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Development of radial optic flow pattern sensitivity at different speeds

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ABSTRACT

The development of sensitivity to radial optic flow discrimination was investigated by measuring motion coherence thresholds (MCTs) in school-aged children at two speeds. A total of 119 child observers aged 6–16 years and 24 young adult observers (23.66 +/− 2.74 years) participated. In a 2AFC task observers identified the direction of motion of a 5° radial (expanding vs. contracting) optic flow pattern containing 100 dots with 75% Michelson contrast moving at 1.6°/s and 5.5°/s and. The direction of each dot was drawn from a Gaussian distribution whose standard deviation was either low (similar directions) or high (different directions). Adult observers also identified the direction of motion for translational (rightward vs. leftward) and rotational (clockwise vs. anticlockwise) patterns. Motion coherence thresholds to radial optic flow improved gradually with age (linear regression, $p < 0.05$), with different rates of development at the two speeds. Even at 16 years MCTs were higher than that for adults (independent *t*-tests, $p < 0.05$). Both children and adults had higher sensitivity at 5.5°/s compared to 1.6°/s (paired *t*-tests, $p < 0.05$). Sensitivity to radial optic flow is still immature at 16 years of age, indicating late maturation of higher cortical areas. Differences in sensitivity and rate of development of radial optic flow at the different speeds, suggest that different motion processing mechanisms are involved in processing slow and fast speeds.

1. Introduction

The pattern of global motion experienced due to movement in the environment called optic flow (Gibson, 1957) is essential for navigation, speed judgement, avoiding obstacles and collisions in all forms of human locomotion (Raffi & Siegel, 2004; Vaina & Rushton, 2000). Three components, namely translational (e.g., right/left, up/down), radial (expansion/contraction) and rotational motion represent most of the motion patterns experienced in the visual world. Humans are very sensitive to optic flow. Young infants can discriminate different types of optic flow patterns (Gilmore et al., 2007; Hou et al., 2009; Shirai, Kanazawa, & Yamaguchi, 2008; Shirai et al., 2009; Wattam-Bell et al., 2010) with stronger visual evoked potentials to translational patterns compared to radial patterns (Gilmore et al., 2007). By 3–6 months, infants use optic flow information to discriminate gross changes in heading direction (Gilmore, Baker, & Grobman, 2004; Gilmore & Rettke, 2003) and the sensitivity to optic flow continue to improve throughout infancy (Brosseau-Lachaine, Casanova, & Faubert, 2008). However, information on further development of radial optic flow in older children, which is the most commonly experienced motion pattern during locomotion, is limited.

Motion is processed by a complex but relatively well understood neural pathway involving as many as 17 anatomically distinct brain areas (Sunaert et al., 1999). The first stage of motion processing occurs at primary visual cortex (V1), signaling direction of motion in local fields (Randolph, Emily, & Robert, 2003; Smith et al., 1998) with global processing occurring in middle temporal area (MT) and beyond. Speed selectivity is first seen in the neurons of area MT with optimal speed preference of 2–256°/s (Albright, 1993; Perrone & Thiele, 2001; Smith et al., 1998). Area MT is implicated for processing of global translational motion while radial and rotational motion are processed in the higher cortical areas of MST and beyond (Morrone et al., 2000; Tohyama & Fukushima, 2005). Motion coherence threshold (MCT) is the most commonly used measure to evaluate the global motion processing occurring in higher visual cortical areas including MT and MST (Braddick

Abbreviations: MCT, motion coherence threshold; RDK, random dot kinematogram; V1, primary visual cortex; MT, middle temporal area; MST, middle superior temporal.

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et al., 2001). MCT represent the minimum proportion of signal dots required to provide a reliable judgement of direction in presence of noise dots with random direction (Newsome & Pare, 1988). There is inconsistent evidence in the literature to which type of optic flow pattern humans are most sensitive. Some studies report better sensitivity for rotational and radial flow than translational flow (Freeman & Harris, 1992; Lee & Lu, 2010), while others report no difference (Aaen-Stockdale, Ledgeway, & Hess, 2007; Bertone & Faubert, 2003; Blake & Aiba, 1998).

