Research Article

INTACT PERCEPTION OF BIOLOGICAL MOTION IN THE FACE OF PROFOUND SPATIAL DEFICITS: Williams Syndrome

Heather Jordan,[1] Jason E. Reiss,[1] James E. Hoffman,[1] and Barbara Landau[2]

[1]University of Delaware and [2]Johns Hopkins University

Abstract—*Williams syndrome (WS) is a rare genetic disorder that results in profound spatial cognitive deficits. We examined whether individuals with WS have intact perception of biological motion, which requires global spatial integration of local motion signals into a unitary percept of a human form. Children with WS, normal mental-age-matched children, and normal adults viewed point-light-walker (PLW) displays portraying a human figure walking to the left or right. Children with WS were as good as or better than control children in their ability to judge the walker's direction, even when it was masked with dynamic noise that mimicked the local motion of the PLW lights. These results show that mechanisms underlying the perception of at least some kinds of biological motion are unimpaired in children with WS. They provide the first evidence of selective sparing of a specialized spatial system in individuals with a known genetic impairment.*

Williams syndrome (WS) is a rare genetic disorder (1:20,000 live births) resulting from a hemizygous submicroscopic deletion on chromosome 7q11.23. It is typically confirmed using FISH (fluoride in situ hybridization) screening (Ewart et al., 1993; Frangiskakis et al., 1996; Lowery et al., 1995). The syndrome is associated with moderate mental retardation (mean composite IQ = 55–60; Mervis, Morris, Bertrand, & Robinson, 1999) and a range of phenotypic characteristics, including congenital defects in connective tissue that result in heart disorders, characteristic "elfin" facial features, and a distinctive cognitive profile including profoundly impaired spatial cognition together with relatively spared language abilities (Bellugi, Marks, Bihrle, & Sabo, 1988; Mervis et al., 1999). Deficits in the spatial domain are particularly evident in performance on construction tasks, which require people to duplicate a model, either by drawing it (e.g., the Developmental Test of Visual-Motor Integration, or VMI; Beery & Buktenica, 1967) or by constructing a copy using parts (e.g., Differential Abilities Scale, DAS, Pattern Construction subscale; Elliot, 1990). Adolescents with WS are severely impaired on these tasks, with their scores typically falling in the 1st percentile (Bellugi, Marks, et al., 1988; Bellugi, Wang, & Jernigan, 1994; Mervis et al., 1999). In contrast, their language abilities are relatively spared (Bellugi, Marks, et al., 1988; Bellugi, Sabo, & Vaid, 1988). This combination of spared language and impaired spatial capacities is consistent with the notion that selective breakdown can occur across cognitive domains—in this case, in conjunction with genetic impairment (Bellugi, Marks, et al., 1988).

The reasons for visuospatial constructive deficits in individuals with WS remain unclear, although there is some evidence that they are impaired in representing the global arrangement of local elements. For example, Bellugi and colleagues (Bellugi et al., 1994; Bihrle, Bellugi, Delis, & Marks, 1989) asked adolescents with WS to reproduce drawings of hierarchical visual stimuli, that is, figures in which individual local elements were arranged to form various global shapes. Although the teens tended to reproduce the local elements (dots) accurately, they did not place these elements accurately, thus violating the overall configurations (see Fig. 1 for examples of similar results with younger children). This pattern of performance has been replicated in other studies, is consistent with performance in the DAS and VMI tasks, and is now considered to be characteristic of WS (Mervis, 1999). This deficit cannot be accounted for by problems with any low-level vision or motor impairment thus far measured. Although visual defects (e.g., strabismus, amblyopia, and refractive errors) are more common in individuals with WS than in the general population, there is no correlation between the severity of these defects and performance in visuospatial construction tasks (Atkinson et al., 2001). In addition, individuals with WS can accurately trace models that they are unable to reproduce, so defective motor coordination cannot be the sole cause of their visuospatial constructive deficits (Bellugi, Sabo, & Vaid, 1988).

Recent studies have also shown that individuals with WS have difficulty integrating dynamic visual information. Atkinson et al. (1997) asked people to detect coherent motion of signal dots embedded in a background of physically identical, but randomly moving, noise dots. Individuals with WS were less accurate than control participants, suggesting they had a deficit in the capacity to integrate individual moving lights into a coherent percept. The groups performed comparably, however, in a task requiring detection of coherence in an array of static lines differing in orientation (see also Pani, Mervis, & Robinson, 1999), suggesting that impairments in spatial integration were restricted to the motion system. Another study (Milner & Goodale, 1995) found that subjects with WS were also impaired in the posting task, in which a card has to be inserted into a slot that is presented in various orientations, although they performed comparably to control subjects in a corresponding perceptual matching task (see also Dilks, Landau, Hoffman, & Siegfried, 2001).

