlations among chronological age, DAS block construction and KBIT2 (verbal and matrices) scores were non-significant² (p values $> .05$).

2.3. Discussion

In Experiment 1, we found that interpolation functions of WS individuals and typical children did not scale with inter-element separation (i.e., slope $\neq 1.0$), while the interpolation function of typical adults did scale (i.e., slope = 1.0). At near locations, positional thresholds across all participant groups did not differ suggesting that interpolation within this condition was typical in WS and adult-like in typical children. At distant locations, positional thresholds of WS and typical children were elevated compared to those of typical adults suggesting that interpolation within this condition may be mediated by immature mechanisms in WS and typical children. Specifically, interpolation abilities in WS might be arrested or delayed at the level of typical 3- to 4-year olds.

One possible explanation for our results is the idea that in WS individuals and typical children the grouping mechanisms that enable long-range integration of spatial information are immature, consistent with the results of Kovacs and colleagues (Kovacs, 2000; Kovacs, Kozma, Feher, & Benedek, 1999). More generally, they may have difficulty in spatial integration when grouping properties in the stimulus are weak (proximity, in this case; Farran, 2005). This idea is consistent with the results of Palomares et al. (2008), in which nearby illusion context affected size discrimination in WS individuals and typical children to the same degree as typical adults. It is a common observation that the closer things are the more likely they are organized into one group. Classic psychological demonstrations of grouping indicate that children have a stronger bias for perceiving global shapes compared with adults. When presented with a hierarchical figure, such as a letter "A" made up of smaller letters "Bs", typical children and adults respond faster for the identification of global shape, the letter "A". However, the bias for quickly recognizing global forms (global precedence effect) is stronger in younger children and diminishes to adult-like

² The prevalence of non-significant correlations may be due to the narrow range in the KBIT2 and DAS scores of our WS participants, which averaged below the 7th percentile of their chronological age.

levels between the ages of 10 and 14 years (Mondloch, Geldart, Maurer, & de Schonen, 2003). This result is consistent with the Gestaltist viewpoint that integration occurs automatically, and provides evidence that integration occurs early in development.

In fact, our main experimental manipulation, inter-element proximity, corresponds to a Gestalt grouping “law” (Wertheimer, 1923). WS and typical children may be able to detect strong grouping cues inherent in the stimuli as well as typical adults, but they might have difficulty in integrating spatial information across stimuli with weak grouping cues.

To further test this hypothesis in the next experiment, we asked observers to judge positional alignment within the context of illusory contours. Illusory contours have collinearity and closure cues that facilitate grouping of elements into a larger object that may aid in localization judgments. In typical adults, formation of objects via illusory contours improves dot localization thresholds in typical adults (Guttman & Kellman, 2004). If typical children and WS individuals can integrate stimulus-based grouping cues, then the presence of illusory contours should also improve localization thresholds.

3. Experiment 2: Interpolation within illusory contours

The visual system has a tendency to complete contours in an image, despite occluding surfaces (Rauschenberger & Yantis, 2001) and missing segments (Snodgrass & Feenan, 1990). Even in the absence of color, luminance, depth, texture or motion discontinuities, some boundaries are perceived (Grossberg, Mingolla, & Ross, 1997)—these are illusory contours. Psychophysical studies have shown that illusory contours, like real contours, facilitate localization of a dot (Guttman & Kellman, 2004; Pomerantz, Goldberg, Golder, & Tetewsky, 1981) and discrimination of letters (Moore, Yantis, & Vaughan, 1998). These studies are consistent with the idea that objects formed by illusory contours conform to the rules of object-based attention, in which spatial selection is enhanced (Roelfsema, Lamme, & Spekreijse, 1998) or prioritized (Shomstein & Yantis, 2002) more within an object than across objects. This suggests that real and illusory contours are mediated by similar mechanisms.

Illusory contours can be perceived early in development, by as early as 2 months (Curran, Braddick, Atkinson, Wattam-Bell, & Andrew, 1999). Likewise, WS individuals perceive illusory contours like typical adults, despite having atypical ERP signatures (Grice et al., 2003). In this experiment, we added illusory contours to our stimuli to see how grouping cues from illusory contours affect our interpolation task across multiple separations in typical adults, typical children and WS individuals. Although, it is known that the perception of illusory contours is affected by the support ratio (i.e., ratio of distance and size) of their inducers (Kellman & Shipley, 1991), it is currently unknown how localization within the context of illusory contours would be affected by inter-element separation. If illusory contours affect target localization in typical adults, typical children and WS individuals in a similar manner, then it would suggest that the ability of young children and WS to perceive and use additional grouping cues from illusory contours are relatively mature. Alternatively, illusory contours may affect localization in typical children and WS individuals differently from typical adults, which would suggest that mechanisms underlying grouping via illusory contours in young children and WS individuals are different from those of typical adults.

3.1. Methods

3.1.1. Participants

Sixty observers with normal or corrected-to-normal vision participated in this experiment. The individuals in the WS, 5- to

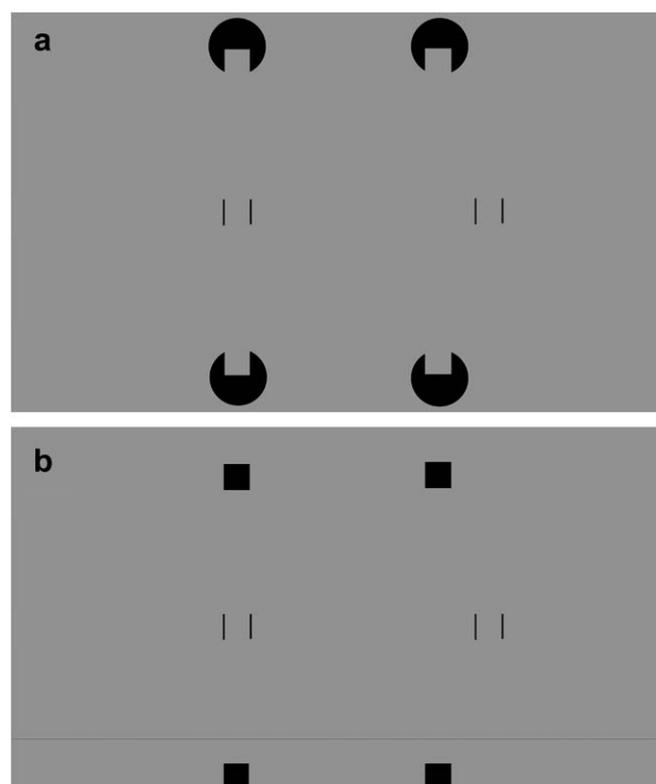


Fig. 4. Schematic of stimuli used in the (a) illusory contour condition and (b) control condition of Experiment 2. Observers were asked which group of objects, left or right, was misaligned.

6-year-old and 7- to 9-year-old group from Experiment 1 also participated in Experiment 2. A new group of typical adults (mean age = 18 years 5 months), and typically developing 3- to 4-year-old children (mean age = 4 years 3 months) were recruited. Each participant group had 12 observers.

