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Normal susceptibility to visual illusions in abnormal development: Evidence from Williams syndrome

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Abstract. The perception of visual illusions is a powerful diagnostic of implicit integration of global information. Many illusions occur when length, size, orientation, or luminance are misjudged because neighboring visuospatial information cannot be ignored. We asked if people with Williams syndrome (WS), a rare genetic disorder that results in severely impaired global visuospatial construction abilities, are also susceptible to the context of visual illusions. Remarkably, we found that illusions influenced WS individuals to the same degree as normal adults, although size discrimination was somewhat impaired in WS. Our results are evidence that illusions are a consequence of the brain's bias to implicitly integrate visual information, even in a population known to have difficulty in explicitly representing spatial relationships among objects. Moreover, these results suggest that implicit and non-implicit integration of spatial information have different vulnerabilities in abnormal development.

1 Introduction

Visual illusions have captivated observers since Aristotle's time, and have been systematically studied since the 1800s (Eagleman 2001). Though the mechanisms mediating illusions are still unclear, recent evidence indicates that the effects of visual illusions produced by neighboring visual context are independent of attentional awareness. Even when experimental conditions leave people *unaware* of the illusion context, illusions still affect perception, suggesting that visuospatial context automatically induces illusions in normal adults (Moore and Egeth 1997). Therefore, contextual visual illusions seem to demonstrate implicit integration(1) of visuospatial information, such that the neighboring context is automatically integrated into the perception of local elements.

Evidence indicates that the neuroanatomical locus of contextual illusions is V1. Patients with visuospatial neglect due to parietal lobe lesions are susceptible to visual illusions (Daini et al 2002) unless there is additional occipital lobe (V1) damage. Murray et al (2006) have also found that the Ponzo illusion context induces an illusory size difference that is correlated with fMRI activation in V1. Here, we asked whether illusions influence Williams syndrome (WS) individuals, who have deficits in their ability to represent visuospatial relationships among objects, and who also have parietal and occipital lobe abnormalities (eg Bellugi et al 1999).

WS is a rare genetic disorder resulting from a microdeletion of ~20 genes on chromosome 7 (Lenhoff et al 1997), producing an uneven cognitive profile that includes relatively intact language with severely impaired visuospatial abilities (Bellugi et al 1999). This profile

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(1) We broadly define integration as the combination or coordination of separate elements into a unified group. There are several tasks that demonstrate integration, including perception of contextual visual illusions, illusory contours, hierarchical figures, and Vernier acuity, in which global perception is contingent upon the combination of information from independent local elements. In contextual visual illusions, local elements are integrated into a global context, which then implicitly influences the perception of the local elements.

suggests the possibility that a genetic deficit might target specific cognitive systems, in this case a system underlying a range of visuospatial tasks. One oft-cited hypothesis is that the WS spatial deficit lies in visuospatial integration (Bellugi et al 1999), resulting in profoundly impaired block construction (Hoffman et al 2003) and drawing performance. For example, when asked to draw a Navon figure (figure 1), which requires the integration of local elements to create a global percept, WS individuals draw the local letters well but do not replicate the configuration of the global object (Bihrle et al 1989).

Model WS male (18; 10) WS female (18; 9)

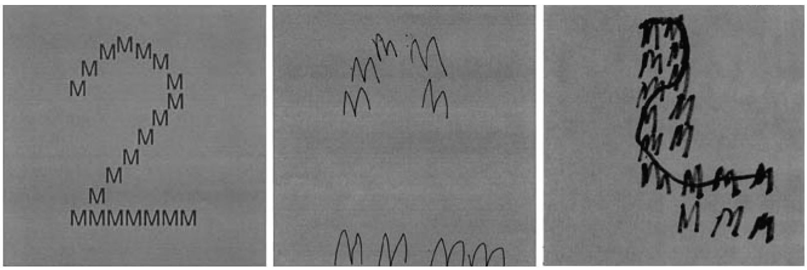

Figure 1. Model and copies by WS participants (age in years; months)

However, the current evidence on visuospatial integration in WS is mixed. On the one hand, WS individuals have deficits in combining elements of a global pattern in construction tasks. They also seem to perceive some global figures in an atypical manner. Farran (2005) found that grouping by shape, orientation, and proximity was poorer in WS individuals than in controls, while grouping by luminance, closure, and alignment was comparable. On the other hand, WS individuals can use grouping properties to facilitate search, suggesting that they can implicitly perceive global organization (Pani et al 1999). They can also perceive both biological motion and motion coherence, which requires integration of spatiotemporal information (Jordan et al 2002; Reiss et al 2005). Thus, the extent to which WS individuals have impaired visuospatial integration is still unsettled.

The idea that basic visual functions such as integration might be impaired in WS is consistent with recent studies showing abnormalities in several visual areas. Anatomical studies also indicate reduced overall brain volume with disproportionate reduction in grey matter in the thalamus and V1 (Reiss et al 2004). Moreover, when viewing illusory contours, WS individuals have abnormal electrophysiological responses in V1 (Grice et al 2003), suggesting that WS individuals may have deficits in basic visual functions, which could include deficits in integration.

