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The development of sensitivity to biological motion in noise

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Abstract. We investigated developmental changes in sensitivity to biological motion by asking 6-year-olds, 9-year-olds, and adults (twenty-four in each group) to discriminate point-light biological motion displays depicting one of a variety of human movements from scrambled versions of the same displays. When tested without noise dots, participants at all ages performed near ceiling levels and no differences in accuracy were found among the three age groups. Age differences emerged in the second task, in which we used a staircase procedure to determine threshold values of the number of noise dots that could be tolerated in producing a percentage correct value corresponding to a d' value of 1.4. Sensitivity to biological motion improved linearly with age ($p < 0.01$), with 6-year-olds performing significantly more poorly than adults. This immature performance contrasts with adult-like accuracy by 4 years of age for sensitivity to global motion (Parrish et al, 2005 *Vision Research* **45** 827 – 837). The comparison implies an immaturity at 6 years of age in the neural networks involved specifically in the processing of biological motion, networks that may include the superior temporal sulcus (STS).

1 Introduction

Adults are highly sensitive to the kinematics defining human activity. This sensitivity is most dramatically revealed when human activity is portrayed by point-light animations created by attaching small lights to the head and major joints of an actor performing different actions in low light. When only the dots are visible, one still experiences a vivid impression of human activity within 200 ms of the onset of the animation (Johansson 1973). Adults are able to use variations in the relative positioning of the point lights as different actions are completed to distinguish and identify these actions (Dittrich 1993; Johansson 1973). More subtle differences in these stimuli allow an observer to recognize, with accuracy that is above chance, the identity of a familiar person by his or her gait, and to distinguish whether a walker is male or female (Barclay et al 1978; Cutting and Kozlowski 1977; Kozlowski and Cutting 1977; Stevenage et al 1999; Troje 2002).

A small developmental literature indicates that even infants are sensitive to point-light displays (see Pinto, 2005, for a review). Infants aged 3 months can discriminate a canonical point-light walker from an inverted walker (Bertenthal et al 1984; Fox and McDaniel 1982). By 5 months of age, infants discriminate a canonical walker from a stimulus with the same motion of individual lights but a scrambling of their position and temporal phase (Bertenthal et al 1982). By 9 months of age babies discriminate displays in which the occlusion of point lights is consistent with the implicit form of a human walker from displays in which the patterns of occlusion are not consistent with those of a walker (Bertenthal et al 1985). Such findings do not necessarily imply that point-light walkers are understood by infants as depicting human motion, but they indicate that, even in the first year of life, infants, like adults, are sensitive to stimulus manipulations that affect the quality of biological motion portrayed by point-light sequences (see Bertenthal et al 1984 for a discussion).

Beyond infancy, there are few comparisons of sensitivity to biological motion of typically developing children and adults. Studies including young children have generally compared the performance of typically developing children with that of children from a special population. For example, children with autism are impaired, relative to control children matched in mental age, in discriminating displays containing biological motion from displays showing scrambled versions of the same motions (Blake et al 2003). In contrast, children with Williams syndrome are better, relative to control children matched in mental age, at judging the direction of walking of a point-light walker embedded in moving noise dots (Jordan et al 2002). Adolescents with motor impairments associated with periventricular leukomalacia are less sensitive to biological motion than a control group of the same age, although their sensitivity is not correlated with the severity of the motor impairment (Pavlova et al 2003). This latter finding is interesting given the largely overlapping neural pathways postulated to underlie the production of movements and the perception of actions (eg Parsons and Fox 1998).

Only four published studies provide evidence on the sensitivity of typically developing children to biological motion in a task also completed by adults. Pavlova et al (2001) found that accuracy in identifying point-light displays of a walking or running dog, bird, and human walker improved between 3 and 5 years of age, at which time performance was at ceiling, like that of adults. This result is consistent with the finding of Blake et al (2003) of no correlation between age and accuracy in a control group of typically developing 5- to 10-year-olds asked to discriminate displays with and without biological motion, likely because performance was near ceiling. As in the study of Pavlova et al (2001), there were no noise elements in the study by Blake et al. Differences in sensitivity to biological motion have, however, been observed between children over 5 years of age and adults when noise dots were included in the stimuli. Specifically, in a study of children with Williams syndrome, a control group of 4- to 7-year-olds was as accurate as an adult group in discriminating the direction in which a walker was moving when added noise dots were static, but less accurate than adults when noise dots moved randomly or were yoked to the movement of the walker (Jordan et al 2002). Similarly, in a discrimination task of displays containing a walker embedded in yoked noise dots and displays containing only noise dots, 14-year-olds were less accurate than adults for both upright and inverted presentations (Pavlova et al 2000). In sum, 5-year-olds are as accurate as adults in perceiving biological motion in displays without noise dots, but performance improves into adolescence when the display includes moving noise dots.