Atkinson et al. (1997) noted that this pattern of results is consistent with Ungerleider and Mishkin's (1982) proposed distinction between a ventral visual system governing object perception (the *what* system) and a dorsal system governing location and motion processing (the *where* system). Each of these systems, in turn, can be decomposed into narrower specialists concerned with particular classes of stimuli, such as faces (Moscovitch, Winocur, & Behrmann, 1997) and objects (Ishai, Ungerleider, Martin, Schouten, & Haxby, 1999). Individuals with WS have relative strengths in face processing (Wang, Doherty, Rourke, & Bellugi, 1995) and object identification (Hoffman & Landau, 2000), both of which are presumably mediated by the ventral stream. In contrast, deficits in motion perception and visually guided action implicate an impaired dorsal stream in WS. This pattern of impaired and preserved abilities in different visual tasks provides additional evidence for the existence of independent, specialized subsystems of spatial cognition. In addition, a careful analysis of this pattern in a subject

Address correspondence to James E. Hoffman, Department of Psychology, University of Delaware, Newark, DE 19716; e-mail: hoffman@udel.edu.

group with a known genetic deficiency may shed light on the link between specific genetic disorders and selective developmental emergence of particular aspects of cognitive architecture. It should be emphasized, however, that the correspondence between these abilities and the dorsal-ventral distinction remains highly speculative.

One domain that could provide further insights into the nature of spatial breakdown in WS is the perception of biological motion. Interpreting the motion of lights that make up a point-light walker (PLW) requires integrating information across individual moving stimuli to extract the form of the animate figure (Johansson, 1973; see Fig. 2).

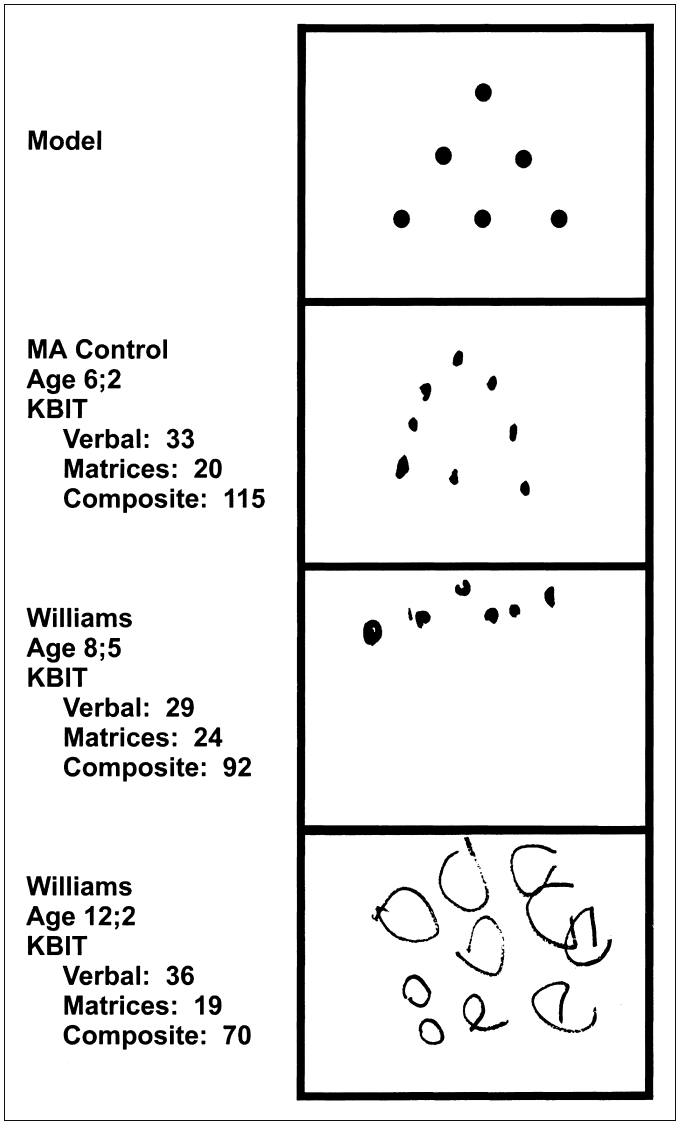

Fig. 1. Examples of reproductions of a hierarchical figure from the Developmental Test of Visual-Motor Integration (Beery & Buktenica, 1967) by two children with Williams syndrome (WS) and a mental-age-matched (MA-matched) peer. Both of the individuals with WS were participants in the experiment reported here. The model (top) was visible until the children reported that they had completed their reproduction; they were under no time pressure to complete the task. The reproductions produced by the children with WS are typical of those seen with this group. Although the children attended to the parts of the figure, the reproductions show little evidence of the spatial arrangement of these parts relative to one another in the model. The faithful reproduction of the local forms, in the absence of the global configuration, has prompted suggestions that individuals with WS have a deficit in global processing. Also shown are the children's scores on the Kaufman Brief Intelligence Test (KBIT; Kaufman & Kaufman, 1990).