Sensitivity to translational optic flow (e.g., right vs. left/up vs. down), is the most commonly investigated motion type and is reported to be adult-like by 6–14 years of age, depending on the stimulus parameters and task complexity (Bogfjellmo, Bex, & Falkenberg, 2014; Gunn et al., 2002; Hadad, Maurer, & Lewis, 2011;Manning et al., 2014; Parrish et al., 2005; Spencer et al., 2000). Generally studies investigating motion detection (Gunn et al., 2002; Spencer et al., 2000) report faster development and maturation than those using discrimination tasks (Falkenberg, Simpson, & Dutton, 2014; Hadad, Maurer, & Lewis, 2011; Parrish et al., 2005). Motion detection is an easier task than discriminating the direction of motion. Discrimination requires the observer to identify a specific target property of the stimulus, compare it to at least two internal templates of the target property before making a judgement, while in detection observers only need to detect the presence of the specific property.

Further, maturation to adult performance also seems to depend heavily on the stimulus parameters such as contrast, speed, size, dot density or field of view (aperture size). The sensitivity to translational motion patterns is reduced at low contrast levels (Aaen-Stockdale, Ledgeway, & Hess, 2007; Edwards, Badcock, & Nishida, 1996; Simmers et al., 2006). Recently, in a cross sectional study Bogfjellmo, Bex, and Falkenberg (2014) showed that for children between 6 and 15 years of age, low contrast translation optic flow sensitivity did not improve significantly with age. Other studies report better motion sensitivity at faster speeds compared to low or moderate speeds for both local and global motion in children and adults (Ahmed et al., 2005; Bogfjellmo, Bex, & Falkenberg, 2014; Ellemberg et al., 2004, 2005; Falkenberg, Simpson, & Dutton, 2014; Hadad, Maurer, & Lewis, 2011; Manning, Aagten-Murphy, & Pellicano, 2012; Manning et al., 2014; Snowden & Kavanagh, 2006). The sensitivity to detection and discrimination of translational motion has been found to be adult like by 11 years of age for 6°/s, while still immature at this age for 1.5°/s (Manning, Aagten-Murphy, & Pellicano, 2012). Psychophysical and electrophysiological studies also report evidence for independent processing for detection of slower and faster speed (Edwards, Badcock, & Smith, 1998; Heinrich et al., 2004; Hou et al., 2009; Khuu & Badcock, 2002). However another study (van Boxtel & Erkelens, 2006) suggested a single motion system with differential sensitivity to slow and fast speeds.

Information on normal sensitivity and development of complex radial motion patterns processed at higher cortical areas is important for understanding the maturation of the overall motion pathway. As the motion pathway is vulnerable to different neurological and cognitive developmental disorders (Grinter, Maybery, & Badcock, 2010; Ridder, Borsting, & Banton, 2001; Simmers et al., 2003, 2006; Spencer et al., 2000; Tibber et al., 2014), further knowledge on development and maturation of the motion sensitivity could help to better understand the effect of early insults to the motion processing mechanism. With these perspectives in mind, we evaluated the development and maturation of motion coherence thresholds to radial optic flow in children at a relatively slow and faster speed and investigated differences between different optic flow types in adults.

2. Methods

2.1. Observers

125 children between the ages of 6 and 16 years recruited from two primary schools in Kathmandu valley participated in this cross sectional, prospective study. 24 young adult observers (mean age 23.66 +/− 2.74 years) were recruited from the University College in Kathmandu to determine adult level of performance. Child observers only participated in the radial optic flow experiment while adults performed all three optic flow experiments. See Table 1 for description of the observers. Three naive adult observers and the author participated in a pilot study (Experiment 1) to investigate the effect of contrast and dot speed on motion coherence threshold for translational, radial and rotational optic flow. All observers had normal visual health, with a best corrected visual acuity of log MAR 0.0 (Snellen 6/6) for 8 years and older and log MAR 0.18 (Snellen 6/9) for children less than 8 years of age. Visual acuity was evaluated using the Freiburg test (Bach, 1996, 2007). An optometrist (MRJ) performed the vision screening. Informed consent was obtained from all children and their guardians and adult participants. The study was carried out in accordance with The Code of Ethics of the World Medical Association (Declaration of Helsinki) and approved by the Nepal Health Research Council. Of the 125 children included in the study, six were excluded from final data analysis; two children were not able to complete the test and data from four children did not converge to reliable psychometric fit.