Many observations are also compatible with the hypothesis that the locus of WS damage is the dorsal visual pathway (eg Atkinson et al 2003). Relative to normal controls, WS dorsal visual areas involved in attention and visuospatial integration are smaller in size (Bellugi et al 1999) and show fMRI hypoactivation, whereas ventral visual areas seem comparable to those of controls (Meyer-Lindenberg et al 2004). Ventral stream functions such as object (Landau et al 2005) and face (Paul et al 2002; Tager-Flusberg et al 2003; but see also Deruelle et al 1999; Karmiloff-Smith et al 2004 for contrasting view) recognition seem functionally normal in WS as well.

As one approach in determining the extent to which visuospatial integration is impaired in WS, we asked if WS individuals are susceptible to visual illusions, which represent a clear case of implicit visuospatial integration. If WS individuals are impaired in some aspects of global visuospatial integration as suggested by partial deficits in perceptual organization (Farran 2005), then they might be less susceptible to visual illusions than controls. Alternatively, if WS individuals have intact implicit visuospatial integration, then they should show normal susceptibility to visual illusions.

This would suggest that their impairment might lie in mechanisms required for explicit representation of visuospatial information. A pattern of normal susceptibility to illusions along with impairment in explicitly representing spatial relationships among elements would be evidence for the functional separation of two different mechanisms of visuospatial integration.

2 Methods

2.1 *Participants*

One hundred participants with normal or corrected-to-normal vision were tested on four illusions: Ponzo, Müller-Lyer, Kanizsa-occlusion, and Ebbinghaus (figures 2 and 3a). Participants included people with WS aged 10–41 years ($n = 22$; mean age $= 20$ years, 9 months), normally developing 3–4-year-olds ($n = 20$; mean age $= 3$ years, 11 months), 5–6-year-olds ($n = 20$; mean age $= 5$ years, 9 months), 7–10-year-olds ($n = 15$; mean age $= 8$ years, 7 months), and normal adults ($n = 23$; mean age $= 19$ years, 9 months). All normal children and WS participants were tested on the four illusions with the exception of one WS participant and two 3–4-year-olds, who did not complete the Ebbinghaus illusion. Twenty-three adults were tested on the Ponzo, Müller-Lyer and Kanizsa-occlusion illusions, and a separate group of fifteen adults was tested on the Ebbinghaus illusion. All WS participants were positively diagnosed by a geneticist with a fluorescent in-situ hybridization test.

WS participants were given the Kaufman Brief Intelligence Test (KBIT), an intelligence test that measures both vocabulary (verbal) and nonverbal analytical skills (matrices). The KBIT is widely used in neuropsychological, developmental, and WS studies (eg Mervis et al 2000). The WS group had average raw KBIT scores of 37 (range of 23 to 50) for the verbal and 19 (range of 14 to 24) for the matrices components. The raw scores correspond to those of normal 8-year-olds (verbal) and 6.5-year-olds (matrices) at the 50th percentile. The mean normalized IQ of the WS group was 60 (range of 40 to 90), within the range of other studies (eg Hoffman et al 2003). A subset of our WS participants ($n = 16$) was also given the Differential Abilities Scales (DAS) block-construction subtest. These WS participants had average raw block-construction scores of 95 (range of 67 to 126), which is between $<$ 1st and 7th percentile for their chronological age. These DAS scores correspond to those of normal 5-year-olds at the 50th percentile, and are typical for people with WS.

2.2 *Stimuli*

All four illusions (figures 2 and 3a) required participants to make a judgment of size. All illusion stimuli were typical of those in the literature (Bruno and Bernardis 2002; Coren and Girgus 1978), were drawn in Adobe Photoshop (figure 2), and were printed via laser printer on 8.5 inch $\times$ 11 inch white letter paper.[2]

2.2.1 *Ponzo illusion.* In the Ponzo illusion, targets were two black horizontal lines separated vertically by 6.9 deg. One line (randomly either the upper or lower one) was always 3.4 deg, and the other line varied in length over trials from 4.0 to 3.4 deg. Flanking the horizontal lines, the inducers were two black lines at $\pm 15°$ angle, which were always angled narrower at the top part of the figure. Thus when the horizontal target lines were equal in length, the upper line (where the angled lines were closer) looked longer than the lower line (figure 3a).

2.2.2 *Müller-Lyer illusion.* In the Müller-Lyer illusion, targets were two black vertical lines presented 6.9 deg apart. One line (either the left or the right) was always 3.4 deg, and the other line varied in length over trials from 4.0 to 3.4 deg. The inducers

[2] The stimuli were printed on paper and bound as a booklet to maximize portability. Ten of the WS participants were tested at the 2004 Williams Syndrome National Convention.

