VISION

Vision Research 62 (2012) 102-107

Contents lists available at SciVerse ScienceDirect



Vision Research

journal homepage: www.elsevier.com/locate/visres

The effect of dot speed and density on the development of global motion perception

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ARTICLE INFO

Article history: Received 28 October 2011 Received in revised form 3 February 2012 Available online 11 April 2012

Keywords: Global motion perception Visual development Speed Density Psychophysics

1. Introduction

Global motion perception represents one of the fundamental aspects of visual processing. It refers to the ability to combine local motion signals into a global percept in order to obtain speed and direction information. Global motion perception has typically been studied using random-dot kinematograms (RDKs) (Nakayama, 1985). The RDK stimulus facilitates the measurement of global motion perception even in the absence of form and position information. The RDK stimulus consists of signal dots that move coherently in one direction and noise dots that move in random directions. The task is to identify the overall direction of motion. Performance is most commonly measured as a motion coherence threshold: the minimum proportion of signal dots required for correct identification of the global motion direction (Newsome & Paré, 1988). Higher coherence thresholds indicate poor performance on this task. RDK stimuli have commonly been used to study global motion perception, including its development and underlying mechanisms, in human and nonhuman primates (Albright, 1984; Born & Tootell, 1992; De Bruyn & Orban, 1988; Edwards & Badcock, 1995; Hess et al., 2007; Kiorpes & Movshon, 2004; Kiorpes, Tang, & Movshon, 2006; MacKay et al., 2005; Nakamura et al., 2003; Scase et al., 1998; Smith, Snowden, & Milne, 1994; Wattam-Bell, 1994).

Human infants are not born with motion direction selectivity, but it appears within the first few months of life (Atkinson et al., 2004; Wattam-Bell, 1991). Using the preferential looking technique, Wattam-Bell (1996a, 1996b) demonstrated that there is

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ABSTRACT

The purpose of this study was to investigate the effect of dot speed and dot density on the development of global motion perception by comparing the performance of adults and children (5–6 years old) on a direction-discrimination task. Motion coherence thresholds were measured at two dot speeds (1 and 4 deg/s) and three dot densities (1, 15, 30 dots/deg²). Adult coherence thresholds were constant at approximately 9%, regardless of speed or density. Child coherence thresholds were significantly higher across conditions, and were most immature at the slow speed and at the sparse density. Thus, the development of global motion perception depends heavily on stimulus parameters. This finding can account for some of the discrepancy in the current developmental literature. Our results, however, caution against making general claims about motion deficits in clinical populations based on only a single measurement at a specific combination of speed and density.

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no evidence for direction-discrimination in 1-month old infants for speeds up to 43 deg/s. Direction discrimination for global motion appears to emerge by 6–8 weeks of age (Banton, Dobkins, & Bertenthal, 2001; Dannemiller & Freedland, 1991), but coherence thresholds remain much higher than those of adults (Atkinson et al., 2004; Banton, Bertenthal, & Seaks, 1999; Wattam-Bell, 1994) even at 27 weeks (Mason, Braddick, & Wattam-Bell, 2003). Newborn macaques show significant immaturities in the properties of direction-selective neurons in cortical area MT (Movshon et al., 2004).

The age at which global motion perception reaches adult levels, remains unclear. Psychophysical testing using motion coherence threshold measures has shown various maturation curves for global motion perception. While we found that global motion perception matured before 3 years of age (Parrish et al., 2005), another group of researchers found maturation by 6 years of age (Ellemberg et al., 2002) or even later (Hadad, Maurer, & Lewis, 2011). Gunn et al. (2002) reported maturation after 10 years of age, but their motion stimulus measured coherence thresholds for motiondefined form, an aspect of motion perception that is known to mature later than global motion (Parrish et al., 2005). Kiorpes and Movshon (2004) found that adult levels of global motion sensitivity are achieved by about 3 years of age in macaques, which is roughly equivalent to 13 human years (Boothe, Dobson, & Teller, 1985). This was attributed to the delayed maturation of extra-striate mechanisms.