3.1.2. Stimuli, design and procedure

There were two kinds of stimuli in Experiment 2: one that created illusory contours and a control condition that did not (Fig. 4a and b). These were presented in a within-subjects design. In the illusory contour condition, observers were asked to localize two parallel line segments between two notched circles (Fig. 4a). These stimuli created the perception of an illusory rectangle “on top” of two black circles. The diameter of the notched circle was 2.5 deg. The size of the notch was a 1.0×1.0 deg square located at the bottom or top edge of the circle. In the control condition, observers were asked to localize the line segments between two squares (Fig. 4b). The size of the squares was 1.0×1.0 deg. In both of these conditions, the parallel line segments were 1.0 deg long and were 1.0 deg apart. All conditions (i.e., presence/absence of illusory contours and five inter-element separations) were presented in separate blocks. Apart from the stimuli used, the procedure in this experiment is identical to Experiment 1 (see Footnote 1).

3.2. Results

3.2.1. Thresholds of Williams Syndrome individuals and typical adults

We compared positional threshold of WS individuals and typical adults with and without illusory contours over a wide range of distances. We found that illusory contours improved positional thresholds of WS individuals and typical adults for distant elements, but not for near elements (Fig. 5a and b). In other words, the presence of illusory contours did not change Weber fractions

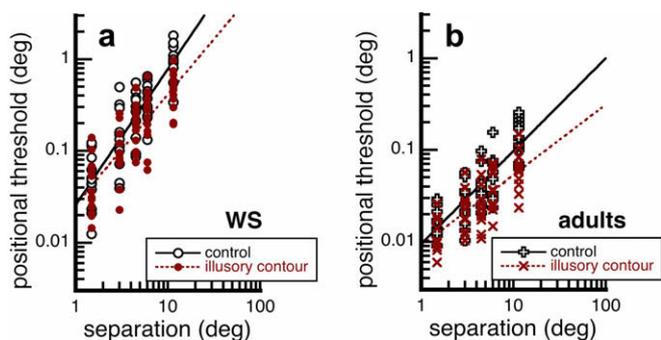


Fig. 5. Data for WS individuals and normal adults in Experiment 2. (a) In the WS group, interpolation functions had slopes of 1.48 and 1.21 for the control and illusory contour conditions, respectively. (b) In normal adults, slopes were 1.01 and 0.77. Illusory contours improved positional thresholds at larger inter-element separations.

at the closest inter-element separation, but it decreased Weber fractions at the farthest separation. For WS individuals, the interpolation function had a log–log slope of 1.48 ($R = .857$) in the control condition and 1.21 ($R = .746$) in the illusory contour condition. For typical adults, the interpolation function had a log–log slope of 1.01 ($R = .801$) in the control condition and 0.77 ($R = .682$) in the illusory contour condition.

To complement our regression analysis, a 5 (inter-element separation) \times 2 (participants group: WS vs. typical adults) \times 2 (illusory contour condition) ANOVA on log thresholds shows significant effects of participant group, $F(1,22) = 342.357$; $p < .001$, inter-element separation, $F(4,88) = 96.682$; $p < .001$ and illusory contour condition, $F(1,22) = 38.102$; $p < .001$. Tukey post-hoc analyses showed that positional thresholds of WS individuals were higher than positional thresholds of typical adults across all inter-element separations in both the control and illusory contour condition (Supplementary Table 1). More importantly, however, the interaction between inter-element separation and participant group, $F(4,88) = 4.840$; $p = .001$, was significant, which reflects the difference in slopes of the interpolation function between WS and typical adults. The interaction between inter-element separation and illusory contour condition, $F(4,88) = 2.437$; $p = .053$, was also nearly significant, which reflects the uneven effect of illusory contours across inter-element separation.

Notably, interactions between condition and participant group, $F(1,22) = 0.002$; $p = .968$, and among condition, participant group and inter-element separations, $F(4,88) = 0.238$; $p = .916$, were non-significant, which implies that there were no differences between WS and typical adults in how illusory contours affected interpolation. These results show that WS individuals are able to use collinear and/or closure grouping cues from illusory contours to the same extent as typical adults, despite the fact that ERP signatures for detecting illusory contours have been reported to be atypical in WS (Grice et al., 2003).

Since we found the effect of participant group was most different at the endpoints of our interpolation functions in Experiment 1, planned t -tests were also conducted on the nearest (1.5 deg) and farthest (11.5 deg) separations to isolate the effects of illusory contours and participant group. We found that positional thresholds at 1.5 deg inter-element separation were not affected by illusory contours in either WS, $t(11) = 0.527$, $p = .609$, or typical adults, $t(11) = 1.521$, $p = .157$, while positional thresholds at 11.5 deg were significantly affected in both WS, $t(11) = 4.609$, $p = .001$, and typical adults, $t(11) = 4.549$, $p = .001$. These results show that the presence of illusory contours mainly facilitates interpolation of distant elements, but provides no significant benefit for interpolating near elements in both groups of WS individuals and typical adults. In

all conditions, we also found that thresholds of WS participants were higher than thresholds of typical adults: in 1.5 deg control, $t(22) = 4.529$; $p < .001$, 11.5 deg control, $t(22) = 10.598$; $p < .001$, 1.5 deg illusory contour, $t(22) = 4.846$; $p < .001$, and 11.5 deg illusory contour, $t(22) = 9.814$; $p < .001$, conditions. These are unlike the results of Experiment 1, in which there was no difference between thresholds of WS and adults at the nearest inter-element separation. It is not obvious why this difference may exist, but one explanation could be the degree of inter-element similarity. The elements were identical squares in Experiment 1 (Fig. 2), but were dissimilar lines and notched circles in Experiment 2 (Fig. 4). Because similarity is a Gestalt grouping cue (Wertheimer, 1923), the presence of highly similar elements may have improved thresholds of WS participants at the nearest separation in Experiment 1. Interpolation of identical elements may be easier than non-identical elements because the observer may be able to use the edges of the elements as well as their centers of mass.

3.2.2. Thresholds of typically developing children

We also looked at how illusory contours affected interpolation in typical development (Figs. 5b and 6a–c). A 5 (inter-element separation) \times 4 (participant group) \times 2 (illusory contour condition) ANOVA on log thresholds of typical adults and children showed that there were main effects of inter-element separation, $F(4,176) = 289.248$; $p < .001$, age group, $F(3,44) = 69.900$; $p < .001$ and illusory contour condition, $F(1,44) = 47.970$; $p < .001$. These data reflect the graded effect of inter-element separation over typical development. There was a significant interaction of age and inter-element separation, $F(12,176) = 2.688$; $p = .002$, which reflects the decreasing slopes in the interpolation functions over development. In the control condition, interpolation functions had log–log slopes of 1.46 ($R = .872$) for 3- to 4-year olds, 1.50 ($R = .800$) for 5- to 6-year olds, 1.28 ($R = .851$) for 7- to 9-year olds and 1.01 ($R = .801$) for adults. In the illusory contour condition, log–log slopes were 1.12 ($R = .826$) for 3- to 4-year olds, 1.15 for 5- to 6-year olds, 0.79 ($R = 0.724$) for 7- to 9-year olds and 0.77 ($R = .682$) for adults. Here, a log–log slope of less than 1.0 indicates that the facilitatory effects of illusory contours in interpolation are greater at farther positions than at nearer positions.