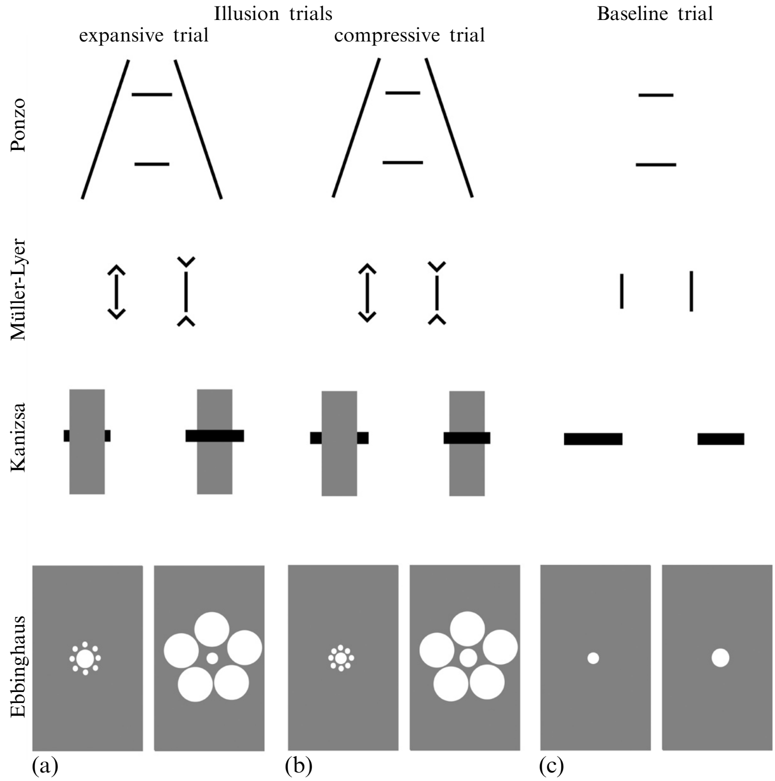

Figure 2. Pair of illusion context trials, (a) and (b), and baseline trial, (c), in the Ponzo, Müller-Lyer, Kanizsa-occlusion, and Ebbinghaus illusions. *Illusion trials*: Though the physical target size difference is identical in both expansive (a) and compressive (b) trials, the size difference between the targets is perceptually increased in the expansive trials (a), while it is perceptually reduced in the compressive trials (b). In both expansive and compressive trials, the position of the illusion context is constant. For the Ponzo illusion the longer target line is on top for the expansive trials, and on the bottom for the compressive trials. For the Müller-Lyer and Kanizsa-occlusion illusions the longer target line is on the right for the expansive trials, and on the left for the compressive trials. For the Ebbinghaus illusion the larger target circle is on the left for the expansive trials, and on the right for the compressive trials. In our experiment, we noted the difference in size at which the participant made the first error on a compressive trial in the illusion condition, which reflects the physical size difference perceptually nullified by the illusion context. *Baseline trials*: The longer/larger target is on the bottom, right, left, and right for the Ponzo, Müller-Lyer, Kanizsa-occlusion, and Ebbinghaus illusions, respectively. The physical target-size difference is identical across the baseline and illusion trials.

were opposing arrowheads whose location was held constant throughout the trials; the left target had arrowheads pointing away from the line, while the right target had arrowheads pointing toward the line. The closest corner of the arrowhead was 0.57 deg away from the endpoints of the lines. When the target lines were equal in length, the line surrounded by arrowheads pointing in toward the line looked longer than the line with outward pointing arrowheads (figure 3a).

2.2.3 *Kanizsa-occlusion illusion.* In the Kanizsa-occlusion illusion, targets were two black horizontal rectangles 13.7 deg apart center-to-center. One was always 4.6 deg long, while the other varied in length over trials from 5.2 to 4.6 deg; both were 1.1 deg tall. Inducers were 50% grey vertical rectangles 3.4 deg wide by 10.3 deg tall, which were either 'in front of' (left stimuli) or 'behind' (right stimuli) the targets. When the horizontal rectangles were equal in length, the one that passed in front of its inducer appeared longer (figure 3a).