Developmental changes in sensitivity to biological motion are interesting in light of what is known about its putative neural concomitants. Perception of biological motion requires the integration of local motion information over time and space. The extrastriate area most closely associated with this integrating function in the perception of biological motion is the posterior region of the superior temporal sulcus (STS) (eg Beauchamp et al 2003; Grossman and Blake 2001; for reviews see Grossman, 2005; Puce and Perrett 2003). For example, fMRI studies indicate that upright point-light biological motion displays produce larger neural responses in STS than do identical but inverted displays (Grossman and Blake 2001), and larger responses than point-light displays of tools undergoing their characteristic patterns of motion (Beauchamp et al 2003). Importantly, fMRI studies have shown that it is specifically the coordinated semirigid motion typical of humans that elicits the strongest responses in the STS, rather than atypical rigid body movements such as rotation about a fixed axis (Beauchamp et al 2002), or complex nonbiological motion (Pelphrey et al 2003).

Although studies directly comparing sensitivity to biological motion of children in middle childhood and adults are lacking, a handful of studies have compared such children and adults on tasks that, like processing of biological motion, are dependent on extrastriate cortical structures and involve the integration of local signals across the visual field. On four of these tasks there is improvement during the school-age years. First, on a contour integration task, thought to depend on neural networks including V4 and feedback to V1 from a number of extrastriate visual areas, children improve significantly between 5 and 14 years of age, at which time they are as accurate as adults (Kovács et al 1999). Similarly, 4-year-olds can differentiate among individual faces solely on the basis of differences in the spacing of the internal features (Freire and Lee 2001), but even 14-year-olds are not quite as accurate as adults (Mondloch et al 2003b). Further, 6-year-olds can readily see that noise dots in Glass patterns have been paired to form a global concentric pattern, a skill believed to depend on neural networks in the ventral stream beyond primary visual cortex including area V4v. However, when the global dot pattern is degraded by randomizing a fraction of the dot pairs (thereby adding noise to the display), the threshold of 6-year-olds is worse than that of 9-year-olds, who do not differ from adults (Lewis et al 2004). Finally, developmental studies of sensitivity to form-from-motion, in which variations in the direction of global motion define shapes, indicate that accuracy in identifying motion-defined letters reaches adult accuracy by the age of 8 years (Giaschi and Regan 1997); when dots moving in opposite directions and with varying degrees of coherence define oriented stripes, adult level performance is reached at the age of 10 – 11 years (Gunn et al 2002). Sensitivity to form-from-motion depends on a number of structures including the kinetic-occipital region (KO), an extrastriate region that is anatomically distinct from both V5/MT and V3 (eg Grossman et al 2000; van Oostende et al 1997). Thus, in all four of these cases, 6-year-old children are not as good as adults on tasks that require processing the relationship between local features and that depend on extrastriate networks.

The above findings are consistent with the hypothesis that children aged 5 and 6 years are poorer than adults on tasks requiring the integration of local elements and hence extrastriate neural networks. However, 6-year-olds perform as well as adults on some measures of sensitivity to the direction of global motion, which requires integration of local motion signals and is dependent on extrastriate regions in the dorsal stream including the middle temporal complex (MT+) and putative V3A (eg Benton and Curran 2003; Braddick et al 2001; Maunsell and Newsome 1987). The global motion task involves discriminating the direction of motion in a random-dot kinematogram in which a small percentage of dots moves coherently in one direction. In a study of the effects of visual deprivation due to cataract on the perception of global motion, the control group of 6-year-old children had thresholds as good as those of adults (Ellemberg et al 2002). Moreover, a recent study indicates that even 4-year-olds can perform as well as adults on at least some global motion tasks (Parrish et al 2005). This finding indicates that 6-year-olds are not immature on all tasks dependent on extrastriate cortex and requiring the integration of local signals over the visual field.

