

## Motion processing specialization in Williams syndrome

Jason E. Reiss<sup>a,\*</sup>, James E. Hoffman<sup>a</sup>, Barbara Landau<sup>b</sup>

<sup>a</sup> *Department of Psychology, University of Delaware, Newark, DE 19716, USA*

<sup>b</sup> *Department of Cognitive Science, Krieger Hall, Johns Hopkins University, Baltimore, Maryland 21218, USA*

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### Abstract

Williams syndrome (WS) is a rare genetic disorder characterized by severe spatial deficits and relatively spared language. Although initial research suggested that WS entails a generalized motion processing deficit, later work demonstrated intact biological motion perception in people with WS, reflecting a sparing of a specific motion perception system. The present study examined whether this sparing is unique to biological motion, or extends to other motion tasks as well. WS children and adults and normal controls were tested to examine developmental changes across a variety of motion tasks. Results indicated that WS individuals performed at normal levels for motion coherence and biological motion tasks but had elevated thresholds for the 2-D form-from-motion task, a profile that extended into adulthood. These findings provide evidence that a genetic impairment can lead to a selective motion processing deficit and argue against characterizing WS as including a general motion processing impairment. The nature of the motion deficit is considered, including the implications for WS dorsal/ventral processing.

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### 1. Introduction

Williams syndrome (WS) is a rare (1:20,000 live births) congenital deficit resulting from a submicroscopic deletion on chromosome 7q11.23, a region known to help regulate elastin and LIM-kinase1 expression (Bellugi, Lichtenberger, Jones, Lai, & St. George, 2000; Frangiskakis et al., 1996). People with WS commonly exhibit features such as ‘elfin’ facial appearance, connective tissue malformations, cardiovascular problems, generally reduced brain volume, a hypersocial personality, and an overall Composite IQ (as measured using the Kaufman Brief Intelligence Test, KBIT, Kaufman & Kaufman, 1990) in the mild to moderately retarded range (Bellugi, Marks, Bihle, & Sabo, 1988; Bellugi et al., 2000; Mervis, Morris, Bertrand, & Robinson,

1999a). What has attracted psychologists and neuroscientists to this population is their strikingly uneven cognitive profile, which consists of relative strengths in language, together with severe impairments in visuo-spatial abilities (Bellugi et al., 1988; Mervis et al., 1999a). This profile raises the possibility that a genetic defect might developmentally target specific domains of cognition, or brain areas that underlie these domains.

The spatial deficit in WS people is most pronounced in visuo-constructive tasks such as ‘block construction’ (e.g., Pattern Construction subscale of the Differential Abilities Scale, DAS, Elliot, 1990) and copying (e.g., the Developmental Test of Visual–Motor Integration, VMI, Beery & Buktenica, 1967) which require individuals to replicate the configural arrangement of a model (Bellugi et al., 1988; Bellugi, Wang, & Jernigan, 1994; Mervis et al., 1999a). In contrast, perception of objects (Landau, Hoffman, & Kurz, submitted) and faces in people with WS (Tager-Flusberg, Plesa-Skwerer, Faja, & Joseph, 2003) appears to be normal.

\* Corresponding author. Tel.: +1 302 831 1137; Fax: +1 302 831 3645.

E-mail address: [jreiss@udel.edu](mailto:jreiss@udel.edu) (J.E. Reiss).

Although initial studies suggested that the WS visuo-spatial deficit resulted from a failure to group local features into coherent global percepts (Bellugi et al., 1994; Bihrlé, Bellugi, Delis, & Marks, 1989), subsequent studies have reported normal performance in a variety of global integration tasks (Atkinson et al., 1997, 2003; Jordan, Reiss, Hoffman, & Landau, 2002; Key, Pani, & Mervis, 1998; Pani, Mervis, & Robinson, 1999; Tager-Flusberg et al., 2003). More recent attempts (Atkinson et al., 1997, 2001, 2003; Galaburda et al., 2001; Jernigan, Bellugi, Sowell, Doherty, & Hesselink, 1993; Wang, Doherty, Rourke, & Bellugi, 1995) to account for the pattern of preserved and impaired visual abilities in people with WS invoke the distinction between ‘dorsal’ and ‘ventral’ visual streams proposed by Milner and Goodale (1995). People with WS perform normally on a variety of tasks that are thought to be carried out by ventral visual areas, including recognition of objects (Landau et al., submitted) and faces (Tager-Flusberg et al., 2003). In contrast, they are impaired in a variety of dorsal stream tasks such as visually-guided actions (Atkinson et al., 1997; Dilks, Landau, & Hoffman, submitted) and perception of some kinds of motion (Atkinson et al., 1997, 2003).

Atkinson and colleagues (1997, 2003) tested the hypothesis of dorsal breakdown with ventral sparing by directly comparing performance on a pair of tasks that require similar judgments but are based on information derived from each of the two visual streams. They found that although a subgroup of WS individuals performed poorly on both tasks—suggesting a general deficit in visual processing—a separate subgroup of WS individuals could successfully detect a 2-D shape that required integration of *static* oriented line segments into a global form but were impaired when perception of a form required integration of local *motion* signals. This finding is consistent with normal ventral stream function but impaired dorsal functioning because previous research in both humans and monkeys indicates that a key cortical region for detecting forms (V4, Gallant, Shoup, & Mazer, 2000; Girard, Lomber, & Bullier, 2002) lies along the ventral stream; whereas a key brain area critical for detecting motion (V5/MT, Newsome & Paré, 1988; Zeki et al., 1991) resides in the dorsal stream (see also Braddick, O’Brien, Wattam-Bell, Atkinson, & Turner, 2000).<sup>1</sup>