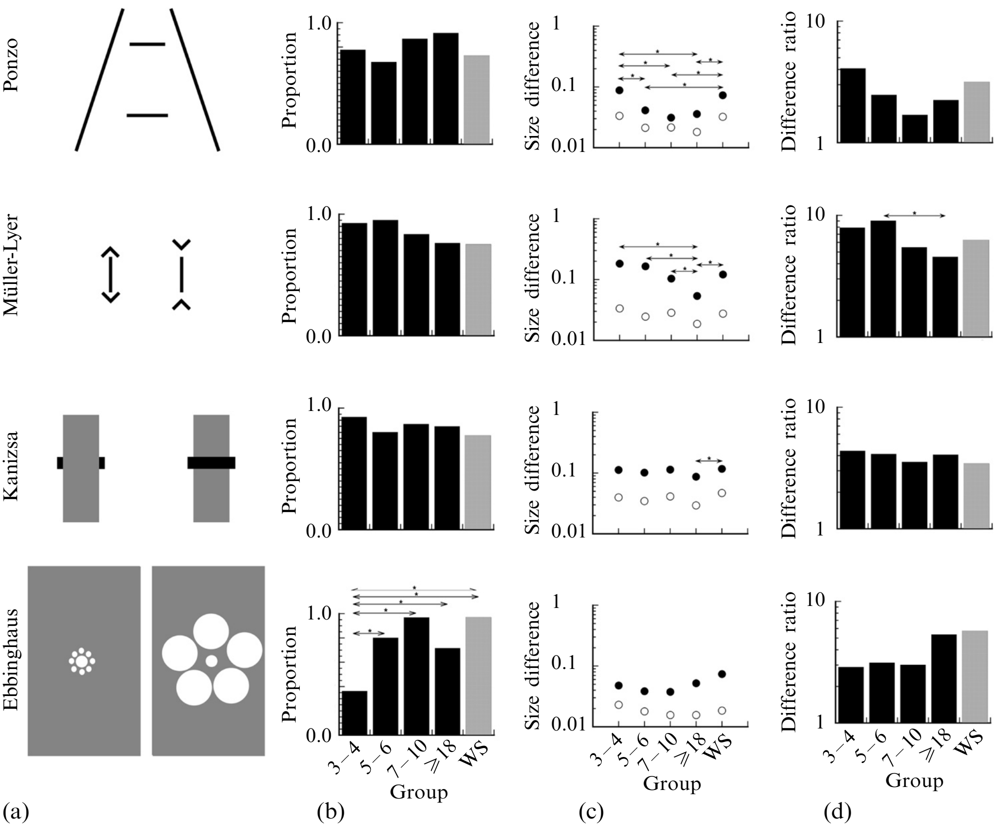

Figure 3. (a) Ponzo, Müller-Lyer, Kanizsa-occlusion, and Ebbinghaus stimuli. The central lines or circles are physically the same size, but are perceptually different in size. (b) Mean proportion of responses consistent with the illusion when the central lines or circles were physically the same size. Proportions were not reliably different between normal adults ($\geqslant$ 18-year-olds) and WS. In the Ebbinghaus illusion, mean proportion of 3 – 4-year-olds was not significantly different from chance (0.50), and was significantly different from the other participant groups. (c) The difference in size (geometric mean) at which the participant made the first error on baseline trials without the illusion context (open circles), or on critical trials with the illusion context (solid circles). Size differences averaged over context and no context conditions were reliably lower in normal adults than in WS or in 3 – 4-year-olds. (d) Crucially, geometric means of different ratios (illusory size/baseline size), which represent the illusion magnitude, were not reliably different between normal adults and WS participants. This suggests that WS individuals perceive visual illusions to the same degree as normal adults (*significant a posteriori Tukey HSD between participant groups at $p < 0.05$).

2.2.4 *Ebbinghaus illusion.* In the Ebbinghaus illusion, the stimuli were white circles on 50% grey background. The two target circles were 12.5 deg apart center-to-center. One target circle always had a 1.15 deg diameter, while the other varied in diameter over trials from 1.71 to 1.15 deg. In the illusion condition, inducers were eight circles with 0.57 deg diameters (left stimuli) or five circles with 3.43 deg diameters (right stimuli). These surrounded the target circles whose location was held constant throughout the trials. When the target circles were the same size, the one surrounded by small inducers appeared larger than the one surrounded by large inducers (figure 3a).

2.3 *Design and procedure*

We designed our experiment such that young children and WS individuals could easily understand and quickly perform the task. Our procedure is modeled after a descending method of limits, similar to the 'eye chart' procedure for measuring letter acuity.

For each illusion, there were fifteen trials: five baseline trials, in which inducers were absent, followed by ten illusion context trials in which they were present. One baseline and two illusion practice trials were presented before the experimental trials. Participants sat approximately 63 cm from the stimuli. The experimenter wrote down the participants' answers.

2.3.1 *Baseline trials.* In the baseline trials (figure 2c), the size difference between the target pairs decreased after every trial (eg 0.5727, 0.2864, 0.1432, 0.0716, and 0 deg). The size difference at which the participant made the first error was taken to be the categorical boundary or 'threshold' at which a difference between two targets becomes indiscriminable. Because the size differences in the initial trials were obvious and size differences in subsequent trials became indistinguishable, the first error was considered an error due to guessing (ie chance performance).

2.3.2 *Illusion trials.* In the illusion context trials, trials were presented in pairs (figures 2a and 2b), and the size difference decreased every *two* trials until the lines or circles had the same size. (The size differences were the same as in the baseline trials.) The position of the inducing context was constant as described in section 2.2. For example, for the Müller-Lyer illusion the inducer that tends to lead to a 'larger' response (ie the inward-pointing arrowheads) was always on the right. What was counterbalanced in each condition were the positions of the shorter and longer lines. In one randomly selected trial within a pair of trials the longer line was on the right and on the other trial it was on the left. Participants indicated which target line was longer or which circle was larger, by pointing. Participants pointed to the top or bottom target for the Ponzo illusion and to the left or right target for the Müller-Lyer, Kanizsa-occlusion, and Ebbinghaus illusions.

The reason for the use of paired trials in the illusion condition is as follows. As exemplified in figure 2, at a given size difference (say 0.29 deg) the illusion context would have the effect of either exaggerating or reducing the perceived size difference between the target lines. In *non-critical* or *expansive* trials (figure 2a), the illusion context would make the long line look longer and the short line look shorter, and therefore one would expect relatively accurate size judgments. In fact, errors occurred on only 1.2% of expansive trials, and they were not considered further. Because a subject could be correct on such a trial either by falling sway to the effect of the illusion or by accurately perceiving the size of the target lines, these trials were not exclusively diagnostic of the effects of the illusory context. They were only presented to counterbalance target position. In pilot trials, presenting unbalanced stimuli (eg comparing a single line and a line with arrowheads) increased the number of young children who had biased responses for choosing targets with inducing context. Presenting balanced stimuli (ie comparing targets with compressive and expansive inducers) eliminated this bias.

