Running Head: DEVELOPMEMNT OF GLOBAL AND BIOLOGICAL MOTION

Long Trajectory for the Development of Sensitivity to Global and Biological Motion

Bat-Sheva Hadad, Daphne Maurer, & Terri L. Lewis

Department of Psychology, Neuroscience & Behaviour

McMaster University

Hamilton, Canada

Submitted for Publication September 2010. Do not cite without permission.

Keywords: global motion; biological motion; development; integration of local motions; random-dot kinematograms

Abstract

We used a staircase procedure to test sensitivity to (1) global motion in random-dot kinematograms moving at 4 and 18 degrees/second 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 7, 10, and 13-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 7 and 13 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.

Processing motion and its direction provide 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, Attkinson, & 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 have assessed the development of sensitivity to motion and the results have been inconsistent. 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. 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.

Both the perception of global motion and biological motion involve integration of local motion signals into a global pattern of motion over space and time by neural networks in 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 have been found to 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 network of areas in the extra-striate cortex involving primarily a region on the ventral bank of the occipital extent of the superior-temporal sulcus (STS; Grossman et al., 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 direction of global motion emerges sometime between 6 to 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; Parrish et al., 2005; Maunsell & Newsome 1987). 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 dots moving at different speeds. For example, while Ellemberg et al. (2002) used dots moving at a relatively fast speed of 18° s^{-1}, Parrish et al (2005) used dots 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 than global motion. Even newborn babies show a preference for upright over inverted biological motion displays (Simion, Regolin, & Bulf, 2008; see Bertenthal et al., 1984; Fox & McDaniel, 1982), 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 et al., 2003; Pavlova et al., 2001), this sensitivity improves well into middle childhood or even into adolescence when the display includes moving noise dots (Friere et al., 2006; Jordan et al., 2002; Pavlova et al., 2000). Thus although the perception of both global and biological motion involve 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, and the biological motion displays were contrasted to scrambled displays in which the local motions followed the same trajectories but with altered phase.

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 der Grind, van Hof, van der Smagt, & Verstraten, 2001). In children, different developmental changes to slow and fast speeds have been found; however, these differences were obtained in local motion

tasks where the slow motion was below 2° s^{-1} (Ahmed et al., 2005). 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, twenty in each, participated in the experiment: 7-year-olds (mean age = 7.10; range = 6.0-8.9 years, 9 females), 10-year-olds (mean age = 10.00; range = 9.0-11.9 years, 10 females), 13-year-olds (mean age = 12.74; range = 12.0-14.9 years, 9 females), and adults (mean age = 20.2; 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 6.0- to 6.9-year-olds met the same criteria except that their acuity was tested with the Cambridge Crowding cards (catalogue # 4116022). An additional three 7-year-olds, two 13-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, whilst the remaining half were tested with the right eye. The eye not being tested was patched with 3M Micropore™ 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 360º 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 71% 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.

Insert Fig 1 about here

To assure that the overall direction of motion could not be determined by local motion detectors, the signal dots were assigned random birthdates and each dot was replaced after a lifetime of 200 msec (15 frames) or 400 msec (30 frames) for the faster and slower speeds, respectively. At the end of its lifetime, the dot was redrawn in a new, random location in the display area, before resuming its motion. That is, on every frame, some dots, chosen randomly from the entire group of signal dots, were reborn. 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.

Apparatus and Stimuli. Stimuli were generated on Apple Macintosh LC475 computer and presented on a monochrome monitor, 29° high by 37° wide, 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 were presented against a square gray background subtending 17.5° x 17.5°. Each dot had a mean luminance of 14 cd/m^2 whilst the background had a mean luminance of 116 cd/m^2. The Michelson contrast between the dots and their background was 78%.

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 watched the participant’s viewing eye continuously to ensure that he/she was looking at the center of the screen.

To familiarize them with the displays, the participants were shown four demonstration trials at 100% coherence, 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 before moving on to the second speed, at which they completed two additional staircases.

Coherence thresholds were measured for dots that moved at speeds of 4° and 18º 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), whilst the remaining dots moved in random directions. For these noise dots, the direction of motion continued for one frame, after which it was replaced randomly by another direction of

motion.

