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PAPER

Vision for perception and vision for action: normal and unusual development

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Abstract

Evidence suggests that visual processing is divided into the dorsal ('how') and ventral ('what') streams. We examined the normal development of these streams and their breakdown under neurological deficit by comparing performance of normally developing children and Williams syndrome individuals on two tasks: a visually guided action ('how') task, in which participants posted a card into an oriented slot, and a perception ('what') task, in which they matched a card to the slot's orientation. Results showed that all groups performed worse on the action task than the perception task, but the disparity was more pronounced in WS individuals and in normal 3–4-year-olds than in older children. These findings suggest that the 'how' system may be relatively slow to develop and more vulnerable to breakdown than the 'what' system.

Introduction

It is widely accepted that visual information is processed along two functionally specialized streams in the brain – the ventral and dorsal streams (Ungerleider & Mishkin, 1982; Milner & Goodale, 1995). Although their exact function is debated, most investigators agree that the dorsal stream (hereafter referred to as the Action system) processes spatial information involved in visually guided action. By contrast, the ventral stream (henceforth called the Perception system) governs perception of the enduring properties of objects (e.g. size, shape) used for tasks such as the identification of objects and faces. Striking evidence for such a distinction comes from Milner and Goodale's case study of patient DF, who has extensive damage to her ventral stream pathway (James, Culham, Humphrey, Milner & Goodale, 2003). DF was not able to judge the orientation of a visual slot but was able to guide her hand towards and into the slot as if to post a letter (for a review see Milner & Goodale, 1995). In contrast, patients with optic ataxia who have intact ventral streams but impaired dorsal streams can judge the orientation of a visual slot without being able to guide their hand movements towards and into the slot (Perenin & Vighetto, 1988).

Although evidence supports this functional specialization in adults, relatively little is known about its development – whether its foundations can be detected early in development, whether it undergoes significant developmental change, and whether the two systems might show differential impairment in cases of early neurological insult. In this paper, we address these questions by examining visually guided action and perception in normally developing children as well as children and adults with Williams syndrome (WS) – a rare genetic developmental disorder which gives rise to an unusual cognitive profile of severe spatial deficit coupled with relatively spared language. Evidence from normally developing children can shed light on the typical developmental trajectory for the Action and Perception systems, addressing the question of when and how the systems become differentiated. Evidence from children and adults with WS can elucidate whether the two systems are differentially susceptible to the effects of altered genetics. In the case of WS, previous research suggests that there is differential impairment in ventral and dorsal stream functions (Atkinson, King, Braddick, Nokes, Anker & Braddick, 1997). Most important for our paper, the combination of evidence from normally developing children at different ages and individuals with WS can elucidate the nature of any differences between the groups – for example, whether they reflect delay and/or arrest in one system relative to the other, or qualitative difference in the organization of one or both systems. Indeed, we will show that insights from normal development are crucial to understanding cases of unusual development (Landau & Hoffman, 2007).

In the following sections, we first review evidence supporting the idea that the two visual systems normally develop at different rates. We then discuss the existing literature suggesting differential breakdown of the two systems in the case of unusual development.

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The dorsal and ventral streams – normal development

The idea of two visual systems has motivated developmental psychologists to ask whether the systems might develop along different trajectories, with several reports suggesting that the Action system may undergo more prolonged development relative to the Perception system. Piaget (1954) first reported that infants do not reach for an occluded object until they are 8 or 9 months old. This failure to recover the hidden object was originally interpreted as evidence that infants do not have 'object permanence' – the capacity to represent objects that are not perceptually present. However, abundant evidence over the past 20 years has shown that the capacity for object representation may be available at birth or soon thereafter (e.g. Baillargeon & DeVos, 1992; Spelke, Breinlinger, Macomber & Jacobson, 1992). The infant's failure in action tasks combined with the success in looking time experiments seems to be contradictory; however, Bertenthal (1996) attempts to reconcile these differences in terms of a developmental dissociation between action and perception. Specifically, he suggested that the Action system may develop a few months later than the Perception system. Other researchers have argued that the most widely cited error pattern in infant search tasks – the A-not-B error – may be explained by an action system in infancy that lags behind the perception system (Diamond & Goldman-Rakic, 1989; Diamond, Zola-Morgan & Squire, 1989; Munakata, 1997). The A-not-B error occurs in tasks where an infant observes an object hidden in one location (A), and is permitted to search after a brief delay. After repeated trials of this type, the object is hidden in a different location (B) which is visually quite similar and close to A. On these B trials, 8- to 10-month-old infants often reach back to location A, making the A-not-B error. This pattern of errors is consistent with the idea that the action system lags perception at this age. The possibility of a slow-developing action system is also consistent with the idea that there is relatively prolonged development for a variety of dorsal stream functions, including action. For example, Atkinson and colleagues found that thresholds for judging form coherence (a putative ventral stream function) remain stable from 4 years onward in children, while thresholds for judging motion coherence (a putative dorsal stream function) undergo significant development between ages 4 and 6 (Atkinson, Braddick, Anker, Curran, Andrew, Wattam-Bell & Braddick, 2003; Braddick, Atkinson & Wattam-Bell, 2003).

Neuro-imaging data are also consistent with the hypothesis that the dorsal stream may undergo more prolonged development relative to the ventral stream (for a review see Johnson, Mareschal & Csibra, 2001). During the first year of life, functions that are guided by the dorsal stream in adults appear to be underdeveloped. For example, ERP studies reveal that 6-month-olds show clear face sensitive responses at temporal leads (ventral stream; de Haan, Pascalis & Johnson, 2002), whereas parietal leads (dorsal stream) do not show characteristic pre-saccadic spike potentials (a sharp positive-going deflection that precedes the saccade by 8–20 ms) (Csibra, Tucker & Johnson, 1998). Pre-saccadic components at parietal leads are generally attributed to the planning of target-directed saccades via the parietal eye movement centers, and these do not appear to be developed until the age of 12 months (Johnson *et al.*, 2001).