Deficits in visually-guided action and perception of motion are consistent with the hypothesis of a *generalized* deficit in dorsal stream functioning in WS (Atkin-

son et al., 1997, 2003); however, research both in adults with cortical lesions (Covey & Vaina, 2000; McLeod, Dittrich, Driver, Perrett, & Zihl, 1996; Schenk & Zihl, 1997; Vaina, Lemay, Bienfang, Choi, & Nakayama, 1990) and with normal adults (Beintema & Lappe, 2002; Grossman & Blake, 1999) has revealed that motion processing is not a unitary function. Instead, it appears to be comprised of several dissociable ‘classes’ of motion perception (e.g., motion coherence, form-from-motion, biological motion, etc.), consistent with the existence of several motion processing ‘specialists’ in the normally developed brain. These behavioral dissociations have been supplemented by findings that different classes of motion perception rely on distinct neural circuitry. Specifically, even though V5/MT is a key motion processing area and appears to be the primary center for processing motion coherence, additional cortical areas have also been implicated for the other two motion classes. For example, single-cell research in monkeys as well as human brain-imaging studies report that the superior temporal sulcus (STS, which integrates information originating from both ventral and dorsal streams) responds specifically to biological motions (Allison, Puce, & McCarthy, 2000; Bonda, Petrides, Ostry, & Evans, 1996; Oram & Perrett, 1994; Vaina, Solomon, Chowdhury, Sinha, & Belliveau, 2001) and is part of a larger network (which includes the fusiform face area, Kanwisher, McDermott, & Chun, 1997) involved in the perception of biological stimuli. In contrast, perception of form-from-motion stimuli appears to be achieved through V5/MT projections to ventral stream areas such as V4 (Maunsell & Van Essen, 1983; Ungerleider & Desimone, 1986) or LO (Schoenfeld et al., 2003), which allow additional ventral stream areas such as inferior temporal cortex to complete perceptual processing (also see discussion by Milner & Goodale, 1995). In light of this evidence for multiple motion systems, the present paper asks whether there may be dissociable patterns of performance among different motion tasks in people with WS.

Recent research has, in fact, shown that at least one kind of motion perception is preserved in WS: biological motion (Jordan et al., 2002). This study demonstrated that, like mental-age-matched (MA) children and normal adults, WS individuals could easily identify various actions of a point-light character (e.g., slipping on a banana, doing jumping jacks, etc.; see Johansson, 1973). In addition, WS children were comparable to or better than MA controls in their ability to discriminate the direction of locomotion of a point-light-walker (PLW) embedded in dynamic noise.

These findings suggest that WS entails selective sparing of some types of motion perception even when they require global integration of local features (i.e., the integration of local lights into limbs and eventually a human form, Bertenthal & Pinto, 1994; Lorenceau & Shiffrar,

<sup>1</sup> Milner and Goodale (1995) propose that crosstalk between streams makes it difficult to conclude that visuo-spatial deficits are due solely to dorsal stream damage. For example, although V5/MT lies along the dorsal stream, the prolific connections it has with regions along both pathways make its exclusive assignment to either individual stream uncertain.

1999). The finding of intact biological motion in WS argues against characterizing this population as having a generalized motion processing deficit, suggesting that some aspects of their dorsal stream functioning may indeed be preserved. On the other hand, biological motion may constitute a special stimulus class for WS individuals due to their intense interest in social stimuli such as faces (Bellugi et al., 2000; Jones et al., 2000; Mervis et al., 1999a; Tager-Flusberg & Sullivan, 2000), such that sustained attention to biological motion during development may insulate this system from the deficits affecting other dorsal stream structures.

The present study was designed to assess the hypothesis that biological motion is 'special' in WS, by examining their performance on three different motion tasks. The *motion coherence* task required subjects to detect coherently moving signal dots embedded in incoherent noise dots. The *2-D form-from-motion (FFM)* task also presented signal dots embedded in incoherent noise. In this case, however, signal dots that were located in a rectangular figure region moved in the opposite direction from signal dots in the background. Subjects were required to discriminate whether the rectangular form was oriented horizontally or vertically. It should be noted that the task used by Atkinson and colleagues (1997, 2003) required subjects to detect a rectangular area in which coherently moving signal dots moved in a direction opposite to the background signal dots, similar to our 2-D form-from-motion task. However, their subjects were not required to discriminate the shape of that region. Therefore, it appears that their task lies somewhere between our motion coherence and form-from-motion tasks, albeit closer to the latter. In the *biological motion* task, subjects had to detect a point-light-walker embedded in noise. Although it was not possible to match every aspect of the stimulus parameters across all tasks, we attempted to make them as similar as possible (for example, all three tasks used dots having the same size and contrast).

Within each of these motion tasks, we followed the approach taken by Jordan et al. (2002) by comparing the performance of WS children to that of normal, mental-age-matched (MA), children and normal adults. The decision to use mental-age matches was motivated by the fact that, because WS individuals are retarded, it can be difficult to interpret their pattern of performance without testing against children of commensurate mental age. For example, comparisons against chronological-age matches can be problematic because any group differences could be due to differences in mental age. Additionally, because it was possible that WS children might show intact perception of some types of motion (Jordan et al., 2002), the inclusion of normal adults served as an index of fully developed motion processing ability. Finally, we also tested a group of WS adults to explore developmental patterns across motion tasks in this population. For example, although it has been claimed that poor motion

perception in WS reflects a developmental delay (Atkinson et al., 2003), it is currently unknown whether this ability eventually catches up to normal levels later in adulthood. To date, this issue has not been addressed in the literature since the existing research on WS motion processing has been limited to children.