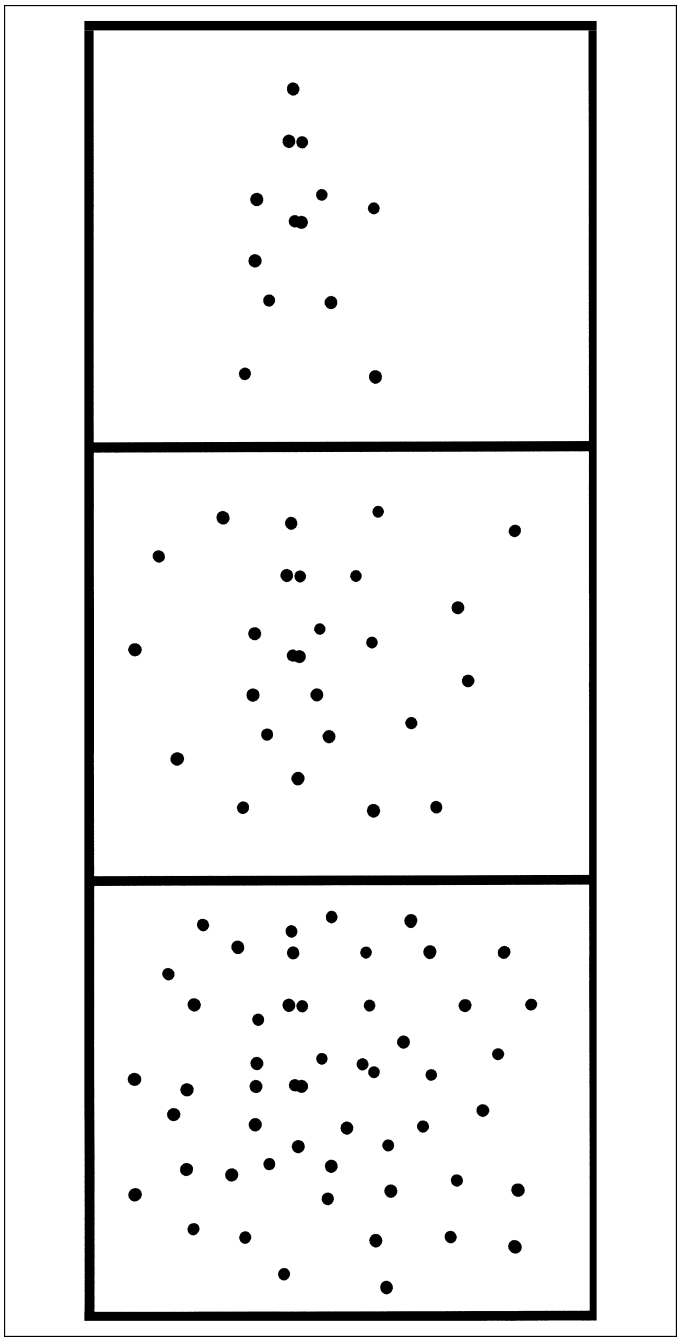

Fig. 2. Scale illustrations of the point-light walker used in pilot work (top), as well as the 1:1 (center) and 1:3 (bottom) signal-to-noise conditions of the current experiment. In all cases, the signal and noise elements appeared as white lights on a black background.

When the PLW is in motion, any single light is insufficient to specify a particular motion. For example, a light attached to the elbow will simply oscillate horizontally like a pendulum, providing little clue about its true origin. However, when its motion is perceived relative to that of the shoulder and wrist joints, the two pairs of lights can be perceived as the ends of connected, rigid rods (upper and lower arm).

Although the motion characteristics of the individual lights attached to a hand, an elbow, and a shoulder may be very different, the visual system integrates this information across the triad to produce the percept of an arm. Similarly, the entire arm can be seen in motion relative to the body. This hierarchical nesting of reference frames for the perception of motion ultimately yields the unmistakable global percept of a person walking. PLW displays are visually compelling to most observers, including infants (Bertenthal, Proffitt, Kramer, & Spetner, 1987), and people can extract a wide variety of social information, including the gender and affective state of the walker, from this degraded visual information (Dittrich, Troscianko, Lea, & Morgan, 1996; Mather & Murdoch, 1994).

Research demonstrating the orientation selectivity (upright vs. inverted) of biological motion perception (Bertenthal & Pinto, 1994; Pavlova & Sokolov, 2000) suggests that global spatial analyses are the primary means of extracting biological motion from this type of visual information, much as faces are analyzed globally (Farah, Tanaka, & Drain, 1995). Because people with WS appear to have a deficit in the ability to globally integrate motion across spatially distributed elements, they might be expected to have difficulty seeing PLW displays. However, other factors suggest that this ability may be spared. First, perception of biological motion in a PLW display, unlike detection of motion coherence, involves the extraction of a three-dimensional shape from the moving lights. Surprisingly, this kind of higher-order motion perception appears to be separable from the ability to detect motion coherence. Vaina, LeMay, Bienfang, Choi, and Nakayama (1990) described a patient who could see biological motion and other structure-from-motion but was severely impaired in motion-coherence tasks similar to those used by Atkinson et al. (1997). Conversely, Schenk and Zihl (1997) studied a group of patients who could not see form-from-motion but had normal motion-coherence thresholds. Thus, it may be possible for people with WS to perceive biological motion even if their perception of motion coherence is impaired.

Second, there is evidence from single-cell recordings in monkeys and brain-imaging experiments with humans that an area of the brain in or near the superior temporal sulcus (STS) may be specialized for perceiving "human actions" (Allison, Puce, & McCarthy, 2000). Because perceiving the direction of another person's gaze or actions is important in inferring that person's intentions, STS is thought to be an important component of the system responsible for the perception and interpretation of socially relevant stimuli (Allison et al., 2000). Given the pronounced proclivity of WS children for social stimuli (Mervis et al., 1999; Tager-Flusberg & Sullivan, 2000), one might expect this area to be preserved in WS. It might also mediate preserved perception of biological motion.

A key component of perceiving biological motion in PLW displays is finding the appropriate correspondences between lights (e.g., the wrist and shoulder lights), even though other (false) correspondences may be obtained for lights that are actually closer together (e.g., those on the wrist and hip). Introducing noise lights into PLW displays complicates this correspondence process. If the signal and noise lights are identical in terms of such features as color, shape, and local motion, a process that computes relative motion between pairs of nearby lights will occasionally establish an incorrect correspondence between signal and noise lights, thereby producing an "illusory" candidate part, which can be rejected only when it violates the constraints of coherent biological motion across all the parts making up the figure.