2.2. Apparatus and stimuli

The experimental stimuli were programmed in Matlab (MATLAB, 2009) using PsychToolBox software (Brainard, 1997; Pelli, 1997) and displayed on a 15.4″ Mac Book Pro laptop Glossy widescreen LCD display with 1440 by 900 pixels resolution at a 75 Hz refresh rate. A 22″ CRT monitor with a resolution of 32 bit and a refresh rate of 75 Hz was used for pilot study. The mean luminance was 50 cd/m^2 and the display was calibrated with a luminance meter (Spyder™, Datacolour, Lawrenceville, NJ, US). The stimulus consisted of 100 black and white dots presented within an 8° circular window at the center of the display at a viewing distance of 57 cm. The dot diameter was 0.188°, and the density was two dots per degree^2. In the pilot study 10 dot contrast levels (between 3% and 80%) were tested at a dot speed of 4.8°/s. Different contrast levels were achieved by changing the luminance of dots with respect to the uniform gray background. Subsequently, 9 levels of speed (between 0.9°/s and 5.5°/s) were evaluated at a contrast of 75% (see Fig. 2).

The expansion and contraction radial optic flow (Fig. 1) was generated by calculating the shift required for global rotation and adding ±90°. The dot speed depended on eccentricity, and based on the pilot study, a global speed of 0.3 or 1.2 rotations per second (1° or 4° angular degrees per frame, respectively), producing dot speeds of approximately 1.6°/s or 5.5°/s at half eccentricity were chosen for the main experiment. All dots moved in a certain trajectory for three frames before disappearing and then reappearing at a different random location anywhere within the stimulus. Noise dots moved in random directions. To match the speed distributions of signal and noise dots, noise dots moved at a speed drawn from the distribution of speeds of the signal elements. This was the same for the rotation experiment, whereas for the translation experiment all dots moved with a speed of 1.6°/s or 5.5°/s to the right or to the left. A central fixation dot with a diameter of 0.25° (8 pixels) was present for the duration of each trial. Each trial lasted 500 ms.

Table 1
Age and visual acuity of participants.

Age (years)	Enrolled participants*	Sample size	Log MAR visual acuity (mean)	
			RE	LE
6	8 (3)	5	0.02	0.02
7	13	13	−0.02	0.01
8	11 (1)	10	−0.07	−0.09
9	13 (1)	12	−0.09	−0.11
10	12	12	−0.06	−0.16
11	11	11	−0.03	−0.02
12	12	12	−0.14	−0.14
13	11	11	−0.12	−0.06
14	10 (1)	9	−0.11	−0.13
15	11	11	−0.18	−0.13
16	13	13	−0.16	−0.17
Total	125	119		
Adults†	24	24	−0.10	−0.11

* The number in the parenthesis represents the six excluded observers.
† Adults: mean age of 23.66 +/− 2.74 years.

2.3. General procedure

The observer viewed the stimuli binocularly in a dark room where the display was the only source of light. In a two-alternative forced choice task observers identified the direction of motion in a radial optic flow pattern. Observers were explained that the pattern of dots would either be coming towards them (expansion) or going away from them (contraction), and to respond accordingly with appropriate keyboard presses. For children 10 years and younger, a verbal response was given to the investigator (blinded to the stimulus display) who pressed the appropriate key. Observers were given immediate feedback by changing the fixation dot color; green for a correct response and red for an incorrect response. Observers performed two practice runs consisting of 15 trials to become familiar with the experiment and the task. Motion coherence thresholds for each speed were estimated from two interleaved runs of 50 trials using the functional adaptive sequential testing (FAST) method for psychometric function fits in Matlab (Vul, Bergsma, & MacLeod, 2010). The FAST method estimated the stimulus strength (coherence level) to be presented in each trial depending upon the simulated psychometric function fit parameters (threshold and slope) from all preceding trials. Adult observers also identified the direction of motion for translational (rightward vs. leftward) and rotational (clockwise vs. anticlockwise) optic flow patterns. The whole experiment (including vision screening, instructions and practice sessions) took no longer than 40 min to complete for children, and 1 h for adults who were tested with all three optic flow patterns.

All data were analyzed using SPSS software and statistical toolbox of Matlab. ANOVA, linear regression analysis and bootstrap analysis (Wichmann & Hill, 2001) were used to determine differences in motion coherence thresholds with age, contrast, speed and task.