## 2. Method

### 2.1. Participants

Ten WS children (age range 9;3–18;4 years,  $M = 14;3$  years)<sup>2</sup> and 10 WS adults (age range 20;4–39;8 years,  $M = 25;3$  years) participated in this study, along with 10 normally developing children matched for mental age (MA) to the WS children (age range 4;11–7;7 years,  $M = 6;1$  years) and 10 normal adults (age range 18;5–23;8 years,  $M = 20;5$  years). Williams syndrome children were recruited through the Williams Syndrome Association and all had been diagnosed by a geneticist. In all but one case, the child had also received a FISH screening (fluorescence in situ hybridization; Ewart et al., 1993; Frangiskakis et al., 1996; Lowery et al., 1995) and these were also positive. Williams syndrome and MA-matched children were individually matched through their performance on the KBIT. This test yields an overall Composite IQ scaled score, as well as raw scores for two components, Verbal and Matrices. The Verbal subtest requires children to name objects depicted as black and white line drawings, while the Matrices subtest—a nonverbal component testing conceptual abilities—requires children to judge which objects or patterns 'go together'. WS children had a mean Verbal score of 38.30 ( $SE = 2.44$ ) and mean Matrices score of 20.80 ( $SE = 1.33$ ). Control children's mean Verbal score was 34.40 ( $SE = 1.65$ ) along with a mean Matrices score of 20.10 ( $SE = 1.06$ ). Overall, mean Composite IQ scores for the WS and MA-matched children groups were 63.70 ( $SE = 5.05$ ) and 119.50 ( $SE = 2.86$ ), respectively. WS adults were also given the KBIT providing a mean Verbal score of 48.90 ( $SE = 2.26$ ), mean Matrices score of 21.80 ( $SE = 1.50$ ) and mean Composite IQ of 66.40 ( $SE = 3.77$ ). Additionally, WS and MA-matched control children completed the Differential Abilities Scale (Elliot, 1990) Pattern Construction sub-scale.<sup>3</sup> Impaired block construction is a hallmark of

<sup>2</sup> The reason that the WS child age range goes up to 18;4 years is that one of the WS children began testing when he was 17;9 but didn't complete all tasks until he was 18;4. A reanalysis of our results without this participant does not change the patterns of our data (although the MA versus WS children effect in biological motion now becomes marginally significant;  $p = 0.06$ ).

<sup>3</sup> DAS Pattern Construction scores were unavailable for two of the MA-matched control children and the WS adults.

the WS cognitive profile and was evident in the current WS sample as well. While the MA-matched children's mean performance was 112.75 ( $SE = 4.72$ , mean percentile of 65.38), WS children's mean performance was much lower ( $M = 91.30$ ,  $SE = 6.13$ , mean percentile of 2.56) with all but two WS children scoring in the 1st percentile. Taken together, these data depict a cognitive profile consistent with that typically found in WS (Mervis et al., 1999a).

All subjects provided written informed consent. In the case of MA-matched children, WS children and (when necessary) WS adults, legal guardians provided written consent. These experiments were approved by the Human Subjects Review Boards of both Johns Hopkins University and the University of Delaware. All participants (or, when necessary, legal guardians) reported that they had normal or corrected-to-normal acuity.

## 2.2. Apparatus

The current experiments were conducted using stimuli presented on a Compaq 1.7 GHz computer running custom software written with Microsoft Visual Basic 6.0 and presented on a DTI 15-in. flat-panel LCD screen (1024 × 768 pixel resolution; 60 Hz frame rate).

## 2.3. Stimuli

### 2.3.1. General

On each trial, two motion animations comprised of individual white dots (white pixels arranged to form a filled circle  $0.38^\circ$  visual angle in diameter; luminance =  $148.83 \text{ cd/m}^2$ ) were simultaneously presented in separate black regions (luminance =  $0.83 \text{ cd/m}^2$ ) located on the left and right sides of the display. Each region subtended  $13.65^\circ \times 13.65^\circ$  visual angle in height and width. To avoid confusion associated with making 'left'/right' verbal responses, a small picture (heart/diamond, respectively) was located under each display panel and children made their response by saying 'heart' or 'diamond' and pointing to the appropriate panel. Animations were presented for up to 6150 ms—discontinued early if a participant responded before the animation ended—at a rate of 20 frames/s (i.e., each frame lasted 3 screen refreshes or 50 ms).

### 2.3.2. Motion coherence

Both panels in this experiment contained randomly positioned elements. Signal elements all moved together in the same direction (either to the left or to the right on an individual trial) at a rate of  $2.51^\circ$  visual angle/s (equivalent to the average velocity for the PLW signal dots in the biological motion task) while noise elements were randomly repositioned to a new location somewhere within the panel. Signal elements that moved beyond the panel border wrapped around to the other side.

Participants were instructed to indicate which panel contained the signal elements that 'moved together like a school of fish' (see Fig. 1A).

Experimental trials began with 11 elements (either all signal or all noise) in each panel. As participants 'passed' a given coherence level, additional noise elements were added to each panel. If a participant failed a given coherence level, noise elements were removed. To keep participants from identifying the target by tracking an individual element over the course of a trial, a limited lifetime technique was utilized (Newsome & Paré, 1988)—in which the designation of an individual element as signal or noise was random on each frame.