In pilot work, we presented participants with 10 brief animated videos of PLWs carrying out five different actions, doing a back handspring, doing a cartwheel, performing jumping jacks, slipping on a banana, and waving. Children with WS, as well as control participants, accurately described the action of the PLW, with expressions such as "He's doing jumping jacks" and "He fell over," indicating that the animated PLWs were indeed perceived as humans engaging in action. In a second experiment, we presented side views of a PLW and required observers to indicate the direction in which the figure was walking. All three groups tested were highly accurate at reporting the PLW's direction of apparent motion: adults, 100%; mental-age-matched (MA-matched) children, 98.5%; and children with WS, 100%.

In the current experiment, we introduced noise lights in ways that should incrementally increase the difficulty of the correspondence process. First, we varied the ratio of signal to noise lights, which is directly related to the number of false correspondences that must be considered and rejected. Even though individuals with WS can correctly perceive PLW displays without noise, they might have "fragile" global integration capacities that would lead to a breakdown in performance at signal-to-noise (S/N) ratios that still yield perfect performance in control subjects. Second, we varied the type of noise, including additional elements that were static, moving randomly, and moving in yoked fashion relative to the signal lights contained in the PLW. Each of these variations should have made it more difficult for all observers to perceive the PLW's direction of motion (Cutting, Moore, & Morrison, 1988), and hence allowed us to determine whether the capacities of children with WS are more fragile than those of normally developing children.

METHOD

Participants

Ten children with WS (mean age = 11 years 7 months, range: 9 years 4 months to 15 years 7 months), 10 MA-matched normally developing children (mean age = 6 years 0 months, range: 4 years 3 months to 7 years 3 months), and 10 undergraduates (ages 19–21 years) participated. Children with WS were identified through the National Williams Syndrome Association, and had been positively diagnosed by a geneticist, the FISH test, or both. The normally developing children were matched individually to the children with WS, using the Kaufman Brief Intelligence Test (Kaufman & Kaufman, 1990), which yields Verbal and nonverbal (Matrices) scores. The Matrices subtest does not have many spatial items, and hence does not unfairly penalize children with WS for their spatial impairment. The children with WS had a mean verbal score of 33.15 (SE = 1.93) and a mean Matrices score of 18.50 (SE = 0.81); corresponding scores for the MA-matched control subjects were 31.60 (SE = 2.48) and 19.10 (SE = 1.45). The mean IQ scores for the two groups were 62.60 (SE = 4.97) for the children with WS and 116.40 (SE = 3.11) for the control children. In addition, both groups were tested on the DAS Pattern Construction subtest, which is the hallmark test used to diagnose WS spatial impairment (DAS scores were unavailable for 1 of the MA-matched children). The DAS scores were as follows: children with WS, M = 85.80, percentile = 2.00, SE = 4.70; MA-matched children, M = 106.78,

percentile = 56.00, *SE* = 5.90. All but 2 of the children with WS fell into the 1st percentile of performance. The scores of the children with WS are similar to those reported in other studies of WS (see Mervis et al., 1999). All participants signed informed assent forms.

Stimuli and Procedure

On each trial, participants observed a side view of a PLW that performed a walking motion directed toward either the left or the right of the screen, although it remained in the same location throughout the trial (and therefore appeared to walk as if on a treadmill). Participants were asked to indicate whether the PLW was walking to the left or right, by raising their corresponding hand and by verbally reporting which of two icons (heart-left, diamond-right) was the PLW's destination. Children were pretrained to make these responses, and none had any difficulty or confusion doing so. Participants heard computer-produced applause on correct trials.

The PLWs were computer-generated using the Character Studio R2.2 plug-in for 3D Studio Max R3.1 and consisted of 13 white lights (each subtending 0.25° visual angle) attached to the joints, head, and trunk of an invisible human form. Each animation showed the person walking for 2 s (see Fig. 2, top panel) and was played three times in a continuous loop, at the rate of 20 frames/s. Each PLW subtended 6.20° visual angle in height when at full stride and viewed from a distance of approximately 92 cm.[1]

Each PLW was presented in one of two locations in the display (left or right of midline); location was randomly selected on each trial. The PLW walked toward the left or right of the display with equal probability. The same figure was viewed from cameras placed in mirror-symmetric locations on either side of the figure to create the separate left and right views.

In the high-S/N condition (S/N ratio = 1:1), the PLW was embedded in 13 noise lights (Fig. 2, center panel). In the low-S/N condition (S/N ratio = 1:3), there were 39 noise lights (Fig. 2, bottom panel). The two S/N conditions were presented in separate blocks (1:1 and then 1:3). This factor was combined with three different noise types (static, random, and yoked). Within each S/N condition, all participants were tested in 12 trials per noise type, for a total of 36 trials, presented in random order. The experiment lasted approximately 15 min.

