PAPER

Long trajectory for the development of sensitivity to global and biological motion

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Abstract

We used a staircase procedure to test sensitivity to (1) global motion in random-dot kinematograms moving at 4° and 18° s^{-1} and (2) biological motion. Thresholds were defined as (1) the minimum percentage of signal dots (i.e. the maximum percentage of noise dots) necessary for accurate discrimination of upward versus downward motion or (2) the maximum percentage of noise dots tolerated for accurate discrimination of biological from non-biological motion. Subjects were adults and children aged 6–8, 9–11, and 12–14 years (n = 20 per group). Contrary to earlier research, results revealed a similar, long developmental trajectory for sensitivity to global motion at both slower and faster speeds and for biological motion. Thresholds for all three tasks improved monotonically between 6 and 14 years of age, at which point they were adult-like. The results suggest that the extrastriate mechanisms that integrate local motion cues over time and space take many years to mature.

Introduction

Processing motion and its direction provides information for interpreting visual scenes. Psychophysical and physiological studies have distinguished between local motion processing – sensitivity to the direction of motion in a small region of the image – and global motion processing – sensitivity to the overall direction of motion in extended regions that often correspond to surfaces and objects (Braddick, Atkinson & Wattam-Bell, 2003; Braddick & Qian, 2000). Global motion processing involves integration of disparate local motion signals so that, for example, an observer gets a sense of the global direction of a flock of birds taking to the air despite the wide range of local motions created by the wings flapping vertically.

Although motion perception and its underlying mechanisms have been studied extensively in adults, only a handful of studies has assessed the development of sensitivity to motion and the results have been inconsistent (e.g. Ellemberg, Lewis, Maurer, Brar & Brent, 2002; Parrish, Giaschi, Boden & Dougherty, 2005). This paper traces the development of the ability to integrate spatially separate local motion signals into a global flow of motion. This ability was examined both for global motion and for biological motion, a special case formed by a moving animate organism. Sensitivity to global motion is often tested with a random dot display in which some fraction of the dots are 'signal' dots that

share a common 'coherent' motion, while the remaining 'noise' dots move in random directions (e.g. Newsome & Paré, 1988). Sensitivity is typically measured as a coherence threshold, defined as the minimum percentage of signal dots required to accurately determine the overall direction of motion (i.e. the inverse of the maximum percentage of noise dots tolerated). Biological motion involves point-light animations created by attaching lights to the head and major joints of a human body performing different actions. Thresholds are typically defined as the maximum number of noise dots tolerated for accurate discrimination (e.g. Grossman & Blake, 1999).

The perception of both global motion and biological motion involves integration of local motion signals into a global pattern of motion over space and time by neural networks in the extrastriate cortex, unlike the processing of local motion, which depends on neurons with smaller directional receptive fields in area V1 (Movshon, Adelson, Gizzi & Newsome, 1985; Smith, Snowden & Milne, 1994; Williams & Sekuler, 1984; see Movshon, 1990, for a review). However, global and biological motions activate different areas in the extrastriate visual cortex. Global motion activates a network of areas in the dorsal stream involving primarily the MT/MST complex located on the tempro-parieto-occipital junction. In contrast, biological motion, the perception of which also depends on the spatial organization of the relevant motion tokens (e.g. Grossman & Blake, 1999), activates in addition a

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network of areas in the extrastriate cortex involving primarily a region on the ventral bank of the occipital extent of the superior-temporal sulcus (STS; Grossman, Donnelly, Price, Pickers, Morgan, Neighbor & Blake, 2000), an area that receives input from both the dorsal and ventral streams (e.g. Schenk, Mai, Ditterich & Zihl, 2000).

Consistent with these differences in the activated brain areas, previous research suggests that there may be different developmental trajectories for the processing of global and biological motion. Although sensitivity to the direction of global motion emerges sometime between 6 and 10 weeks of age (Wattam-Bell, 1996), coherence thresholds at 11 weeks (Wattam-Bell, 1994) and 24 weeks (Banton, Bertenthal & Seaks, 1999) are much higher than those of adults. Children aged 3 to 6 years, however, have been shown to perform as well as adults on some measures of sensitivity to the direction of global motion (e.g. Benton & Curran 2003; Braddick, O'Brien, Wattam-Bell, Atkinson & Turner, 2001; Ellemberg *et al.*, 2002; Maunsell & Newsome 1987; Parrish *et al.*, 2005). For example, in a study of the effects of visual deprivation caused by cataract on the perception of global motion, the control group of visually normal 6-year-old children exhibited adult-like coherence thresholds (Ellemberg *et al.*, 2002). A more recent study of visually normal children indicated that even 4-year-olds perform as well as adults on at least some global motion tasks (Parrish *et al.*, 2005).