The effect of illusory contours also varied over inter-element separation, as shown by the significant interaction between condition and inter-element distance, $F(4,176) = 7.066$; $p < .001$. Illusory contours were effective in facilitating interpolation of distant elements in typical adults and children (Fig. 6a–c). The interaction among condition, age group and inter-element separation was non-significant, $F(12,176) = 0.978$; $p = .472$. However, the interaction between condition and age group was significant, $F(3,44) = 3.595$; $p = .021$, which may be due to relatively elevated thresholds of 7- to 9-year olds in the illusory contour condition.³ In both the control and illusory contour condition, positional thresholds generally decrease over development (Fig. 7; for significant Tukey HSD results, see Supplementary Table 2).

3.2.3. Comparing thresholds of typically developing children and WS

Three independent 5 (inter-element separation) \times 2 (participant group: WS and typical children) \times 2 (illusory contour condition) ANOVAs comparing thresholds of WS to thresholds of 3- to 4-year olds, 5- to 6-year olds and 7- to 9-year olds were also per-

³ For 7- to 9-year-old participants, the elevated thresholds in the illusory contour condition were specifically due to elevated thresholds at the inter-element separation of 1.5 deg (see Supplementary results). At this separation, thresholds in the control condition were significantly higher than thresholds in the illusory contour condition, $t_{\text{one-tail}}(11) = -2.107$; $p = .03$ for this age group. No other participant group at any inter-element distance show this effect. It is unclear why this should be the case and might be noise in the data.

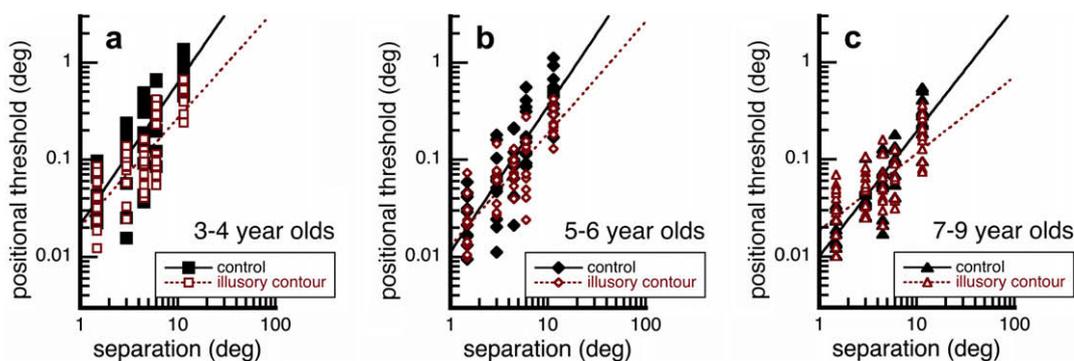


Fig. 6. Data for normal children in Experiment 2. (a) Three- to four-year olds had interpolation functions with slopes of 1.46 and 1.12 for the control and illusory contour conditions, respectively. (b) In 5- to 6-year olds, slopes were 1.50 and 1.15. (c) In 7- to 9-year olds, slopes were 1.28 and 0.79. Illusory contours improved positional thresholds at larger inter-element separations.

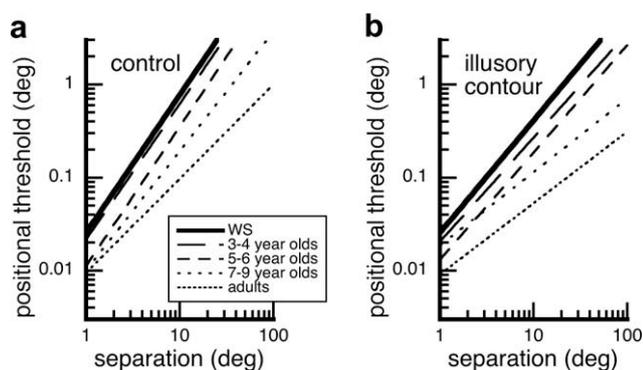


Fig. 7. Interpolation functions in the (a) control and (b) illusory contour condition for all participants.

formed. The main effects of inter-element separation were significant in the analysis of WS versus 3- to 4-year olds, $F(4, 88) = 121.908$; $p < .001$, WS versus 5- to 6-year olds, $F(4, 88) = 130.355$; $p < .001$ and WS versus 7- to 9-year olds, $F(4, 88) = 98.284$; $p < .001$. The main effects of illusory contour condition were significant in the analysis of WS versus 3- to 4-year olds, $F(1, 22) = 36.360$; $p < .001$, WS versus 5- to 6-year olds, $F(1, 22) = 20.501$; $p < .001$ and WS versus 7- to 9-year olds, $F(1, 22) = 13.932$; $p = .001$. These results show that inter-element separation and the presence of illusory contours affected positional thresholds across participants.

The main effects of participant group were significant in the analysis of WS versus 3- to 4-year olds, $F(1, 22) = 9.145$; $p = .006$, WS versus 5- to 6-year olds, $F(1, 22) = 51.712$; $p < .001$ and WS versus 7- to 9-year olds, $F(1, 22) = 181.058$; $p < .001$, indicating that thresholds of WS individuals were higher than those of typical children (see Table 1 for significant Tukey HSD results.) More importantly, however, interactions between inter-element separation and participant group were not significant in the analysis of WS versus 3- to 4-year olds, $F(4, 88) = 1.344$; $p = .260$ and WS versus 5- to 6-year olds, $F(4, 88) = 0.707$; $p = .589$, but was significant for WS versus 7- to 9-year olds, $F(4, 88) = 3.707$; $p = .008$. The slopes of the interpolation functions reflect these results. With and without illusory contours, slopes of WS individuals were similar to slopes of 3- to 4-year olds and 5- to 6-year olds (Fig. 7a and b), suggesting that the mechanisms underlying visuospatial interpolation in WS may be developmentally retarded or arrested at the level of typical children under the age of six. These results are slightly different from the results of Experiment 1, in which the magnitude and slope of the interpolation function of WS individuals were not significantly different from the interpolation function of 3- to

4-year olds. In Experiment 2, interpolation functions of WS individuals were significantly higher than 3- to 4-year olds, but did not differ in slope from interpolation functions of 3- to 4- and 5- to 6-year olds. Again, it is unclear why the difference between experiments may exist, but one explanation could be the degree of inter-element similarity in the stimuli. The effect of illusory contours across groups was similar across participant groups, with the exception of 7- to 9-year olds. The interaction between condition and participant group were not significant in the analysis of WS versus 3- to 4-year olds, $F(1, 22) = 0.854$; $p = .365$ and WS versus 5- to 6-year olds, $F(1, 22) = 0.109$; $p = .744$, but was significant for WS versus 7- to 9-year olds, $F(1, 22) = 5.478$; $p = .029$. However, the significant interaction of condition and participant group for WS versus 7- to 9-year olds may be noise in the data since there is no clear hypothesis about why thresholds from this age group should differ from thresholds from other typically-developing children, adults and WS individuals (see Footnote 3).

There were significant interactions between condition and inter-element separation in the analysis of WS versus 5- to 6-year olds, $F(4, 88) = 4.017$; $p = .005$ and WS versus 7- to 9-year olds, $F(4, 88) = 4.528$; $p = .002$, and a nearly significant interaction in the analysis of WS versus 3- to 4-year olds, $F(4, 88) = 2.192$; $p < .076$. The interactions across these separate analyses reflect the graded effect of the illusory contour; that they are less effective for near elements than for far.