In the static condition, all noise elements remained static as the PLW elements moved. Such noise elements should produce little interference, because false correspondences with noise lights can be eliminated on the basis of the single feature of motion. Random noise consisted of lights moving through random trajectories at the same mean velocity as the signal lights. False correspondences based on this kind of noise will often result in parts that may not be rigid or whose motion may not correspond to the motion of known parts such as an arm. In the yoked condition, each noise element was paired with a signal light and moved with the same velocity and on the same trajectory (either in or out of phase) as that signal. This type of noise should often produce correspondences between pairs and triads of lights. In some cases, the resulting parts can be rejected only when they fail to fit into the global figure defined by all of the parts taken together. In the 1:1 displays, each yoked noise light moved 180° out of horizontal-axis phase with its paired signal light. In the 1:3 display, two noise elements moved 180° out of horizontal-axis phase with their paired signal light, and one noise element moved in phase with the same paired signal light. For example, if a signal light was moving up and to the left of the displays, one of the paired noise lights would also move up and to the left while the other two paired noise lights would move up and to the right. Therefore, the noise lights moved with the same velocity and on the same trajectory (either in or out of phase) as the corresponding signal light. This method produced drift-controlled displays (Chubb & Sperling, 1988), in which the average direction of motion in each horizontal direction was equal across the entire array.

In all conditions, the noise elements were randomly dispersed across the display. The camera view was divided into 16 equal three-dimensional volumes, and noise elements were randomly distributed among these volumes. So that the density of lights across the display would be as equivalent as possible, only a limited number of noise elements was placed in volumes containing the walker. Following inspection of the animation, individual noise elements were repositioned to provide relative homogeneity of density. For example, individual noise elements were repositioned if an element moved out of the camera view during the animation or if obvious "holes" were created by the elements' movement.

RESULTS AND DISCUSSION

Percentage correct (PC) in a two-alternative, forced-choice task can be reduced by extreme bias toward one of the alternatives. We evaluated this possibility by converting our PC measure to a bias-free measure, PC_{max}, using the method of Green and Swets (1966, p. 410). Group averages changed by less than 2%, and none of our reported significance levels were affected by this procedure. Therefore, we report our results in terms of the uncorrected PC scores.

The percentages of correct judgments across groups and conditions are shown in Figure 3. Two of the children, 1 in each of the WS and MA-control groups, completed the study but exhibited diminishing attention to the task. Their scores fell more than 3 *SD*s below the mean for the remainder of their group in the static condition by the second block (the low-S/N condition), and data from these 2 subjects were excluded in the following analyses. However, the overall pattern of their data was consistent with the patterns illustrated in Figure 3.

The data were submitted to a 3 (group) × 2 (S/N ratio) × 3 (noise type) mixed-model repeated measures analysis of variance. There were main effects of all three factors. The adults performed best (95.97%), followed by the children with WS (90.90%) and the MA-matched children (83.49%), $F(2, 25) = 11.33$, $p < .001$. Tukey HSD post hoc comparisons showed that the adults and children with WS performed reliably better than the normally developing children (ps < .001 and .05, respectively). There was no reliable difference between the adults and the children with WS. Participants also performed reliably better with less noise (1:1 ratio, $M = 95.30\%$; 1:3 ratio, $M = 84.94\%$), $F(1, 25) = 73.20$, $p < .001$. Finally, a significant S/N Ratio × Noise Type interaction revealed that the type of noise lights had different effects depending on the S/N ratio, $F(2, 50) = 19.81$, $p < .001$. To further analyze this interaction, we conducted a separate 3 (group) × 3 (noise type) mixed-model repeated measures analysis of variance for each S/N ratio (1:1 and 1:3).

In the high-S/N condition (1:1 S/N ratio), a main effect of noise type, $F(2, 50) = 7.76$, $p < .005$, showed that participants performed better when the noise lights were static ($M = 99.39\%$) than when they were moving (average of random noise, $M = 93.83\%$, and yoked

1. Examples of the stimuli used in this experiment can be found on the Web at http://hoffman.psych.udel.edu/research/emdemo/WilliamsPage.htm.