### 2.3.3. Biological motion

Point-light-walkers (Johansson, 1973) in the target display were computer generated using the Character Studio R2.2 plug-in for 3D Studio Max R3.1 and consisted of 11 signal elements—attached to the major joints (2 hands, 2 elbows, 1 shoulder, 2 feet, 2 knees, and 1 hip) and head of an invisible human form (presented from side-view, subtending approximately  $8.21^\circ$  visual angle in height at full stride). During the trial, the PLW remained fixed in the display's center while performing a one step/s walking motion towards either the participant's left or right (i.e., moving as if on a treadmill). Distractor panels also contained 11 elements attached to the major joints and head of an invisible human form. However, while these individual distractor elements moved through identical paths as the corresponding elements in the target display, the distractor elements' trajectories were temporally out of phase with each other (i.e., instead of a corresponding 'hand' and 'elbow' moving forward together, these two elements might now move in opposite directions; phase for each distractor element was selected randomly with the same set of phases used across trials and participants). Therefore, while central display density and overall spatial arrangement was controlled across panels, the phase-scrambled nature of the distractor elements was inconsistent with the perception of a person walking. Participants were instructed to indicate which panel portrayed a 'person walking nice and upright' (see Fig. 1B).

The experiment began with the 11 target and 11 phase-scrambled distractor PLW signal elements in their respective panels. As participants 'passed' a given coherence level, additional noise elements were added to each display. If a participant failed to pass a given coherence level, noise elements were removed. These noise elements moved in accordance with the trajectories of corresponding target PLW signal elements but were randomly positioned in the display region, thus disrupting the spatial configuration of a walker percept. This type of noise has been shown to be an effective mask in the perception of biological motion (Cutting, Moore, & Morrison, 1988).



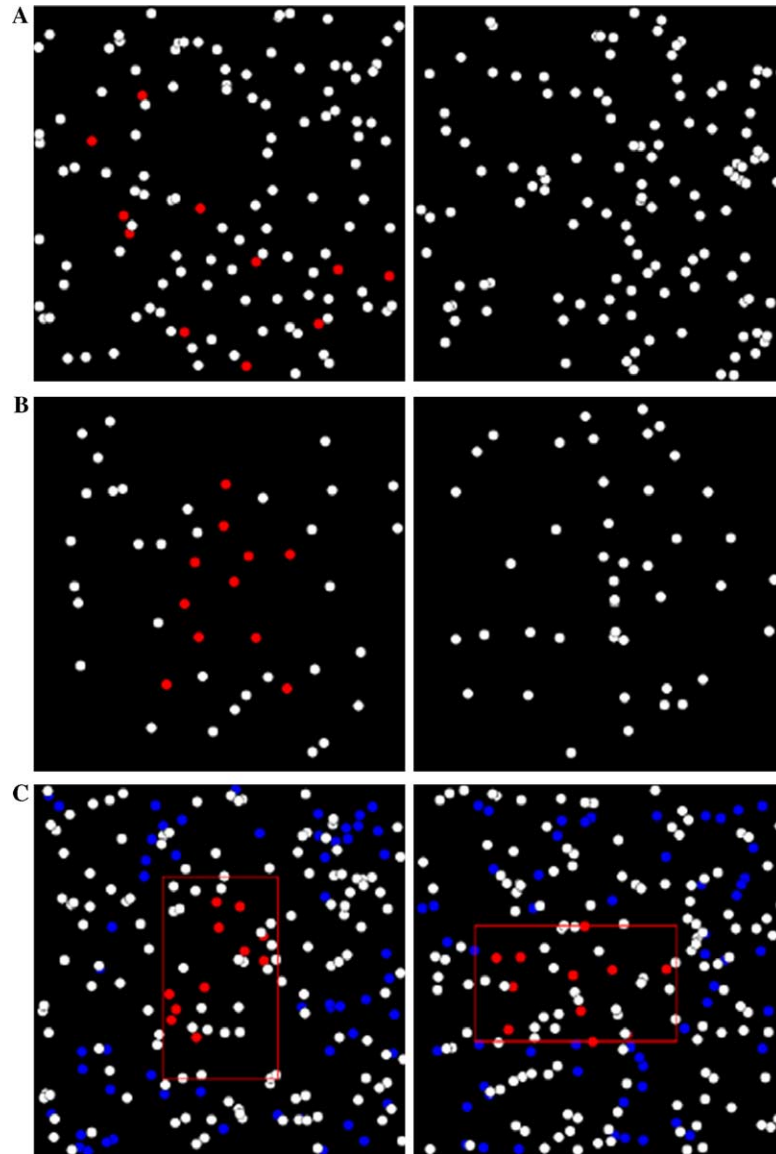


Fig. 1. Scale illustrations of (A) motion coherence, (B) biological motion and (C) form-from-motion displays. For illustration purposes, signal elements are indicated in red (background signal elements in the form-from-motion task are indicated in blue) while noise elements are colored white. During the actual experiments, all elements appeared as white lights on a black background and no rectangles appeared in the form-from-motion displays.