3.2.4. Correlations

We calculated correlations in order to determine whether our measures of visuospatial interpolation are related to WS scores on standardized tests. All correlations with DAS block construction scores (p values $>.05$) and KBIT2 verbal raw scores (p values $>.05$) were non-significant.² We found that KBIT2 matrices raw scores and thresholds at 1.5 inter-element separation in the illusory contour condition ($R = -.590$; $p = .043$) correlated negatively, which may suggest that nonverbal ability is related to integrating elements that have multiple grouping cues (i.e., proximity, collinearity and closure). All other correlations with KBIT2 matrices scores were non-significant (p values $>.10$).

3.3. Discussion

In Experiment 2, we found that illusory contours facilitated visuospatial interpolation in WS individuals, typical children and adults similarly. Across all participants, illusory contours facilitated thresholds at distant separations, but not at near separations. This suggests that WS individuals perceive illusory contours in a typical way (see also Grice et al., 2003). Consistent with Experiment 1, we found that the interpolation functions of WS individu-

als and typical children had higher slopes than the interpolation function of typical adults, suggesting that WS difficulties in visuospatial interpolation might be due to arrested or delayed visual functions. These results support the hypothesis that WS and typical children can detect strong grouping cues as well as typical adults, but that they have difficulty in integrating spatial information across stimuli when grouping cues are weak. WS and typical children can detect grouping cues inherent in the stimuli as well as typical adults, but they have difficulty in integrating spatial information across stimuli with weak grouping cues.

Moreover, since the effect of illusory contours did not vary with participant group, while effect of separation did vary, our results imply that visuospatial integration within a single object (within illusory contours) and across multiple objects (across three squares) may have different developmental trajectories. They further indicate that these two types of integration have different susceptibilities to damage in atypical development.

4. General discussion

We explored how WS individuals, typical children and typical adults integrate visuospatial information across space. We manipulated two factors: inter-element separation and the presence of illusory contours. We found a consistent difference between interpolation of near versus far elements: There was no effect of participant group for integrating over near elements, while thresholds of WS individuals and typically developing children were higher than thresholds of typical adults for integrating over far elements (Fig. 3). There was no effect of illusory contours for integrating over near elements, while the presence of illusory contours improved thresholds of all participant groups for integrating over far elements (Figs. 5–7). These results suggest that visuospatial integration is highly dependent on inter-element proximity (see Quinn, Bhatt, & Hayden, 2008; Kubovy, Holcombe & Wagemans, 1998).

More importantly, we found that the effect of inter-element separation varied over participant group, while the effect of illusory contours did not. WS individuals and typical children had higher thresholds than typical adults (Figs. 3 and 7), but visuospatial interpolation by all participants was facilitated by illusory contours to the same degree (Figs. 6 and 7). We found that the integration of distant elements has a different trajectory in typical development, and a different susceptibility to damage in atypical development than the integration of illusory contour cues. Together, these findings are consistent with the idea that visuospatial integration involves various visual areas, whose computational contributions depend on the grouping cues inherent in the stimuli. When grouping cues such as proximity, closure or collinearity are weak, voluntary attention may be necessary to integrate visuospatial information in a top–down manner.

We hypothesize that our results can be explained in terms of two different kinds of integration: bottom–up and top–down. We now lay out the reasoning in support of this hypothesis, which includes current theories on the mechanisms of bottom–up vs. top–down integration, their apparent brain bases, and the developmental patterns in people with WS that suggest the possibility of impairment in top–down integration but not bottom–up integration.

4.1. Mechanisms of bottom–up and top–down visuospatial integration

4.1.1. Theoretical and behavioral support

There are two broad theories on how integration occurs. On the one hand, Gestalt psychologists in the 1920s and 1930s observed that elements are organized into whole objects readily and effortlessly. They proposed six fundamental laws of grouping: proximity,

similarity, good continuation, common fate, closure and “goodness of form” (Wertheimer, 1923). On the other hand, Treisman and colleagues found that search for a complex, multi-featured object among distractors required more effort than search for simple features. They formulated Feature Integration Theory (Treisman & Gelade, 1980; Treisman & Schmidt, 1982), which contended that integration of multiple features was effortful and requires visual attention. We suggest that Gestalt laws are the bases for bottom–up integration, while voluntary attention is the basis for top–down integration.

This hypothesis is consistent with human adult psychophysics, in which the proximity (Polat & Sagi, 1993) and alignment (Popple, Polat, & Bonnef, 2001) of flankers modulate grating contrast sensitivity. Moreover, as we have seen in our current data (Figs. 3, 6 and 7), proximity and collinearity/closure also improves positional alignment thresholds of high contrast stimuli (Popple et al., 2001; but see also Keeble & Hess, 1998). Waugh and Levi (1993) measured contrast thresholds and Vernier acuities of line segments across various separations. They found that Vernier acuities depended on contrast at small separations, but were independent of contrast at large separations. These authors proposed that position acuity is governed by local spatial filters (i.e., receptive fields) at small separations and by a “local sign” mechanism, in which absolute positions are tagged and compared to obtain relative position information, at large separations. Since the degree of Gestalt grouping cues in the stimuli affect psychophysical data in adults, we speculate that it also accounts for our developmental data.

4.1.2. Possible neural basis

There is a growing body of evidence that the horizontal connections in layers 2/3 of V1 encode grouping properties in the stimuli (Chisum & Fitzpatrick, 2004). Gilbert and colleagues (Gilbert, Das, Ito, Kapadia, & Westheimer, 1996; Gilbert, Ito, Kapadia, & Westheimer, 2000; Kapadia, Ito, Gilbert, & Westheimer, 1995; Li & Gilbert, 2002) have consistently found that neuronal response in V1 is modulated by contextual stimuli. Single-cell recordings in monkey have resulted in increased neuronal firing rate to an oriented bar when a collinear line segment is presented outside of its classical receptive field. Firing rate is dependent on the inter-element separation, on the relative positional offset as well as on the relative orientation between the oriented bar and the neighboring line segment (Gilbert et al., 1996).

Several other areas of the ventral visual pathway in addition to V1 seem to be modulated by stimulus-driven grouping cues. Altmann, Bulthoff, and Kourtzi (2003) have found that viewing collinear contours increases fMRI signals in V1, V2, VP, V4v and LOC relative to viewing randomly oriented gratings. Moreover, perception of grouped stimuli seems to alter fMRI activation in both V1 and LOC (Murray, Kersten, Olshausen, Schrater, & Woods, 2002). These findings suggest that both primary visual cortex and higher occipitotemporal areas are responsible for encoding grouping properties found within the stimuli.

Whereas primary and ventral visual areas may mediate bottom–up integration, top–down visuospatial integration may be mediated by cortical area involved in visual attention. fMRI studies have found that attentional selectivity over multiple elements depends on dorsal visual areas (Culham, Cavanagh, & Kanwisher, 2001), particularly the parietal lobe. The findings of Ritzl et al. (2003) are particularly consistent with our hypothesis. They asked observers to identify simple polygons (e.g. triangles, squares and diamonds) composed of outlines, inducers that form illusory contours and reversed inducers that do not form illusory contours. They found significant activation in posterior parietal cortex when brain activations in the illusory contour and outline conditions were subtracted from the activation in the reversed inducer condition. When brain activation in the reversed inducer condition was

subtracted from the activation from the illusory contour and outline conditions, there were greater activations in the LOC. They also found that when activation in the outline condition was subtracted from activation in the illusory contour condition, there was more activation in the occipital cortex, while the reverse of this contrast, (i.e., illusory contour condition subtracted from the outline condition) activated temporal areas. The results of Ritzl et al. (2003) suggest that the same task (shape identification) increases activation in different brain areas depending on the grouping properties available in the stimuli.