The dorsal and ventral streams – unusual development

In addition to the claim that the dorsal stream may have a prolonged developmental trajectory, some have suggested that this stream might be relatively vulnerable in unusual development, and hence be partially responsible for a variety of developmental disabilities (for a review see Neville & Bavelier, 2000). Several researchers have provided evidence that disabilities such as Specific Language Impairment and Dyslexia may be associated with altered dorsal stream functions (Eden, VanMeter, Rumsey, Maisog, Woods & Zeffiro, 1996; Lovegrove, Garzia & Nicholson, 1990). For example, Eden and colleagues found abnormal motion processing (a supposed dorsal stream function) in adult dyslexics, even though their primary symptom is deficient reading. Neville and Lawson (1987a, 1987b, 1987c) found that congenitally deaf adults showed greater ERP signal alterations in response to visual stimuli in the peripheral fields, compared to those presented foveally (Neville, Schmidt & Kutas, 1983). The former are associated with dorsal stream processing and the latter with ventral stream processing. Although the neural and/or genetic bases of these disorders are not well understood, the possible similarity in the locus of brain- and cognitive-based changes raises the intriguing possibility that certain brain regions are particularly susceptible to the effects of altered genetics and/or unusual environment.

Most important for the present paper, some have suggested that WS may be best characterized as an impairment of the dorsal stream relative to the ventral stream (Atkinson *et al.*, 1997; Wang, Doherty, Rourke & Bellugi, 1995). WS is a rare genetic disorder (with the most current prevalence estimates as high as 1 in 7500 births) associated with a hemizygous submicroscopic deletion of chromosome 7q11.23 (Stromme, Bjornstad & Ramstad, 2002; Morris, Ewart, Sternes, Spallone, Stock, Leppert & Keating, 1994). Phenotypically, the syndrome is associated with moderate retardation (Mean IQ = 55–60), a distinctive set of facial features (often described as 'elfin'), certain malformations of connective tissue often leading to heart malfunction, and an overall reduced brain volume. WS individuals show an unusual cognitive profile of severe spatial deficits coupled with relatively stronger language abilities (Bellugi, Bihrle, Neville, Doherty & Jernigan, 1992; Mervis, Morris, Bertrand & Robinson, 1999).

The spatial deficits in WS are most evident in visual-spatial construction tasks such as object assembly, block copying, and copying by drawing (Bellugi *et al.*,

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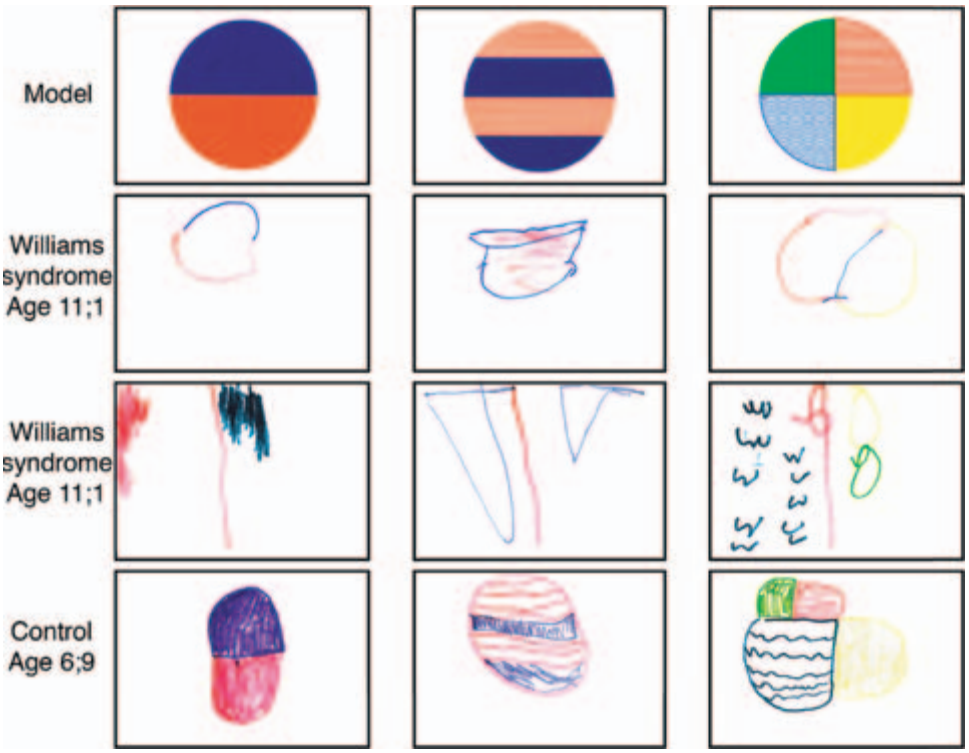

Figure 1 *Sample drawings by WS children, and one normally developing child who was matched for mental age. Matching is done using raw scores on the Kaufman Brief Intelligence Test (KBIT).*
Note: The WS children did participate in this study while the Control child did not.

1992; Mervis *et al.*, 1999; Hoffman, Landau & Pagani, 2003, see Figure 1). But despite these profound spatial deficits, recent evidence suggests that there are also a number of spared abilities *within* the broader system of spatial representation. A number of these abilities are thought to engage the ventral stream of processing in adults (Kanwisher, McDermott & Chun, 1997; Kourtzi & Kanwisher, 2000; Palmieri & Gauthier, 2004). For example, Landau, Hoffman and Kurz (2006) found that individuals with WS, relative to mental-age matched controls, do not show deficits in basic mechanisms of object recognition. Similarly, Jordan, Reiss, Hoffman and Landau (2002) and Reiss, Hoffman and Landau (2005) found that WS individuals perceive biological motion displays at levels equivalent to or better than mental-age matched controls, and in some cases, at the same levels as normal adults. And Tager-Flusberg, Plesa-Skwerer, Faja and Joseph (2003) found that people with WS can encode and recognize faces holistically, as do normal chronological age matches (but see Deruelle, Mancini, Livet, Casse-Perrot & de Schonen, 1999; Elgar & Campbell, 2001; Gagliardi, Frigerio, Burt, Cazzaniga, Perret & Borgatti, 2003; Karmiloff-Smith, 1997; Karmiloff-Smith, Scerif & Thomas, 2002).