However, a direct comparison across studies of the development of global motion is difficult, as different studies have examined subjects at different ages, with different densities of dots moving at different speeds. For example, while Ellemberg *et al.* (2002) used low density dots (0.75 dots/deg^2) moving at a relatively fast speed of $18°\,s^{-1}$, Parrish *et al.* (2005) used high density dots (32 dots/deg^2) moving at $1.2°\,s^{-1}$, a slow speed that does not fall within the optimal speed range for neurons in the MT/MST complex (Britten, Shadlen, Newsome & Movshon, 1993). Furthermore, in some developmental studies, the lifetime of signal dots was unclear (e.g. Ellemberg *et al.*, 2002). Sensitivity to global motion could have been overestimated in these studies because it could have been based on processing the trajectory of only an individual dot rather than on the global integration of the trajectories of multiple dots.

Biological motion appears to have a different developmental trajectory from global motion. Even newborn babies show a preference for upright over inverted biological motion displays (Simion, Regolin & Bulf, 2008; see Bertenthal, Proffit & Cutting, 1984 and Fox & McDaniel, 1982, for evidence from older infants), suggesting that infants, like adults, are sensitive to parameters that affect the perception of biological motion (see Bertenthal *et al.*, 1984, for a discussion). Developmental studies beyond infancy, however, show that while 5-year-olds are as sensitive as adults to biological motion in displays without noise dots (Blake, Turner, Smoski,

Pozdol & Stone, 2003; Pavlova, Krageloh-Mann, Sokolov & Birbaumer, 2001), this sensitivity improves well into middle childhood or even into adolescence when the display includes moving noise dots (Freire, Lewis, Maurer & Blake, 2006; Jordan, Reiss, Hoffman & Landau, 2002; Pavlova, Krageloh-Mann, Sokolov & Birbaumer, 2000). Thus although the perception of both global and biological motion involves extrastriate cortex, and both types of motion require the integration of spatially separate local motion signals over the visual field, the current developmental literature suggests that the perception of global motion is faster to mature than biological motion. However, no study to date has compared the development of these two types of motion in the same participants with dots moving at the same speed. That was the purpose of the current study. In addition, we constructed the tasks so that they could not be performed accurately based on local motion cues: the lifetime of each dot was limited in the global motion task to assure that accurate performance could be achieved only by integrating local motions into a global coherent motion (e.g. Bex & Dakin, 2003), and the biological motion displays were contrasted to scrambled displays in which the local motions followed the same trajectories but with altered phase (e.g. Grossman & Blake, 1999).

We tested sensitivity to global motion both at a slower speed ($4°\,s^{-1}$) that matched the mean speed in the biological motion task and at a faster speed ($18°\,s^{-1}$) that was used in a previous study by our group (Ellemberg *et al.*, 2002). Earlier studies have found evidence for two independent motion channels for processing these speeds in adults (e.g. Heinrich, van der Smagt, Bach & Hoffmann, 2004; van de Grind, van Hof, van der Smagt & Verstraten, 2001). In children, different developmental patterns have been found for slower and faster speeds (Ahmed, Lewis, Ellemberg & Maurer, 2005); however, these differences were obtained in tasks where the slower motion was below the $2°\,s^{-1}$ cut-off for optimal responding of MT/MST neurons (Britten *et al.*, 1993). Here we aimed to look at developmental trends for global motion by contrasting two speeds both within the optimal range for MT/MST neurons, that is, above $2°\,s^{-1}$.

General method

Participants

Four age groups, 20 in each, participated in the experiment: 6- to 8-year-olds (mean age = 7.10; range = 6.0–8.9 years; nine females), 9- to 11-year-olds (mean age = 10.00; range = 9.0–11.9 years; 10 females), 12- to 14-year-olds (mean age = 12.74; range = 12.0–14.9 years; nine females), and adults (mean age = 20.02; range = 18.0–26.2 years, 11 females). All met our criteria on a visual screening examination. Specifically, participants had a linear letter acuity (Lighthouse Visual Acuity Chart) of at least 20/20 in each eye with a maximum of −2

diopters of optical correction (to rule out myopia greater than 2 diopters, which would reduce vision at our testing distance of 50 cm), worse acuity with a +3 diopter add (to rule out hypermetropia greater than 3 diopters), fusion at near on the Worth four dot test, and stereo acuity of at least 40 arcsec on the Titmus test. The 6-year-olds met the same criteria except that their acuity was tested with the Cambridge Crowding cards (catalogue # 4116022). An additional five children (three 6- to 8-year-olds, two 12- to 14-year-olds) and three adults were excluded from the final sample for not passing visual screening.

Procedure

The experimental protocol was approved by the Research Ethics Board, McMaster University. The procedures were explained and informed consent was obtained from the adults and from the parents of the children. In addition, informed assent was obtained from the children age 7 and older.