Moreover, Gestalt properties of the stimuli have been found to improve bisection, which is also a visuospatial interpolation task. Bisection of square activated the LOC (Fink, Marshall, Weiss, et al., 2000), while bisection of a line activated parietal cortex (Fink, Marshall, Shah, et al., 2000), suggesting that different brain areas are recruited for the same task depending on the number of grouping cues (i.e., closure) within the stimuli. In addition, the presence of illusory contours improved bisection performance in people with hemispatial neglect due to parietal lobe damage (Vuilleumier, Valenza, & Landis, 2001). This result suggests that the parietal lobe is not necessary for the perception of illusory contours. It further suggests that functions primarily mediated by the parietal lobe are improved by activity in areas responsible for illusory contours (e.g. V1, V2, and LOC).

4.2. Integration in typically developing children and people with WS

Our results highlight the importance of investigating perceptual and cognitive functions in neuropsychological and developing populations, which may provide insight into what mechanisms underlie functions in a typical and mature system. Previous studies in typical adults have yielded Weber's Law in judging relative position as a function of inter-element separation, but they did not give information on how this function might change across development.

We have replicated results from other studies of typical adults, in which we found near perfect scaling, log–log slope of 1.0, of positional thresholds with inter-element separation (Fig. 3a). This scaling of positional judgment with inter-element distance may reflect the equilibrium between the relative activities in bottom-up and top-down grouping within a typical and mature visual system. More informatively, however, positional thresholds of typical children and WS individuals did not scale with inter-element separation (Fig. 3b–d). In other words, Weber fractions of typical children were different between near and far separations, while the Weber fraction of typical adults was the same. The interpolation functions of typical children and WS individuals were steeper than that of typical adults due to higher positional thresholds for interpolating distant elements. Since attentional mechanisms may be immature in typical children (Gogtay et al., 2004) this violation of scaling (i.e., slope \neq 1.0) may reflect the imbalance between the relative activities in the mechanisms involved in bottom-up and top-down integration.⁴

Notably in our experiments, the effect of separation cannot be isolated from the effect of viewing eccentricity. Unless the task is cognitively demanding, peripheral acuity of 6- to 7-year olds (Whiteside, 1976) and the extent of visual fields of 2- to 3-year olds (Cummings, van Hof-van Duin, Mayer, Hansen, & Fulton, 1988) are adult-like. This suggests that the differences between typical

adults and children are not likely due to acuity differences between their foveal and peripheral vision, but may be due to differences in integrating information over wide distances.

The difficulty of WS people in voluntarily integrating positional information from multiple locations is consistent with abnormalities in brain areas responsible for visual attention such as the parietal lobe⁵ (Meyer-Lindenberg et al., 2004). We propose that bottom-up integration of stimulus-driven grouping properties are intact in WS, while top-down integration by voluntary attention is immature to the level of typical children under the age of 6 years.⁶

Interestingly, WS individuals have gross anatomical abnormalities in the occipital lobe (Bellugi et al., 1999, Galaburda, Holinger, Bellugi & Sherman, 2002); but these do not give rise to atypical perception of illusory contours (Grice et al., 2003) or contextual visual illusions (Palomares et al., 2008). Grice et al. (2003) did find atypical ERP signatures in the WS occipital lobe for typical perception of illusory contours. Of course more detailed psychophysical investigation may yet reveal perceptual abnormalities, but it is possible that atypical ERP signals come from the anatomical compression of the posterior portion of the WS brain rather than reflecting the integrity of neuronal connectivity in V1, which mediates the perception of illusory contours (Grosf, Shapley & Hawken, 1993, Grossberg et al., 1997). The typical perception of various visual illusions (Palomares et al., 2008), and the facilitative effect of illusory contours on interpolation in the present study suggest that the mechanisms underlying illusory perception are not impaired in people with WS.

Other studies have found that WS individuals have difficulty perceiving positional information at a distance. When asked to judge the location of a dot relative to a central rectangle, Landau and Hoffman (2005) found that performance of WS children (8–14 years old) was no different from typically developing children matched for verbal and non-verbal abilities (3–6 years old) when the dot and rectangle were close; but that it was impaired when the dot and rectangle were more distant. The performance of WS individuals declined more sharply over distance than performance of controls—a finding that echoes our present results. In addition, Farran and Jarrold (2005) asked WS adults to determine the position of a “ball” relative to the position of a “bat.” They found that WS adults have broader positional tuning than typical adults, but are comparable to tuning of typically developing 4- to 6-year olds (Farran & Jarrold, 2005). This is consistent with our findings in Experiment 2, in which positional thresholds of WS were elevated relative to typical adults even at the nearest distance (Fig. 7). Farran and Jarrold (2005) also found that the peak of the spatial tuning was somewhat shifted in WS. We cannot assess this bias in our data since we asked observers to determine which group of elements was misaligned, and not to determine the direction of the misalignment. Nonetheless, our results, along with these studies, suggest that judgment of relative position for distant elements is somewhat impaired in WS.

⁵ Abnormalities in the parietal lobe are consistent with a more general hypothesis that dorsal visual functions are impaired in people with WS (e.g. Atkinson et al., 2003). However, WS individuals show deficits in many, but not all, of these functions. For example, WS individuals are able to detect motion coherence, but they have difficulty detecting form from motion (Braddick, Atkinson, & Wattam-Bell, 2003; Reiss, Hoffman, & Landau, 2005).

⁶ The difference between bottom-up and top-down integration of visual information in WS and typical development might be related to the difference in the basic representation of implicit and explicit information in development. Implicit and explicit representations in visuospatial cognition (Palomares et al., 2008; Farran & Cole, 2008) and memory (Krinsky-McHale, Kittler, Brown, Jenkins, & Devenny, 2005) have been found to be functionally different in WS and typically-developing children.

⁴ Our data can be described as $y = cx^{(b-d)}$, where b and d independently modify the Weber fraction and c is a constant. The exponent b (top-down integration of separated elements) varies with age, and ranges from 1 (adults) to 1.5 (3- to 4-year olds) in our data. However, the exponent d (bottom-up integration of collinear/closure cues from illusory contour) is invariant with age, and is estimated to be 0.3 (see Appendix for details).

5. Conclusions

Our study provides insight into the nature of visuospatial integration over typical development and in people with WS who have severe spatial impairment. First, we found that developmental progression of near and distant elements were qualitatively different. WS individuals and typically developing children had higher positional thresholds than typical adults for integrating distant spatial information, but had adult-like thresholds at proximate distances. Second, we found that WS individuals and typically developing children were adult-like in their ability to use closure and collinearity cues from illusory contours to improve positional thresholds. Taken together, our data suggest that visuospatial integration—our “position sense”—may recruit multiple mechanisms with variable developmental trajectories, whose relative contributions depend on the grouping cues (e.g. proximity, collinearity and closure) available in the stimuli.

