The development of speed discrimination abilities

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ABSTRACT

The processing of speed is a critical part of a child's visual development, allowing children to track and interact with moving objects. Despite such importance, no study has investigated the developmental trajectory of speed discrimination abilities or precisely when these abilities become adult-like. Here, we measured speed discrimination thresholds in 5-, 7-, 9-, 11-year-olds and adults using random dot stimuli with two different reference speeds (slow: 1.5 deg/s; fast: 6 deg/s). Sensitivity for both reference speeds improved exponentially with age and, at all ages, participants were more sensitive to the faster reference speed. However, sensitivity to slow speeds followed a more protracted developmental trajectory than that for faster speeds. Furthermore, sensitivity to the faster reference speed reached adult-like levels by 11 years, whereas sensitivity to the slower reference speed was not yet adult-like by this age. Different developmental trajectories may reflect distinct systems for processing fast and slow speeds. The reasonably late development of speed processing abilities may be due to inherent limits in the integration of neuronal responses in motion-sensitive areas in early childhood.

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1. Introduction

Children develop in a dynamic world, with retinal motion constantly being invoked by eye movements, self-motion and moving objects. Motion information also contributes to a range of other visual functions such as scene segmentation, perception of depth, registering trajectories and identifying objects. The ability to process such information is therefore an integral part of visual development.

The development of many aspects of motion processing has been well studied, such as directional selectivity, optokinetic responses, segmentation from motion, optic flow responses and coherent motion perception (see Braddick, Atkinson, and Wattam-Bell (2003) for review). One aspect that has received little attention, however, is children's ability to discriminate the speed of moving objects. The speed of a moving object needs to be coded in order to keep the object focused on the retina and to direct accurate reaches and grasps towards the object. Also, locomotion requires an accurate representation of the relative speeds of objects in the visual scene. The ability to process speeds should also have real-world implications, such as in making judgments about whether to cross a road, which critically relies on the perception of how fast a vehicle is moving. Understanding how speed discrimination develops in children is therefore vital.

Much is known about the speed processing abilities of adults, including the way that speed is perceived and discriminated, in which neural regions it is coded, and the nature of such representations. Human adult observers can discriminate differences in speeds as small as 5–7% of the reference speed (de Bruyn & Orban, 1988). Adult speed discrimination thresholds show a U-shaped dependence on the reference speed used, with optimal discrimination between 4 and 64 deg/s, and lower sensitivities to speeds above and below this range (de Bruyn & Orban, 1988).

Single neuron recordings have revealed a proportion of speed-tuned cells in primate area MT (Lagae, Raiguel, & Orban, 1993; Liu & Newsome, 2003; Maunsell & Van Essen, 1983; Perrone & Thiele, 2001; Priebe, Cassanello, & Lisberger, 2003) and MT lesions lead to impaired speed discrimination of macaques (Orban, Saunders, & Vandenbussche, 1995). Additionally, microstimulating MT can bias the speed judgments of rhesus monkeys (Liu & Newsome, 2005). Studies with human adults also confirm a role of MT/V5 in speed processing. A functional Magnetic Resonance Imaging (fMRI) study revealed higher activity in MT during a speed discrimination task than a contrast discrimination task (Huk & Heeger, 2000), and a Positron Emission Tomography (PET) study reported more activity in the middle temporal area during attention to speed compared to attention to shape or colour (Corbetta et al., 1991).

Many models have been proposed for how speed is represented in the brain (see Burr and Thompson (2011) for review), including

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spatiotemporal energy models (e.g., Adelson & Bergen, 1985), ratio models (e.g., Harris, 1986; Smith, 1987; Smith & Edgar, 1994) and Bayesian models (e.g., Ascher & Grzywacz, 2000; Weiss, Simoncelli, & Adelson, 2002). Despite varying in their precise computations, there is a consensus amongst theorists that speed cannot be coded by single neurons alone, but by populations of neurons (e.g., Churchland & Lisberger, 2001). Therefore, we can expect performance in speed discrimination tasks to rely on integration of signals in motion-sensitive areas such as area MT.