The relatively late maturation of global motion perception reported in some studies appears to be at odds with evidence that the sensitive period for the disruption of global motion perception by visual deprivation in human infants (Ellemberg et al., 2002) or kittens (Mitchell, Kennie, & Kung, 2009) is very short. It is,

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^{0042-6989/\$ -} see front matter © 2012 Elsevier Ltd. All rights reserved. http://dx.doi.org/10.1016/j.visres.2012.02.016

therefore, important to determine if there is a straightforward explanation for the conflicting results.

Most obvious is the different stimulus parameters, specifically dot speed and dot density, that vary considerably across these studies. Parrish et al. (2005) reported early maturation with a dense display (32 dots/deg²) at a slow speed (1.2 deg/s). Hadad, Maurer, and Lewis (2011) reported later maturation with a sparse display $(0.75 \text{ dots/deg}^2)$ at two faster speeds (4 and 18 deg/s). Results with the sparse display $(0.75 \text{ dots/deg}^2)$ at the fastest speed (18 deg/s), however, have been inconsistent. Global motion perception was found to be adult-like by age 6 (Ellemberg et al., 2002) or still developing between age 4 and 8 (MacKay et al., 2005; Taylor et al., 2009). The difference in dot speed could be crucial because it has been shown that global motion direction-discrimination matures earlier for faster speeds (6 or 9 deg/s) than for slower speeds (1.5 deg/s: Ellemberg et al., 2004). Other aspects of motion perception also appear to mature earlier for fast speeds than for slow speeds (Ahmed et al., 2005; Aslin & Shea, 1990; Hayward et al., 2011; Kaufmann, 1995). This known dependence of maturation on speed, however, is in the wrong direction to explain the early maturation of global motion perception observed by Parrish et al. (2005) with a slow speed.

The effect of dot density on the development of global motion perception is not known, and the effect of dot density in adults is inconsistent. Coherence thresholds were found to decrease as density increased (Barlow & Tripathy, 1997), increase as density increased (Hutchinson, Allen, & Ledgeway, 2011) or be unaffected by changes in density (Eagle & Rogers, 1997; Talcott et al., 2000; Welchman & Harris, 2000).

The purpose of the current study was to investigate the effect of speed and dot density on the development of global motion perception by comparing the performance of adults and children (5–6 years old) on a direction-discrimination task over a range of speeds and densities. We predict that performance will be more mature with dense displays based on our previous results (Parrish et al., 2005).

2. Methods

The study was approved by the University of British Columbia Research Ethics board.

2.1. Participants

Eleven children (aged 5-6 years) and 11 adults (aged 18-24 years) participated in the study. Prior to data collection, informed consent was obtained from the parents (on behalf of the children) and from the adult participants. Verbal or written assent was obtained from each child. For most participants visual acuity was measured using the Regan high contrast (96%) vision chart (Regan, 1988). A picture chart (Lighthouse Low Vision Products) was used to assess visual acuity in some of the children who did not know the alphabet reliably. Stereopsis was measured using the Randot preschool test (Stereo Optical Co. Inc.). All participants had best corrected decimal visual acuity of at least 1.1 on the Regan chart or at least 0.8 on the picture chart (Chen et al., 2006; Dobson et al., 2009), stereo acuity of 40 arc seconds and no ocular pathology. The tasks were completed monocularly using the eye with the best visual acuity. The other eye was occluded with an opaque eye patch.

2.2. Apparatus

The stimulus was generated using a Macintosh Power G4 laptop computer and presented on a 17" Sony monitor with a resolution of 1024 (horizontal) \times 768 (vertical) pixels. The monitor had a refresh rate of 75 Hz. Participant responses were collected using a Gravis game pad pro controller. The room was dimly illuminated using diffuse lights to avoid glare during the test session.

2.3. Stimulus

A randomly generated array of square white dots (98.5 cd/m^2) was presented on a black background $(1 \text{ cd}/\text{m}^2)$. The visual display subtended 7.65° horizontally and 5.75° vertically at a viewing distance of 2.5 m. The dot size was fixed at 0.015 deg². On each trial, the dots were presented in 10 successive frames (frame duration: 40 ms, trial duration: 400 ms). The dots were displaced between frames by 6 or 24 pixels to create apparent motion of 1 deg/s or 4 deg/s. A proportion of dots moved coherently in the same direction (signal dots). The remaining dots moved in random directions at the same speed (noise dots). We tested a total of six conditions – three dot densities $(1 \text{ dot/deg}^2, 15 \text{ dots/deg}^2 \text{ and } 30 \text{ dots/deg}^2)$ at two dot speeds (Fig. 1). We chose these densities and dot speeds to match as closely as possible the stimulus parameters used by earlier studies investigating global motion (Hadad, Maurer, & Lewis, 2011; Parrish et al., 2005) or motion-defined form (Hayward et al., 2011) maturation.