We used a 2-down, 1-up staircase procedure (Levitt, 1971) to measure motion coherence thresholds which we 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 71% accuracy. The initial coherence level was 100% and the initial step size was one octave (where an octave is a halving or a doubling of a value). The step size decreased to a half octave after the first reversal and to a quarter octave at all subsequent reversals. The staircase ended at the eighth reversal after the first quarter octave step. The coherence threshold was taken as the geometric mean of the last six reversals.

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 2-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. Density of the 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, Lewis, Maurer, and Blake (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 two frames, not successive in the animation, from a normal biological sequence and two non-successive frames from a phase-scrambled sequence created from the same animations, in this case of the actor, 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 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.

Insert Fig 2 about here

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. Specifically, before running each subject, half of the biological motion sequences and their phase-scrambled counter-parts 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 min of arc at the viewing distance of 50 cm, and the biological motion figures subtended approximately 6° x 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 direction and variable distance from the center of the 19.2° x 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 long 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 2-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 6 noise dots before the staircase task). Then, to ensure that the subjects understood the task, criterion trials were presented. 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 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. The staircase terminated after 20 reversals. Subsequent to the first 12 reversals, 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. 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. During the test phase, the experimenter sat to the side of the monitor and controlled presentation of displays, but could not see the displays themselves.

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.

Motion Coherence

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.

Insert Fig 3 about here

A mixed designed ANOVA with speed as a within-subjects and age as a between-subject factor revealed a significant effect of speed, $F(1,76) = 11.84$, $p < .001$, 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, $F(3,76)=12.74$, $p < .0001$. Curve fitting indicated that sensitivity increases exponentially with age, for both fast and low speeds, $R^2=0.25$, $y = -0.01x^2 + 0.34x + 1.49$, and post-hoc Dunnett tests revealed that adults had lower thresholds than both the 7- and the 10-year-olds ($ps < .0001$) but not the 13-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 in Figure 3, as dashed and smooth black curves, 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 Figure 4A. A between-subjects ANOVA revealed a significant effect of age on *d*', $F(3,76) = 7.32$, $p < .0001$ (means: 3.41, 3.94, 4.3, and 4.34 for 7-year-olds, 10-year-olds, 13-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*', $R^2=0.25$, $y = -0.01x^2 + 0.34x + 1.49$, and post-hoc Dunnett tests revealed a significant difference in sensitivity between the 7-year-olds and adults ($p < .0001$). Sensitivity of the 10-year-olds and 13-year-olds did not differ from that of adults ($ps > .10$). The best-fitting

quadratic function is shown as a smooth black curve in Figure 4A.

Staircase task. A between-subjects ANOVA revealed a significant improvement in thresholds with age ($F(3,76) = 14.67$, $p < .0001$; means: 48.53, 59.29, 70, and 80.58 for 7-year-olds, 10-year-olds, 13-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, $y = -0.15x^2 + 6.81x + 8.16$, $R^2 = .36$, and post-hoc Dunnett tests showed that both 7-year-olds and 10-year-olds could tolerate fewer noise dots than adults while perceiving biological motion (*p*s< .001) but that the 13-year-olds were adult-like ($p > .15$).

Insert Fig 4 about here

Discussion

The results reveal a long developmental trajectory for the ability to integrate local motion signals into a global flow of motion. Only the 13-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 after 12 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 fast moving dots than for the slower ones in all age groups, developmental trends did not differ across 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 accounts 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 Parish et al. (32 dots /deg^2) may explain the longer development of global motion observed here. Additionally, some of the earlier developmental studies had the same signal dots presented for the entire trial. Such unlimited lifetime allows an observer to 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 these studies might in fact reflect their sensitivity to the direction of local rather than to global flow of motion. In fact, previous studies indicate that sensitivity to local motion is nearly adult-like at least by 5 years of age (Ellemberg et al., 2003). The present results suggest that when integration across time and space is required, presumably mediated by extrastriate cortex, a much longer

developmental trajectory occurs, at least under some testing conditions.

Biological Motion. The results for biological motion revealed a similar protracted development as those for global motion. Seven-year-olds were less able to discriminate biological motion animations from phase-scrambled ones, even when those 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., 2007), 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. 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 rendered the displays in the present study more challenging, resulting in relatively elevated thresholds even in adults, and in immature performance at 6 years of age, even when no noise is presented.

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 7- and 10-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 after 12 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 to 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 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. Six-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 thresholds, with sensitivity increasing with age over the groups tested at 6, 8, and 18 years of age. This raises the possibility of small gains in processing biological motion past 9 years of age, and therefore is largely consistent with the prolonged development observed here.