In the present study, we compared the performance of typically developing 6-year-olds, 9-year-olds, and adults on two biological motion tasks. In the yes/no task, participants discriminated coherent and scrambled versions of biological motion stimuli depicting a variety of activities. These stimuli did not include noise dots. The yes/no task served as a warm-up task, and was included also as an attempt to replicate a previous finding that, by 5 years of age, children recognize biological motion displays as well as adults if noise dots are not included (Pavlova et al 2001). The second task comprised the discrimination of biological motion from scrambled biological motion displays presented in noise. Unlike previous studies, we varied the number of noise dots in the display according to a staircase procedure, to determine a threshold number of noise dots for which a participant could discriminate intact from scrambled displays at above chance rates.

Given the results of two previous studies (Jordan et al 2002; Pavlova et al 2000), we expected adults to be more accurate than children and, unlike those studies, planned to quantify age differences in sensitivity. We included 6-year-olds because children at that age are adult-like in sensitivity to direction of global motion in random-dot kinematograms (Ellemberg et al 2002; Parrish et al 2005), but immature in sensitivity to contour integration (Kovács et al 1999), spacing of features in faces (Mondloch et al 2002), the global form in Glass patterns (Lewis et al 2004), and form-from-motion (Giaschi and Regan 1997; Gunn et al 2002; Parrish et al 2005). We included 9-year-olds because children at that age are adult-like in processing the global form in Glass patterns (Lewis et al 2004), but still immature in processing of contour integration (Kovács et al 1999), the spacing of features in faces (Mondloch et al 2002), and form-from-motion (Giaschi and Regan 1997; Gunn et al 2002; but see Parrish et al 2005).

2 Method

2.1 *Participants*

Participants were twenty-four 6-year-olds (±3 months; twelve boys, twelve girls), twenty-four 9-year-olds (±3 months; fifteen boys, nine girls), and twenty-four adults (range $18-26$ years, mean $= 20.1$ years; ten men, fourteen women). All participants had no history of eye problems and met our criteria on a visual screening exam. Specifically, 9-year-olds and adults had a linear letter acuity on the Lighthouse Distance Visual Acuity Test chart of at least 20/20 in each eye without optical correction, worse acuity with a $+3$ D add (to rule out hypermetropia of greater than 3 D), fusion at near on the Worth four-dot test, and stereoacuity of at least 40 s of arc on the Titmus test. The criteria for 6-year-olds were the same except acuity was tested with the Good-Lite Crowding cards.

2.2 *Apparatus and stimuli*

Visual displays were generated with MatLab© and the Psychophysics Toolbox (Brainard 1997), and were shown on a ViewSonic Professional Series PS790 19 inch monitor with a refresh rate of 75 Hz. The experiment was run under the control of a Macintosh G4 computer.

The techniques used to generate the biological motion sequences have been described elsewhere (Grossman and Blake 1999). In brief, video recordings were made of an adult engaged in a variety of familiar activities, including running, kicking, climbing, throwing, and jumping. These recordings were then transcribed to the computer, and markers were placed on the joints in each frame of the movie sequence. Those individual frames were then converted to matrices that could be animated and manipulated in MatLab©. Figure 1 shows two frames, not successive in the animation, from a normal biological sequence and two nonsuccessive frames from a phase-scrambled sequence created from the same animation—in this case the actor is shown in sagittal view, walking from left to right. The phase-scrambled animations consisted of the same number of individual dots undergoing the same local motions as in the normal animations they were derived from, but with their temporal phases scrambled. The x, y starting position of dots in the scrambled animations were located within a region approximating that of the corresponding biological motion stimulus. This form of scrambling perturbs the hierarchical, pendular motions characteristic of biological motion while preserving local motion trajectories, and the resulting animations look distinctly different from their biological counterparts.