Much less is known about the way that speed processing abilities develop both behaviourally and neurally. Studies with human infants suggest that there is a differential sensitivity to distinct speeds even early in development. Volkmann and Dobson (1976) reported that the fixation preferences of 1-, 2- and 3-month-old infants for a dynamic checkerboard over a stationary checkerboard were stronger for rapid rates of movement (up to 31 deg/s) than slower rates of movement. Furthermore, Aslin and Shea (1990) found that 6-week-old infants could not discriminate stationary stripes from stripes moving slower than 9 deg/s, whereas 12-week-old infants could not discriminate stationary stripes from those moving under 4 deg/s. It therefore seems that, in the first few months of life, sensitivity to slow moving stimuli is less mature than sensitivity to faster moving stimuli, but that there is a reasonably rapid development of sensitivity.

There is only one existing study that has investigated speed discrimination in childhood. Ahmed et al. (2005) compared the speed discrimination thresholds of 5-year-olds ($n = 48$) and adults ($n = 48$) using sinusoidal grating stimuli for both a reference speed of 1.5 and 6 deg/s. They found that 5-year-olds were immature in their discrimination abilities for both reference speeds, but that they were disproportionately worse at the slower reference speed. Ahmed et al. suggested that there was a less rapid development of sensitivity for slow speeds than that for faster speeds, offering some continuity from infant studies. Ahmed et al. (2005) further suggested that developmental changes in speed discrimination abilities might reflect changes within MT. Specifically, they proposed a population coding explanation for a differential rate of development for slow and faster speeds. Neurons encoding speeds might be less sharply tuned in children than adults, but as there are fewer neurons tuned to slow speeds (at least in adult monkeys; Liu & Newsome, 2003), such immature tuning may have a greater effect on discriminating slower than faster speeds, leading to different rates of development.

Yet Ahmed et al. (2005) assessed only one age group of children (5-year-olds) in their study and were therefore unable to test the possibility of different *rates* of development for discriminating slow and fast speeds. Indeed, one alternative possibility is that sensitivities to slow and faster speeds follow *similar* developmental rates but that the onset of sensitivity to certain (e.g., slow) speeds may lag behind the onset of sensitivity to other (e.g., faster) speeds, resulting in different ages of adult-like sensitivity being reached. Furthermore, Ahmed et al. manipulated reference speed between participants, rendering it possible that the particularly poor performance of 5-year-olds for the slow reference speed may be attributable, at least in part, to cohort effects.

The current study therefore measured the speed discrimination thresholds of 5-, 7-, 9-and 11-year-old children and adults using a child-friendly, developmentally-sensitive procedure. We addressed two key aims: (1) to investigate the developmental trajectory of speed discrimination abilities, and (2) to determine the age at which these abilities become adult-like. We used a 2-interval-forced choice (2-IFC) procedure using the same reference speeds as Ahmed et al. (2005), but made three main modifications to their experimental paradigm. First, whereas Ahmed et al. manipulated reference speed between participants, the current study manipulated reference speed within a stronger, within-participants de-

sign. Second, Ahmed et al. used sinusoidal grating stimuli with constant spatial frequency, causing temporal frequency to vary directly with speed and therefore making it possible that developmental differences reflected temporal sensitivity rather than speed sensitivity per se. We therefore used random dot stimuli in order to eliminate the consistent relationship between temporal frequency and speed and to preclude the possibility of using counting strategies. Finally, we attempted to reduce adaptation effects by randomising the location of stimuli and direction of motion between trials.

The current study allowed us to test Ahmed et al.'s claim that sensitivities to slow and fast speeds follow different developmental rates, with sensitivities to slow speeds showing a slower rate of development than sensitivities to faster speeds. It also enabled us to investigate whether the age at which maturity is reached is different for sensitivities to slow and fast speeds. It is difficult to predict precisely the point at which sensitivity to speed discrimination might become adult-like. It is possible that speed discrimination might mature at a similar developmental time-point as other aspects of motion processing that require integration of MT neurons' responses, such as motion coherence (Britten et al., 1992). Coherence thresholds for random dot stimuli appear to follow a protracted developmental trajectory, with reports of adult-like levels being reached somewhere between 10 and 13 years old for stimuli moving between 4 and 18 deg/s (Gunn et al., 2002; Hadad, Maurer, & Lewis, 2011). Yet the minimum speed thresholds for motion-defined form perception and the maximum displacement for which directional motion can be perceived matures somewhat earlier, by 7–8 years (Hayward et al., 2011; Parrish et al., 2005). We therefore hypothesised that speed discrimination should also mature during mid childhood, with sensitivities to the slower reference speed maturing later in this period.