Developmental changes in motivation or in attentional control may contribute to the later development of sensitivity to global and biological motion in noise than to motion signals without noise (i.e., yes/no biological motion task in the present study). Indeed, it has been shown that children are poorer than adults at ignoring irrelevant information (e.g., Goldberg, Maurer, & Lewis, 2001). However, two lines of evidence suggest that age changes in attention cannot explain our findings, and hence that children are not as sensitive as adults to global and

biological motion *per se*. The first line of evidence comes from the fact that 6-, and 7-year-olds perform as well as adults on different tasks requiring them to detect a signal in noise. Six-year-olds are as accurate as adults on a form coherence task in which line segments, tangentially arranged to form concentric circles, have to be identified in a display embedded in a field of randomly oriented line segments (i.e., noise; Gunn et al 2002; but see Lewis et al, 2004). Similarly, 7-year-olds are as accurate as adults on a contour integration task in which a contour made up of collinear Gabors is embedded in a field of randomly oriented Gabors (Hadad, Maurer, & Lewis, 2010). The second line of evidence comes from the fact that although the perception of the global flow of motion is stronger for faster moving dots than for the slower ones in all age groups, developmental trends did not differ across these two speeds. If poorer motivation or attention of children underlies the age-related changes obtained, worse performance would have been expected in the condition proven to be more demanding (i.e., global motion at the slower speed). This was not the case, however. The results showed no significant difference in developmental changes across the two speeds, although the slower speed was clearly more difficult than the faster speed for all observers.

Consistent with this overall effect of speed on global motion processing are findings that visually normal infants and patients treated for congenital cataract have relatively poor motion processing at slow speeds (Ellemberg, Lewis, Maurer, & Brent, 2000; Ellemberg, Lewis, Maurer, Lui, & Brent, 1999). 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 slowly 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.

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 (Kovacs, 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 et al., 2004), configural face processing (Mondloch, Le Grand, & Maurer, 2002; but see Crookes & McKone, 2009), and configural processing of hierarchical patterns (Burack, Enns, Iarocci, & Randolph, 2000; Kimchi, Hadad, Behrmann, & Palmer, 2005; Mondloch, Geldart, Maurer, & de Schonen, 2003). Immature cortical connections downstream of V1 may underlie the protracted development of these perceptual integration processes. Results from monkeys are consistent with this explanation of our results: in a study of infant monkeys aged 103-561 days and adults monkeys, at the younger age, activation in V1 was strong, while activation in extrastriate areas involved in processing global motion (MT/MST) and form (V4) could not be found (Kourtzi, Augath, Logothesis, 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).

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 between 10 and 13 years of age, at least when tested monocularly.

Acknowledgments

This research was supported by grants from the Canadian Institutes of Health Research (MOP-458 36430) and the James S. McDonnell Foundation. We thank Randolph Blake for providing us with the stimuli and Kathleen Lee for her help in data collection. Some of these data were presented at the 2010 annual meeting of the Vision Sciences Society, Naples, Florida.

References

Ahmed, I. J., Lewis, T. L., Ellemberg, D., & Maurer D. (2005). Discrimination of speed in 5-year-olds and adults: Are children up to speed? *Vision Research*, 45, 2129 – 2135.

Banton, T., Bertenthal, B. I., & Seaks, J. (1999). Infants' sensitivity to statistical distributions of motion direction and speed. *Vision Research*, *39*, 3417–3430.

Benton, C. P., & Curran, W. (2003). Direction repulsion goes global. *Current Biology, 13*, 767–771.

Bertenthal, B. I., Proffit, D. R., & Cutting, J. E. (1984). Infant sensitivity to figural coherence in biomechanical motions. *Journal of Experimental Child Psychology,* 37, 213–230.

Blake, R., Turner, L. M., Smoski, M. J., Pozdol, S. L., & Stone, W. (2003). Visual recognition of biological motion is impaired in children with autism. *Psychological Science*, 14, 151-157.

Braddick, O. J., O'Brien, J. M., Wattam-Bell, J., Atkinson, J., & Turner, R. (2001). Brain areas sensitive to coherent visual motion. *Perception,* 30, 61–72.

Braddick, O., Atkinson, J., & Wattam-Bell, J. (2003). Normal and anomalous development of visual motion processing: motion coherence and dorsal-stream vulnerability. *Neuropsychologia*, 41, 1769-84.