A dorsal stream deficit with relative sparing of the ventral stream would predict special impairment on action tasks for WS individuals. Indeed, evidence suggests that individuals with WS perform more poorly on visual-manual tasks compared to perceptual matching tasks that do not engage the visual-motor system (Atkinson *et al.*, 1997). Following Milner and Goodale (1995), Atkinson and colleagues asked WS children (ages 4–14) to either *post* a card into an oriented slot (a proposed dorsal stream function) or *match* the orientation of a card to the same oriented slot (a proposed ventral stream function). About half of the WS children performed within the range of normal controls (aged 4–20) in the perception task, but only two WS children did so in the action task. This led Atkinson *et al.* to suggest that spatial deficits in WS may be linked to an impairment of the dorsal stream relative to the ventral stream. Their hypothesis receives support from recent neuro-imaging studies. For example, evidence from structural magnetic resonance imagining (MRI) studies indicates reductions in both occipital and parietal areas (Eckert, Hu, Eliez, Bellugi, Galaburda, Korenberg, Mills & Reiss, 2005; Meyer-Lindenberg, Kohn, Mervis, Kippenhan, Olsen, Morris & Berman, 2004). Additionally, Meyer-Lindenberg and colleagues carried out a functional magnetic resonance imagining (fMRI) study in which WS individuals performed tasks thought to involve the dorsal and ventral streams. None of the ventral tasks (e.g. passively viewing pictures of house, faces; identifying such pictures, etc.) revealed different activation patterns compared to normal chronological age matched controls. However, the WS individuals did show abnormal brain activity (i.e. hypoactivation) in the dorsal stream for such tasks as location judgments and a simplified version of the block construction task (tasks thought to tap the dorsal stream).

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Table 1 *Participant characteristics*

	WS children (n = 12)			MA controls (n = 12)		
	M	*SE*	Range	*M*	*SE*	Range
Chronological age	12;0	0;7	8;3–16;2	6;3	0;4	4;7–9;6
Verbal KBIT (raw score)	34	2	23–46	35	2	26–48
Matrices KBIT (raw score)	19	1	13–24	20	1	13–29
	3–4-year-olds (n = 12)			WS adults (n = 10)		
	M	*SE*	Range	*M*	*SE*	Range
Chronological age	3;8	0;1	3;3–4;7	23;9	1;7	19;3–32;3
Verbal KBIT (raw score)	22	2	13–29	44	3	35–57
Matrices KBIT (raw score)	15	2	4–23	19	2	12–32

The notion of a dorsal stream deficit is appealing in its simplicity, and would suggest that the two different visual streams might develop abnormally in the case of WS. Given the separate literature positing *normal* developmental differences in functions of the two streams, this raises intriguing unanswered questions about the relationship between the WS profile for action vs. perception tasks and that shown by normally developing children of different ages. Are these profiles related or are there obvious differences? If there are differences, are they quantitative or qualitative? Can we understand the spatial deficit in WS by examining normal developmental patterns? Can WS shed additional light on the nature of normal development?

To answer these questions, we carried out a series of studies examining the performance of WS individuals and normally developing children carrying out two tasks thought to tap the two visual systems. We used the benchmark tasks developed by Milner and Goodale (1995) and adapted by Atkinson *et al.* (1997). In Experiment 1, we asked whether the spatial deficit in WS reflects targeted damage to the Action system with relative sparing of the Perception system, and whether this pattern of performance is qualitatively different from normally developing children. While Atkinson *et al.* (1997) used chronological-age (CA) matched controls, this type of control may set the bar too high, since people with WS have moderate mental retardation. Therefore, we used a control group of normally developing children matched for mental age (MA), and tested to see whether we still found the WS deficit in action. In addition, we examined detailed patterns of performance to determine whether any deficit in the WS group was due to quantitative or qualitative differences from the normally developing children.

Experiment 1

Participants

Twelve children with WS between the ages of 8 and 17 and 12 normally developing mental-age matched controls ranging in age from 4 to 10 participated in the study (see Table 1). The WS age range might appear relatively large, but as will be seen, performance of this group showed about the same variability as the normal control group. The children with WS were recruited through the Williams Syndrome Association, and all had been positively diagnosed by a geneticist and also received the FISH test which checks for a microdeletion on the long arm of chromosome 7. All children were tested on a standardized intelligence test, the Kaufman Brief Intelligence Test (KBIT; Kaufman & Kaufman, 1990). This test yields an overall IQ score, as well as scores for two components, Verbal and Non-verbal (Matrices) (see Table 1). The Verbal subtest requires children to name objects depicted as black and white line drawings and the Matrices subtest (which does not have many spatial items, and hence does not unfairly penalize WS individuals for their spatial impairment) requires children to judge which objects or patterns 'go together'. Each WS child was individually matched to a normally developing child on the raw scores of the Verbal and Matrices components.[1] No significant differences were found between groups on either the mean raw Verbal KBIT or Matrices KBIT (ts = 0.35, 0.81, df = 22, ps = 0.73, 0.42, respectively).[2]

Design, stimuli and procedure

Participants performed two tasks: an Action task, in which they posted a card (disguised as a dollar bill) into an oriented slot, and a Perception task, in which they matched a rigid card (also disguised as a dollar bill) to the slot's orientation (see Figure 2). Tasks were counterbalanced across participants. In both tasks, participants were seated approximately 61 cm (2 ft) in front of a box with a slot (10 cm × 2 cm) cut into its front face. The slot could be turned to any of four target orientations: 0

[1] Matching was done as closely as possible, with a maximum difference of 3 points on the Verbal (N = 1) and 5 points on the Matrices (N = 1). The modal difference was 3 points.

[2] These KBIT scores were not reliably correlated with performance on either the Action or Perception tasks, all ps > .20.

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Figure 2 *Pictures of Action task (left) and Perception task (right).*

(vertical), 90 (horizontal), 45 right of vertical, or 45 left of vertical. Changes in the orientation of the slot were made between trials while it was hidden from view by a black cloth. Trials were not time limited, and no feedback was given.

In the Action task, participants were instructed to pick up a 15 cm × 8 cm plexiglass 'dollar bill' from the table in front of them and 'put it quickly into the slot of the piggy bank'. If participants wanted to repeat a trial, they were allowed to do so. Participants were tested at each of the four target orientations for six trials each, for a total of 24 trials. Trial order was randomized over participants. Responses were videotaped from overhead and from the side and the two video signals were integrated into a single videotape for later analysis.

In the Perception task, participants viewed the same apparatus, and the slot was positioned at the same target orientations. In front of the participant was a mannequin 'hand' attached to a pulley and lever set-up, which allowed the experimenter to rotate it through 180-degrees.[3] The participant was told that the hand would move, and that he or she should say 'stop' such that 'Mr Hand' holding the dollar bill would be 'just ready to put the dollar bill into the slot in the piggy bank'. The hand was moved via a dial by a second experimenter who looked away from the procedural set-up during all trials. The participant was allowed to correct the motion (by saying, e.g. 'go a little bit more, a little less', etc.) until he or she was content that the dollar bill was ready for posting. When satisfied, the second experimenter called out the angle reading from the dial, and the first experimenter recorded it. Participants were tested six times at each target orientation for a total of 24 trials, randomized over participants.