Each participant was tested with three tasks on the same day: global motion with the dots moving at $4° s^{-1}$, global motion with the dots moving at $18° s^{-1}$, and biological motion. Half the participants in each group were tested first with the global motion tasks and half were tested first with the biological motion task. For the global motion tasks, half of the participants were tested first with dots moving at $4° s^{-1}$ and half were tested first with dots moving at $18° s^{-1}$. In order to provide norms for children with monocular eye problems, each participant was tested monocularly from a viewing distance of 50 cm. Half of the participants in each group were tested with the left eye, while the remaining half were tested with the right eye. The eye not being tested was patched with 3M Micropore[TM] tape.

Global motion

The perception of global motion was examined using the well-established random-dot kinematogram displays (Newsome & Paré, 1988). A randomly chosen subset of dots (signal) was constrained to move in the same direction at a specified speed for a number of frames (Figure 1). The other (noise) dots in the display moved at the same speed but in random directions, covering the entire 360° range. Signal strength was manipulated by varying the proportion of signal dots. Thresholds were defined as the lowest proportion of signal dots that must move coherently for the observer to correctly identify the direction of coherent motion 82% of the time, that is, the inverse of the maximum number of noise dots tolerated for accurate discrimination. A high motion coherence threshold is indicative of poor integration of the dots into a global direction of motion.

To assure that the overall direction of motion could not be determined by local motion detectors, the dots had a limited lifetime of 200 msec (15 frames) or
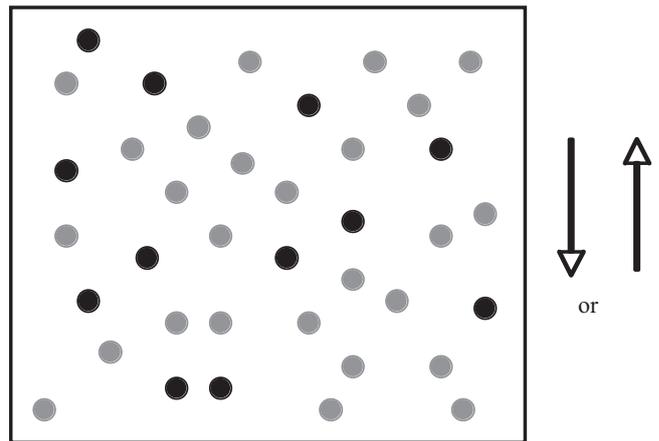

Figure 1 *Static illustration of a global motion display with 30% coherence. The illustration shows signal dots (those moving up or down) in black and noise dots (those moving in random directions) in gray. In the actual displays, all dots were black. Thresholds were defined as the minimum percentage of coherently moving signal dots necessary for accurate identification of upwards versus downwards motion.*

400 msec (30 frames) for the faster and slower speeds, respectively. When expired, each dot reappeared at a random position within the display area for a subsequent 200- or 400-ms lifetime. The phase of each dot's lifetime cycles was shifted randomly to prevent all dots from being reborn at the same time. Signal dots moved coherently in a common direction across lifetimes, giving the impression of a global motion, while the noise dots had a random initial direction of displacements every subsequent lifetime. The direction of the global pattern could thus be determined only by integrating the local signals over a larger summation field and not by following a single dot (e.g. Bex & Dakin, 2003).

Apparatus and stimuli

Stimuli were generated on an Apple Macintosh LC475 computer and presented on a monochrome monitor, 29° high by 37° wide when viewed from 50 cm, with a refresh rate of 75 Hz. The stimuli consisted of limited lifetime RDKs. Each frame contained 300 dots, giving a density of 0.75 dots/deg^2. The black dots (each 30×30 arcmin) were presented against a square gray background subtending $17.5° \times 17.5°$. Each dot had a mean luminance of 14 cd/m² while the background had a mean luminance of 116 cd/m². The Michelson contrast between the dots and their background was 78%.

Procedure

Participants were instructed to fixate a cross at the center of the screen, which disappeared during the presentation of each RDK, and were asked to judge whether the global motion of the dots was upward or downward. Specifically, both adults and children were told:

'There will be dots moving either up or down on the screen. At first, all the dots will be moving together but then some of them will start moving in many different directions. Your job is to tell me whether the dots that are moving together are going up or down the screen.'

Subjects responded verbally and/or by pointing. The experimenter entered the responses into the computer by pressing a key on the keyboard. No feedback was given during the test but children were praised periodically and were reminded to watch carefully. The experimenter, seated so that she could not see the display, watched the participant's viewing eye continuously and pressed a key to initiate the next trial only when the participant was fixating the center of the screen.

To familiarize them with the displays, the participants were shown four demonstration trials at 100% coherence at the first speed they were to be tested on, two with each type of motion (upward and downward). Then, to ensure that the subjects understood the task, criterion trials were presented. To pass criterion, subjects had to achieve two correct judgments at 100% coherence and two correct judgments at 50% coherence on four consecutive trials. The subjects were given three chances to achieve criterion, and all met this criterion, usually in the first block. After passing the criterion, subjects completed two staircases at the first speed and then two additional staircases at the second speed.