Braddick, O., & Qian, N. (2000). The organization of global motion and transparency. In J.M. Zanker, & J. Zeil (Eds.), *Computational, neural and ecological constraints of visual motion.* Berlin: Springer.

Britten, K, Shadlen, M. N., Newsome, W. T. & Movshon, J. A. (1993). Responses of neurons in macaque MT to stochastic motion signals. *Visual Neuroscience*, 10, 1157-1169.

Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision,* 10*,* 433-436.

Burack, J. A., Enns, J. T., Iarocci, G., & Randolph, B. (2000). Age differences in visual search for compound patterns: long- versus short-range grouping. *Developmental Psychology,* 36, 731-740.

Carter, E. J. & Pelphrey, K. A. (2006). School-aged children exhibit domain-specific responses to biological motion. *Social Neuroscience,* 1, 396-411.

Crookes, K., & McKone, E. (2009). Early maturity of face recognition: no childhood development of holistic processing, novel face encoding, or face-space. *Cognition,* 111, 219-247.

Ellemberg, D., Lewis, T. L., Maurer, D., Lui, C. H., & Brent, H. P. (1999). Spatial and temporal vision in patients treated for bilateral congenital cataracts. *Vision Research*, 39, 3480–3489.

Ellemberg, D., Lewis, T. L., Maurer, D., & Brent, H. P. (2000). Influence of monocular deprivation during infancy on the later development of spatial and temporal vision. *Vision Research*, 40, 3283–3295.

Ellemberg, D., Lewis, T.L., Meghji, K.S., Maurer, D., Guillemot, J.-P., & Lepore, F. (2002). Comparison of sensitivity to first- and second-order local motion in 5-year-olds and adults. *Spatial Vision*, *16*, 419-428.

Ellemberg, D., Lewis, T. L., Maurer, D., Brar, S., & Brent, H. P. (2002). Better perception of global motion after monocular than after binocular deprivation. *Vision Research*, 42, 169-179.

Fox, R., & McDaniel, C. (1982). The perception of biological motion by human infants. *Science,* 218, 486–748.

Freire, A., Lewis, T. L., Maurer, D., & Blake, R. (2006). The development of sensitivity to biological motion in noise. *Perception*, 35, 647–657.

Goldberg, M., Maurer, D., Lewis, T. L. (2001). Developmental changes in attention: The effects of endogenous cueing and of distractors. *Developmental Science*, 4, 209-219.

Grossman, E. D., & Blake, R. (1999). Perception of coherent motion, biological motion and form-from-motion under dim-light conditions. *Vision Research.* 39*,* 3721-3727.

Grossman, E. D., et al. (2000). Brain areas involved in the perception of biological motion. *Journal of cognitive Neuroscience,* 12*,* 711-720.

Gunn, A., Cory, E., Atkinson, J., Braddick, O., Wattam-Bell, J., Guzzetta, A., & Cioni, G. (2002). Dorsal and ventral stream sensitivity in normal development and hemiplegia" Neuroreport, 13, 843-847.

Hadad, B. S., & Kimchi, R. (2006). Developmental trends in utilizing perceptual closure for grouping of shape: effects of spatial proximity and collinearity. *Perception & Psychophysics, 68(8)*, 1264-1273.

Hadad, B., Maurer, D., & Lewis, T.L. (2010). The effects of spatial proximity and

collinearity on contour integration in adults and children. *Vision Research*, *50*, 772-778.

Heinrich, S. P., van der Smagt, M. J., Bach, M., & Hoffmann, M. B. (2004).Electrophysiological evidence for independent speed channels in human motion processing. *Journal of Vision*, 4, 469–475.

Hess, R.F., Hutchinson, C.V., Ledgeway, T. & Mansouri, B. (2007). Binocular influences on global motion processing in the human visual system. *Vision Research*, 47, 1682-1692.

Jordan, H., Reiss, J. E., Hoffman, J. E., Landau, B. (2002). Intact perception of biological motion in the face of profound spatial deficits: Williams syndrome. *Psychological Science*, 13, 162-167.

Kimchi, R., Hadad, B., Behrmann, M., & Palmer, S. E. (2005). Microgenesis and ontogenesis of perceptual organization: Evidence from global and local processing of hierarchical patterns. *Psychological Science, 16*, 282-290.