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Appendix A

For judging relative position across a range of inter-element separations, the underlying function follows Weber's law—a function with a log–log slope of 1. This means that the Weber fraction is constant across inter-element separation. In the equation below, c is a constant that represents the Weber fraction.

$$y = cx \tag{A.1}$$

It is not known how WS individuals judge relative position. It has been reported that WS individuals are less precise in their judgment (Farran & Jarrold, 2005). One alternative is that WS individuals' interpolation function also follows Weber's law, but with a higher Weber fraction. The graphs below depict interpolation functions of typical adults and WS individuals if both follow Weber's law. The left panel has log–log coordinates while the right panel has linear–linear coordinates. Notice that the functions in the left panel are parallel, with the function in the right panel converge at the origin and diverge at farther separations (Fig. A1). In the examples below, $c = 0.01$ for adults and $c = 0.02$ for WS.

If the thresholds were normalized by dividing the threshold by the inter-element separation (Fig. A2), then we would get flat interpolation functions (slope = 0) for both WS individuals and typical adults.

The second alternative is that the interpolation function of WS individuals follows a Power law. That is, WS individuals may have different Weber fractions for judging relative position at different inter-element separation. This pattern of results would suggest that interpolation function of WS individuals is different from the

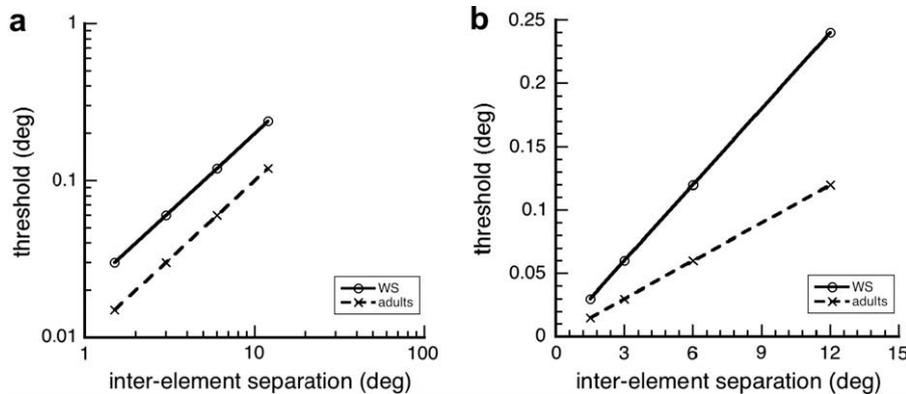


Fig. A1. Prediction 1 shows that positional thresholds follow Weber's Law in log–log coordinates (a) and in linear–linear coordinates (b).

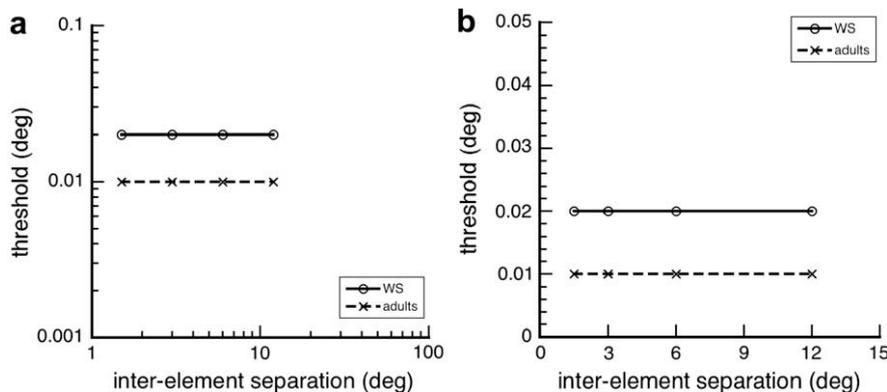


Fig. A2. Normalized positional thresholds from Prediction 1 in log–log coordinates (a) and in linear–linear coordinates (b).

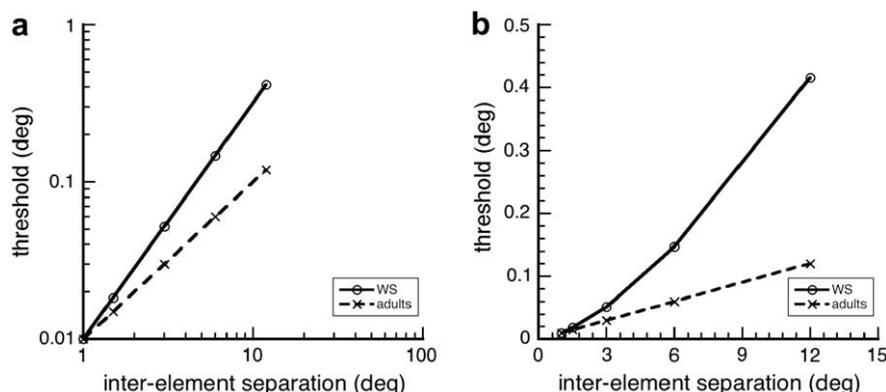


Fig. A3. Prediction 2 shows that positional thresholds of typical adults follow Weber's Law, while thresholds of WS individuals follow Power law in log–log coordinates (a) and in linear–linear coordinates (b).

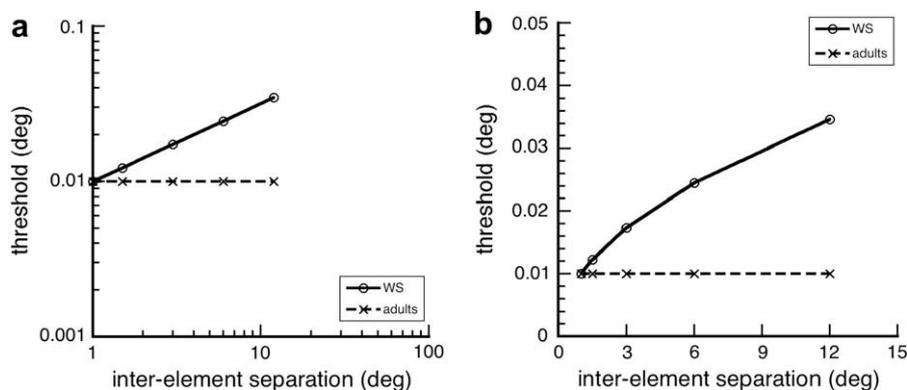


Fig. A4. Normalized positional thresholds from Prediction 2 in log–log coordinates (a) and in linear–linear coordinates (b).

interpolation function of typical adults. In the equation below, c is a constant, and b is an exponent that modifies the Weber fraction. As you can see, the Power law is a more generalized form of Weber's law.

$$y = cx^b \tag{A.2}$$

The example graphs depict interpolation functions of typical adults following Weber's law and of WS individuals following a Power law. The left panel has log–log coordinates while the right panel has linear–linear coordinates. Notice that the functions in both panels converge at the origin and diverge at farther separations in Fig. A3. The slope of the log–log function corresponds to the exponent, b . In these examples, $c = 0.01$; $b = 1.5$ for WS and $b = 1.0$ for typical adults.

If the thresholds were normalized by dividing the threshold by the inter-element separation, then we would get flat interpolation functions (slope = 0) for typical adults, but not for WS individuals (log–log slope = 0.5) as in Fig. A4.