2. Method

2.1. Participants

Five groups of participants were tested, with 20 5-year-olds ($M = 5$ years; 6 months, range 4;11–6;1, 9 females), 21 7-year-olds ($M = 7$ years; 4 months, range 6;11–7;11, 11 females), 21 9-year-olds ($M = 9$ years; 4 months, range 8;11–9;9, 11 females), 20 11-year-olds ($M = 11$ years; 5 months, range 10;9–11;10, 10 females) and 18 adults ($M = 22$ years; 6 months, range 18;5–28;2, 9 females) included in the final dataset. Children were recruited from schools in Surrey, UK. Normal or corrected-to-normal visual acuity was confirmed by binocular testing with the Cambridge Crowding cards for children and with a Snellen acuity chart for adults, using optical corrections where necessary. Normal acuity was defined as a binocular crowded-letter acuity of 6/9 or better for 5- and 7-year-olds (because acuity is still maturing in this age range; Adams & Courage, 2002; Ellemberg et al., 1999) and 6/6 or better for 9- and 11-year-olds. All adults had binocular Snellen acuities of 20/12 or better.

An additional seven 5-year-olds were excluded from the dataset, with one child failing to pass the visual acuity screening, two not completing both reference speed conditions, one failing to reach criterion (see Section 2.3.2) and three being excluded due to poorly fitting psychometric functions either in the fast condition ($n = 2$) or both conditions ($n = 1$) (see Section 2.5). Six additional 7-year-olds were not included in the final dataset, with one participant failing to complete both conditions, two failing to reach criterion, and three having poorly fitting psychometric curves in either the slow ($n = 2$) or fast ($n = 1$) reference speed conditions. Finally, three 9-year-olds were also excluded, with two failing to pass the acuity criterion, and one reporting having abnormal binocular vision.

2.2. Apparatus and stimuli

The stimuli were presented using MATLAB (The Mathworks Ltd.) using elements of the Psychophysics Toolbox software (Brainard, 1997; Kleiner, Brainard, & Pelli, 2007; Pelli, 1997). Stimuli were displayed on a Philips 107E CRT monitor measuring 34.03° × 25.91° when viewed at a distance of 50 cm, controlled by a Dell Precision M6500 laptop. The monitor had a frame rate of 80 Hz with a pixel resolution of 1024 × 768.

The screen was black with a central rocket-shaped fixation point (1.54° × 3.12°) with a red square border (11° × 11°) to the left and a blue square border (11° × 11°) to the right of fixation. The colour of the fixation point marked different trial events: green to prompt participants to fixate before the trial commenced, red to signal stimulus presentation during test trials, and yellow for when participants were making their response (see Fig. 1). The stimuli were white random dot patterns moving with 100% motion coherence for 1000 ms (120 monitor refreshes) in either border (red, blue). Dots were displaced 0.0125 or 0.05 deg/frame in the slow (1.5 deg/s) and fast (6 deg/s) reference speed conditions, respectively. Each dot was 0.34° in diameter and there were 100 dots in each stimulus. The dots had a limited lifetime of 12 monitor refreshes (approximately 150 ms), with each dot displayed at the beginning of a trial being randomly assigned a starting life. On reaching its decay lifetime, each dot was replaced by another dot in a new random location, maintaining a constant dot density of 0.83 dots/deg^2.

2.3. Procedure

Following Abramov et al. (1984), the task was presented in the context of a fun space-related game. Participants completed two "games", one for each of two reference speed conditions similar to Ahmed et al. (2005): 1.5 deg/s (or "slow-moving stars") and 6 deg/s (or "fast-moving stars"). The order of presentation of conditions was counterbalanced across participants. Within each game, there was an initial introductory phase followed by three levels: a criterion phase ("level 1" in the space game), a practice phase ("level 2"), and a threshold estimation phase ("level 3"). In all phases, a trial consisted of a pair of stimuli (a reference and comparison stimulus) presented sequentially, with a stimulus in the left (red) border followed by a stimulus in the right (blue) border and vice versa (see Fig. 1). The direction of motion (leftwards, rightwards) was the same for both stimuli within a trial, but randomised across trials.

2.3.1. Introductory phase

Participants were shown an animation depicting a blue and a red rocket in a space scene. They were told that they would have to judge which rocket was moving faster based on how fast the "stars" travelled past the windows of the rockets. To aid motivation, children were told that they were competing against a cartoon character, "Astro". The experimenter used hand gestures to demonstrate to participants that they should judge the overall motion of the stimulus rather than the rate the dots decayed (or "twinkled"). Pilot testing showed that the 5-year-old participants showed some difficulties understanding this part of the procedure. They were therefore presented with a demonstration trial with one stimulus moving very slowly (0.1 deg/s) and the other moving more rapidly (7 deg/s or 18 deg/s). This additional trial helped to illustrate the point to the youngest age group, whereas verbal and gestural descriptions appeared sufficient for the older age groups.