Kourtzi, Z., Augath, M., Logothetis, N. K., Movshon, A., & Kiorpes, L. (2006). Development of visually evoked cortical activity in infant macaque monkeys studied longitudinally with fMRI. *Magnetic Resonance Imaging,* 24, 359-366.

Kovács, I. (2000). Human development of perceptual organization. *Vision Research, 40*, 1301-1310.

Levitt, H. J. (1971). Transformed up–down methods in psychophysics. Acoustical Society of America, 49, 467–477

Lewis, T. L., Ellemberg, D., Maurer, D., Dirks, M., Wilkinson, F., & Wilson, H. R. (2004). A window on the normal development of sensitivity to global form in Glass patterns. *Perception*, 33, 409-418.

Liu, J., & Newsome, W. T. (2003) Functional organization of speed tuned neurons in visual area MT. *Journal of Neurophysiological*, 89, 246 –256.

Maunsell, J. H., Newsome, W. T. (1987). Visual processing in monkey extrastriate Cortex. *Annual Review of Neuroscience*, 10, 363-401.
Maunsell, J.H., &Van Essen, D.C. (1983) Functional properties of neurons in the middle temporal visual area of the macaque monkey. II. Binocular interactions and the sensitivity to binocular disparity. *Journal of Neurophysiology*, 49, 1148-1167.

Mondloch, C. J., Geldart, S., Maurer, D., & de Schonen, S. (2003). Developmental changes in the processing of hierarchical shapes continue into adolescence. *Journal of Experimental Child Psychology,* 84, 20-40.

Mondloch, C. J., Le Grand, R., & Maurer, D. (2002). Configural face processing develops more slowly than featural face processing. *Perception,* 31, 553-566.

Movshon, J. A. (1990). Visual processing of moving images. In *Images and Understanding*, ed. M. Weston-Smith, H. B. Barlow and C. Blakemore. New York: Cambridge University Press.

Movshon, J. A., Adelson, E. H., Gizzi, M. S., and Newsome, W. T. (1985). The analysis of visual moving patterns. In Chagas, C., Gattass, R., & Gross, C., (Eds.), *Pattern recognition mechanisms*, 117-151. Springer, New York.

Newsome, W. T., & Pare, E. B. (1988). A selective impairment of motion perception following lesions of the middle temporal visual area. *Journal of Neuroscience*, 8, 2201–2211.

Parrish, E. E., Giaschi, D. E., Boden, C., Dougherty, R. (2005). The maturation of form and motion perception in school age children. *Vision Research,* 45, 827-837.

Pavlova, M., Krageloh-Mann, I., Sokolov, A., & Birbaumer, N. (2000). Simultaneous masking of a point-light walker in children, in Fechner Day 2000 Ed. C. Bonnet (Strasbourg: ISP) pp 279-284.

Pavlova, M., Krageloh-Mann, I., Sokolov, A., & Birbaumer, N. (2001). Recognition of point-light biological motion displays by young children. *Perception*, 30, 925-933.

Perrone, J. A., & Thiele, A. (2002). A model of speed tuning in MT neurons. *Vision Research*, 42, 1035-1051.

Smith, A. T., Snowden, R. J., & Milne, A. B. (1994). Is global motion really based on spatial integration of local motion signals? *Vision Research,* 34, 2425-2430.

Williams, D. W., & Sekuler, R. (1984). Coherent global motion percepts from stochastic local motions. *Vision Research*, 24, 55–62.

Schenk, T., Mai, N., Ditterich, J. & Zihl, J. (2000). Can a motion-blind patient reach for moving objects? *European Journal of Neuroscience,* 12, 3351-3360.

Simion, F., Regolin, L., & Bulf, H. (2008). A predisposition for biological motion in the newborn baby. *Proceedings of the National Academy of Science, 105*, 809-813.

van de Grind, W. A., van Hof, P., van der Smagt, M. J., & Verstraten, F. A. J. (2001). Slow and fast visual motion channels have independent binocular rivalry stages. *Proceedings of the Royal Society London*, B, 268, 437-443.

Wattam-Bell, J. (1994). Coherence thresholds for discrimination of motion direction in infants. *Vision Research*, *34*, 877–883.

Wattam-Bell, J. (1996). The development of visual motion processing. In F. Vital-Durand, O. Braddick, & J. Atkinson (Eds.), *Infant vision*. Oxford: Oxford University Press.