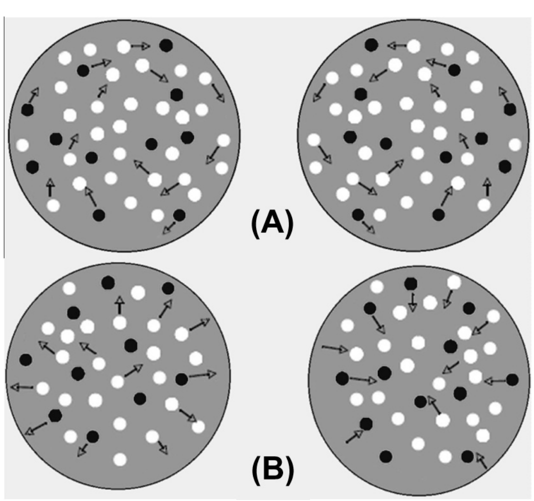

Fig. 1. Schematic representation of the rotation (A) and radial (B) stimuli. The arrows represent the direction of motion of the signal dots; clockwise and anticlockwise for rotation (A) and expansion and contraction for radial flow (B). Noise dots moved in a random direction. For translation the signal dots moved either right or left (not illustrated).

3. Results

3.1. Experiment 1: Optic flow sensitivity in adults

A pilot study with four observers was conducted to determine the contrast and speed parameters to use in the main experiment. Fig. 2A shows that motion coherence thresholds (MCTs) for three optic flow types improve rapidly up to 8% contrast, but remain constant between 10% and 80% contrast. ANOVA with contrast level and motion type as fixed factors revealed a significant effect of contrast level ($F(9, 332) = 77.64$, $p < 0.05$), but no effect of motion type or interactions between contrast level and motion type ($p > 0.05$). Post-hoc analysis showed that motion coherence thresholds at contrast less than 10% were significantly worse than at higher contrasts (Bonferroni correction: $p < 0.001$), with no significant difference between thresholds at higher contrast levels. Fig. 2B shows MCTs for radial, rotational and translational motion as a function of speed. It can be seen that thresholds improve with higher dot speed. ANOVA with motion type and dot speed as fixed factors revealed significant effects of type ($F(2, 393) = 64.50$, $p < 0.05$) and speed ($F(8, 393) = 101.92$, $p < 0.05$). The interaction between type and speed was also significant ($F(16, 393) = 7.43$, $p < 0.05$). Post-hoc analysis of motion type and dot speed factor revealed that for speeds of 1.6°/s and below, MCTs for translational patterns was higher than for radial and rotational patterns (Bonferroni correction: $p < 0.017$). For dot speeds over 2.3°/s MCTs did not improve further and there was no significant difference between three stimuli (Bonferroni corrections: $p > 0.05$). Since there was no significant effect of medium to high contrast levels on MCT and significant effect of slow and fast dot speeds, the contrast of 75% and two dot speeds of 1.6°/s and 5.5°/s were selected for the main developmental experiment.

Fig. 3 shows motion coherence thresholds for 24 naive adult observers as a function of motion type and speed. For all motion types, MCTs were higher for 1.6°/s than for 5.5°/s. An ANOVA with speed and type of pattern as fixed factors, confirmed a significant effect of speed ($F(1, 138) = 40.9$, $p < 0.05$), but no effect of type and no interaction between speed and type of optic flow pattern ($p > 0.05$). At 1.6°/s, the threshold for translation was significantly higher than for radial optic flow ($p < 0.0167$) but there was no significant difference between the flow types at 5.5°/s ($p > 0.05$) after the Bonferroni correction.

3.2. Experiment 2: Development of radial optic flow in children

Radial optic flow sensitivity was measured as a function of age and speed. Fig. 4 shows that there is a gradual and significant improvement in MCT to radial optic flow for both speeds between the age of 6–16 years, (linear regressions: 1.6°/s ($F(1, 117) = 16.45$, $p < 0.05$, $R^2 = 0.12$); 5.5°/s ($F(1, 117) = 17.45$, $p < 0.05$, $R^2 = 0.13$). To further explore the improvement of the MCT with age and effects