2.3.2. Criterion phase

Participants were instructed to fixate the coloured central fixation point throughout stimulus presentation. The experimenter continuously monitored participants' eye movements, providing regular reminders to maintain central fixation and initiated trials only when the participant was attending. Following Ahmed et al. (2005), the comparison speed was 7 deg/s in the slow reference speed (1.5 deg/s) condition and 18 deg/s in the faster reference speed (6 deg/s) condition. The order of presentation of the reference and comparison stimulus was randomised on each trial. Participants were shown a pair of stimuli and asked whether the "stars" moved faster in either the blue or red "window". They responded either verbally or by pointing and the experimenter pressed the corresponding response key. Visual and verbal feedback and encouragement were provided. The number of trials needed to reach a criterion of four consecutive correct responses was recorded. Those participants who failed to reach criterion after 20 trials (n = 3) were given a short version of the task and excluded from further analyses.

2.3.3. Practice phase

The procedure was the same as in the criterion phase, but included eight trials and comparison speeds fixed at eight percentages of the reference speed in a fixed order (300%; 25%; 250%; 50%; 200%; 75%; 150% and 90%). Participants received feedback as before, but there was no criterion for proceeding to the next level in this phase.

2.3.4. Threshold estimation phase

The threshold was estimated using the QUEST technique (Watson & Pelli, 1983). Four QUEST functions ran interleaved with a 2 × 2 design, varying both temporal order (reference speed presented first vs. comparison speed presented first) and starting
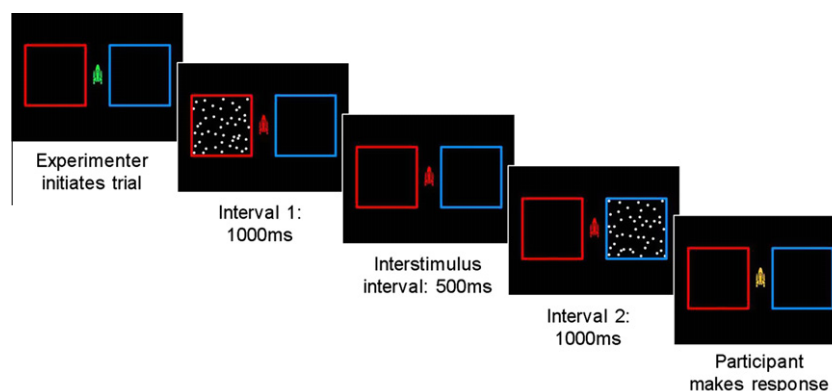

Fig. 1. Schematic representation of a single trial structure. Red (left) and blue (right) borders and a rocket-shaped fixation point remain on the screen throughout the trial. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

speed (above vs. below reference speed). Two QUEST functions therefore started with an initial comparison speed of 25% of the reference speed (0.38 deg/s for the slow condition, and 1.50 deg/s for the fast condition) and two QUEST functions started with an initial comparison speed of 175% of the reference speed (2.63 deg/s for the slow condition, and 10.50 deg/s for the fast condition). Each QUEST consisted of 20 trials, yielding 80 trials in total for each speed condition (slow, fast). Each QUEST had a beta value of 3 and a lapse rate set to 0.01.

As recommended by Watson and Pelli (1983), a random 'jitter' was added to values suggested by the QUEST, of up to plus or minus 0.75 deg/s and 1.5 deg/s for the slow and fast conditions, respectively. The values suggested by the QUEST were limited to a range between 0.05 and 15 deg/s to ensure that (a) slow-moving stimuli were not completely static and (b) fast-moving stimuli were presented within the limits of the screen's temporal resolution. No feedback was given regarding performance, although the experimenter gave general encouragement throughout (e.g., "You're doing so well!"). A short break was given after a block of 20 trials in which the participant was shown a simulated graph of the "points" s/he and Astro had attained. These points were fixed for all participants to minimise reward and motivation effects on threshold estimates.