On *critical* or *compressive* trials (figure 2b), however, the illusion context would normally induce a percept that is opposite from the targets' actual relative sizes by making a long line look shorter and a short line look longer. This would effectively reduce the perceived size differences between the targets, and, if the target lines were similar enough, could result in a reversal in their apparent sizes (which would result in an error). In the illusion condition, the size difference at which the participant made the first error on a compressive trial was taken to be the categorical threshold.

In the current experiment, we assumed that the size difference at which the participant made the first error represents the size difference at which the participant begins to perceive a reversal of the actual sizes, or at which the participant cannot perceptually distinguish a physical size difference. Since participants were forced to choose which target was longer or bigger, they could make correct guesses at the smallest size difference we tested, which could result in no error for a condition. When this occurred (16% of trials across all participants, illusions, and conditions), we assumed that people would be at chance performance on the next step size, which is the smallest physical size difference decreased by a factor of two (ie 0.357 deg). This assumption seems reasonable since the smallest size difference that we tested (eg 0.0716 deg) corresponded to Vernier thresholds for comparing elements at separations between 5.0 and 12 deg (Levi and Klein 1990; Levi et al 1988; Palomares et al 2008) and to normal letter acuity at fixation (eg Arditi and Cho 2007).

In a separate procedure, we asked normal adults to discriminate line lengths or circle diameters that were different by 0.0357 deg (ie half of the smallest size difference in the main experiment), which is below hyperacuity thresholds for similar inter-target separations (eg Levi and Klein 1990). These stimuli were identical to the baseline stimuli in the main experiment. For lines, we found that thirteen out of twenty-three people correctly discriminated length (one-tailed sign test, $p = 0.3388$). For circles, we found that twelve out of twenty people correctly discriminated size (one-tailed sign test, $p = 0.2517$). These results suggest that ability of normal adults to discriminate objects with a size difference of 0.0357 deg was not reliably better than chance. As categorical thresholds are essentially the difference in stimuli that would elicit chance performance, it does not seem implausible to use size difference in the supplementary experiment as the proxy step size in the main experiment.(3)

3 Results

Data from WS children (< 18 years old; $n = 10$) and WS adults ($\geqslant 18$ years old; $n = 12$) were collapsed, since KBIT raw scores, block-construction scores, size discrimination, illusion prevalence, and illusion susceptibility was not reliably different between these groups. All t-tests had p-values > 0.05.

3.1 *Illusion prevalence*

To determine whether or not participants were subject to the visual illusions we examined the mean proportion of responses consistent with the illusion on trials when the target lines or circles were physically the same size (figures 3a and 3b). Participants in all groups perceived the illusions at greater than chance levels (50%), with the exception of 3–4-year-olds in the Ebbinghaus illusion (figure 3b). The WS group was not different from normal adults in any of the illusions. A one-way ANOVA showed no significant differences(4) across the five participant groups for the Ponzo illusion ($F_{4,95} = 2.267$, $p = 0.068$), Müller-Lyer illusion ($F_{4,95} = 2.179$, $p = 0.077$), or Kanizsa-occlusion illusion ($F_{4,95} = 0.709$, $p = 0.588$).

Only the Ebbinghaus illusion showed a significant effect of participant group ($F_{4,84} = 9.443$, $p < 0.001$), with Tukey a posteriori analyses showing that 3–4-year-olds had significantly lower proportions than any of the other groups: 5–6-year-olds ($p = 0.001$), 7–10-year-olds ($p < 0.001$), normal adults ($p = 0.012$), and WS individuals ($p < 0.001$).

(3) As a precaution, we also carried out analyses without proxy scores, which affected 29% of participants in the Ponzo illusion, 36% in the Müller-Lyer illusion, 21% in the Kanizsa-occlusion illusion, and 50% in the Ebbinghaus illusion. Since proxy scores mostly affected normal adults in the baseline conditions, normal adults were not included in the analyses for the Ponzo and Müller-Lyer illusions. We also did not analyze data from the Ebbinghaus illusion due to lack of power. Even with fewer participants, results from these analyses were consistent with the main data reported in section 3. Across the three remaining illusions, participant group did not affect illusion magnitude. Participant group did not affect size discrimination in the Müller-Lyer and Kanizsa-occlusion illusions, while 8–9-year-olds had better size performance than 3–4-year-olds in the Ponzo illusion (Tukey a posterior HSD; $p < 0.05$).

(4) One-way ANOVAs for the Ponzo and Müller-Lyer illusions approached significant levels ($p < 0.10$). Tukey a posteriori analyses show the smallest p-values between groups were from proportions of 5–6-year-olds compared to adults ($p = 0.072$) in the Ponzo illusion, and proportions of 5–6-year-olds compared to WS individuals ($p = 0.164$) in the Müller-Lyer illusion. All other differences between groups had p-values > 0.20.

Like Káldy and Kovács (2003), we found that young children may be less susceptible to this particular illusion since we found that the mean proportion of responses of 3–4-year-olds were not significantly different from chance.

3.2 *Illusion magnitude*

An additional measure was used to determine the *magnitude* of the illusion, the ratio of the size differences at which participants made the first error in the illusion and baseline conditions. If the context was effective in inducing the illusion, then the target size difference at which observers first made a perceptual error should be larger in the critical trials of the illusion condition compared to the trials of the baseline condition (figure 3c). The ratio of these size differences measures the amount of perceptual distortion due to the illusion context, and is mathematically equivalent to the interaction between illusion condition and participant group. Ratios were computed for each participant by dividing the size difference in the illusion condition by the size difference in the baseline condition (figure 3d). These size differences and ratios of size differences were converted to log size differences and log ratios of size differences in order to perform statistical tests.