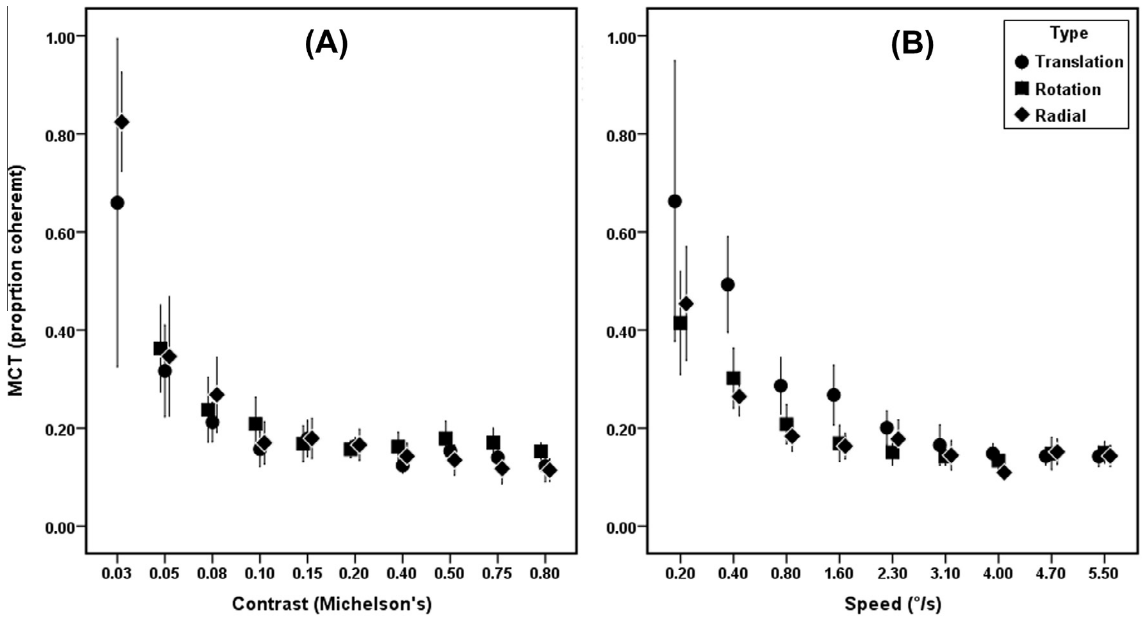

Fig. 2. Mean motion coherence thresholds (MCT) for translational, rotational and radial dot motion as a function of contrast level at 4.8°/s (A) and dot speed at 75% contrast (B) for 4 adult observers. Error bars represent 95% confidence intervals.

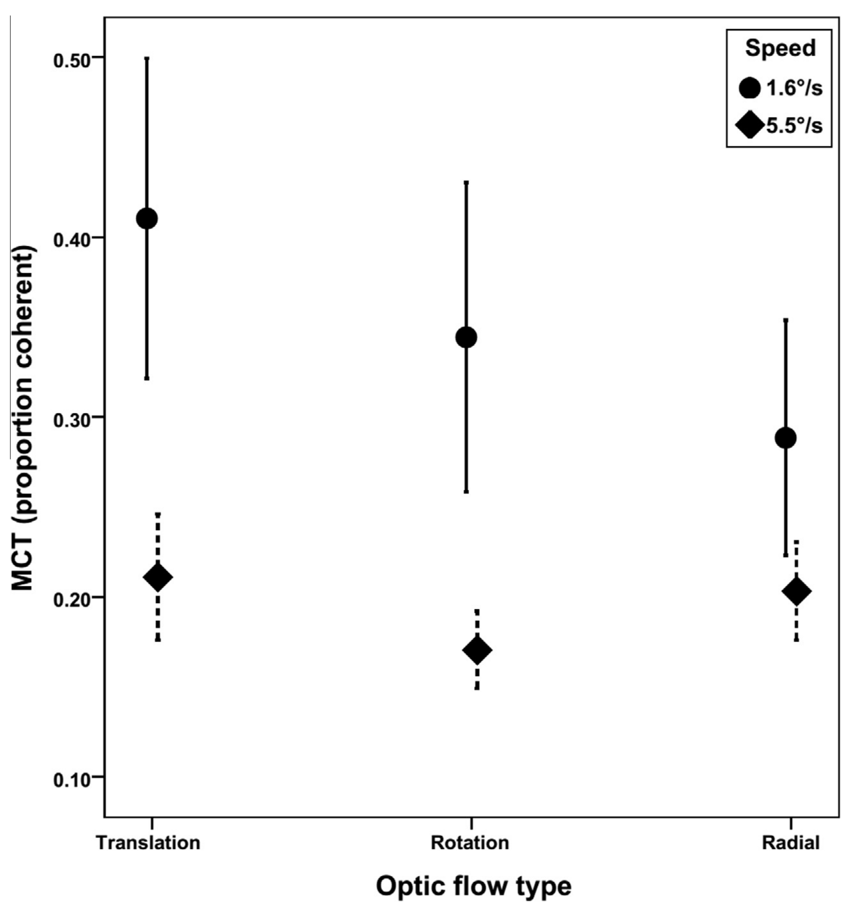

Fig. 3. Mean adult motion coherence thresholds (MCT, $n = 24$) for translational, rotational and radial optic flow with a dot motion of 1.6°/s and 5.5°/s and dot contrast of 75%. Error bars represent 95% confidence intervals.