2.4. General procedure

The procedure was approved by the Institute's Faculty Research Ethics Committee. All adult participants and parents of child participants gave their informed consent, and children provided their verbal assent. Children were seen individually either at school in two or three sessions each lasting approximately 15 min, or in a single session outside school. Adults were generally seen on one occasion only. Participants were tested binocularly in a darkened room seated at a distance of approximately 50 cm from the computer monitor. They were given a 'Space Cadet Training Record' with which they recorded their progress through the experimental session.

2.5. Data analysis

Trials at the extremes of the QUEST range were excluded from analysis, resulting in a mean number of trials of 71.66 (SD: 4.43) and 76.55 (SD: 2.40) in the slow and fast conditions, respectively. Each participant's data for each condition were bootstrapped (Efron & Tibshirani, 1993), drawing N random samples (with replacement) from the data of a particular condition (where N is the number of trials). Next, these sampled data were fit with a cumulative Gaussian function, using the 'maximum likelihood' (MLH) fitting method described by Watson (1979) to obtain an estimate of the slope in log units. This procedure was repeated 10,000 times, and the average slope and standard error of the slope were calculated. All analyses were conducted with the average slope values in log units and, for comparability to previous studies (e.g., Ahmed et al., 2005), converted to Weber fractions using the following formula: Weber fraction = $10^{(slope)} - 1$. Mean Weber fractions for each group are plotted in Fig. 2.

Preliminary data screening was conducted on the individual psychometric curves. Participants whose fits were unable to account for more than 30% of the variance in the data (bootstrapped R^2 value <0.30) in one or both conditions were excluded, as they were deemed to represent participants who were unable to perform the task adequately. Finally, the data were screened for potential outliers. z scores were calculated using the mean slope values and standard deviations for each age group in each condition. Outliers were identified as data-points with z scores of absolute values above 3. Screening revealed two such outlying points:
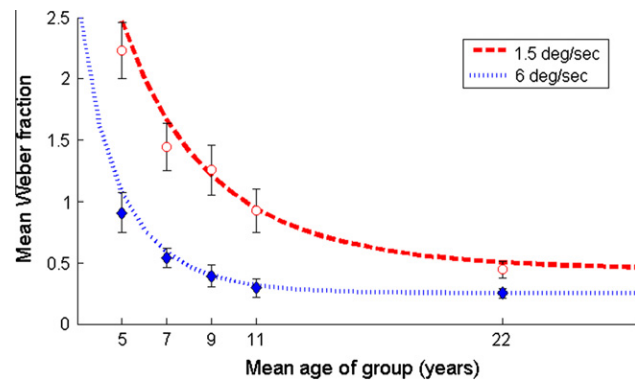

Fig. 2. Mean Weber fractions for speed discrimination for a slow (1.5 deg/s) (open circles) and faster (6 deg/s) (filled diamonds) reference speed as a function of age. Error bars represent ±1 standard error of the mean (SEM). Red dashed and blue dotted lines represent the best-fitting exponential curves for the slow reference speed condition [$y = 0.94 \times \exp(-0.18x) + 0.16$, $R^2 = 0.31$] and faster reference speed condition [$y = 1.45 \times \exp(-0.38x) + 0.10$, $R^2 = 0.33$], respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

one for a 9-year-old and one for an 11-year-old in the fast condition. Removing these outliers did not change the pattern of the ANOVA results and so we retained these points in the sample to increase statistical power but replaced the outlying scores with slope values corresponding to a z score of ±2.5 (Tabachnick & Fidell, 2007).

3. Results

Examination of Fig. 2 suggests that there were age-related improvements in sensitivity for both reference speeds, with greater sensitivity to the faster reference speed (6 deg/s) than the slow reference speed (1.5 deg/s) at all ages. This pattern was confirmed with a mixed-design ANOVA on raw thresholds with age group (5, 7, 9, 11 years and adults) as the between-participants factor and reference speed condition (1.5 and 6 deg/s) as the within-participants factor. A preliminary analysis revealed a non-significant effect of order of reference speed presentation (fast first, slow first), $F(1,90) = 3.79$, $p = .06$, $\eta^2 = .04$. Importantly, order did not have a significant interacting effect with reference speed condition, $F(1,90) = .52$, $p = .47$, or age group $F(4,90) = 1.10$, $p = .36$, so this factor was not included in the main analysis.