#### 2.3.4. Form-from-motion

Each panel in the form-from-motion task contained randomly positioned elements placed into a rectangular figure region ( $7.38^\circ \times 4.22^\circ$  visual angle) and a surrounding background. To eliminate any cues created by the disappearance of both figure and background elements at the figure's edge, these two regions overlapped by  $0.19^\circ$  visual angle (equivalent to half the diameter of an individual element; The figure dimensions listed above were computed from the midline of this overlapping zone). The target panel contained a vertical figure while the distractor panel contained a horizontal figure. Figure regions were randomly positioned at the begin-

ning of each trial with the constraint that their borders had to be at least  $1.36^\circ$  visual angle from each panel edge. Signal elements in both figure and background regions moved coherently, at a rate of  $2.51^\circ$  visual angle/s, but in opposite directions (i.e., if figure signal elements moved to the right, background signal elements moved to the left). Additionally, noise elements were randomly positioned in each of these regions, individually moving to a new random position each frame. In this task, participants were to indicate which panel contained the moving elements that formed the shape of a vertical rectangle (e.g., the 'tall up and down rectangle that looks like a door', see Fig. 1C). Participants were shown solid

(e.g., not made of dots) vertical and horizontal rectangles in a pre-training trial to ensure that they could differentiate them. In addition, a small vertical rectangle picture was always present at the top of the computer screen to serve as a reminder of the target shape.

Unlike the previous two conditions where the total number of elements/panel varied with performance, accurate form-from-motion perception is quite difficult with small numbers of elements. Therefore, the current experiment kept both the number of elements (204 elements/panel; density = 1.09 dots per degree) and their assignment to figure and background regions (34 and 170 elements, respectively) constant across trials. Difficulty was adjusted by varying the proportion of elements in each region that moved as signal or noise elements. If a signal element's motion path took it out of its respective region, either it wrapped around to the other side or, as can occur in the background, it 'jumped' across to the other side of the figure. The experiment began with all elements moving coherently as signal elements. As participants 'passed' a given coherence level, the proportion of signal elements in each region decreased. Conversely, if a participant failed a given coherence level, the proportion of signal elements increased. As was the case in the motion coherence task, a limited signal lifetime technique was utilized such that the assignment of an element as signal or noise was random on each frame.

#### 2.4. Procedure

Participants completed all three types of motion tasks in separate blocks presented in counterbalanced order.<sup>4</sup> Across tasks, participants were seated approximately 60.96 cm in front of a flat-panel LCD computer screen while each trial was presented in two animated displays. Participants specified which panel contained the target, both by pointing to the correct animation panel and verbally indicating either the 'heart' (left) or the 'diamond' (right) side. Pre-training guaranteed that there was no difficulty or confusion in responding in this fashion. Computer-generated applause sounded after each correct response. Detection difficulty for each task was

adjusted following a 2-down/1-up adaptive staircase rule. Across tasks, the coherence level was defined as the number of signal elements divided by the total number (signal + noise) of elements within the target panel.

Experimental trials for each motion task began with only signal elements in the target panel (no noise elements, equivalent to a coherence level of 1.00) and coherence levels were adjusted on subsequent trials until a participant made seven staircase reversals. If an individual made an error at a coherence level of 1.00, no change in coherence level was made for the next trial (this almost never happened). Otherwise, in the case of motion coherence and biological motion, coherence was adjusted by adding or subtracting 22 (first two reversals) or 11 (last five reversals) noise elements. For example, during the first two reversals, correctly identifying the target panel on two consecutive 1.00 coherence trials (i.e., target panel contains 11 signal dots + 0 noise dots) resulted in the addition of 22 dots to each panel on the next trial (corresponding to a 0.33 coherence level; target panel contains 11 signal dots + 22 noise dots). Form-from-motion signal coherence levels were adjusted in step sizes of 20% (first two reversals) or 10% (last five reversals) of the current coherence level.

Target motion direction (left or right) and display panel (left or right) were randomized and counterbalanced across groups of eight trials. Prior to experimental trials for a given motion task, subjects were given instructions along with a small number of practice trials to familiarize them with the procedure and the stimuli. Practice trials were identical to those in the experiment with the exception that the staircase step size was reduced (motion coherence and biological motion, 11 and 2 elements; form-from-motion, 10% and 5%). Finally, in order to ensure that coherence thresholds reflected true perceptual ability uncontaminated by extraneous factors such as failing to look at the display, trials during which MA-matched child, WS child and WS adult participants were not paying attention were replayed.<sup>5</sup>

<sup>4</sup> During the course of the experiment, several participants exhibited diminished attention and/or confusion regarding task instructions and were therefore rerun on the affected motion tasks (motion coherence reruns = 1 MA-matched child; biological motion reruns = 1 normal adult, 1 MA-matched child and 2 WS children; form-from-motion reruns = 3 WS children—one of which also appears in the biological motion rerun count). Including these subjects' original data produced the same pattern of performance found in Fig. 2. Several additional participants (3 normal adults, 1 MA-matched child and 3 WS adults) did not understand/follow the task instructions but were unable to return for retesting. These individuals were eliminated from all analyses and were not included in Section 2's sample sizes.

<sup>5</sup> For the WS children and adults, the use of replays was rare (on average less than 12% of trials). Mental-age-matched children did appear to be more likely to see a replay though. Separate One-way ANOVAs of replay percentages across participant groups (including normal adults who were allowed zero replays) revealed that WS individuals did not exhibit a significant number of replay trials (i.e., not different than zero) in any motion task. However, MA-control children exhibited higher replay percentages than normal adults on motion coherence and higher replay percentages than all other groups (normal adults, WS children, and WS adults) on biological motion. The WS pattern of replays confirms that accurate WS performance on motion coherence and biological motion was not confounded by additional exposure to the animations. Additionally the finding that MA children required higher biological motion replays is consistent with our conclusion that they struggled with this task.