of speed, mixed model ANOVA was conducted with age as between subject factor and speed as within subject factor. There was significant effect of both age ($F(11, 131) = 7.09$, $p < 0.05$) and speed ($F(1, 131) = 193.43$, $p < 0.05$) but no significant interaction between age and speed ($F(11, 131) = 1.75$, $p > 0.05$). Pairwise comparisons with independent *t*-test revealed significantly higher MCT for all

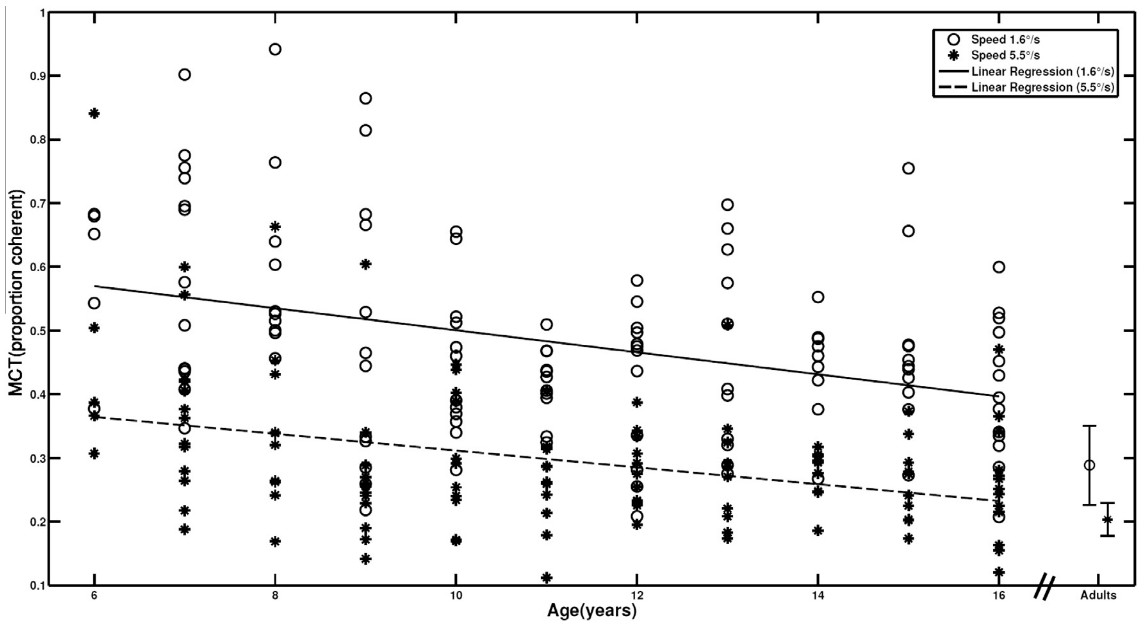

Fig. 4. Radial motion coherence thresholds (MCT) for individual children as a function of age for the two dot speeds. Lines show fitted regression lines. For comparison mean adult values ($n = 24$) with 95% confidence intervals is added to the plot.

children groups (6–16 years) at both speeds compared to adults (p's < 0.05). For all observers over 7 years of age, the MCT was better at 5.5°/s than 1.6°/s (matched paired t-test, $p < 0.05$). For the 6 years olds the difference was not significant ($p = 0.05$) due to one observer.

A bootstrapping procedure was used to investigate whether the rate of development (slope of the fitted regression lines) differed for the two speeds. The thresholds for each age group at the two speeds were used to independently sample 1000 sets of simulated mean threshold estimates in a bootstrapping analysis (Wichmann & Hill, 2001). A linear regression model was then fit to each mean data set to obtain independent slope of fits. The comparison of the slopes for two speeds showed significant difference (independent t-test, $p < 0.05$), suggesting that radial MCT develop at different rates for fast and slow speeds.