The main dependent variable was the difference between the orientation of the target and the posted or judged orientation of the dollar bill and was coded as follows. In the Action task, the videotapes were used to measure the orientation of the dollar bill near the end of its trajectory (i.e. 2.5 cm from the slot).[4] A second rater coded 25% of the trials and reliability of this measure of orientation was 97%. In the Perception task, the orientation of the dollar bill on each trial was the angle reported by the second experimenter from the dial on the Mr Hand apparatus. The slot was wide enough that participants were still able to successfully post the bill if they were within 10 of the target slot's orientation.

Results and discussion

Figure 3 (Panel A) shows the mean absolute error magnitude in degrees for the two tasks for mental-age matched controls (MA controls) and WS children. Both groups performed better (i.e. exhibited less error) on the Perception task than the Action task, but the WS children appear to perform worse than controls, especially on the Action task. Planned comparisons confirmed these impressions.[5] Both groups of children performed significantly worse on the Action than the Perception task, ts = 3.98, 4.24, $df = 11$, $p < .01$ for the MA controls and the WS children, respectively. Children with WS performed significantly worse than the MA controls in the Action task, $t(22) = 3.07$, $p < .01$, and marginally worse on the Perception task, $t(22) = 2.08$, $p = .06$. Crucially, comparing across tasks, WS children exhibited a greater disparity between tasks than MA controls, $t(22) = 2.11$, $p < .05$ (one-tailed).[6] These results reveal that, compared to mental-age controls, WS children are more impaired in the Action task

[3] Unlike the original Milner and Goodale perception task, which required participants to orient their hand to match the slot, we altered the procedure slightly following Atkinson *et al.*'s (1997) perception task for ease of comparison. In a later task, Milner and Goodale tested their patient, DF, with a so-called rotating hand, and her performance was equally poor on this task as on the original task.

[4] The orientation was determined by measuring the width of the dollar bill (from the videotapes) and then converting this measurement to degrees. The conversion was derived using previously developed 'standards' – that is, the dollar bill was videotaped at every angle (from 0 to 180) and the corresponding width was recorded.

[5] Planned comparisons were used given the *a priori* hypothesis that WS children exhibit worse performance on the Action task than the Perception task, as reported in Atkinson *et al.* (1997).

[6] A one-tailed test was used considering the Atkinson *et al.* (1997) finding that WS children perform worse on the Action task, relative to the Perception task.

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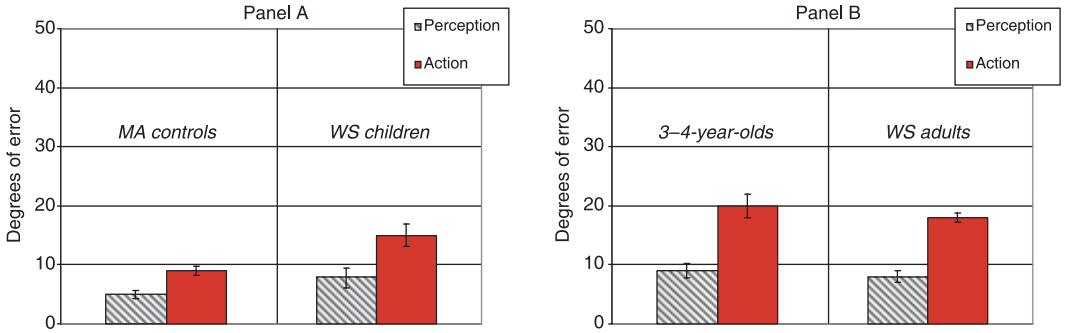

Figure 3 *Mean error magnitude in degrees for the Perception and Action tasks for (A) WS children and MA controls, and (B) 3–4-year-olds and WS adults.*

than the Perception task, consistent with the hypothesis that people with WS have a dorsal stream deficit relative to the ventral stream (Atkinson *et al.*, 1997).

Although these results suggest that WS children are primarily impaired in the Action task, they do not address the nature of their responses. It could be the case that the greater decrement in performance on the Action task results from a *quantitatively* different pattern of performance (e.g. a broader tuning function around the various orientations – that is, a WS child might accept 65 to the right as 45 to the right). Alternatively, the poorer performance could result from a *qualitatively* different pattern of performance (e.g. WS children could systematically make errors at particular orientations that are different from normal children, or they could make mirror reflections – that is, match 45 to the left as 45 to the right). Even with similar overall performance, as seen in the Perception task, the children with WS might still show qualitatively different patterns of performance relative to the normal children. To address this issue, we carried out analyses examining patterns of performance across the different target orientations for each task separately.

In the Action task, a 2 (Group) × 3 (Target Orientation) repeated measures ANOVA showed a significant main effect of Group, $F(1, 22) = 9.61$, $p < .01$, with WS children performing worse than MA controls, and a significant main effect of Target Orientation, $F(2, 44) = 10.16$, $p < .01$, with both groups performing worse on Obliques than Horizontals (Tukey's HSD, $p < .01$). There was no reliable interaction between the factors, $F(2, 44) = 0.90$, $p = .41$. In the Perception task, the same analysis revealed a significant main effect of Group, $F(1, 22) = 5.01$, $p < .05$, with the WS children performing worse overall than MA controls. There was no significant main effect of Target Orientation (Horizontal, Vertical, Oblique), $F(2, 44) = 3.13$, $p = .06$, and no significant interaction, $F(2, 44) = 0.43$, $p = .66$. Both of these analyses reveal that the pattern of performance on the different orientations was the same for both groups. Thus, these results suggest that the greater decrement in performance by the WS children on the Action task compared to the MA controls is one of a quantitative nature, as opposed to a qualitative one.

A radial plot of individual performances also supports this claim. Figures 4 and 5 show individual responses (non-bolded lines in the figure) for each target orientation in the Action and Perception tasks, respectively. The rectangular box denotes the target orientation (and the 10 allowance around the target orientation). Recall that the slot was wide enough such that if participants were 10 off from the target orientation, they could still fit the dollar bill into the slot. We used this 10 allowance as the criterion for 'accuracy'.