Coherence thresholds were measured for dots that moved at speeds of $4°$ and $18°\ s^{-1}$. The duration of each trial was 2 seconds. On any given trial, a percentage of the dots moved either upwards or downwards, each for a limited lifetime (see above), while the remaining dots moved in random directions.

The percentage of signal dots was varied over trials using the VPIXX VPEST adaptive staircase that is similar to Harvey's (1986) ML-TEST. Thresholds were defined as the minimum percentage of dots that had to be moving in the same direction for the subject to detect the overall direction of motion with 82% accuracy. The staircase terminated when the 95% confidence interval of the estimated threshold was within ±0.1 log units.

Biological motion

As in our previous study of the development of biological motion (Freire et al., 2006), we measured children's and adults' thresholds for detecting a point-light human figure in 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 and the task served as a warm-up. The second biological motion task used a two-interval forced-choice procedure to test the discrimination of biological motion from scrambled biological motion displays, with both presented in noise. Because the motion of the noise dots and the local motion of the target figure were identical, the human figure could not be detected from local motion cues and required integration of the trajectories across space and time, that is, a global processing mechanism. The number of noise dots was increased systematically over trials. Thresholds were defined as the maximum number of noise dots that could be tolerated for accurate identification of the interval containing the figure 71% of the time.

Apparatus and stimuli

Visual displays were generated with MatLab and the Psychophysics Toolbox (Brainard, 1997), and were shown on the same computer and monitor as the global motion task.

The biological motion stimuli were identical to those described in Freire et al. (2006). 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 2 shows a frame from a normal biological sequence and a frame from a phase-scrambled sequence created from the same animations, in this case of the actor jumping. The phase-scrambled animations consisted of the same number of individual dots undergoing the same local motions as in the normal animations from which they were derived, but with their temporal phases scrambled. The x, y starting positions 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.

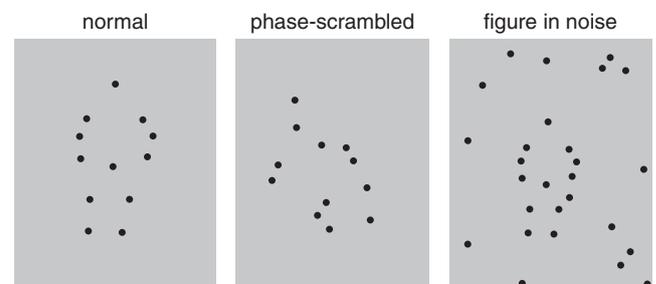A total of 48 animations, 24 depicting normal biological motion and 24 depicting phase-scrambled

Figure 2 *Static illustration of biological motion displays depicting jumping (left panel), scrambled displays of the actor (middle panel) and the same biological motion embedded in noise (right panel). Adapted from Freire et al. (2006) with permission.*

sequences, were used in the yes/no and staircase tasks. Specifically, before running each subject, half of the biological motion sequences and their phase-scrambled counterparts were assigned randomly to the yes/no task, and a new set comprising all remaining animations was assigned to the staircase task. In all animations, black dots appeared against a light-gray background (60 cd/m^2). Individual dots subtended approximately 10 arcmin at the viewing distance of 50 cm, and the biological motion figures subtended approximately 6° × 3° of visual angle. The duration of each animation was 1 sec and average speed within a sequence was about 4° s^{-1}. On each trial, the spatial location of the biological motion or scrambled stimulus was displaced in a random and variable distance from the center of the 19.2° × 14.4° display window. Dot step-size was optimized to yield the most natural appearing biological motion sequences.

In the yes/no task, participants were shown 25 biological motion and 25 scrambled stimuli, sampled randomly with replacement, from the biological and scrambled stimulus pools for this phase. Following each 1-sec animation, participants judged whether or not they saw a person. Specifically, the participants were told:

> 'What you are going to see on the screen are a bunch of moving dots. Sometimes the dots will look like a person doing something, for example maybe kicking a ball or jumping. Other times they will look only like a bunch of moving dots and not like a person. Your job is to say "yes" if you see a person and "no" if you do not.'

For the two-interval staircase task, a trial consisted of two point-light animations, one a biological motion stimulus and the other a scrambled version of the same stimulus, sampled randomly from the stimulus pools for this phase. Participants judged whether the person appeared in the first or second 1-sec interval. Specifically they were told:

> 'I'll show you some moving dots and you tell me when you see a person. But now it's going to get harder because the person will be hiding in a bunch of extra moving dots, so it will be like a person hiding in the snow. Also, now you'll see two movies each time and it will always be the case that there is a person in one of the two movies but not in the other. So, your job is to tell me if you see a person hiding in the dots in the first movie, or if the person is hiding in the second movie. If you see a person in the first movie, say "1" and if you see a person in the second movie, say "2".'