Figure Captions

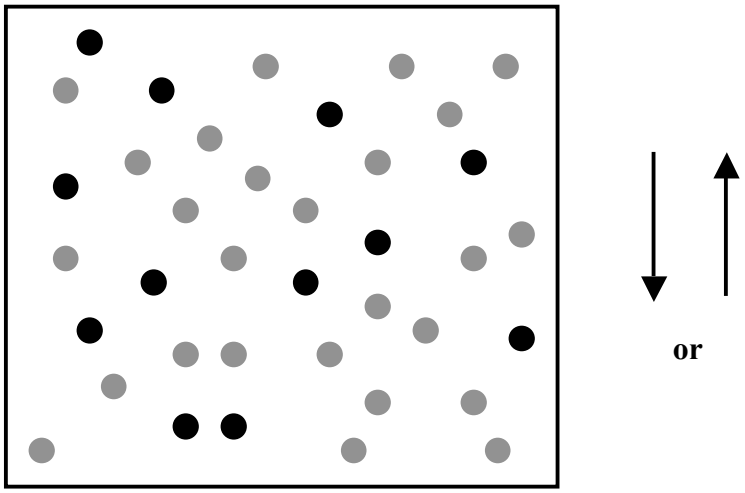
Figure 1. Static illustration of a global motion display with 30% coherence. The illustration shows signal dots (those moving up or down) in black and noise dots (those moving in random directions) in gray. In the actual displays, all dots were black. Thresholds were defined as the minimum percentage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

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

Figure 3. Motion coherence thresholds (in percentage) as a function of age with the best fitting functions for 4 (dashed line) and 18 (solid black line) deg/sec. Each symbol represents the threshold for one subject at the age indicated.

Figure 4. d' for the yes/no task (A) and thresholds (number of noise dots tolerated) for the (B) biological motion tasks, as a function of age. Each symbol represents the threshold for one subject at the age indicated. The best fitting functions are represented by the curved smooth lines.