As shown in Figure 4, in the Action task, the MA controls and WS children showed similar spread around the different orientations, with more spread around the Obliques for both groups. Clearly, however, the WS children showed dramatically more noise, resulting in lower accuracy. In these plots, MA controls were 80% accurate and the WS were 60% accurate. Both groups, however, performed significantly better than chance at each of the orientations,[7] MA group: ts = 47.52, 21.82, 34.60, 20.64, $df = 11$, $p < .001$; WS group: ts = 8.54, 24.51, 30.66, 5.70, $df = 11$, $p < .001$. The similar patterns of spread suggest that the difference between the WS children and their MA controls in the Action task is of a quantitative nature, as opposed to a qualitative one. Finally, in the Perception task, the MA controls and WS individuals also showed nearly identical responses around all axes (Figure 5). The average accuracy across orientations was 90% for the MA controls and 80% for the WS children. Both groups performed significantly better than chance at each of the orientations, MA group: ts = 67.11, 64.03, 72.91, 28.01, $df = 11$, $p < .001$; WS group: ts = 36.39, 12.01, 18.59, 14.60, $df = 11$, $p < .001$.

These results suggest that, compared to mental-age controls, WS children are more impaired in the Action task than the Perception task, consistent with the hypothesis that people with WS may have a dorsal stream deficit. However, the *qualitatively similar* pattern of responses across groups suggests that the deficit might actually reflect developmental delay or arrest. If so, we would expect similar patterns of responding for children

[7] Regardless of target orientation, the greatest error one could achieve was 90 . Thus, the average error if one were guessing is 45 .

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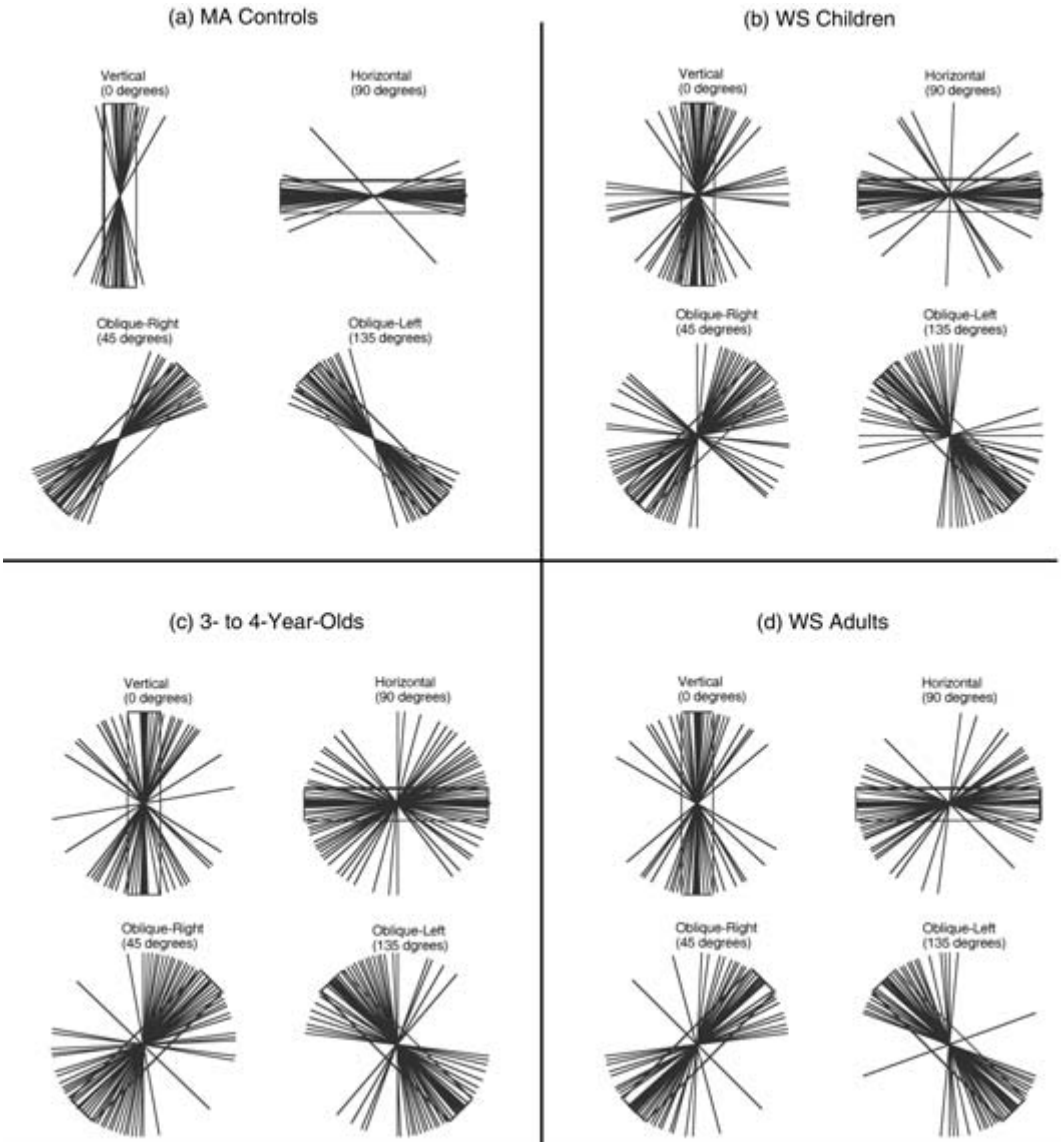

Figure 4 *Radial plots of individual responses for each target orientation in the Action task. Individual responses are denoted by non-bolded lines and the rectangular box indicates the 10 allowance around the target slot.*

with WS and normally developing children younger than the mental-age matches whom we tested.

Testing the hypothesis of developmental delay and/or arrest requires several additional comparisons which we carried out in Experiment 2. First, we need to know how normal children perform at an earlier developmental point than the mental-age matches tested in Experiment 1. If WS children are developmentally delayed, then their performance should be similar to normal children at an earlier point. Second, we need to know how WS adults perform in order to evaluate whether any initial developmental delay is accompanied by improvement over age, and perhaps even catch-up to the level of a mental-age match or better. Improvement or catch-up might involve some sort of cortical reorganization or compensatory strategies (or continued development). In any case, however, developmental catch-up would predict stronger performance among WS adults than WS children (or possibly even the mental-age matched children). Arrest would predict no difference between the WS adults and WS children. Third, the addition of a younger control group of children allows us to assess the developmental trajectories of the two visual systems in normal populations.