A total of 48 animations, 24 depicting normal biological motion and 24 depicting phase-scrambled sequences, were used in the yes/no and staircase tasks described below. Specifically, half of the biological motion sequences and their phase-scrambled counterparts were used in the yes/no task, and a new set comprising all remaining animations

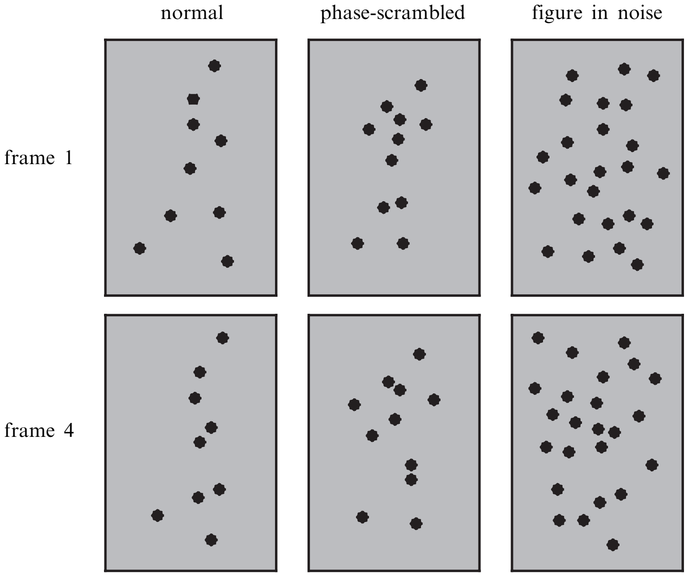

Figure 1. Sample (non-consecutive) frames from a biological motion stimulus depicting walking, a scrambled version of the walker, and the same frame embedded in noise.

was used for the staircase task. In all animations, dots appeared black against a light-gray background (60 cd m^{-2}). Individual dots subtended approximately 10 min of arc at the viewing distance of 60 cm, and the biological motion figures subtended approximately 6 deg × 3 deg of visual angle. The duration of each animation was 1 s and average speed within a sequence was about 4 deg s^{-1}. On each trial, the spatial location of the biological motion or scrambled stimulus was displaced in a random direction and variable distance from the center of the 19.2 deg × 14.4 deg display window; for he displays masked with noise dots, this spatial jittering prevented participants from making their judgments on the basis of just a few tell-tale dots located at a given location in the display window.

3 Procedure

The procedures were explained, and written consent was obtained from the parents of the children and from the adults who participated. All participants provided verbal assent. The experimental protocol was approved by the McMaster University Research Ethics Board.

Participants were tested individually in a room illuminated only by the computer monitor, and were adapted to the lighting conditions prior to the test. Parents of children sat in the testing room out of their child's sight and were asked to remain silent during testing. All testing was binocular.

3.1 *Yes/no task*

The experimenter explained to the participants that they would see brief patterns of dots moving on the screen, and that some of the patterns would look like a person doing something, for example walking or throwing a ball, while others would not look like a person. Participants were instructed to say "yes" if they saw a person and "no" if the moving dots did not look like a person. The task began with two demonstration trials followed by criterion trials.

3.1.1 *Demonstration trials.* Two stimuli were presented, first a biological motion stimulus and then a scrambled stimulus, selected randomly from the set of biological motion and scrambled stimuli, respectively. Immediately following presentation of the biological motion stimulus the experimenter explained the depicted action and asked the participant if it looked to him or her like a person performing the stated action. After presentation of the scrambled stimulus, the experimenter stated that a person was not present and asked the participant if she/he agreed.

3.1.2 *Criterion trials.* Criterion trials were included to verify that the participant understood the task. Single animations were shown, in random order, and the participant responded "yes" or "no". If an error occurred, the experimenter gave feedback and presented two additional demonstration displays. Using this procedure, participants had three opportunities to reach a criterion of four consecutive correct responses. All participants passed criterion within two tries.

3.1.3 *Test.* The participant was shown 25 biological motion and 25 scrambled stimuli, sampled randomly with replacement, from the biological motion and scrambled stimulus pools. The participant said "yes" or "no" after each display and the experimenter entered responses on the computer keyboard. The experimenter sat to the side of the monitor and controlled presentation of displays, but could not see the displays themselves. The experimenter also ensured that the participant was looking at the screen prior to initiating each trial. Encouragement was provided periodically to the children, although it was not contingent on the accuracy of responses.