Appendix B. Supplementary data

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.visres.2008.08.012](https://doi.org/10.1016/j.visres.2008.08.012).

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(4), 342–349.

Atkinson, J., Braddick, O., Anker, S., Curran, W., Andrew, R., Wattam-Bell, J., et al. (2003). Neurobiological models of visuospatial cognition in children with

Williams syndrome: Measures of dorsal-stream and frontal function. *Developmental Neuropsychology*, 23(1–2), 139–172.

Bellugi, U., Lichtenberger, L., Mills, D., Galaburda, A., & Korenberg, J. R. (1999). Bridging cognition, the brain and molecular genetics: Evidence from Williams syndrome. *Trends in Neurosciences*, 22(5), 197–207.

Bihrlé, A. M., Bellugi, U., Delis, D., & Marks, S. (1989). Seeing either the forest or the trees: Dissociation in visuospatial processing. *Brain and Cognition*, 11(1), 37–49.

Braddick, O., Atkinson, J., & Wattam-Bell, J. (2003). Normal and anomalous development of visual motion processing: Motion coherence and 'dorsal-stream vulnerability'. *Neuropsychologia*, 41(13), 1769–1784.

Brainard, D. H. (1997). The psychophysics toolbox. *Spatial Vision*, 10(4), 433–436.

Carkeet, A., Levi, D. M., & Manny, R. E. (1997). Development of Vernier acuity in childhood. *Optometry and Vision Science*, 74(9), 741–750.

Chisum, H. J., & Fitzpatrick, D. (2004). The contribution of vertical and horizontal connections to the receptive field center and surround in V1. *Neural Networks*, 17(5–6), 681–693.

Culham, J. C., Cavanagh, P., & Kanwisher, N. G. (2001). Attention response functions: Characterizing brain areas using fMRI activation during parametric variations of attentional load. *Neuron*, 32(4), 737–745.

Cummings, M. F., van Hof-van Duin, J., Mayer, D. L., Hansen, R. M., & Fulton, A. B. (1988). Visual fields of young children. *Behavioral and Brain Research*, 29(1–2), 7–16.

Curran, W., Braddick, O. J., Atkinson, J., Wattam-Bell, J., & Andrew, R. (1999). Development of illusory-contour perception in infants. *Perception*, 28(4), 527–538.

Elliot, C. D. (1990). *Differential abilities scale*. San Diego: Harcourt, Brace, Jovanovich.

Fang, M. S., Enoch, J. M., Lakshminarayanan, V., Kim, E., Kono, M., Strada, E., et al. (2000). The three point vernier alignment or acuity test (3Pt VA test): an analysis of variance. *Ophthalmic and Physiological Optics*, 20(3), 220–234.

Farran, E. K. (2005). Perceptual grouping ability in Williams syndrome: Evidence for deviant patterns of performance. *Neuropsychologia*, 43(5), 815–822.

Farran, E. K., & Cole, V. L. (2008). Perceptual grouping and distance estimate in typical and atypical development: Comparing performance across perception, drawing and construction tasks. *Brain and Cognition* (Epub ahead of print).

Farran, E. K., & Jarrold, C. (2003). Visuospatial cognition in Williams syndrome: Reviewing and accounting for the strengths and weaknesses in performance. *Developmental Neuropsychology*, 23(1–2), 173–200.