As expected, there was a significant main effect of speed, $F(1,95) = 130.23$, $p < .01$, $\eta^2 = .58$, with the slower reference speed condition yielding higher mean thresholds than the faster reference speed (slower: $M = 1.20$, SD = 0.59; faster: $M = 0.46$, SD = 0.30), suggesting greater sensitivity to speed differences in the faster condition. There was also a significant main effect of age group, $F(4,95) = 14.42$, $p < .01$, $\eta^2 = .38$, with mean raw thresholds decreasing with age, suggesting age-related improvements in sensitivity to speed differences (5-year-olds: $M = 1.48$, SD = 0.45; 7-year-olds: $M = 0.94$, SD = 0.27; 9-year-olds: $M = 0.77$, SD = 0.33; 11-year-olds: $M = 0.58$, SD = 0.28; adults: $M = 0.34$, SD = 0.09).

These main effects were qualified by a significant interaction between speed condition and age group, $F(4,95) = 3.47$, $p = .01$, $\eta^2 = .13$. To determine the source of this interaction we first examined whether the difference between reference speed conditions was significant within each age group. Planned t-tests confirmed that the thresholds were elevated for slow compared with fast speeds for all age groups (5-year-olds: $t(19) = 5.91$, $p < .01$; 7-year-olds: $t(20) = 4.92$, $p < .01$; 9-year-olds: $t(20) = 5.80$, $p < .01$; 11-year-olds: $t(19) = 5.94$, $p < .01$; and adults: $t(17) = 3.74$, $p < .01$).

Next, we examined whether the magnitude of the difference between reference speed conditions varied as a function of age group

using repeated planned contrasts. These analyses showed that the degree of difference in thresholds between fast and slow reference speed conditions did not differ between 5- and 7-year-olds, $t = 0.60$, $p = .55$, 7- and 9-year-olds, $t = -0.20$, $p = .84$ and 9- and 11-year-olds, $t = 0.78$, $p = .44$, but did differ between 11-year-olds and adults, $t = 2.21$, $p = .03$, where 11-year-olds showed a greater difference between sensitivities for the fast and slow speed conditions than adults. The interaction between age group and reference speed condition therefore appears to be driven by differences between 11-year-olds and adults.

We further examined age-related improvements within each reference speed condition. As expected, one-way ANOVAs revealed main effects of age group for slow, $F(4,95) = 10.81$, $p < .01$, $\eta^2 = .31$, and fast, $F(4,95) = 11.96$, $p < .01$, $\eta^2 = .34$, speed conditions. To determine the point at which sensitivity to speed differences reaches adult-like levels for each reference speed condition, the thresholds of the adult group were compared with each of the other groups using a bootstrap sign test (Ross & Burr, 2010), which has the advantage of making very few assumptions about the underlying distributions under test. For the slow reference speed condition, adults had significantly lower mean thresholds than 5-year-olds, $p < .01$, 7-year-olds, $p < .01$, 9-year-olds, $p < .01$ and 11-year-olds, $p < .01$. For the fast reference speed condition, adults had significantly lower mean thresholds than 5-year-olds, $p < .01$, 7-year-olds, $p < .01$, and 9-year-olds, $p < .01$, but their performance was not significantly different to 11-year-olds, $p = .11$. These results therefore suggest that sensitivity is adult-like by 11 years of age for the fast but not the slow reference speed.

Finally, we examined the *rates* of development in the discrimination of slow- and faster-moving speeds. To address this issue, the data were best fit with exponential curves that captured the plateau at adult levels for each condition, using the mean adult threshold level as a constant in the equation. Note that without this constant, the exponential equation failed to capture the tail-ends of the data, and underestimated the thresholds of the 5-year-old and adult groups (i.e., predicting higher sensitivity than obtained). Sensitivity therefore increased exponentially with age for both slow speeds, $y = 0.94 \times \exp(-0.18x) + 0.16$, $R^2 = 0.31$, and faster speeds, $y = 1.45 \times \exp(-0.38x) + 0.10$, $R^2 = 0.33$. The best-fitting curves for the slow and fast condition are shown as dashed lines and dotted lines, respectively, in Fig. 2. The slope value for the exponential curve of the slow reference speed (−0.18) fell outside the 95% confidence intervals defined for the fast reference speed condition (−0.21 to −0.55), suggesting that the slope of the function relating sensitivity to age was significantly less steep for the slow compared to the fast condition.