3.2 *Staircase task*

The experimenter explained that a second task was to be completed, similar to the first. Again, the participant's job was to say which displays showed a person and which did not by answering "yes" or "no", except that now there would be extra dots such that it would be like "looking for a person in the snow".

3.2.1 *Demonstration and criterion trials.* Demonstration and criterion trials were carried out exactly as for the yes/no task, except that displays included six noise dots in addition to the dots comprising the biological motion and scrambled stimuli, and the experimenter drew attention to the fact there were extra dots compared to the previous task. All participants passed criterion within two tries.

3.2.2 *Test.* The experimenter explained that there would be a long series of displays and that the participant's job was always to respond "yes" or "no", indicating whether there was a person or not. The experimenter also explained that, at the start, the displays would have only a small number of extra dots but later there would be many more extra dots so that it would get more difficult to decide whether there was a person present in each display. Each participant completed two staircases with a short break after completion of the first. Within a staircase, biological motion or scrambled stimuli were displayed randomly, with equal probability. The staircase used a 2-up/1-down rule that estimates the noise level producing a percentage correct value corresponding to a d' value of 1.4 (see Grossman et al 2004). The first display did not include noise dots; 6 dots were added to each ensuing display until the first error was made, at which point the number of noise dots was reduced by 6. Thereafter, two consecutive correct responses were required for the addition of 6 noise dots in the next trial, and a single incorrect response led to 6 fewer noise dots in the next trial. After the first 12 reversals in the staircase, the number of noise dots added or removed was lowered to 3, in order to obtain a more precise estimate of the participant's threshold. The staircase ended after 36 reversals, with threshold defined as the mean number of noise dots in all trials within the final 10 reversals. As in the yes/no task, the experimenter entered the participant's responses and provided periodic encouragement to the children but feedback was not tied to accuracy.

4 Results

4.1 *Yes/no task*

Figure 2a shows results for the yes/no task for the three age groups. As evident in the figure, all groups performed near ceiling. A one-way between-subjects ANOVA of the number of correct responses confirmed that there was no difference between the three age groups for this task ($F_{2,69} = 0.97$, ns). Several individuals in each age group responded correctly on all 50 trials. The lowest number of correct responses for 6-year-olds, 9-year-olds, and adults was 45, 43, and 42, respectively.

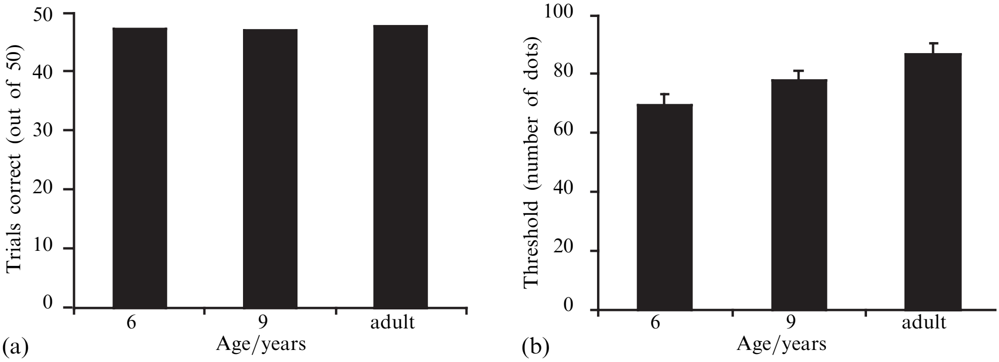

Figure 2. (a) Mean correct trials, out of 50, for all ages in the yes/no task; (b) threshold values obtained by each age group for the staircase task, in terms of the number of dots tolerated (+1 SE). Values indicated represent the mean of the two completed staircases.