Experiment 2

Participants

Twelve normally developing children, ages 3 and 4 (henceforth referred to as 4-year-olds), and 10 adults

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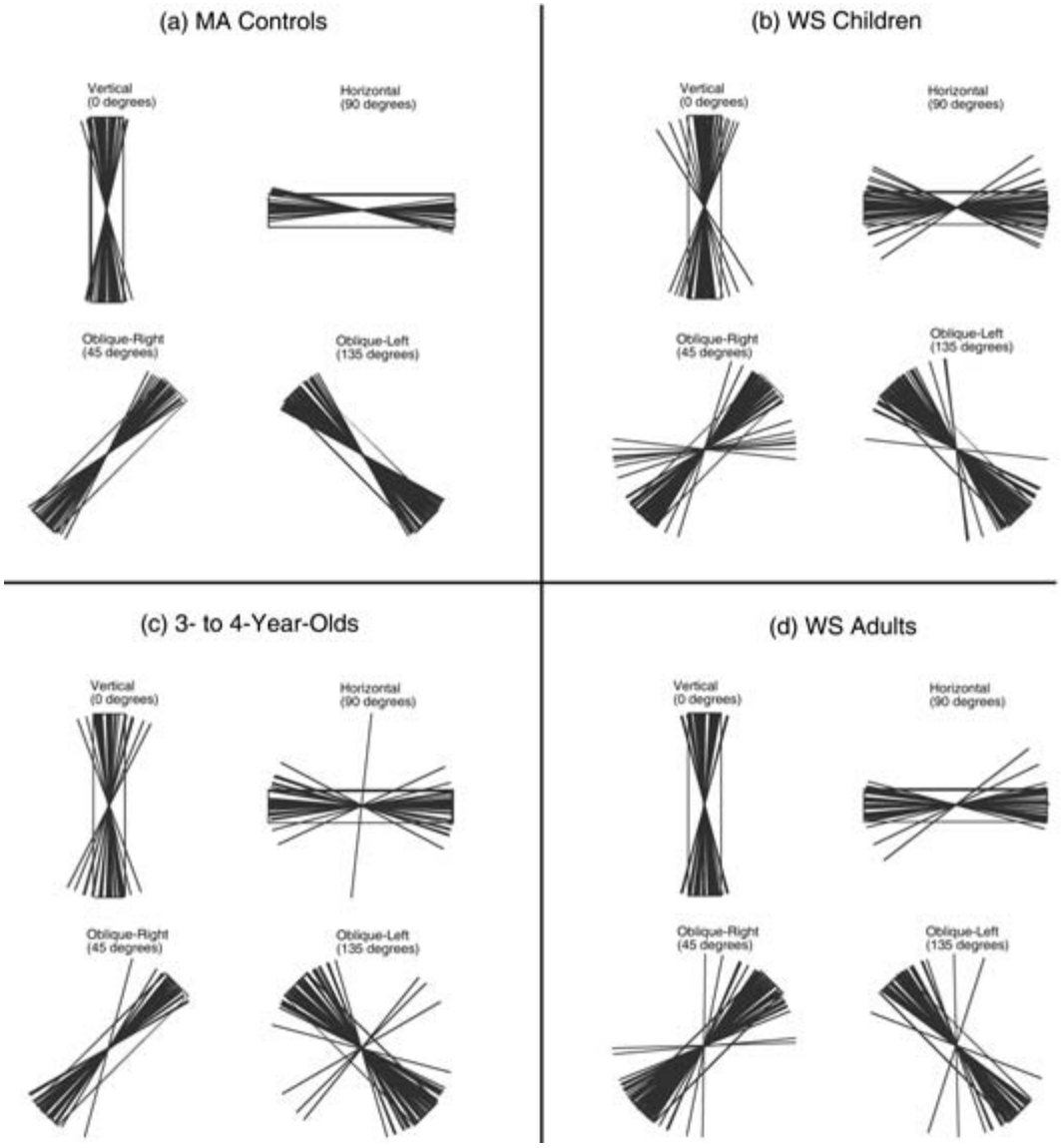

Figure 5 *Radial plots of individual responses for each target orientation in the Perception task. Individual responses are denoted by non-bolded lines and the rectangular box indicates the 10 allowance around the target slot.*

with WS between the ages of 19 and 33 were tested (see Table 1). The 4 year-old group was chosen because in several other tasks (e.g. block construction) the WS children perform at the level of 4-year-old normally developing children. The WS adults had all been diagnosed for the elastin deletion by a geneticist using the FISH test. Both groups of participants were tested on the Verbal and Matrices components of the KBIT (see Table 1B).[8] The mean raw Verbal KBIT of WS adults was reliably higher than both the WS children and MA controls tested in Experiment 1 and the 4-year-old normal children tested in this experiment, *t*s = 3.10, 2.98, 7.01, *df*s = 19, 19, 16, $p < .01$. By contrast, no reliable differences in mean raw Matrices KBITs were found across any other groups with the exception that the mean raw Matrices KBIT for the MA controls was significantly higher than the 4-year olds, $t(18) = 2.19$, $p < .05$.

Design, stimuli and procedure

These were identical to Experiment 1.

Results and discussion

Developmental delay? WS children versus 4-year-olds

We first examined overall error among the 4-year-olds (see Figure 3, Panel B) and compared it to that of the WS children from Experiment 1 (see Figure 3, Panel A). Planned comparisons revealed no significant differences between the 4-year-olds and the WS children in either

[8] These KBIT scores were not reliably correlated with performance on either the Action or Perception tasks, all *p*s > .20.

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the Perception, $t(22) = 0.20$, $p = .84$, or the Action tasks, $t(22) = 1.56$, $p = .13$. In addition, there was no greater disparity across tasks for the 4-year-olds than the WS children, $t(22) = 1.79$, $p = .09$.

The two groups were also similar in the qualitative nature of their responses for both tasks. In the Action task, an ANOVA showed a significant main effect of Target Orientation, $F(2, 44) = 6.77$, $p < .01$, with both groups performing worse on Obliques than Horizontals (Tukey's HSD, $p < .05$). There was no significant main effect of Group, $F(1, 22) = 3.40$, $p = .08$, nor any significant interaction between the factors, $F(2, 44) = 0.34$, $p = .71$. The same analysis for the Perception task also showed a significant main effect of Target Orientation, $F(2, 44) = 4.46$, $p < .05$, with both groups performing worse on Obliques than Verticals (Tukey's HSD, $p < .05$). There was no significant main effect of Group, $F(1, 22) = .02$, $p = .88$, and no significant interaction between the factors, $F(2, 44) = 0.06$, $p = .94$. These results suggest quantitative and qualitative similarity between the 4-year-olds and the WS children.