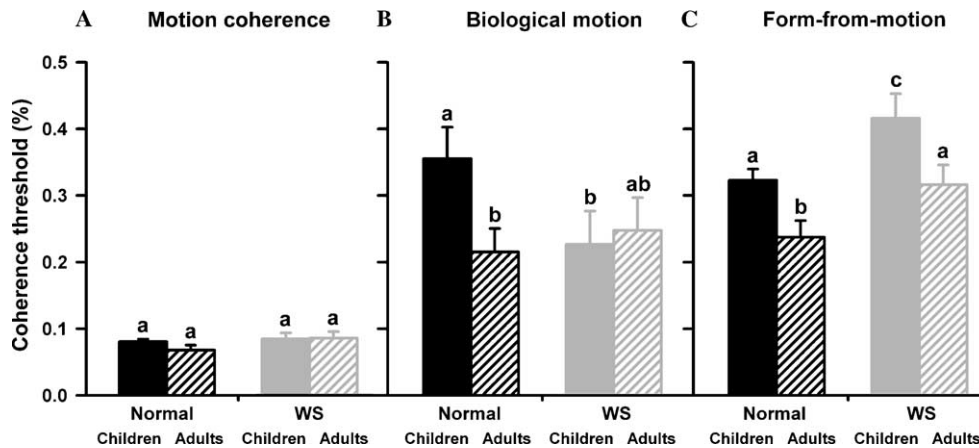


Fig. 2. Coherence thresholds (mean coherence level from last 5 adaptive staircase reversals; lower values indicate greater sensitivity) for correctly reporting the target display in (A) motion coherence, (B) biological motion and (C) form-from-motion conditions across the participant groups. Within each motion task panel, means with different letters above them are significantly different from each other based on planned one-tailed  $t$  test comparisons. For example, in the form-from-motion task, MA children are not significantly different from WS adults but are significantly different from both normal adults and WS children. Error bars represent one standard error of the mean.

### 3. Results

Coherence thresholds for each participant were computed as the mean of coherence levels corresponding to that participant's last five staircase reversals in a given motion task.<sup>6</sup> Fig. 2 presents the coherence thresholds across participant groups and motion tasks. These data were submitted to a 4 (Group)  $\times$  3 (Motion Task) mixed-model repeated-measures analysis of variance (ANOVA). There were significant effects for both Group ( $F(3, 36) = 3.10, p < 0.04$ ) and Motion Task ( $F(1.60, 57.74) = 73.70, p < 0.001$ , Greenhouse–Geisser correction) main effects as well as their interaction ( $F(4.81, 57.74) = 3.32, p < 0.02$ , Greenhouse–Geisser correction). To assess the significant Group  $\times$  Motion Task interaction, planned one-tailed  $t$  tests were conducted which compared the performance of all pairs of groups separately for each motion task. No group differences were statistically significant in the motion coherence thresholds (all  $t$ s  $< 1.52$ ), indicating preservation of this motion ability in WS (see Fig. 2A). Importantly, this means that motion coherence is at adult levels by age 6 in normally developing children and that there is no decrement among WS children and adults. For biological motion (see Fig. 2B), WS children and adults performed comparably to normal adults ( $t(18) = 0.19$  and  $0.54, ns$ ) while MA-matched children performed worse than both normal adults ( $t(18) = 2.38, p < 0.02$ ) and WS children ( $t(18) = 1.87, p < 0.04$ ). Perception of biological motion improves over normal development

and there is no decrement associated with WS since WS children and adults exhibit normal adult-level abilities. In contrast to their intact perception of motion coherence and biological motion, WS children performed worse than normal adults in perceiving form-from-motion,  $t(18) = 4.01, p < .001$ . In fact, both WS groups were impaired relative to their developmental controls in perceiving 2-D form-from-motion stimuli (see Fig. 2C; WS children versus MA-matched children,  $t(18) = 2.30, p < 0.02$ ; WS adults versus normal adults,  $t(18) = 2.04, p < 0.03$ ).<sup>7</sup> While the results indicate developmental improvement in both normal ( $t(18) = 2.84, p < 0.006$ ) and WS ( $t(18) = 2.11, p < 0.03$ ) groups, the developmental trajectory in WS appears to be slow and prematurely arrested, as WS adults fail to perform at levels beyond that of a normal 6-year-old child ( $t(18) = 0.19, ns$ ). This extends previous findings of impairments in the ability of WS children to detect a 2-D area defined by motion 'borders' (Atkinson et al.,

<sup>6</sup> To assess whether performance patterns derived by mean reversals were inappropriately affected by outliers, analyses were repeated with either the median of the last five reversals or the lowest coherences level passed by each participant. In both cases, the patterns of results were very similar to that described in the main text.

<sup>7</sup> Conceivably, accurate performance in the form-from-motion task might have been achieved without the perception of a motion-defined 2-D shape. For example, perhaps participants identified the target panel by detecting vertically oriented flickering "zones" created by signal element appearance/disappearance at the left and right figure borders (i.e., both the vertical height and horizontal spacing of such zones is predictive of figure shape). To evaluate this claim, a control task was run that removed the presence of opposing motion. In this task, all signal elements continued to appear and disappear at figure borders and were still confined to their respective figure/background regions, but traveled in the same horizontal direction on each trial. Performance on this control task (run with normal adults in counterbalanced order along with the three standard motion tasks) was much poorer (coherence threshold;  $M = 0.88, SE = 0.01$ ) than on the standard form-from-motion task ( $t(9) = 24.07, p < 0.001$ ) suggesting that participants were unable to use stimulus features aside from opposing figure/background motion vectors to accurately perceive the target rectangle.