4.2 *Staircase task*

Figure 2b shows performance on the staircase task for the three age groups. Preliminary analyses revealed no significant gender differences at any of the ages tested, so results were collapsed across gender. Preliminary analyses also indicated no significant difference between the means for the first and second thresholds at any age (ie there was no systematic improvement or drop in performance between the first and second staircases for any of the groups). Therefore, analyses were based on the mean of the two staircases for each individual.⁽¹⁾

A univariate general linear model revealed a significant effect of age on threshold ($F_{2,69} = 6.00$, $p < 0.01$). Polynomial contrasts were used to test the significance of the linear trend. As shown in figure 2b, thresholds increased linearly across age groups ($p < 0.01$; means = 69.26, 77.76, and 86.86 for 6-year-olds, 9-year-olds, and adults, respectively). A posteriori Dunnett *t*-tests comparing the two children's groups to the adult group showed a significant difference between the 6-year-olds and adults ($p < 0.01$), but no significant difference between 9-year-olds and adults ($p > 0.1$, ns).

5 Discussion

There was no difference among the three age groups in performance on the yes/no task, with very few errors made overall at any age. Differences did emerge, however, in the threshold task. Specifically, 6-year-olds tolerated a significantly smaller number of noise dots than did adults. The overall pattern was a linear increase in performance among the three groups, although performance of 9-year-olds was not significantly different from that of the adult group.

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(1) For the average threshold values, deviant scores were replaced by using the procedure outlined by Kirk (1989). Each average threshold was converted to a Z-score by using the group mean and standard deviation for that age group. Z-scores greater than +2.5 or less than −2.5 were replaced by the group mean with the deviant scores included. A total of two data points were replaced in this way: one in the 9-year-old group, and one in the adult group. Subsequent analyses were completed by using the replacement scores.

Findings in the yes/no task are consistent with those of two previous developmental studies of the perception of biological motion in the absence of noise (Blake et al 2003; Pavlova et al 2001). In both studies, children as young as 5 years of age performed as well as adults and at ceiling levels. Together with results of these two studies, our results in the yes/no task highlight the remarkable ability of even very young children to interpret point-light biological motion stimuli as depicting the human form.

Six-year-olds, however, are not adult-like when the biological motion task is made more difficult via the addition of noise: the threshold number of noise dots was 69 and 87 for 6-year-olds and adults, respectively. That pattern is consistent with two previous studies (Jordan et al 2002; Pavlova et al 2000). Specifically, children 4 to 7 years old in Jordan et al's study were less accurate than adults in discriminating the direction of walking of a point-light walker in noise, while 14-year-olds in the study by Pavlova et al were less accurate than adults in a walker-detection task in which displays were composed of either a point-light walker in noise or noise alone. Reduced motivation or increased fatigue are unlikely to account for poorer performance of the 6-year-olds because the mean number of dots that they tolerated was (non-significantly) higher in the second block of trials than in the first: sixteen of twenty-four 6-year-olds scored better in the second run than in the first, whereas only eleven 9-year-olds and twelve adults did so.

Developmental changes in attentional control may contribute to the age difference in threshold because it would be more likely to affect sensitivity to biological motion signals embedded in noise than those without noise. Indeed, there is evidence that adults' thresholds for perceiving biological motion in noise are correlated with other measures of attentional control (Ian Thornton, personal communication) and that children are poorer than adults at ignoring irrelevant information (eg Goldberg et al 2001).

However, two lines of evidence suggest that age changes in attention cannot explain our findings, and hence that 6-year-olds are not as sensitive as adults to biological motion per se. The first line of evidence comes from the fact that 6-year-olds perform as well as adults on two other tasks requiring them to detect a signal in noise. Both 6-year-olds and adults have equivalent thresholds in a task measuring sensitivity to the direction of global motion, in which a subset of elements in a random-dot kinematogram moves in a uniform direction (Ellemberg et al 2002; Parrish et al 2005). Specifically, Ellemberg et al (2002) found that 6-year-olds are as accurate as adults in detecting the direction of motion at the adults' threshold, that is when the display is composed of 92% noise dots and only 8% signal dots. Similarly, Parrish et al (2005) found that even children aged 3 to 4 years did not differ significantly from adults in detecting the direction of global motion accurately in a procedure using up to 84% noise dots, the highest value presented. Further, 6-year-olds are as accurate as adults on a form coherence task in which short line segments, tangentially arranged to form concentric circles, have to be identified in a display embedded in a field of noise (ie randomly oriented line segments—Gunn et al 2002). Children aged 6 years need a 20% signal to perform this task, a value not significantly different from the 16% signal required by adults (see Parrish et al 2005 for evidence of adult-like accuracy by the age of 4 years on a similar task). The second line of evidence comes from the fact that improvements with age in ignoring irrelevant information in a visual display continue past the age of 10 years (Goldberg et al 2001), yet 9-year-olds' thresholds did not differ significantly from those in adults in the present study. Thus, it seems likely that adults are more sensitive to biological motion than are 6-year-olds, rather than just being better able to deploy attention to ignore distracting noise dots.