3.2.1 *Effect of the illusion.* To directly compare the perceived magnitude of the illusion between WS individuals and normal adults, we carried out planned comparisons of size difference ratios. Histograms of the illusion magnitude show that the majority of normal adults and WS individuals are affected by the illusion (figure 4).[5] We found no reliable difference between WS individuals and normal adults (figure 3d) ($t_{43}^{\text{Ponzo}} = 0.664$, $p = 0.510$, power $= 0.100$; $t_{43}^{\text{Muller-Lyer}} = 2.219$, $p = 0.144$, power $= 0.308$; $t_{43}^{\text{Kanizsa-occlusion}} = 1.681$, $p = 0.523$, power $= 0.097$; $t_{43}^{\text{Ebbinghaus}} = 0.403$, $p = 0.996$, power $= 0.050$). There were also no differences in magnitude of the illusion over participant groups for the Ponzo ($F_{4,95} = 1.390$, $p = 0.243$), Kanizsa-occlusion ($F_{4,95} = 0.124$, $p = 0.973$), or Ebbinghaus ($F_{4,84} = 2.137$, $p = 0.087$) illusions. There was a significant effect of participant group for the Müller-Lyer illusion ($F_{4,95} = 2.533$, $p = 0.045$) owing to higher ratios of 5–6-year-olds compared to normal adults (Tukey HSD, $p = 0.035$).

3.2.2 *Size discrimination: Baseline condition only.* We carried out four one-way ANOVAs on the size discrimination scores in the baseline condition to see if there were any differences across participant groups. We found a significant effect of participant group in the Ponzo illusion ($F_{4,95} = 4.614$, $p = 0.002$), near-significant effects in the Müller-Lyer illusion ($F_{4,95} = 2.372$, $p = 0.059$) and Ebbinghaus illusion ($F_{4,84} = 2.067$, $p = 0.092$), and no effect in the Kanizsa illusion ($F_{4,95} = 1.391$, $p = 0.243$). Tukey a posteriori analyses showed that size discrimination was poorer in WS than in normal adults only in the Ponzo illusion ($p = 0.012$). Size discrimination also was worse for 3–4-year-olds than for normal adults in the Ponzo ($p = 0.002$), Müller-Lyer ($p = 0.058$), and Ebbinghaus ($p = 0.113$) illusions.

3.2.3 *Size discrimination: Collapsed over baseline and illusion condition.* To increase the power of analyses, it seems justifiable to also conduct analyses on size discrimination errors collapsed over baseline and illusion context conditions since there was only a main effect of condition with no significant interaction between condition and participant group (figure 3b). The target size difference at which observers made size discrimination errors significantly varied over participant group in the Ponzo illusion ($F_{4,95} = 11.285$, $p < 0.001$), Müller-Lyer illusion ($F_{4,95} = 11.005$, $p < 0.001$), and Kanizsa-occlusion illusion ($F_{4,95} = 2.581$, $p = 0.042$), but only approached significance for the Ebbinghaus

[5] The magnitude of the illusion is represented by a difference between the baseline and the illusion conditions, rather than a ratio in other studies. However, if we convert our ratios to differences, the effect of the illusions is similar to those in other studies on normal children and adults (eg Káldy and Kovács 2003; Ropar and Mitchell 1999).