- Farran, E. K., & Jarrold, C. (2005). Evidence for unusual spatial location coding in Williams syndrome: An explanation for the local bias in visuo-spatial construction tasks? *Brain and Cognition*, 59(2), 159–172.
- Fink, G. R., Marshall, J. C., Shah, N. J., Weiss, P. H., Halligan, P. W., Grosse-Ruyken, M., et al. (2000). Line bisection judgments implicate right parietal cortex and cerebellum as assessed by fMRI. *Neurology*, 54(6), 1324–1331.
- Fink, G. R., Marshall, J. C., Weiss, P. H., Shah, N. J., Toni, I., Halligan, P. W., et al. (2000). 'Where' depends on 'what': A differential functional anatomy for position discrimination in one- versus two-dimensions. *Neuropsychologia*, 38(13), 1741–1748.
- Galaburda, A. M., Holinger, D. P., Bellugi, U., & Sherman, G. F. (2002). Williams syndrome: Neuronal size and neuronal-packing density in primary visual cortex. *Archives of Neurology*, 59(9), 1461–1467.
- Georgopoulos, M. A., Georgopoulos, A. P., Kurz, N., & Landau, B. (2004). Figure copying in Williams syndrome and normal subjects. *Experimental Brain Research*, 157(2), 137–146.
- Gilbert, C. D., Das, A., Ito, M., Kapadia, M., & Westheimer, G. (1996). Spatial integration and cortical dynamics. *Proceedings of the National Academy of Sciences of the United States of America*, 93(2), 615–622.
- Gilbert, C., Ito, M., Kapadia, M., & Westheimer, G. (2000). Interactions between attention, context and learning in primary visual cortex. *Vision Research*, 40(10–12), 1217–1226.
- Gogtay, N., Giedd, J. N., Lusk, L., Hayashi, K. M., Greenstein, D., Vaituzis, A. C., et al. (2004). Dynamic mapping of human cortical development during childhood through early adulthood. *Proceedings of the National Academy of Sciences of the United States of America*, 101(21), 8174–8179.
- Grice, S. J., Haan, M. D., Halit, H., Johnson, M. H., Csibra, G., Grant, J., et al. (2003). ERP abnormalities of illusory contour perception in Williams syndrome. *Neuroreport*, 14(14), 1773–1777.
- Grosfod, D. H., Shapley, R. M., & Hawken, M. J. (1993). Macaque V1 neurons can signal 'illusory' contours. *Nature*, 365(6446), 550–552.
- Grossberg, S., Mingolla, E., & Ross, W. D. (1997). Visual brain and visual perception: How does the cortex do perceptual grouping? *Trends in Neurosciences*, 20(3), 106–111.
- Guttman, S. E., & Kellman, P. J. (2004). Contour interpolation revealed by a dot localization paradigm. *Vision Research*, 44(15), 1799–1815.
- Hess, R. F., & Hayes, A. (1993). Neural recruitment explains "Weber's law" of spatial position. *Vision Research*, 33(12), 1673–1684.
- Hess, R. F., & Hayes, A. (1994). The coding of spatial position by the human visual system: Effects of spatial scale and retinal eccentricity. *Vision Research*, 34(5), 625–643.
- Hoffman, J. E., Landau, B., & Pagani, B. (2003). Spatial breakdown in spatial construction: Evidence from eye fixations in children with Williams syndrome. *Cognitive Psychology*, 46(3), 260–301.
- Kapadia, M. K., Ito, M., Gilbert, C. D., & Westheimer, G. (1995). Improvement in visual sensitivity by changes in local context: Parallel studies in human observers and in V1 of alert monkeys. *Neuron*, 15(4), 843–856.
- Karmiloff-Smith, A. (2002). Elementary, my dear, Watson, the clue is in the genes... or is it? *Proceedings of the British Academy*, 117, 525–543.
- Karmiloff-Smith, A. (2007). Atypical epigenesis. *Developmental Science*, 10, 84–88.
- Keeble, D. R., & Hess, R. F. (1998). Orientation masks. 3. Gabor alignment performance. *Vision Research*, 38(6), 827–840.
- Kellman, P. J., & Shipley, T. F. (1991). A theory of visual interpolation in object perception. *Cognitive Psychology*, 23(2), 141–221.
- Kim, E., Enoch, J. M., Fang, M. S., Lakshminarayanan, V., Kono, M., Strada, E., et al. (2000). Performance on the three-point Vernier alignment or acuity test as a function of age: Measurement extended to ages 5 to 9 years. *Optometry and Vision Science*, 77(9), 492–495.
- Kovacs, I. (2000). Human development of perceptual organization. *Vision Research*, 40(10–12), 1301–1310.
- Kovacs, I., Kozma, P., Feher, A., & Benedek, G. (1999). Late maturation of visual spatial integration in humans. *Proceedings of the National Academy of Sciences of the United States of America*, 96(21), 12204–12209.
- Kovacs, I., Lukacs, A., Feher, A., Racsmány, M., & Pleh, C. (2001). Contour integration deficit in Williams Syndrome children (abstract). *Journal of Vision*, 1(3), 146. 146a. Available at: <<http://journalofvision.org/1/3/146/>>, doi: 10.1167/1.3.146.
- Krinsky-McHale, S. J., Kittler, P., Brown, W. T., Jenkins, E. C., & Devenny, D. A. (2005). Repetition priming in adults with Williams syndrome: Age-related dissociation between implicit and explicit memory. *American Journal of Mental Retardation*, 110(6), 482–496.
- Kubovy, M., Holcombe, A. O., & Wagemans, J. (1998). On the lawfulness of grouping by proximity. *Cognitive Psychology*, 35(1), 71–98.
- Landau, B., & Hoffman, J. E. (2005). Parallels between spatial cognition and spatial language: Evidence from Williams syndrome. *Journal of Language and Memory*, 53(2), 163–185.
- Lenhoff, H. M., Wang, P. P., Greenberg, F., & Bellugi, U. (1997). Williams syndrome and the brain. *Scientific American*, 277(6), 68–73.
- Levi, D. M., Klein, S. A., & Yap, Y. L. (1987). Positional uncertainty in peripheral and amblyopic vision. *Vision Research*, 27(4), 581–597.
- Li, W., & Gilbert, C. D. (2002). Global contour saliency and local colinear interactions. *Journal of Neurophysiology*, 88(5), 2846–2856.
- Meyer-Lindenberg, A., Kohn, P., Mervis, C. B., Kippenhan, J. S., Olsen, R. K., Morris, C. A., et al. (2004). Neural basis of genetically determined visuospatial construction deficit in Williams syndrome. *Neuron*, 43(5), 623–631.
- Mondloch, C. J., Geldart, S., Maurer, D., & de Schonen, S. (2003). Developmental changes in the processing of hierarchical shapes continue into adolescence. *Journal of Experimental Child Psychology*, 84(1), 20–40.
- Moore, C. M., Yantis, S., & Vaughan, B. (1998). Object-based visual selection: Evidence from perceptual completion. *Psychological Science*, 9(2), 104–110.
- Murray, S. O., Kersten, D., Olshausen, B. A., Schrater, P., & Woods, D. L. (2002). Shape perception reduces activity in human primary visual cortex. *Proceedings of the National Academy of Sciences of the United States of America*, 99(23), 15164–15169.
- Palomares, M., Ogbonna, C. O., Landau, B., & Egeth, H. (2008). Normal susceptibility to visual illusions in abnormal development: Evidence from Williams Syndrome. *Perception*, 37, doi:10.1068/p6044.
- Pani, J. R., Mervis, C. B., & Robinson, B. F. (1999). Global spatial organization by individuals with Williams Syndrome. *Psychological Science*, 10(5), 453–458.
- Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision*, 10(4), 437–442.
- Polat, U., & Sagi, D. (1993). Lateral interactions between spatial channels: Suppression and facilitation revealed by lateral masking experiments. *Vision Research*, 33(7), 993–999.
- Pomerantz, J. R., Goldberg, D. M., Golder, P. S., & Tetewsky, S. (1981). Subjective contours can facilitate performance in a reaction-time task. *Perception & Psychophysics*, 29(6), 605–611.
- Popple, A., Polat, U., & Bonneh, Y. (2001). Collinear effects on 3-Gabor alignment as a function of spacing, orientation and detectability. *Spatial Vision*, 14(2), 139–150.
- Quinn, P. C., Bhatt, R. S., & Hayden, A. (2008). Young infants readily use proximity to organize visual pattern information. *Acta Psychologica (Amsterdam)*, 127(2), 289–298.
- Rauschenberger, R., & Yantis, S. (2001). Attentional capture by globally defined objects. *Perception & Psychophysics*, 63(7), 1250–1261.
- Reiss, J. E., Hoffman, J. E., & Landau, B. (2005). Motion processing specialization in Williams syndrome. *Vision Research*, 45(27), 3379–3390.
- Ritzl, A., Marshall, J. C., Weiss, P. H., Zafiris, O., Shah, N. J., Zilles, K., et al. (2003). Functional anatomy and differential time courses of neural processing for explicit, inferred, and illusory contours: An event-related fMRI study. *Neuroimage*, 19(4), 1567–1577.
- Roelfsema, P. R., Lamme, V. A., & Spekreijse, H. (1998). Object-based attention in the primary visual cortex of the macaque monkey. *Nature*, 395(6700), 376–381.
- Shomstein, S., & Yantis, S. (2002). Object-based attention: Sensory modulation or priority setting? *Perception & Psychophysics*, 64(1), 41–51.
- Snodgrass, J. G., & Feenan, K. (1990). Priming effects in picture fragment completion: Support for the perceptual closure hypothesis. *Journal of Experimental Psychology—General*, 119(3), 276–296.
- Treisman, A. M., & Gelade, G. (1980). A feature-integration theory of attention. *Cognitive Psychology*, 12(1), 97–136.
- Treisman, A., & Schmidt, H. (1982). Illusory conjunctions in the perception of objects. *Cognitive Psychology*, 14(1), 107–141.
- Vuilleumier, P., Valenza, N., & Landis, T. (2001). Explicit and implicit perception of illusory contours in unilateral spatial neglect: Behavioural and anatomical correlates of preattentive grouping mechanisms. *Neuropsychologia*, 39(6), 597–610.
- Waugh, S. J., & Levi, D. M. (1993). Visibility and Vernier acuity for separated targets. *Vision Research*, 33(4), 539–552.
- Wertheimer, G. (1923). Untersuchungen zur Lehre von der Gestalt II, Psychologische Forshung, 301–350. In W. D. Ellis (Ed.), *A Source Book of Gestalt Psychology* (Vol. 4, pp. 71–88). London: Harcourt, Brace and Javanovich.
- Westheimer, G., & McKee, S. P. (1977). Integration regions for visual hyperacuity. *Vision Research*, 17(1), 89–93.
- Whiteside, J. A. (1976). Peripheral vision in children and adults. *Child Development*, 47(1), 290–293.
- Yebara-Pimentel Vilar, E., Giraldez-Fernandez, M. J., Enoch, J. M., Lakshminarayanan, V., Knowles, R., & Srinivasan, R. (1995). Performance on three-point vernier acuity targets as a function of age. *Journal of the Optical Society of America A—Optical Image Science and Vision*, 12(10), 2293–2304.