To familiarize them with the displays, the participants were first shown three demonstration trials before each

task (without noise before the yes/no, and with six noise dots before the staircase task). Then, to ensure that the subjects understood the task, criterion trials were presented (each with no noise for the yes/no task and with six noise dots for the staircase task). To pass criterion, subjects had to achieve correct judgments on four consecutive trials. The subjects were given three chances to achieve criterion, and all met this criterion, usually in the first block.

The first two trials in the test phase of the staircase task included no noise dots. Six noise dots were added to each display after two consecutive correct responses, and six were subtracted after one incorrect response. Subsequent to the first 12 reversals, the number of noise dots added or removed was lowered to three, in order to obtain a more precise estimate of the participant's threshold. The staircase terminated after eight more reversals, resulting in a total of 20 reversals. Threshold was defined as the mean number of noise dots in the final six reversals and represents an estimate of the noise level producing a percent correct value of 71%. Each participant completed two staircases with a short break after completion of the first and the results are based on the mean. In both the yes/no and staircase tasks, the experimenter provided periodic encouragement but feedback was not tied to accuracy. As in the global motion task, the experimenter was seated so that she could not see the display during the test phase, watched the participant's viewing eye continuously, and pressed a key to initiate the next trial only when the participant was fixating the center of the screen.

Results

Preliminary analyses revealed no significant gender differences or order effects at any of the ages tested. Therefore, analyses for each of the tasks were based on the mean of the two staircases for each individual, collapsed across gender and order.

Global motion

The coherence thresholds for sensitivity to the direction of global motion for the two speeds are plotted as a function of age in Figure 3. A mixed design ANOVA with speed as a within-subjects and age as a between-subjects factor revealed a significant effect of speed, $F(1, 76) = 11.84$, $p < .001$, $\eta_p^2 = .14$, with higher sensitivity to global motion for the faster moving dots (means: 39.5% and 30.5% for 4° and 18° s^{-1}, respectively). Sensitivity also varied significantly with age, $F(3, 76) = 12.74$, $p < .0001$, $\eta_p^2 = .33$. Curve fitting indicated that sensitivity increases exponentially with age, for both fast and slow speeds, $y = 130.8 * \exp(-0.11x)$, and post-hoc Dunnett tests revealed that adults had lower thresholds
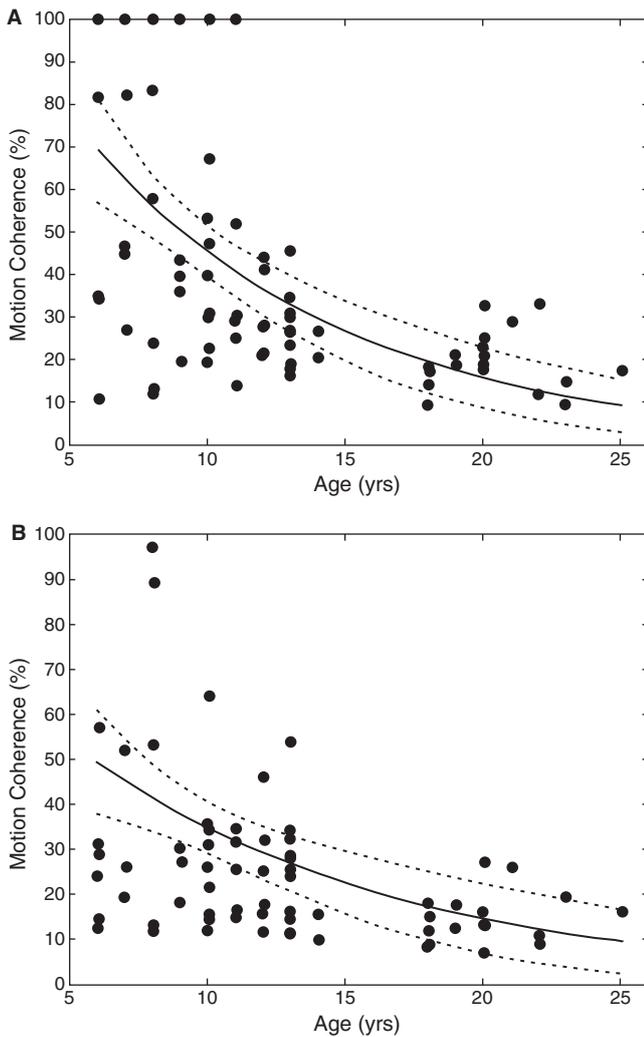
Figure 3 *Motion coherence thresholds (in percentage) as a function of age for 4° (A) and 18° s⁻¹ (B). Each symbol represents the threshold for one subject at the age indicated. The solid line in each figure represents the best-fitting function and the dashed lines show the 95% confidence limits on curve fits.*

Figure 4 *d′ for the yes/no task (A) and thresholds (number of noise dots tolerated) for the biological motion tasks (B), as a function of age. Each symbol represents the threshold for one subject at the age indicated. The solid line in each figure represents the best-fitting function and the dashed lines show the 95% confidence limits on curve fits.*

than both the 6- to 8-year-olds and the 9- to 11-year-olds ($ps < .0001$) but not the 12- to 14-year-olds ($p > .10$). The interaction between age and speed did not reach significance, suggesting a similar developmental trajectory for the two speeds, $F(3, 76) = 1.95$, $p > .10$. The best-fitting exponential functions for slow and fast speeds are shown as black solid lines in Figure 3A and B, respectively.