To determine how much worse children performed compared to adults, the MCT ratio for each age group was compared to adult values. Fig. 5 shows that MCTs improve in childhood, but performance is still immature at 16 years of age. A ratio of one represents equal performance to adults, and a higher ratio indicates worse performance. Children 8 years and younger are approximately two times worse than adult at both speeds, while the 16 year old are about 1.3 times worse. It can also be seen that apart from the 6 year old group, all ratios are higher for 1.6°/s compared to 5.5°/s (paired t-tests, p's < 0.05), indicating that motion direction discrimination is more difficult at slow speed than faster speed.

Similarly when the development of radial MCT were projected to adult levels, there was a significant reduction in the threshold with increasing age for both slow ($F(1, 141) = 57.23$, $p < 0.05$, $R^2 = 0.29$) and fast speed ($F(1, 141) = 34.50$, $p < 0.05$, $R^2 = 0.20$) with significantly different slope after bootstrapping ($p < 0.05$).

4. Discussion

The development of motion coherence thresholds to radial optic flow was investigated at two speeds in school-aged children. Our study shows that there is a gradual development in radial optic flow sensitivity and that 16 year olds are still immature in discriminating radial optic flow patterns. Further, the results show that children are more immature at slow speed compared to faster speed, with different rates of development.

As far as we are aware of, no other study have investigated the development of radial optic flow sensitivity in school aged children, but our results of late development complement findings that illusory self-movement (vection) is stronger in children beyond 14 years of age than in adults (Shirai, Seno, & Morohashi, 2012; Shirai et al., 2014). Since radial flow is the most commonly experienced flow type during the self-motion, the relative immaturity of radial motion discrimination would also affect any function dependent on its inputs. As we did not collect data on the development of translation optic flow, it is not possible to do a direct comparison of development of different types of optic flow patterns. Nevertheless, a wide range of studies using different stimulus parameters and procedure show that the sensitivity to translation mature between 8 and 14 years of age (Bogfjellmo, Bex, & Falkenberg, 2014; Gunn et al., 2002; Manning, Aagten-Murphy, & Pellicano, 2012; Narasimhan & Giaschi, 2012; Parrish et al., 2005; Spencer et al., 2000).

One reason for the relatively late development could be that discriminating radial optic flow is a more complex task than discriminating translational flow. Radial optic flow is processed in the visual area MST which integrates motion input from lower cortical areas (V1, MT). This is supported by studies that suggest that motion functions that require higher cortical processing mature later than those that require lower levels of processing (Ellemberg et al., 2004, 2003; Gilmore et al., 2007; Kovacs et al., 1999; Schrauf, Wist, & Ehrenstein, 1999). For example, Ellemberg et al. (2004, 2005) reported that global translational motion sensitivity (processed mainly in area MT) was more immature in 5-year-olds than local motion sensitivity (processed mainly in area V1). Similarly, dynamic visual acuity processed at area MT, reach adult levels first at the age of 15 years (Schrauf, Wist, & Ehrenstein, 1999). This suggest that the system which processes local features matures earlier than those higher functions that require the integration of input from the lower-level processing areas. It is also known that the visual cortex continues to develop even after the first decade of life. Myelination of axons, cortical