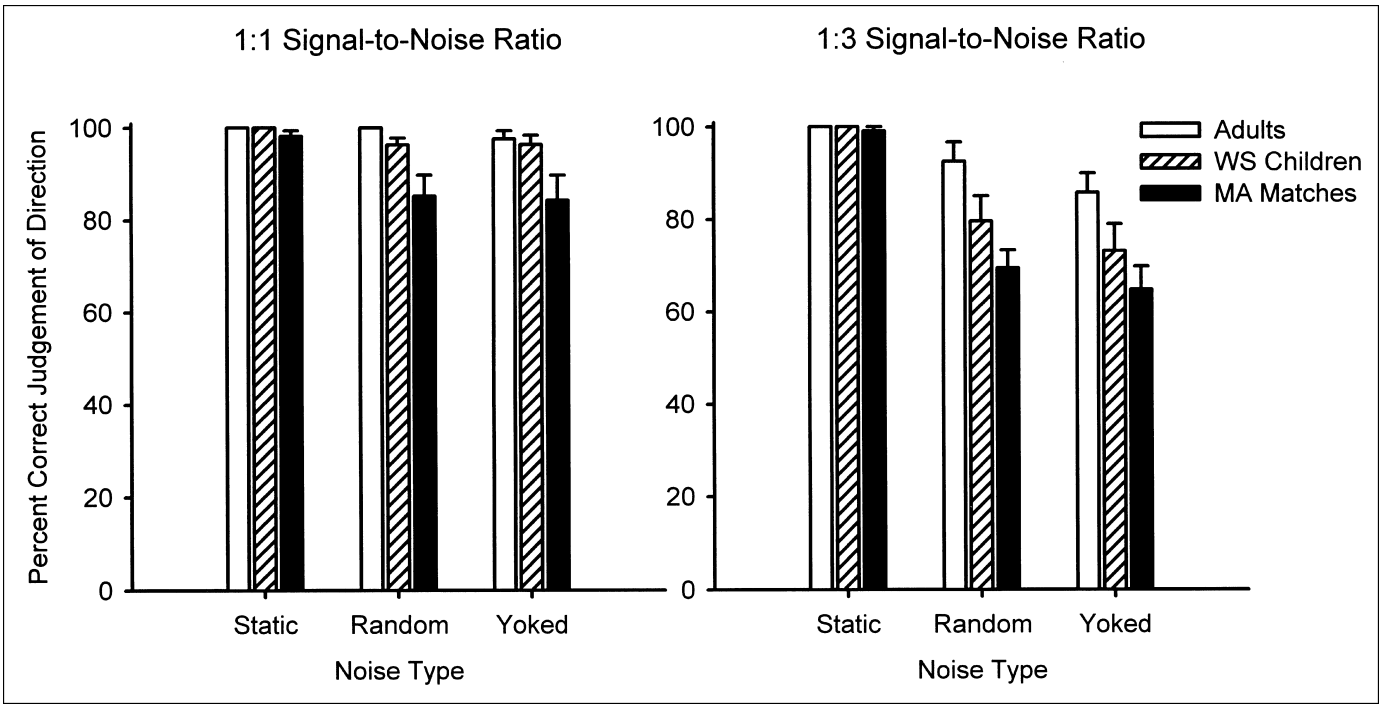

Fig. 3. Mean percentage accuracy of reporting the walking direction of the point-light walker in each of the three noise conditions for the three groups of participants (adults; children with Williams syndrome, WS; and children matched for mental age, MA). Results are shown separately for high (1:1; left) and low (1:3; right) signal-to-noise ratios. Chance performance lies at 50%.

noise, $M = 92.69\%$), $F(1, 25) = 13.40$, $p < .005$. Random and yoked noise did not differ, $F(1, 25) = 0.45$, n.s. A group effect, $F(2, 25) = 9.11$, $p < .005$, showed that adults performed the best (99.17%), followed by children with WS (97.54%) and MA-matched control children (89.20%). Tukey HSD post hoc comparisons showed that, once again, adults and children with WS outperformed MA-matched children (ps $< .005$ and .01, respectively), whereas adults and children with WS were not different from each other. Finally, a Group × Noise Type interaction (static vs. the average of random and yoked), $F(2, 25) = 4.93$, $p < .05$, showed that the presence of moving lights (either randomly or yoked) affected the groups differently. As can be seen in Figure 3 (left panel), performance of MA-matched control children was dramatically reduced by the presence of moving noise lights, but both adults and WS children showed only small decreases in accuracy.

Analysis of performance in the low-S/N condition (1:3 S/N ratio) revealed, once again, an effect of noise type, $F(2, 50) = 37.68$, $p < .001$, with accuracy being better when the noise lights were static ($M = 99.69\%$) than when they were moving (average of random noise, $M = 80.52\%$, and yoked noise, $M = 74.60\%$), $F(1, 25) = 112.81$, $p < .001$. Random and yoked noise did not differ, $F(1, 25) = 2.81$, n.s. A group effect, $F(2, 25) = 9.45$, $p < .005$, showed that adults performed the best (92.77%), followed by children with WS (84.26%) and MA-matched control children (77.78%). Unlike in the previous analyses, Tukey HSD post hoc comparisons showed that although adults outperformed MA-matched control children ($p < .005$), children with WS did not ($p = .18$). Additionally, the difference between performance of adults and children with WS was marginally significant ($p = .054$). The significant Group × Noise Type (static vs. average of random and yoked) interaction, $F(2, 25) = 8.90$, $p < .005$, suggests that adding movement to the noise lights affected the groups differently. Figure 3 (right panel) illustrates this point. Although all three groups performed at or near ceiling in the static condition, adding movement to the noise lights had negligible effects on adults, but reduced the performance of both children with WS and MA-matched control children.

The present experiment examined whether the capacity to perceive biological motion is spared in children with WS. Biological motion stimuli are of interest because they require the perceiver to integrate the local motion of lights in different locations into a global percept of a walking person. Previous research (Bellugi, Sabo, & Vaid, 1988) using stationary stimuli suggests that children with WS are impaired at processing the spatial configuration of local elements. In addition, they appear to have deficits in perceiving coherent motion of dots embedded in random noise (Atkinson et al., 1997). Therefore, it is surprising that our results show that children with WS performed as well as or better than MA-matched children, and in many cases achieved performance comparable to that of normal adults. Even in cases in which adults were below ceiling performance, children with WS performed comparably to MA-matched control children and only marginally worse than normal adults. In contrast, on the hallmark block construction task, children with WS perform much worse than MA-matched children (Hoffman, Landau, & Pagani, 1998; Mervis et al., 1999). Most important, the excellent performance of children with WS in the present experiment shows that they possess the capacity to extract a global figure and its direction of motion from a highly complex set of motion signals. The basic mechanisms underlying the perception of biological motion appear to be intact in these children.