Biological motion

Yes/no task

d′ was calculated for each observer as the differences between z-score of hits (responding 'biological' when a sequence was biological) and those of false alarms (responding 'biological' when a sequence was phase-scrambled). The resulting d′ values are shown in Fig-
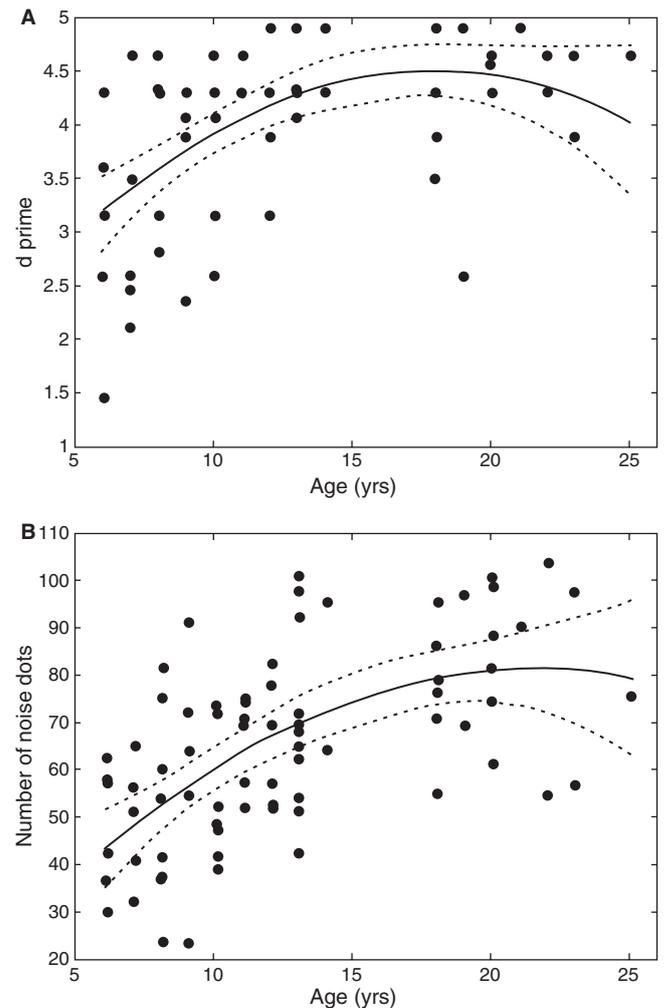
ure 4A. A between-subjects ANOVA revealed a significant effect of age on d′, $F(3, 76) = 7.32$, $p < .0001$, $\eta^2 = .26$ (means: 3.41, 3.94, 4.30, and 4.30 for 6- to 8-year-olds, 9- to 11-year-olds, 12- to 14-year-olds, and adults, respectively), demonstrating lower sensitivity to biological motion in the youngest age group, even when no noise dots are displayed. Curve fitting indicated a quadratic trend in the age-related changes in d′, $y = -0.01x^2 + 0.34x + 1.49$, and post-hoc Dunnett tests revealed a significant difference in sensitivity between the 6- to 8-year-olds and adults ($p < .0001$). Sensitivity of the 9- to 11-year-olds and 12- to 14-year-olds did not differ from that of adults ($ps > .10$). The best-fitting quadratic function is shown as a solid black curve in Figure 4A.

Staircase task

A between-subjects ANOVA revealed a significant improvement in thresholds with age ($F(3, 76) = 14.67$,

$p < .0001$, $\eta^2 = .36$; means: 48.53, 59.29, 70.00, and 80.58 for 6- to 8-year-olds, 9- to 11-year-olds, 12- to 14-year-olds, and adults, respectively), indicating improvement with age in the ability to tolerate noise dots in perceiving biological motion. Curve fitting showed a quadratic trend, $y = -0.15x^2 + 6.81x + 8.16$, and post-hoc Dunnett tests showed that both 6- to 8-year-olds and 9- to 11-year-olds could tolerate fewer noise dots than adults while perceiving biological motion ($ps < .001$) but that the 12- to 14-year-olds were adult-like ($p > .15$).