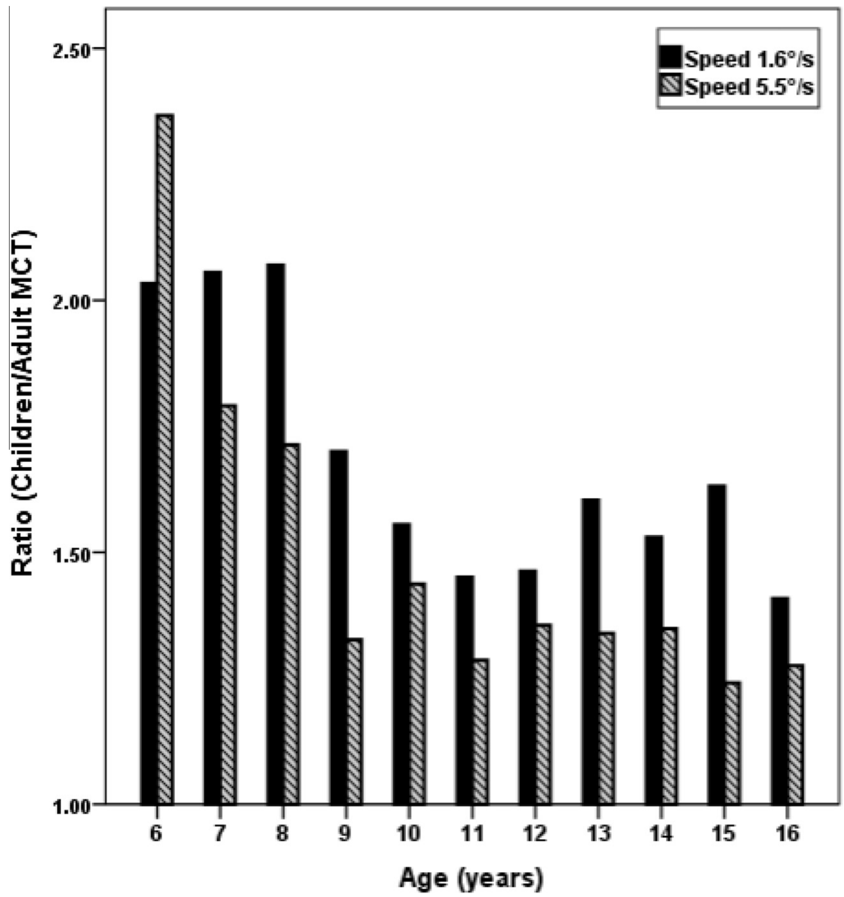

Fig. 5. Motion coherence threshold (MCT) ratios of children compared to adults as a function of age and speed.

thinning (Gogtay et al., 2004; Huttenlocher, 1990; Shaw et al., 2008) and GABAergic signaling mechanisms (Pinto et al., 2010) mature in adolescence, and that the late development is more pronounced for the motion processing pathways (Mitchell & Neville, 2004). This continual cortical development may influence the development of the direction discrimination abilities for complex global motion patterns.

Another reason for higher threshold in children than adults could be that they did not understand the task, or did not pay attention during the experiment. We do not think this explains our results. All children included in the study completed two short practice sessions before the main experiment. Also only observers with good psychometric functions fits were included in the experiment. Further, the pattern of change across age groups, as well as consistent differences in the performance at two speeds suggests that child observer were adequately able to complete the task. We therefore believe that improvement with age seen in this study is due to development of global motion pattern sensitivity.

Both children and adults show lower sensitivity to optic flow at the lowest speed. In addition, the results show that the rate of development for radial optic flow differs for the two speeds. This add to what has already known for both local and global motion (Ahmed et al., 2005; Armstrong, Maurer, & Lewis, 2009; Bogfjellmo, Bex, & Falkenberg, 2014; Ellemberg et al., 2004; Hadad, Maurer, & Lewis, 2011; Narasimhan & Giaschi, 2012). Manning, Aagten-Murphy, and Pellicano (2012) showed that speed discrimination thresholds reached adult levels earlier for the faster (6°/s) than slower speeds (1.5°/s). In contrast, Hadad, Maurer, and Lewis (2011) found that motion coherence thresholds matured by the age of 12–14 years irrespective of speed. The discrepancy could be explained that all/both speeds used in by Hadad et al. were relatively fast 4°/s and 18°/s. Other motion-based visual functions such as motion-defined form perception also matures earlier for relatively faster speeds (Hayward et al., 2011), in line with our results.

Higher sensitivity to faster speed could be explained by separate speed processing mechanisms for slow and fast optic flow patterns, which have previously been suggested (Edwards, Badcock, & Smith, 1998; Khuu & Badcock, 2002), or by a single channel tuned for differential sensitivity at various speeds (van Boxtel & Erkelens, 2006). It could also be due to more neurons in higher cortical areas, such as MT, tuned to faster speeds. This is supported by neurophysiological evidence which show that areas MT and MST contains a high proportion of neurons tuned to faster speeds (Duffy & Wurtz, 1991). Primate studies also show that monkeys from the age of 10 days demonstrate better sensitivity to fast motion, with sensitivity to all speeds continuing to develop beyond 3 years of age (Kiorpes & Movshon, 2004). In addition, primates with amblyopia display larger motion defect for slow compared to faster speed, indicating a later development of the sensitivity to the slow speed (Kiorpes, Tang, & Movshon, 2006). Our results supports the findings that speed processing of complex motion patterns may involve independent mechanisms that develop at different rates.

5. Conclusion

Sensitivity to radial optic flow continues to improve gradually between 6 and 16 years of age, and is still immature in 16 year olds. Both children and adults show higher sensitivity to the faster speed. In addition, the rate of development differs for the two speeds, indicating that fast and slow speeds could be processed by different motion mechanisms.

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