The results indicate a selective sparing of biological motion perception in a population with a genetic disorder resulting in impairment in the perception of some kinds of coherent motion (Atkinson et al., 1997), as well as the ability to integrate visual information across

space (Bellugi, Sabo, & Vaid, 1988; Bellugi et al., 1994; Hoffman et al., 1998; Mervis et al., 1999). Perception of biological motion may depend on a specialized system that is preserved in people with WS, and this selective sparing may be linked to their genetic profile. For example, the relative sparing of social functions, such as perception of faces and other social stimuli, could well be linked to other aspects of their cognitive profile, in particular, the relative preservation of language in WS. This possibility of selective sparing is consistent with findings from human brain imaging (Bonda, Petrides, Ostry, & Evans, 1996) and single-cell recording in nonhuman primates (Oram & Perrett, 1994), which suggest functional specialization subserving the perception of biological motion. Such selective sparing is also consistent with the claim that people with WS are particularly acute in perceiving social stimuli (Frith & Frith, 1999; Tager-Flusberg & Sullivan, 2000). To conclusively determine whether the perception of biological motion is the only form-from-motion ability that is spared in WS—or one of a few such abilities—would require further tests. Impairment in a variety of form-from-motion tasks, combined with sparing in the perception of biological motion, would constitute especially strong evidence for the claim that there is specialization within the domain of spatial cognition.

In conclusion, our experiment provides evidence that there are specialized subsystems in spatial cognition, that selective sparing of one such subsystem might be linked to a specific genetic syndrome, and that this pattern of selectivity can be observed relatively early in development.

Acknowledgments—This work was supported in part by Grants 12-FY99-670 and FY98-0194 from the March of Dimes Birth Defects Foundation, Grant 1 R55 NS37923 from the National Institute of Neurological Disorders and Stroke, and Grant SBR-9808585 from the National Science Foundation to B.L. and J.E.H. The results were originally presented at the annual conference of the Cognitive Neuroscience Society, San Francisco, April 2000. We thank the children and families who participated in the research and the National Williams Syndrome Association, which helped identify participating families. We also thank Andrea Zukowski and Nicole Kurz for their assistance in carrying out this study.

REFERENCES

Allison, T., Puce, A., & McCarthy, G. (2000). Social perception from visual cues: Role of the STS region. *Trends in Cognitive Sciences*, *4*, 267–278.

Atkinson, J., Anker, S., Braddick, O., Nokes, L., Mason, A., & Braddick, F. (2001). Visual and visuospatial development in young children with Williams syndrome. *Developmental Medicine and Child Neurology*, *43*, 330–337.

Atkinson, J., King, J., Braddick, O., Nokes, L., Anker, S., & Braddick, F. (1997). A specific deficit of dorsal stream function in Williams' syndrome. *NeuroReport*, *8*, 1919–1922.

Beery, K.E., & Buktenica, N.A. (1967). *Developmental Test of Visual-Motor Integration.* Cleveland, OH: Modern Curriculum Press.

Bellugi, U., Marks, S., Bihrle, A., & Sabo, H. (1988). Dissociation between language and cognitive functions in Williams Syndrome. In D. Bishop & K. Mogford (Eds.), *Language development in exceptional circumstances* (pp. 177–189). Hillsdale, NJ: Erlbaum.

Bellugi, U., Sabo, H., & Vaid, J. (1988). Spatial deficits in children with Williams Syndrome. In J. Stiles-Davis, M. Kritchevsky, & U. Bellugi (Eds.), *Spatial cognition: Brain bases and development* (pp. 273–298). Hillsdale, NJ: Erlbaum.

Bellugi, U., Wang, P.P., & Jernigan, T.L. (1994). Williams Syndrome: An unusual neuropsychological profile. In S.H. Broman & J. Grafman (Eds.), *Atypical cognitive deficits in development disorders: Implications for brain function* (pp. 23–56). Hillsdale, NJ: Erlbaum.

Bertenthal, B.I., & Pinto, J. (1994). Global processing of biological motions. *Psychological Science*, *5*, 221–225.

Bertenthal, B.I., Proffitt, D.R., Kramer, S.J., & Spetner, N.B. (1987). Infants' encoding of kinetic displays varying in relative coherence. *Developmental Psychology*, *23*, 171–178.

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

Bonda, E., Petrides, M., Ostry, D., & Evans, A. (1996). Specific involvement of human parietal systems and the amygdala in the perception of biological motion. *Journal of Neuroscience*, *16*, 3737–3744.

Chubb, C., & Sperling, G. (1988). Drift-balanced random stimuli: A general basis for studying non-Fourier motion perception. *Journal of the Optical Society of America A—Optics Image Science and Vision*, *5*, 1986–2007.

Cutting, J.E., Moore, C., & Morrison, R. (1988). Masking the motions of human gait. *Perception & Psychophysics*, *44*, 339–347.

Dilks, D., Landau, B., Hoffman, J.E., & Siegfried, J. (2001, April). *Selective impairment of dorsal stream functions in Williams syndrome?* Poster session presented at the annual meeting of the Cognitive Neuroscience Society, New York.

Dittrich, W.H., Troscianko, T., Lea, S., & Morgan, D. (1996). Perception of emotion from dynamic point-light displays represented in dance. *Perception*, *25*, 727–738.

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

Ewart, A.K., Morris, C.A., Atkinson, D., Jin, W., Sternes, K., Spallone, P., Stock, A.D., Leppert, M., & Keating, M.T. (1993). Hemizygosity at the elastin locus in a developmental disorder, Williams syndrome. *Nature Genetics*, *5*(1), 11–16.