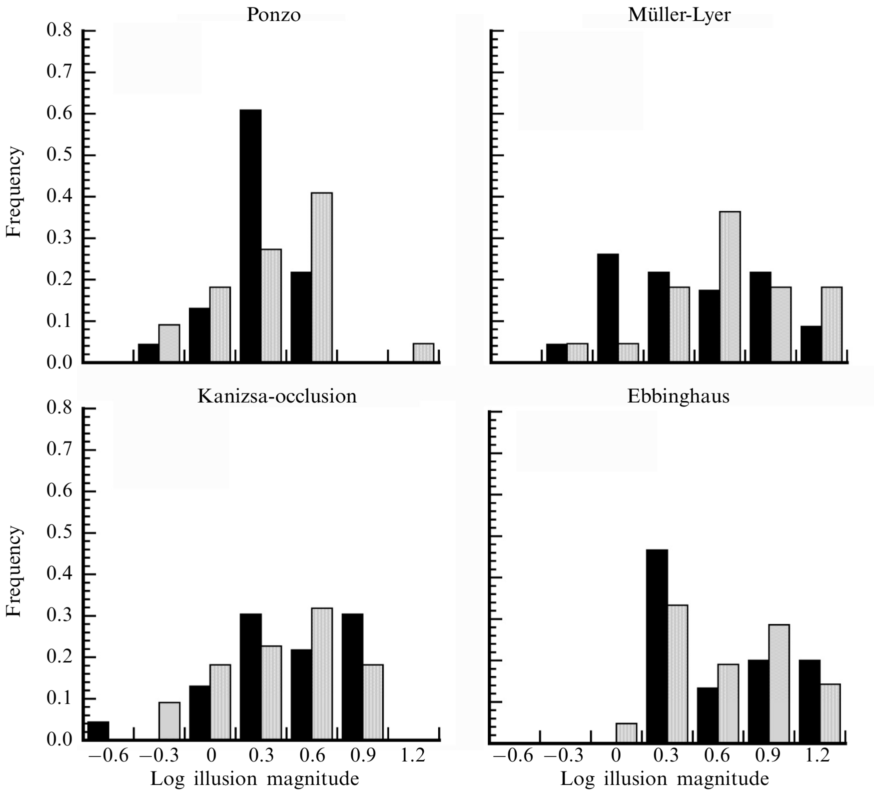

Figure 4. Frequency histograms of illusion magnitude (log difference ratio) in normal adults (black) and WS individuals (grey) for the Ponzo, Müller-Lyer, Kanizsa-occlusion and Ebbinghaus illusions. Scores greater than zero represent an effect of the illusion. Across all four illusions, the distributions between normal adults and WS individuals highly overlap, and are not significantly different (see text for details).

illusion ($F_{4,84} = 2.214$, $p = 0.074$). Although there were no differences between WS people and normal adults in existence or in magnitude of perceiving the illusion, the WS participants were worse than normal adults at discriminating size (figure 3c). The size difference at which WS participants made errors was larger than the size difference at which normal adults made errors in the Ponzo (Tukey HSD, $p < 0.001$), Müller-Lyer (Tukey HSD, $p < 0.001$), and Kanizsa-occlusion (Tukey HSD, $p = 0.031$) illusions. The size differences at which WS participants made errors were not different from those of any of the children's groups, with the exception of 5 – 6-year-olds (Tukey HSD, $p = 0.011$) and 8 – 10-year-olds (Tukey HSD, $p = 0.002$) in the Müller-Lyer illusion. Size discrimination in the Müller-Lyer illusion was worse in WS than in normal children.

In addition, we found that size discrimination improves over normal development (figure 3c). Tukey a posteriori analyses indicate that the size difference at which 3 – 4-year-olds made errors was significantly larger than those at which 5 – 6-year-olds, 7 – 10-year-olds, and normal adults made errors in the Ponzo illusion. Likewise, the size differences at which 3 – 4-year-olds, 5 – 6-year olds, and 7 – 10-year-olds made errors were significantly larger than that at which normal adults made errors in the Müller-Lyer illusion (all ps < 0.01).

3.3 *Correlations*

In order to determine whether size discrimination and illusion susceptibility were related to the hallmark impairment in block construction tasks and measures of verbal and non-verbal abilities, we carried out a subset of correlations on scores of WS participants.

We correlated KBIT (verbal and matrices) and DAS block-construction raw scores with size discrimination and illusion magnitude, and found one significant correlation. We found that DAS block-construction scores weakly correlated with log ratios in the Ebbinghaus illusion ($n = 16$; Pearson $r = +0.517$; $p = 0.049$), which may suggest that certain skills involved in block construction may be linked to the susceptibility to the Ebbinghaus illusion.(6) Susceptibility to the other three illusions did not correlate with block construction (p-values > 0.20). There were also several notable correlations that were nearly significant. The correlations between DAS block-construction scores and size discrimination in the baseline conditions of the Ponzo ($n = 16$; Pearson $r = -0.414$; $p = 0.111$) and Kanizsa-occlusion ($n = 16$; Pearson $r = -0.428$; $p = 0.059$) illusions were *negative*, which suggests that better block-construction skills may be associated with better size-discrimination skills. (Note that the direction of the correlation is negative since a smaller size difference represents better performance.) All other correlations among KBIT scores, DAS scores, size-differences, and ratios of size differences were non-significant (p-values > 0.20). However, these correlations need to be taken with caution: these KBIT and DAS scores have a narrow range, averaging in the 1st percentile of their chronological age.

In addition, raw scores from the non-verbal component of the KBIT (matrices) correlated with the raw scores of the DAS block-construction task ($n = 16$; Pearson $r = +0.578$; $p = 0.019$). Baseline size discriminations in the Ponzo and Kanizsa-occlusion illusions correlated with each other ($n = 22$; Pearson $r = +0.426$; $p = 0.048$), perhaps reflecting the fact that both tasks involved size discrimination of horizontal elements.

4 Discussion

The aim of this study was to determine whether WS individuals are susceptible to visual illusions, and to compare the magnitude of their illusory perception with those of normal children and adults. We found that WS individuals were susceptible to all four illusions: when the targets were physically the same size, WS individuals saw them as different (figure 3b). We also found that the illusions affected WS individuals and normal adults to the same degree (figure 3d) despite the fact that WS individuals made discrimination errors at larger target-size differences than normal adults (figure 3c). Our results are consistent with those of Pani et al (1999), who found that both WS individuals and normal adults show similar effects of grouping on visual search, even though WS individuals had overall slower reaction times. These findings show that WS individuals may have functional implicit processes of grouping and visuospatial integration, even though they are impaired in explicit representation of spatial relationships.

4.1 *Possible mechanisms*

4.1.1 *Susceptibility to contextual illusions and implicit integration.* The normal susceptibility of WS individuals to visual illusions is striking in view of the evidence for their unusual cognitive profile, and the anomalous brain structures and functions that might have prevented them from seeing the illusions. The occipital lobe, which seems to be necessary for perceiving contextual visual illusions (Daini et al 2002; Murray et al 2006), has been found to be abnormal in WS. Structural MRI has shown that WS individuals have reduced grey matter in the thalamus and V1 (Reiss et al 2004).