1997, 2003), by demonstrating that it persists into adulthood.

#### 4. Discussion

The present results reveal an uneven distribution of WS performance across motion tasks. As reported in Jordan et al. (2002), perception of biological motion in children with WS appears to be intact and can be superior to that of normally developing control children matched to the WS children on mental age. Performance of WS adults was also intact and indistinguishable from WS children and normal adults. Comparison of the normal children and adults clearly shows a developmental change in this ability with normal adults detecting point-light-walkers (PLWs) significantly better than the MA-matched children. This suggests that the ability to perceive ‘difficult’ biological motion stimuli (PLWs embedded in dynamic noise), as in the present study, is not normally fully developed until sometime between 6 and 20 years of age (see Pavlova, Krägeloh-Mann, Sokolov, & Birbaumer, 2000). Since the WS children were chronologically older than their MA-matched controls (mean ages = 14;3 versus 6;1 years), findings that both WS children and adults performed equivalently and at normal adult levels are consistent with the idea that, by adolescence, the WS biological motion system has reached the level of a normal adult.

This preserved ability in people with WS does not seem to be restricted to biological motion, however, because we also found normal thresholds on the motion coherence task. All four groups exhibited the same performance level, suggesting that (1) this ability is normally fully developed by at least 6 years of age and that (2) our WS children have successfully reached a fully developed stage.<sup>8</sup> Equivalent performance by all groups in detecting motion coherence is consistent with findings that basic motion processing develops early in infancy and may thus be less vulnerable to disruption from abnormal development or environmental influences (Elleberg, Lewis, Maurer, Brar, & Brent, 2002). However, it is clear that motion coherence is not always immune to damage during development as motion coherence deficits have been reported in children with

other disorders (e.g., developmental dyslexia; see Raymond & Sorensen, 1998).

A quite different pattern was evident in the 2-D form-from-motion condition. Although both normal and WS groups showed improvement over development (see Hollants-Gilhuijs, Ruijter, & Spekrijse, 1998; Schrauf, Wist, & Ehrenstein, 1999), the WS groups were systematically worse than controls, with the WS adults failing to perceive the forms at a level beyond that of normal 6-year-olds. Poor performance by the WS children could be explained by a delayed development of this ability while deficits in WS adults could indicate premature arrest. This pattern would be consistent with other reports suggesting that a variety of WS deficits can be characterized, not as deviant, but as both a developmental delay (see Mervis, Robinson, & Pani, 1999b; Nakamura, Kaneoke, Watanabe, & Kakigi, 2002) and a premature arrest (see Atkinson et al., 2001, 2003; Bellugi et al., 2000; Braddick, Atkinson, & Wattam-Bell, 2003; Georgopoulos, Georgopoulos, Kurz, & Landau, 2004). Factors such as inattention or fatigue are an unlikely explanation for their poor thresholds, since WS individuals detected targets at levels commensurate with normal adults on the other two motion tasks. Likewise, accounts based on task difficulty (i.e., WS individuals simply do poorly on ‘difficult’ tasks) do not fit the data; although normal participants performed equally well on FFM and biological motion tasks (suggesting equivalent difficulty), the WS deficit was limited to FFM perception.

Importantly, despite several methodological differences from previous work, WS children’s performance in the current study was not only qualitatively but also *quantitatively* similar to previous results obtained in comparable motion tasks. For example, Jordan et al. (2002) reported that WS children were 73.2% accurate at a 0.25 coherence level which is quite comparable to WS accuracy in the present study (70.7% accuracy level at a 0.23 coherence level). Additionally, the current study confirmed the findings by Atkinson and colleagues (1997) that WS children’s mean motion-defined form coherence was approximately 0.40 (0.42 in present study versus 0.39 estimated from Atkinson et al., 1997; Fig. 1), in spite of differences in display size, density, speed, and task (detecting a single rectangle in Atkinson et al. versus discriminating a vertical from a horizontal rectangle in the present study). Such consistency across studies suggests that we are measuring properties of the motion processing system that generalize across many differences in the details of the particular task.

##### 4.1. Nature of the WS motion deficit

The finding that WS individuals demonstrate intact perception of motion coherence and biological motion, but struggle with 2-D motion-defined forms, naturally raises questions as to why the 2-D FFM class is so

<sup>8</sup> At first glance, this may seem inconsistent with claims by Atkinson and colleagues (1997, 2003) that motion coherence is abnormal in children with WS. However, as stated in the Introduction, the task used by Atkinson and colleagues required participants to detect a 2-D shape defined by opposing signal motion between figure and background. Therefore, based on the motion classifications used in the present work, the Atkinson et al. (1997, 2003) task is more appropriately referred to as form-from-motion and not motion coherence. This conclusion is supported by the comparison of the data across studies as well (discussed in the main text below).



difficult for WS individuals. One obvious explanation is that WS people had trouble discriminating the horizontal and vertical rectangles. This seems unlikely, however, for several reasons. First, we informally tested WS subjects with solid rectangles of the same size and shape as those used in the motion task and they never made errors in discriminating the orientation of the rectangle (for further evidence of intact vertical and horizontal orientation perception in WS, see Atkinson et al., 1997; Dilks et al., submitted). Second, we found that, when coherence levels were high, WS individuals were nearly perfect. Finally, Atkinson et al. (1997, 2003) also reported impairments in children with WS in a task that, like ours, used motion direction to define a rectangular area; however, their subjects had to simply *detect* the location of the area and were not required to discriminate its shape. Therefore, it appears that shape discrimination per se is not the source of difficulty.