The radial plots further support the finding of qualitative similarity. Both the 4-year-olds and the WS children exhibited a similar broad tuning around the Oblique orientations in the Action task (Figure 4). Average accuracy in this analysis was 50% for the 4-year-olds and 60% for the WS children. Like the WS children, the 4-year-olds performed significantly better than chance at each of the orientations, ts = 5.99, 6.16, 15.53, 7.80, $df = 11$, $p < .001$. Similarly, the 4-year-olds showed nearly identical spread to the WS children around all orientations in the Perception task (Figure 5). Average accuracy was 70% for the 4-year-olds and 80% for the WS children. Like the WS children, the 4-year-olds performed significantly better than chance at each of the target orientations, ts = 54.89, 46.99, 23.76, 8.85, $df = 11$, $p < .001$.

Developmental arrest? WS children versus WS adults

We next examined overall error among the WS adults (see Figure 3, Panel B) relative to the WS children in Experiment 1 (see Figure 3, Panel A). Planned comparisons revealed no significant differences between the two groups in either the Perception, $t(20) = 0.26$, $p = .80$, or Action, $t(20) = 1.00$, $p = .33$, tasks. Moreover, there were no significant differences between the two tasks for WS adults, relative to WS children, $t(20) = 1.16$, $p = .26$. Thus, the WS adults did not perform differently from the WS children.

The analyses examining the nature of their responses further confirmed these findings. In the Action task, there was again a significant main effect of Target Orientation, $F(2, 40) = 5.52$, $p < .01$, with both groups performing worse on Obliques and Verticals than Horizontals (Tukey's HSD, $p < .05$). However, there was no significant main effect of Group, $F(1, 20) = 2.57$, $p = .13$, nor any significant interaction, $F(2, 40) = 2.91$, $p = .08$. In the Perception task, ANOVA showed a significant main effect of Target Orientation, $F(2, 40) = 3.65$, $p < .05$, with both groups performing worse on Obliques than Verticals (Tukey's HSD, $p < .05$). However, there was no significant effect of Group, $F(1, 20) = .10$, $p = .75$, nor any significant interaction, $F(2, 40) = 0.06$, $p = .94$.

The radial plots confirmed the qualitative similarity between groups (Figures 4 and 5). In the Action task, the WS adults and children exhibited similar 'broad tuning' around the target orientations, achieving 60% and 50% average accuracy, respectively. Like WS children, WS adults performed significantly better than chance at each of the target orientations, ts = 5.10, 8.31, 9.65, 17.65, $df = 9$, $p < .001$. In the Perception task, WS adults and children exhibited nearly identical responses around the target orientation, and both groups were on average 80% accurate. Additionally, the WS adults, like the WS children, performed significantly better than chance at each of the orientations, ts = 62.03, 18.45, 41.87, 17.76, $df = 9$, $p < .001$.

Normal development: MA controls (6-year-olds, on average) versus 4-year-olds

Finally, we compared the 4-year-olds to the 6-year-olds (i.e. the MA controls for the WS children) tested in Experiment 1 (see Figure 3, Panel B). Planned comparisons showed that the 4-year-old children performed significantly worse than the 6-year-olds in both the Perception, $t(22) = 2.80$, $p < .05$, and Action, $t(22) = 4.81$, $p < .01$, tasks. In addition, the 4-year-old children showed a greater disparity between tasks than the 6-year-olds, $t(22) = 4.18$, $p < .01$.

Analyses of target orientation showed qualitative similarity across the two groups. In the Action task, there was a significant main effect of Group, with the 4-year-olds performing worse than the 6-year-olds, $F(1, 22) = 28.10$, $p < .01$, and a significant effect of Target Orientation, $F(2, 44) = 5.48$, $p < .01$, with both groups performing worse on Obliques than Horizontals (Tukey's HSD, $p < .05$). Again, there was no significant interaction, $F(2, 44) = 1.40$, $p = .26$. In the Perception task, the analysis of variance showed a main effect of Group, with the 4-year-olds performing significantly worse than 6-year-olds, $F(1, 22) = 9.21$, $p < .01$. There was a significant main effect of Target orientation, $F(2, 44) = 6.43$, $p < .01$, with both groups performing worse on Obliques than Verticals and Horizontals (Tukey's HSD, $p < .05$). However, there was no significant interaction, $F(2, 44) = 0.85$, $p = .44$.

The radial plots show very similar performance in both tasks. In the Action task (see Figure 4), the 6-year-olds (labeled MA controls) and the 4-year-olds again showed similar spread around the target orientations, but the 4-year-olds showed substantially more noise, resulting in lower accuracy (50% versus 75% for the MA controls). As previously discussed, both groups performed significantly better than chance at each of the orientations. In the Perception task (see Figure 5), the 6-year-olds

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(labeled MA controls) and the 4-year-olds showed tight clustering around the target orientations. MA controls were 90% accurate and 4-year-olds were 70% accurate. A previous analysis showed that both groups performed significantly better than chance at each of the orientations.

The findings across Experiments 1 and 2 show several things. First, WS children were disproportionately impaired on the Action task relative to normally developing children who were matched for mental age. Second, the WS children were not different from younger normally developing children (i.e. 4 year-olds) in either the Perception or the Action task, suggesting that the impairment reflects a quantitative, but not qualitative, difference from normal, early developing children. Third, the WS adults were not different from the WS children, suggesting that this impairment reflects developmental arrest, that is, no catch-up later in development. And finally, the comparison of normal 4-year-olds to the 6-year-olds (MA controls) suggests that there is significant development in the Action task, but not in the Perception task in normal development within this age range.

General discussion

In this paper, we sought to examine the development and breakdown of two aspects of visual-spatial representation, specifically, vision-for-action and vision-for-perception. To do so, we studied normally developing children as well as children and adults with WS as they carried out two different tasks. The Action task required people to post a rigid object (a 'dollar bill') through an oriented slot; the Perception task required them to judge when the object was in the proper orientation for someone else to post it through the slot. Within the two visual systems framework, these two tasks would appear to engage two different functional systems, with the Action task engaging primarily dorsal stream functions, and the Perception task engaging more ventral stream functions. Our questions were whether we could uncover evidence for differentiation between the two systems as they emerge in normal development, whether such differentiation might be especially striking in the case of WS, and whether this pattern of performance fits with that of normally developing children at various ages.