(6) The Ebbinghaus illusion might be different from the other illusions we studied. First, we found that susceptibility to the Ebbinghaus illusion did not change with age (figure 3d), while its prevalence increased with age (figure 3b). The effects of the Ebbinghaus illusion have been reported to decrease, increase, or be constant with age (Bondarko and Semenov 2004; Coren and Girgus 1978; Káldy and Kovács 2003), suggesting that this illusion may be sensitive to context proximity, shape, and size that can alter age effects.

Nevertheless, our results suggest that V1 damage in WS is not equivalent to a lesion (Daini et al 2002) as WS individuals were still influenced by the illusion context.

Properties of individual V1 neurons are unlikely to code for visual illusions since their classical receptive fields are generally small (Murray et al 2006). Perhaps the mechanism involved in seeing contextual illusions is the connection among V1 neurons. Long-range horizontal connections in layers 2/3 of V1 (Kapadia et al 1995) have been thought to mediate receptive field center – surround interactions (Chisum and Fitzpatrick 2004), grouping by collinearity (Hess and Field 1999), and early object formation (Grossberg et al 1997). The initial grouping cues that are mediated by horizontal connections in V1 are likely to be the basis for integration of contours and objects that are then relayed to ventral cortical areas such as V4 (Kourtzi et al 2003) and lateral occipital cortex (LOC—Murray et al 2002). Our results suggest that early grouping processes function properly in WS.

Another example of implicit integration is the perception of illusory contours, which may be mediated by long-range connections in V1 (Grossberg et al 1997). Consistent with our results on perception of contextual illusions, Grice et al (2003) found that WS individuals can normally detect illusory contours. However, they also found abnormal event-related potential (ERP) signature in the occipital lobe relative to typical adults when viewing these illusory contours. It is intriguing that WS individuals functionally perceive illusions despite unusual neural activity.

4.1.2 *Size discrimination and explicit integration.* Our data suggest that size discrimination is functionally impaired in WS (figure 3c), while illusion perception is not. These results may reflect the difference between explicit and implicit integration of spatial information. Here, size discrimination is the voluntary comparison of two elements, while illusion perception is the involuntary susceptibility to contextual information. Interestingly, WS individuals seem to have dissociable explicit and implicit memory abilities (Krinsky-McHale et al 2005): the implicit memory scores of WS individuals are comparable to scores of normal controls (Vicari et al 2001) while explicit memory scores are not. Further studies are necessary to determine if there is a link between explicit/implicit integration in perception and in memory.

4.2 *Relationship to general development*

In our study, size discrimination in normal participants improved with age (figure 3c), but the effect of the illusions generally did not change (figures 3b and 3d), perhaps with the exception of the Ebbinghaus illusion (Káldy and Kovács 2003). This might be due to the difference between the maturational periods of the mechanisms involved in implicit and explicit visuospatial integration. These results are consistent with the results of Mondloch et al (2003), which show that typical children, like typical adults, can implicitly group elements into a whole, but have trouble explicitly shifting their attention. They found that children are faster at discriminating shapes at the global level than the local level (global precedence effect), but seems to be less able to shift attention from global to local levels until adolescence.

Although our results show that children as young as 3 years of age are susceptible to visual illusions, it is not known whether this capacity extends to human infants. Infants can detect illusory contours by 2 months of age (Curran et al 1999), indicating that the mechanisms of implicit visuospatial integration are present early in normal development. The perception of Gestalt grouping by shape appears by 6 – 7 months of age while grouping by luminance appears by 3 – 4 months of age, suggesting that different perceptual grouping abilities have varied developmental onsets (Quinn et al 2002).

The ability of WS participants to perceive illusions (and some types of perceptual grouping) might be attributed to the fact that these mechanisms normally develop quite early, and are consequently more resistant to the effect of genetic damage than later-developing visual functions (Gunn et al 2002) such as explicit integration of visuospatial information (Palomares et al 2008). Interestingly, autistic people also perceive illusions (Ropar and Mitchell 1999) and grouping properties of the stimuli (Plaisted et al 2006), and seem to have normal V1 organization (Hadjikhani et al 2004), indicating that implicit integration may be preserved in other cases of abnormal development.

5 Conclusion

Our study increases our knowledge about the peaks and troughs within the visuospatial abilities of WS individuals. The classic evidence of WS visuospatial deficits has been from visuomotor tasks, which require extensive spatial working memory, considerable coordination between visual and motor systems (Farran and Jarrold 2003), and/or sustained attentional switching between local and global spatial information (Pani et al 1999). The robustness of implicit visuospatial integration in WS individuals, ie perception of illusions, suggests that automatic integration mechanisms may be intact and that the WS hallmark spatial impairments might stem from processes underlying the explicit integration of spatial information. The normal susceptibility to visual illusions by WS individuals indicates that the mechanisms underlying implicit visuospatial integration are resistant to damage, and may be present early in development. This implicit integration allows us to put visual features and contours together into whole objects and surfaces. Though a visual illusion is a misrepresentation of the physical world, it is a consequence of the brain's innate bias to integrate visual information that enables us to readily recognize objects and surfaces in our environment.

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