4. Discussion

This study investigated the sensitivities of children aged 5, 7, 9 and 11 years and adults to differences in speed from two reference speeds (slow: 1.5 deg/s; faster: 6 deg/s). At all ages tested, thresholds varied with reference speed, as previously shown in adults (e.g., Bravo & Watamaniuk, 1995; de Bruyn & Orban, 1988; Johnston, Benton, & Morgan, 1999; McKee, Silverman, & Nakayama, 1986) and 5-year-olds (Ahmed et al., 2005). Children and adults obtained lower Weber fractions (i.e., increased sensitivity) for speed discrimination at a reference speed of 6 deg/s compared with a slower reference speed of 1.5 deg/s.

We were especially interested, however, in the nature of the developmental trajectories for each reference speed, and when sensitivity to each reference speed reaches adult-like levels. As expected, we found age-related improvements in speed discrimination thresholds for both reference speed conditions. Furthermore, consistent with Ahmed et al.'s (2005) results, we found a signifi-

cant interaction between age group and reference speed condition, suggestive of a more rapid rate of development for sensitivity to faster speeds compared to sensitivity to slow speeds. In addition, our results revealed that sensitivity to speed differences reaches adult-like levels earlier in development for faster speeds than slower speeds, which matures at some point after 11 years.

At all ages, participants were less sensitive to speed differences from a slow than a faster reference speed, suggesting that non-visual factors, such as attention, motivation, memory and response biases (e.g., Abramov et al., 1984; Bradley & Freeman, 1982), or even differences in the ability to maintain fixation with age (e.g., Ross et al., 1994), were unlikely to be a substantial limiting factor on performance. Furthermore, our careful data screening removed unreliable thresholds, which may have arisen from inattention or strong response biases. We are confident, therefore, that the developmental improvements in sensitivity observed here reflect true differences in speed discrimination abilities.

It should be noted that the Weber fractions obtained in the current study are higher than those reported by Ahmed et al. (2005). This discrepancy may be attributable to (a) genuine differences between mechanisms used to code moving dots and the grating stimuli employed by Ahmed et al. (see Braddick (1974), de Bruyn and Orban (1988), McKee and Nakayama (1984), and Nakayama and Tyler (1981) for discussion); (b) greater adaptation effects in Ahmed et al.'s study due to their centrally presented stimuli always moving in the same direction, leading to overall lower speed discrimination thresholds (Clifford & Wenderoth, 1999); and (c) the fact that Ahmed et al.'s task required participants to discriminate a comparison speed that was always above the reference speed, while the current study examined discrimination both above and below a reference speed. Therefore, subtle methodological differences may have contributed to a discrepancy in absolute Weber values between the current study and that of Ahmed et al. However, such a discrepancy does not detract from our findings of *relative* improvements in Weber fractions with age, since all our participants received the same task under similar conditions.

Our developmental findings have important implications for models of speed perception (e.g., Adelson & Bergen, 1985; Ascher & Grzywacz, 2000; Harris, 1986; Smith, 1987; Smith & Edgar, 1994; Weiss, Simoncelli, & Adelson, 2002), which have been driven almost exclusively by such perception in adults. Specifically, our results suggest that (1) speed discrimination has a reasonably protracted developmental trajectory, reaching adult levels only by mid-to-late childhood, (2) sensitivity to slow speeds shows a more gradual rate of development than that to fast speeds, and (3) sensitivity to slower speeds takes longer to reach adult-like maturity than sensitivity to faster speeds. Any model of speed processing must therefore address these findings.

While motion areas such as MT are recruited from the first few months of life (see review by Braddick, Atkinson, and Wattam-Bell (2003)), it appears that the mechanisms underlying speed discrimination take a relatively long time to reach adult levels of functioning. Ahmed et al. (2005) suggested that MT neurons were less sharply tuned to speeds in children than adults, but that this had a greater effect on discrimination at slow speeds as there are fewer neurons encoding slower speeds than encoding faster speeds. Indeed, different developmental trajectories may be indicative of two distinct systems for processing slow and faster speeds (e.g., Burr, Fiorentini, & Morrone, 1998; van de Grind et al., 2001).

Ahmed et al.'s explanation is consistent with ratio models or Bayesian accounts of speed perception. According to ratio models (e.g., Smith & Edgar, 1994; Thompson, Brooks, & Hammett, 2006), speed is computed by comparing the activity of two or more channels. In this case, age-related improvements in speed discrimination ability cannot be accounted for by changes in responsiveness of these channels individually, but by developmental changes in

the ratio between them. A differential effect of the tuning on different-sized neuronal populations may change this ratio. However, there is no consensus among ratio models as to what these channels might be [e.g., low- and high-speed channels (Thompson, Brooks, & Hammett, 2006), transient-type and sustained-type V1 neurons (Perrone & Thiele, 2002) or magnocellular and parvocellular channels (Hammett et al., 2005; Perrone, 2005)]. The nature of the channels might well need to be resolved before one considers how these might change with development.