Discussion

The results reveal a long developmental trajectory for the ability to integrate local motion signals into a global flow of motion. Only the 12- to 14-year-olds showed adult-like performance and they did so for all three tasks. These results suggest that the extrastriate mechanisms supporting integration of local motion cues over time and space continue to develop increased functionality into later childhood.

Global motion

Sensitivity to the direction of global motion was not adult-like until 12–14 years of age, both when the dots moved slowly at $4°$ s^{-1} and when they moved more quickly at $18°$ s^{-1}. Although, as is apparent in Figure 3, the thresholds for the perception of the global flow of motion are lower for faster moving dots than for the slower ones in all age groups, developmental trends did not differ between these two speeds. The late maturation was found even for the fast speed for which adults showed higher sensitivity.

The results show a much longer developmental trajectory for the perception of global motion than that found in earlier studies. Adult-like performance in a global motion task has been demonstrated in 6-year-olds (Ellemberg *et al.*, 2002) and in children as young as 4 years of age (Parrish *et al.*, 2005). A number of factors likely account for this difference. First, Parish *et al.* used dots moving at $1.2°$ s^{-1}, a slow speed that does not fall within the optimal speed range of neurons in MT/MST (Britten *et al.*, 1993). The implication is that children may be able to perform as well as adults for global motion tasks mediated by a different mechanism or limited by poor neural responses even in adults. Second, the relatively low density of the dots in the present study (0.75 dots/deg^2) compared to that used in Parrish *et al.* (32 dots/deg^2) may explain the longer development of global motion observed here. Additionally, it is unclear whether some of the earlier developmental studies had the same signal dots presented for the entire trial (e.g. Ellemberg *et al.*, 2002) rather than signal dots with a limited lifetime as used here. If so, an observer could determine the direction of the entire pattern by simply following the trajectory of a single dot that moves in the same direction throughout the trial. The high sensitivity in young children demonstrated by those studies might in fact reflect children's sensitivity to the direction of local rather than to global flow of motion.

Another difference between our study and earlier ones is that we used monocular testing, while the previous studies were binocular. This might explain the different results, particularly given that extrastriate visual areas such as MT and MSTd contain cells that are mostly or exclusively binocular (e.g. Maunsell & Van Essen, 1983). In fact, a study that demonstrated a binocular advantage for global motion processing in adults further suggested that the specialized subset of cells in V1 that project to MT are binocular (Hess, Hutchinson, Ledgeway & Mansouri, 2007). Eliminating stereo cues thus may have made the task more difficult, particularly for children.

Whatever the reason for the difference in results from previous studies, the present results suggest that when integration across time and space is required, presumably mediated by extrastriate cortex, the developmental trajectory is long, at least under some testing conditions.

Biological motion

The results for biological motion revealed a similar protracted development as those for global motion. Children who were 6–8 years old were less able to discriminate biological motion animations from phase-scrambled ones, even when the animations were presented without any noise dots. This result indicates that despite the very early emergence of this sensitivity a few hours after birth (Simion *et al.*, 2008), young children are less skilled than adults at processing the kinematics defining human activity. Earlier studies, however, demonstrated adult-like performance in perceiving biological motion without noise in 6-year-olds (Freire *et al.*, 2006; Pavlova *et al.*, 2000). In those studies testing was binocular, while it was monocular in our study, and the elimination of stereo cues, as explained above, might have made the task especially difficult for 6- to 8-year-old children.

We found a longer developmental trajectory for the threshold task where noise dots were presented with the biological motion than for the yes/no task without noise. Here, both 6- to 8-year-olds and 9- to 11-year-olds tolerated significantly fewer noise dots than did adults. A quadratic trend in improvement in tolerance to the noise dots was found with age, indicating adult-like performance only at 12–14 years of age. Together, the results show a late maturation of the integration of spatially separated local motion signals into a global flow of biological motion, similar to the long trajectory for global motion.

The protracted development of sensitivity to biological motion observed in the present study is largely consistent with earlier research (Freire *et al.*, 2006; Jordan *et al.*, 2002; Pavlova *et al.*, 2000). Specifically, children 4–7 years old in the study by Jordan *et al.* (2002) were less accurate than adults in discriminating the direction

of walking of a point-light walker in noise, and 6-year-olds in the study by Freire *et al.* (2006) tolerated less noise when discriminating biological from scrambled displays. Although 9-year-olds in Freire *et al.* (2006) did not differ significantly from adults, their thresholds were about 1.2 times worse than those of adults and were not significantly different from those of 6-year-olds. Furthermore, there was a significant linear trend in biological motion thresholds, with sensitivity increasing with age over the groups tested at 6, 9, and 18 years of age. This raises the possibility of small gains in processing biological motion past 9 years of age. Consistent with that possibility is the finding in the study by Pavlova *et al.* (2000) that 14-year-olds 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. Overall, the results of previous studies agree with the findings reported here of protracted development.