A second possibility is that WS people have difficulty integrating form and motion information and that this causes difficulty in form-from-motion tasks. However, the finding that WS subjects were intact on the biological motion task appears to argue against this possibility, since both biological motion and form-from-motion require integration of form and motion. Similarly, both our FFM task and the task used by Atkinson et al. (1997, 2003) required that subjects discriminate the direction of motion, a requirement not present in motion coherence. One might consider, therefore, that perceiving motion direction is the critical process impaired in WS. However, biological motion also requires discrimination of the direction of motion of the individual lights making up the PLW. Additionally, Nakamura and colleagues (2002, discussed below) report intact WS motion direction discrimination in a variant of the motion coherence task used in the present study.

We speculate that the key difference between FFM and the other tasks has to do with the difficulty of *segmenting* the coherently moving object from its background. In our biological motion and motion coherence tasks, subjects need only detect coherence to perform correctly. In our 2-D FFM and the motion task used by Atkinson et al. (1997, 2003), both figure and background areas contained coherently moving dots. In these tasks, subjects had to segment one area of coherence from another. Segmentation would allow subjects to detect a discontinuity between areas, allowing for a detection response in the Atkinson et al. (1997, 2003) studies and serving as the input for processing of the rectangle orientation in the current work. A failure to segment the coherent areas would produce poor thresholds in both studies. People with WS appear to have a particular difficulty in segmentation, which may be a major contributor to their difficulties in visuo-constructive tasks such as block construction. For example, Hoffman, Landau, and Pagani (2003) showed that even

when blocks were visually segmented from their neighbors by visual borders and spatial separation, WS children were unable to ignore neighboring blocks which contributed to their errors in identifying the attended block. It may be that 2-D form-from-motion tasks are difficult because they require similar processes of segmentation, which are weak in people with WS.

#### 4.2. Motion coherence and the general dorsal stream deficit hypothesis

Previous findings of preserved biological motion perception in WS individuals might be explained in terms of this kind of motion having a special status in this population. WS individuals are known to have an intense interest in faces and other social stimuli (Bellugi et al., 2000) and this attention to social cues might result in preserved functioning of those systems that are important in identifying other individuals. Findings of preserved perception in biological motion *and* motion coherence tasks argue against this notion. In addition, the preservation of some functions that clearly involve structures in the dorsal stream argues against the idea that WS involves a generalized deficit of the entire dorsal stream. Bertone, Mottron, Jelenic, and Faubert (2003) have reached a similar conclusion in the context of autism, a developmental disorder that results in a cognitive profile quite different from that found in WS (see also Blake, Turner, Smoski, Pozdol, & Stone, 2003; Milne et al., 2002; Spencer et al., 2000). Further support for a pattern of differential sparing and impairment in WS motion processing comes from a recent case study by Nakamura and colleagues (2002) describing an individual WS child who demonstrated typical poor visuo-spatial performance, but correctly perceived coherent motion as well as element/group 'Ternus' apparent motion (apparent motion is also MT/V5-driven, Muckli et al., 2002).

One could speculate that an intact ventral stream could become reorganized to compensate for dorsal stream perceptual deficits; in which case, we might conclude that normal motion processing in WS subjects is mediated by ventral stream structures. Nakamura and colleagues (2002) however, challenge this explanation in the context of motion processing. First, they point out that there does not appear to be any systematic cyto-architectural abnormalities in the WS magnocellular pathway (Galaburda & Bellugi, 2000), which serves as the primary input to cortical motion area MT/V5 (Maunsell, Nealey, & DePriest, 1990). Second, they found that their subject's neural activation (as measured by magnetoencephalography, MEG) in response to coherent/incoherent motion resulted in the same spatio-temporal profile found in normal controls, consistent with a V5/MT source (Nakamura et al., 2002). Taken together, the present work and that of Nakamura and colleagues (2002) provides strong converging evidence

of intact perception across several motion classes in WS and thus further weakens the notion of a general deficit in WS dorsal stream processing.

## 5. Conclusions

The data from the present study demonstrate that WS individuals can accurately perceive some, but not all, classes of motion stimuli. Specifically, in addition to intact biological motion perception, WS individuals also have spared perception of motion coherence; a function primarily associated with the dorsal stream region V5/MT. These findings suggest that biological motion is not a 'special' spared stimulus class within the WS population and that these individuals do not suffer from a general motion processing deficit. Therefore, to the extent that impaired motion processing has previously been taken as evidence of a WS general deficit in dorsal stream function, our data suggest that this may not be the case—instead any dorsal stream deficit must be selective. Furthermore, the inclusion of WS adults in the present study allowed us to characterize the nature of their deficit in perceiving motion-defined forms as the premature arrest of a developmentally delayed ability.

More broadly, although research with normal and brain-damaged adult populations indicates that specialized subsystems of motion processing exist in the fully developed brain (Beintema & Lappe, 2002; Cowey & Vaina, 2000; Grossman & Blake, 1999; McLeod et al., 1996; Schenk & Zihl, 1997; Vaina et al., 1990), the present study lends support to the claim that different kinds of motion processing can be selectively damaged as a result of a genetic developmental deficit. This suggests that such specificity may exist early in development due to a link between the deleted genes and the development of the brain's functional capacities (Bellugi et al., 1988; Mervis et al., 1999b).

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