Ahmed et al.'s (2005) explanation also shares similarities with Bayesian models of speed perception (e.g., Ascher & Grzywacz, 2000; Weiss, Simoncelli, & Adelson, 2002). When there are fewer neurons contributing to the population response, the population response itself will have a wider distribution and so discrimination will be less reliable. Noise in the network may therefore have a disproportionate effect on discrimination of slow speeds than faster speeds. Priors (e.g., Weiss, Simoncelli, & Adelson, 2002) might also play an important role in developmental improvements in sensitivity by improving signal-to-noise ratios. Modelling developmental data may help to disentangle the relative contributions of development of the sensory receptors and of priors in age-related improvements in speed discrimination.

The development of neurons in motion areas such as MT is therefore a possible candidate mechanism both for improved speed discrimination and global motion coherence with age (e.g., Britten et al., 1992; Orban, Saunders, & Vandenbussche, 1995; Perrone & Thiele, 2001), and could explain why there are similarities in the development of these two abilities. Like the speed discrimination thresholds reported here, global motion coherence thresholds are also dependent on stimulus speed, with 5-year-olds having higher thresholds at a speed of 1.5 deg/s than 6 deg/s (Ellemberg et al., 2004). Conversely, local motion processing, which does not require integration, develops earlier and does not appear to be speed-dependent. For example, direction discrimination is equally good at 1.5 and 6 deg/s in 5-year-olds (Ellemberg et al., 2003).

Interestingly, Hadad, Maurer, and Lewis (2011) did not find different rates of development for motion coherence thresholds for random dot stimuli moving at 4 deg/s and 18 deg/s. However, for a motion-defined form task, Hayward et al. (2011) reported greater immaturity in sensitivity at the slowest speed tested (0.1 deg/s) compared to faster speeds of 0.9 and 5 deg/s. Together, this body of research suggests that the development of motion processing for intermediate and high speeds may follow similar rates of development, but with a slower rate of development being found with much slower speeds (e.g., 1.5 deg/s and 0.1 deg/s). The integration of neuronal responses is a possible commonality that may limit the development of both global motion perception and speed discrimination, particularly at slower speeds, where fewer neurons potentially contribute to the population response. Investigating the relationship between speed discrimination and global motion coherence thresholds during development is therefore a worthwhile avenue for future research.

The current findings and the putative neural mechanisms underpinning the development of speed processing raise additional questions about speed perception more broadly. First, why has the visual system not evolved to pool neurons encoding slow speeds over a wider area in order to allow more reliable discrimination at slower speeds? Perhaps there is some difference in the relative importance of processing fast and slow speeds. Objects moving slowly across the retina may either be actually moving at a slow speed, or they may be a long distance away, both giving the observer a long time to prepare a response to the object. In contrast, objects moving fast across the retina may be more immediate, where it is important to reliably judge the speed in order to organise a response to it.

Second, the processing of visual motion is often thought to be an important part of visual processing, serving many functions such as determining self-motion, segmenting the visual scene, and processing form-from-motion. It is therefore somewhat remarkable that a particular aspect of visual motion processing – speed processing – reaches adult-like levels of ability reasonably late in development. If children have difficulties perceiving the speed of moving objects, this may lead to difficulties in interacting with objects, such as catching balls, and in safely crossing a road. It is possible, however, that the current study underestimates speed processing abilities in children. In everyday life, children are able to track objects and may make use of additional cues such as temporal frequency information, position cues and static reference points. Future research could assess the use of different cues, and the weighting of such cues, by children at different points in development.

In sum, this study extends that of Ahmed et al.'s (2005) and is the first study probing the developmental trajectory of speed discrimination abilities. We have established that sensitivity to a slow reference speed develops slower and becomes adult-like later than sensitivity to a faster reference speed. More research is needed to study the development of speed discrimination, such as in assessing whether the U-shaped dependence on speed reported in adults (e.g., de Bruyn & Orban, 1988) is present throughout development. Furthermore, such developmental findings need to inform models of speed processing, which currently treat the system as static and unchanging. Developmental models should indeed help to validate and refine adult models of speed perception.

Acknowledgments

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