Fig. 1



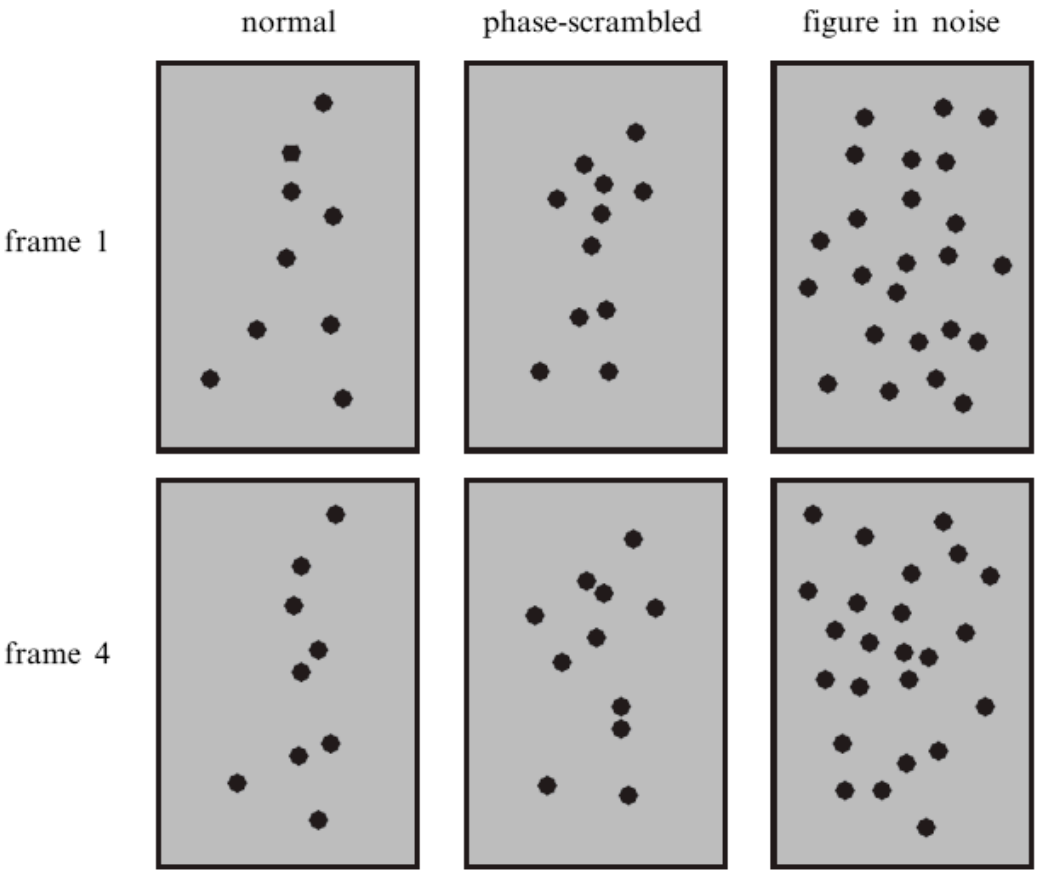
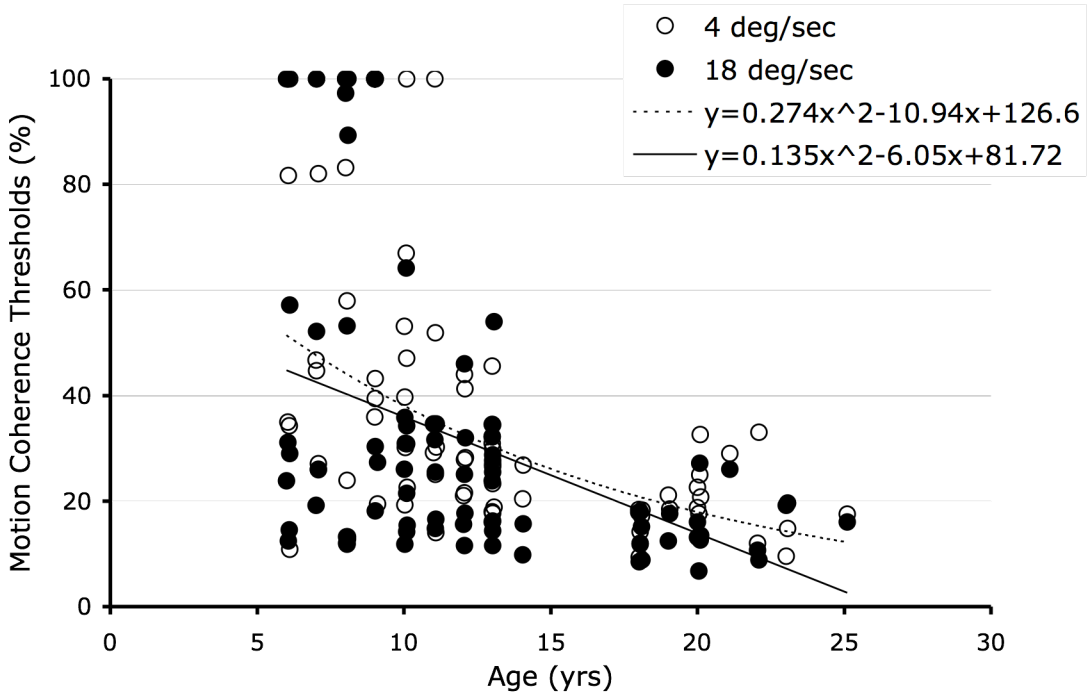
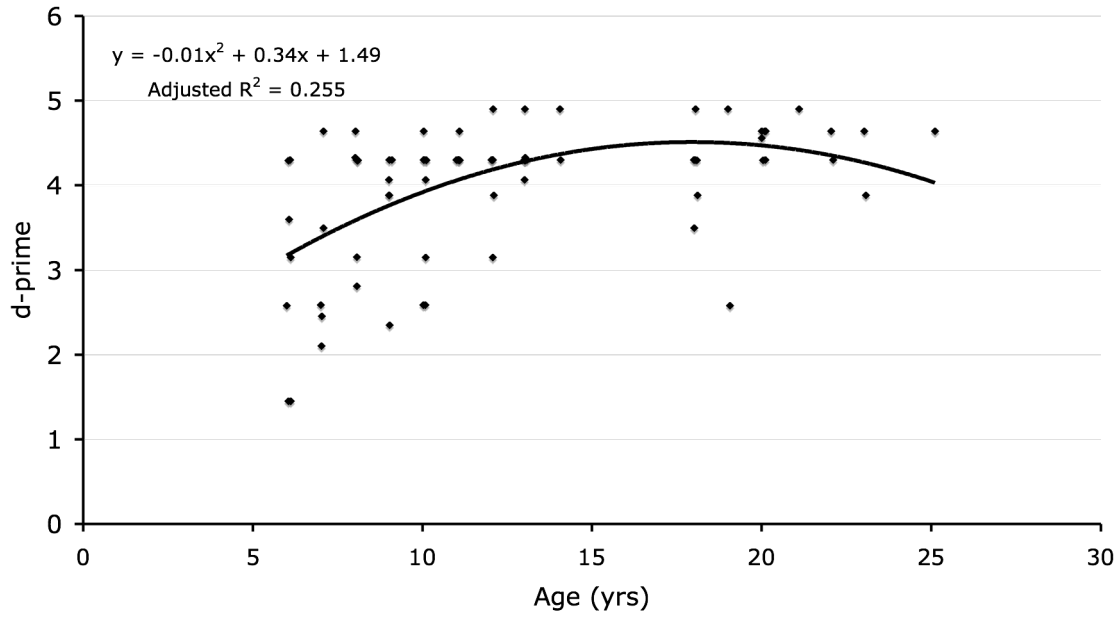