Farah, M., Tanaka, J., & Drain, H.M. (1995). What causes the face inversion effect? *Journal of Experimental Psychology: Human Perception and Performance*, *21*, 628–634.

Frangiskakis, J.M., Ewart, A.K., Morris, C.A., Mervis, C.B., Bertrand, J., Robinson, B.F., Klein, B.P., Ensing, G.J., Everett, L.A., Green, E.D., Proschel, C., Gutowski, N.J., Noble, M., Atkinson, D.L., Odelberg, S.J., & Keating, M.T. (1996). LIM-kinase1 hemizygosity implicated in impaired visuospatial constructive cognition. *Cell*, *86*(1), 59–69.

Frith, C.D., & Frith, U. (1999). Interacting minds—a biological basis. *Science*, *286*, 1692–1695.

Green, D.M., & Swets, J.A. (1966). *Signal detection theory and psychophysics*. New York: Wiley.

Hoffman, J.E., & Landau, B. (2000, April). *Spared object recognition with profound spatial deficits: Evidence from children with Williams syndrome.* Poster session presented at the annual meeting of the Cognitive Neuroscience Society, San Francisco.

Hoffman, J.E., Landau, B., & Pagani, J.H. (1998, November). *Eye fixations during block construction in children with Williams syndrome.* Paper presented at the annual meeting of the Psychonomics Society, Dallas, TX.

Ishai, A., Ungerleider, L.G., Martin, A., Schouten, J.L., & Haxby, J.V. (1999). Distributed representation of objects in the human ventral visual pathway. *Proceedings of the National Academy of Sciences, USA*, *96*, 9379–9384.

Johansson, G. (1973). Visual perception of biological motion and a model for its analysis. *Perception & Psychophysics*, *14*, 201–211.

Kaufman, A.S., & Kaufman, N.L. (1990). *Kaufman Brief Intelligence Test.* Circle Pines, MN: American Guidance Service.

Lowery, M., Morris, C., Ewart, A., Brothman, L., Zhu, X., Leonard, C., Carey, J., Keating, M., & Brothman, A. (1995). Strong correlation of elastin deletions, detected by FISH, with Williams-syndrome—evaluation of 235 patients. *American Journal of Human Genetics*, *57*(1), 49–53.

Mather, G., & Murdoch, L. (1994). Gender discrimination in biological motion displays based on dynamic cues. *Proceedings of the Royal Society of London, Series B—Biological Sciences*, *258*, 273–279.

Mervis, C.B. (1999). The Williams Syndrome cognitive profile: Strength, weaknesses, and interrelations among auditory short-term memory, language, and visuospatial constructive cognition. In E. Winograd, R. Fivush, & W. Hirst (Eds.), *Ecological approaches to cognition: Essays in honor of Ulric Neisser* (pp. 193–227). Hillsdale, NJ: Erlbaum.

Mervis, C.B., Morris, C.A., Bertrand, J., & Robinson, B.F. (1999). Williams Syndrome: Findings from an integrated program of research. In H. Tager-Flusberg (Ed.), *Neurodevelopmental disorders: Developmental cognitive neuroscience* (pp. 65–110). Cambridge, MA: MIT Press.

Milner, A.D., & Goodale, M.A. (1995). *The visual brain in action.* New York: Oxford University Press.

Moscovitch, M., Winocur, G., & Behrmann, M. (1997). What is special about face recognition? Nineteen experiments on a person with visual object agnosia and dyslexia but normal face recognition. *Journal of Cognitive Neuroscience*, *9*, 555–604.

Oram, M.W., & Perrett, D.I. (1994). Responses of anterior superior temporal polysensory (STPa) neurons to "biological motion" stimuli. *Journal of Cognitive Neuroscience*, *6*, 99–116.

Pani, J.R., Mervis, C.B., & Robinson, B.F. (1999). Global spatial organization by individuals with Williams syndrome. *Psychological Science*, *10*, 453–458.

Pavlova, M., & Sokolov, A. (2000). Orientation specificity in biological motion perception. *Perception & Psychophysics*, *62*, 889–899.

Schenk, T., & Zihl, J. (1997). Visual motion perception after brain damage: II. Deficits in form-from-motion perception. *Neuropsychologia*, *35*, 1299–1310.

Tager-Flusberg, H., & Sullivan, K. (2000). A componential view of theory of mind: Evidence from Williams syndrome. *Cognition*, *76*, 59–89.

Ungerleider, L.G., & Mishkin, M. (1982). Two cortical visual systems. In D.J. Ingle, M.A. Goodale, & R.J.W. Mansfield (Eds.), *Analysis of visual behavior* (pp. 549–586). Cambridge, MA: MIT Press.

Vaina, L.M., LeMay, M., Bienfang, D.C., Choi, A.Y., & Nakayama, K. (1990). Intact "biological motion" and "structure from motion" perception in a patient with impaired motion mechanisms: A case study. *Visual Neuroscience*, *5*, 353–369.

Wang, P.P., Doherty, S., Rourke, S.B., & Bellugi, U. (1995). Unique profile of visuo-perceptual skills in a genetic syndrome. *Brain and Cognition*, *29*(1), 54–65.

(RECEIVED 2/9/01; REVISION ACCEPTED 6/11/01)