The results from the above experiments showed consistent differences between the two tasks – both in normal children and in individuals with WS. All groups performed worse on the Action than the Perception task, but the extent of the difference between tasks was greater for some groups than others. It was greater for WS children than for normally developing children who were between 4 and 10 years old, but were matched for mental age. The same particularly strong difference was also observed among WS adults and normally developing 4-year-olds, suggesting that this aspect of WS may represent developmental arrest at the level of a normally developing child around 4 years of age. Finally, the pronounced difference that was observed among WS children and adults and normal 4-year-olds was considerably smaller than that among normal older children (around 6 years old), suggesting that the Action system – as revealed by our task – may normally develop more slowly than the Perception system, only catching up to the Perception system by age 6 (for these two tasks).

Importantly, additional analyses suggested that the differences across groups were quantitative, not qualitative. For example, in both tasks, all groups had difficulty with oblique orientations – a finding which is consistent with abundant literature suggesting that representing obliques is a developmental achievement and is even difficult in adulthood (for reviews see Appelle, 1972; Rudel, 1982). This finding is also consistent with the idea that the deficits shown by WS individuals may best be characterized as noisy structure, rather than qualitative differences in structure. We conclude that genetic deficits need not result in qualitative abnormalities, counter to some claims (Karmiloff-Smith, 1998). While it is always possible that there may be some other measure (e.g. RT, details of trajectory) that reveals a qualitative difference across groups, our analyses of the present tasks revealed only quantitative differences.

Our results suggest that the two visual systems normally develop under different trajectories, with the Action system lagging behind the Perception system, at least in the age range we tested. Performance in the Perception task appears to be close to ceiling level by about 4 years of age, whereas there appeared to be significant development in the Action task between ages 4 and 6. These findings are consistent with the idea that the dorsal stream may be slower to develop than the ventral stream (Atkinson *et al.*, 2003; Bertenthal, 1996; Csibra *et al.*, 1998; de Haan *et al.*, 2002; Diamond *et al.*, 1989; Diamond & Goldman-Rakic, 1989; Gilmore & Johnson, 1997a, 1997b; Johnson *et al.*, 2001; Munakata, 1997). In the case of WS, our results suggest that WS can be characterized as a dorsal stream deficit, as initially proposed by Atkinson and colleagues (Atkinson *et al.*, 1997, 2003).

An obvious question then is whether the dorsal stream impairment in WS stems from low-level visual processing or higher cortical mechanisms. While the answer is not yet clear, there are several studies suggesting that there is relative normalcy in low-level functions. For example, Pani, Mervis and Robinson (1999) found that WS individuals exhibit normal patterns of performance in attention tasks that engage perceptual grouping. Similarly, Palomares, Ogbonna, Landau and Egeth (2007) have shown that WS individuals perceive illusions to the same extent as normal adults, suggesting intact mechanisms of global integration. Moreover, Palomares and colleagues found adult-like thresholds among WS people in tasks requiring the integration of oriented elements into global forms (Palomares, Landau & Egeth, 2007). These findings suggest that damage to early visual processes may not account for the dorsal stream impairment

Importantly, the nature of the dorsal stream deficit can now be more fully spelled out. The fact that WS adults

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performed like normally developing 4-year-old children is consistent with the idea that the deficit in WS reflects an overall persisting immaturity of visuo-spatial processing at an early developmental point – when the Perception system is *normally* developmentally ahead of the Action system. The idea that the Perception system develops more rapidly than the Action system may explain the broader pattern of spared and impaired spatial performance that is characteristic of WS (see Landau & Hoffman, 2007). Children with WS are comparable to MA controls in several perceptual tasks such as processing biological motion (Jordan *et al.*, 2002; Reiss *et al.*, 2005), recognizing and identifying objects in canonical orientations (Landau *et al.*, 2006) and matching faces (Tager-Flusberg *et al.*, 2003). These tasks generally engage neural structures in the ventral stream, here posited to be early developing. In contrast, impairments (defined as poorer performance than MA controls) have been observed in several tasks that appear to engage structures in the dorsal stream, particularly the posterior parietal lobe. Examples include block construction (Hoffman *et al.*, 2003), drawing (Georgopoulos, Georgopoulos, Kurz & Landau, 2004; Bertrand, Mervis & Eisenberg, 1997), and multiple object tracking (O'Hearn, Landau & Hoffman, 2005). Patterns of errors across these tasks, and in the ones reported in the present studies, resemble those of normally developing children who are around 4 years of age. This pattern of strengths and weaknesses is the one that would be expected if brain and cognitive development in WS is arrested at a time when maturation of the ventral stream is developmentally ahead of the dorsal stream.

The posited relative vulnerability of the dorsal stream function might be common to genetic disorders other than Williams syndrome. Individuals with Turner syndrome and Fragile X syndrome are known to show spatial impairment on tasks thought to engage the dorsal stream (e.g. Romans, Stefanatos, Roeltgen, Kushner & Ross, 1998; Kogan, Bertone, Cornish, Boutet, Der Kaloustian, Andermann, Faubert & Chaudhuri, 2004). Thus it is possible that a range of genetic disorders might also suffer from persisting immaturity, as we have posited for WS. Alternatively, it is possible that different syndromes might result from different specific kinds of damage to the dorsal stream, resulting in different detailed profiles of spatial impairment. For example, Meyer-Lindenberg *et al.* (2004) have suggested that the WS deficit results from disruption of information flow moving from early visual areas via the interparietal sulcus (IPS) to higher (dorsal stream) areas. Evidence for structural alteration to the IPS in WS is consistent with this idea. While we cannot directly address whether the WS profile is common across other genetic disorders, the answer has significant implications for interpreting the potential links between genetic change and neural and cognitive structure. For example, if similar patterns exist across many genetic disorders, this would imply that some quite general developmental processes are at play across neurodevelopmental disorders, perhaps resulting in just a few common results for brain structure and cognitive function. By contrast, if different patterns emerge over genetic disorders, then this would imply that different genes or sets of genes can target specific cognitive systems, resulting in highly specific neural and cognitive deficits characteristic of different disorders (see Mervis & Klein-Tasman, 2004). An important future direction for research is the comparison of a variety of dorsal and ventral stream functions across different deficit populations to determine whether the dorsal stream deficit suggested for WS is also common to other neurodevelopmental disorders.

In sum, we have demonstrated that the two visual systems – as embodied in our two tasks – follow different trajectories in normal development, with the Action system lagging behind the Perception system. We have also shown differential impairment in the case of WS, suggesting that the Action system may be more vulnerable to breakdown than the Perception system. Importantly, we have characterized the nature of the breakdown exhibited by individuals with WS as an overall persisting immaturity of visuo-spatial processing at an early developmental point – when the Perception system is *normally* developmentally ahead of the Action system. This conclusion depends on using insights from normal development to understand cases of unusual development.

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