normal
phase-scrambled
figure in noise
frame 1
frame 4

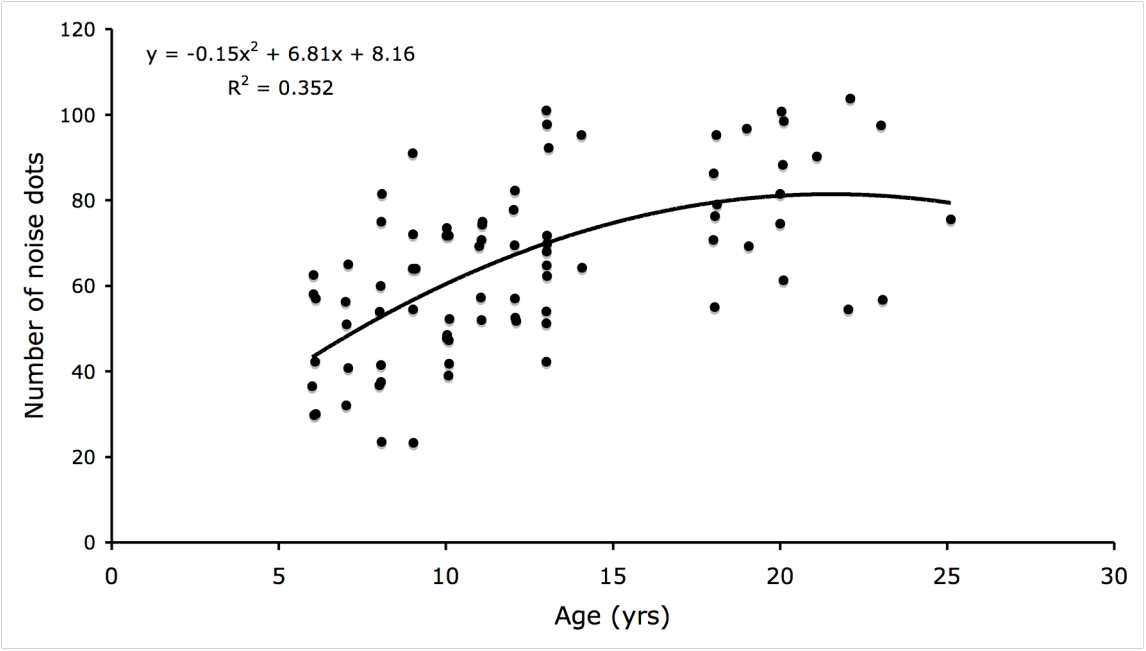
Fig. 3


4 deg/sec
18 deg/sec
y=0.274x^2-10.94x+126.6
y=0.135x^2-6.05x+81.72
Motion Coherence Thresholds (%)
100
80
60
40
20
0
0
5
10
15
20
25
30
Age (yrs)

A


y = -0.01x² + 0.34x + 1.49
Adjusted R² = 0.255
d-prime
Age (yrs)
0
1
2
3
4
5
6
0
5
10
15
20
25
30

B


y = -0.15x² + 6.81x + 8.16
R² = 0.352
Number of noise dots
Age (yrs)
0
20
40
60
80
100
120
0
5
10
15
20
25
30