Children aged 9 years tolerated as many noise dots as adults in the staircase task. At first glance this finding diverges from that of Pavlova et al (2000). As mentioned above, in that study 14-year-olds were less accurate than adults at detecting a walker in noise—specifically, at discriminating displays comprising an 11-dot walker and 66 noise dots from those consisting only of 77 noise dots. However, 14-year-olds, like adults, performed at above chance rates regardless of whether displays were upright or inverted, and, also like adults, were more accurate in upright trials. Our results are compatible with those of Pavlova et al to the extent that, in the present study, we obtained a significant linear trend in the threshold measure, with sensitivity increasing with age (figure 2b). Thus, while sensitivity to biological motion in the present task is immature at 6 years of age, there is no significant difference in thresholds between 9-year-olds and adults. However, this finding does not preclude the possibility of small gains in processing of biological motion past 9 years of age. This pattern of results suggests an immaturity in parts of the neural network involved in the processing of biological motion at 6 years of age, with these substrates developing between the ages of 6 and 9 years, and perhaps into adolescence.

A comparison of our findings with those of two related abilities, processing of global motion and of form-from-motion, allows speculation about the relative rate of development of different parts of the extrastriate pathway. The three abilities are related in that all require the integration of local motion cues (ie from the movement of individual elements) that do not individually provide enough information for correct perception. Further, like biological motion, the processing of both global motion and form-from-motion is carried out beyond V1, in extrastriate cortex. Processing of global motion is associated with the dorsal visual stream, primarily area V5/MT and putative V3A (eg Benton and Curran 2003; Braddick et al 2001). As assessed by sensitivity to random-dot kinematograms, sensitivity to global motion reaches adult levels by the age of 4 years (Parrish et al 2005). However, even in 5-year-olds, the degree of immaturity in sensitivity to global motion varies as a function of stimulus speed, displacement, and whether the direction of motion is specified by first-order or second-order cues (Ellemberg et al 2004).

Development proceeds more slowly if variations in global motion are used to define different shapes (form-from-motion). Adult accuracy on a task requiring identification of letters or shapes defined by dots moving coherently in opposite directions is reached only at the age of 7 – 8 years (Giaschi and Regan 1997; Parrish et al 2005). When the form (oriented stripes) is defined by dots moving in opposite directions overall but with varying levels of coherence, children reach adult levels of accuracy only at the age of 10 – 11 years (Gunn et al 2002). As indicated in the introduction, neuroimaging studies have implicated a broad network of structures in the dorsal and ventral streams in the processing of form-from-motion, including the kinetic-occipital region (KO) (eg Grossman et al 2000; van Oostende et al 1997).

Combined with our results, these studies indicate that the processing of global motion matures prior to the processing of biological motion and of form-from-motion. The relative rates of development of sensitivity to biological motion and form-from-motion, and thereby of the neural structures critical to these abilities, is less clear. Regardless, the overall pattern of results does suggest that regions in the STS that are associated with processing of biological motion mature later than areas V5/MT and V3A, associated with processing of global motion. A comparatively slow rate of development of the STS is consistent with the finding that children's ability to match direction of eye gaze, another skill in which the STS is implicated, does not reach adult levels until 10 years of age (Mondloch et al 2003a). It is also consistent with the finding that it is only by about 10 years of age that children make consistent use of paralinguistic cues such as prosody when evaluating speaker affect, with an over reliance on lexical content prior to this age (Friend 2000; Friend and Becker 2000). As with processing of biological motion and eye gaze, fMRI studies have indicated that the STS may be involved in processing of paralinguistic aspects of language (Belin et al 2002).

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