Possible reasons for long developmental trajectories

Non-visual factors, such as differences between children and adults in motivation or in ability to pay attention, may have contributed to the observed age-related differences in thresholds. However, non-visual factors are unlikely to be the only explanation for these age-related differences. First, we found similar developmental trends for global motion across the two speeds despite lower thresholds for the perception of the global flow of motion for faster moving dots than for the slower ones in all age groups. If general cognitive factors played a major role in performance, we would have expected larger age-related changes for the more demanding task (i.e. global motion perception at the slower speed) compared to the less demanding one (i.e. global motion perception at the faster speed) (Crookes & McKone, 2009). This, however, was not the case in the present study. Thus, similar developmental trends at the two speeds, both of which fall within the optimal speed range for neurons in the MT/MST complex and are likely to involve the same high-level integration process, are more likely to reflect development in a specific global motion mechanism rather than in more general cognitive abilities.

Furthermore, a large body of recent evidence from our lab indicates that children reach adult-like levels of sensitivity at different ages for different visual abilities: on some tasks, children are adult-like at an early age, ruling out non-visual explanations for their immaturities on other tasks tested with the same procedures but showing long developmental trajectories. These patterns hold across experiments using added noise to measure thresholds and either simultaneous presentations or two-interval forced-choice procedures, as were used here for global motion and biological motion, respectively. For example, children are adult-like by 7 years when processing local motion for second-order displays, which contain noise, but are immature even at age 10 for first-order motion containing the same noise (Armstrong,

Maurer & Lewis, 2009). Similarly, sensitivity for second-order form, which contains noise, is adult-like even at 5 years of age, whereas it is not adult-like for first-order form with the same noise until 7–10 years of age (Armstrong *et al.*, 2009). Furthermore, sensitivity to spatial frequency, one of the building blocks of vision, is not adult-like until after 7 years of age, and this is true whether children are tested with a two-alternative forced-choice procedure or simultaneous discrimination (Patel, Maurer & Lewis, 2010). These different developmental trends for the different visual abilities cannot be explained easily by general cognitive factors and are more likely to reflect different rates of development for different types of visual processing.

The ability to integrate local motions into a global pattern of motion is related to a group of visual functions with protracted developmental sequences. Each of these visual functions involves integration among elements into a global visual pattern. Developmental studies beyond the second year of life suggest that many abilities involving such integration remain immature well into childhood, namely the ability to integrate Gabor elements into a contour (Hadad, Maurer & Lewis, 2010; Kovács, 2000), the ability to use collinearity to enhance the perception of a closed shape (Hadad & Kimchi, 2006), the detection of a global form in Glass patterns (Lewis, Ellemberg, Maurer, Dirks, Wilkinson & Wilson, 2004), sensitivity to the spacing of features in faces (Mondloch, Le Grand & Maurer, 2002; but see Crookes & McKone, 2009) or houses (Robbins, Shergill, Maurer & Lewis, 2011), configural processing of hierarchical patterns (Burack, Enns, Iarocci & Randolph, 2000; Kimchi, Hadad, Behrmann & Palmer, 2005; Mondloch, Geldart, Maurer & de Schonen, 2003), and the ability to integrate visual depth cues (Nardini, Bedford & Mareschal, 2010). Immature cortical connections downstream of V1 may underlie the protracted development of these perceptual integration processes. Consistent with this explanation of the results are ERP data in humans demonstrating substantial reorganization of extrastriate networks between infancy and adulthood (Wattam-Bell, Birtles, Nystrom, von Hofsten, Rosander, Anker, Atkinson & Braddick, 2010). Similarly, fMRI recordings in infant monkeys aged 103–561 days show strong activation in area V1 but no activation in the extrastriate areas involved in processing global motion (MT/MST) and form (V4) (Kourtzi, Augath, Logothetis, Movshon & Kiorpes, 2006). Furthermore, in humans, fMRI recordings indicate that the superior temporal sulcus (STS) becomes more selective to biological motion as opposed to non-biological motion over the age range of 7 to 10 years (Carter & Pelphrey, 2006).

At all ages, we found that sensitivity was poorer at the slower than at the faster speed of global motion. This relatively poor processing of slowly moving dots at all ages might be attributed to the fact that only a few neurons in MT are tuned to slow speeds, at least in adult monkeys (Liu & Newsome, 2003). Alternatively, or in

addition, this disadvantage of processing slow speeds might be at the level of the initial filters integrating temporal and spatial frequencies (Perrone & Thiele, 2002). Whatever the cause, the finding that both adults and children are less sensitive to slow than to fast moving dots is consistent with the hypothesis that it is the same mechanism of motion processing that is tapped at all ages.

In sum, the present results reveal a protracted development of sensitivity to global and biological motion. Comparing these two types of motion perception in the same groups of subjects indicates, contrary to earlier studies, that both the perception of global motion and its special case formed by a moving animate organism, become adult-like only after 11 years of age, at least when tested monocularly.

Acknowledgements

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