2.4. Procedure

The participant's task was to identify the overall direction of motion of the stimulus, left or right, by pressing the corresponding



Fig. 1. Schematic of the global motion stimulus. (a) Dense condition – 30 dots/deg^2 and (b) sparse condition – 1 dot/deg^2 . The long arrows indicate the direction of motion of the signal dots and the short arrows indicate the direction of motion of the noise dots.

button on the gamepad. The proportion of signal dots was manipulated in a two-down, one-up staircase in which coherence level was decreased when two successive trials were correct or increased by the same step size when one trial was incorrect. A run started at a motion coherence level of 1.0 with an initial step size of 0.1. After the third response reversal, step size was halved in both directions at each reversal. Each participant began with a practice staircase of 20 trials to ensure that they understood and were able to perform the task. This was followed by one staircase for each of the six conditions, with order counterbalanced across participants. These staircases ended after 50 trials or 10 response reversals. The session lasted for 1.5 h.

2.5. Analysis

For each participant and each condition, a coherence threshold was estimated by fitting a Weibull function to the data using a maximum-likelihood minimization procedure (Watson, 1979). The point of maximum slope on the fitted curve (82% correct) was taken as the measure of coherence threshold (Strasburger, 2001). A χ^2 test (p < 0.05) was used to check the adequacy of the fit provided by the Weibull function.

3. Results

Mean motion coherence thresholds for direction discrimination are plotted in Fig. 2. A 1 between (age group) \times 2 within (speed, density) mixed-model ANOVA showed a significant group by speed interaction, *F*(1.00,20.00) = 10.680, *p* = 0.004, as well as a significant group by density interaction, *F*(1.42,28.401) = 4.275, *p* = 0.035. Both interactions had large effect sizes (*f* = 0.73 for speed; *f* = 0.46 for density; Cohen, 1988). As the Mauchly's test of sphericity indicated that the data were non-spherical, the degrees of freedom were adjusted with the Greenhouse–Geisser method.

The significant interactions were followed up with simple effects analyses. The effect of group was significant at both speeds (p < 0.001). The effect sizes for the slow and fast speeds were large at 1.51 and 0.97, respectively. The effect of group was also significant at all three densities (p < 0.001) and the effect sizes were large (f = 1.147 for 30 dots/deg²; f = 1.310 for 15 dots/deg²; f = 1.182 for 1 dot/deg²). Post-hoc pair-wise comparisons were calculated with a Bonferroni correction to maintain an overall α -level of 0.05. The children performed worse than the adults for the two speeds as well as the three densities (all p < 0.001).

Table 1 shows the threshold elevation for each of the six conditions. For a specific combination of speed and density, threshold elevation is the ratio of the mean coherence threshold for the children relative to the mean coherence threshold for the adults. Threshold elevation was higher at the slow speed (1 deg/s) especially for the sparse density (1 dot/deg²).

4. Discussion

We have shown that global motion direction-discrimination thresholds were significantly higher in 5–6 year old children than in adults for the three densities (30, 15 and 1 dots/deg²) at both the slow (1 deg/s) and fast (4 deg/s) speeds. The adult coherence thresholds were around 9% irrespective of the speed or density. The difference in threshold between the two groups was more pronounced at the slow speed and especially for the sparse density, with child thresholds more than six times higher than adult thresholds (Table 1 and Fig. 2).

Our speed finding confirms previous results (Ellemberg et al., 2004; Hayward et al., 2011). We believe this is the first report of the effect of dot density on the development of global motion perception. The early maturation reported by Parrish et al. (2005) was probably partially driven by the dense pattern used (32 dots/deg²), while the late maturation reported by Hadad, Maurer, and Lewis (2011) and Gunn et al. (2002) was due to the sparse patterns used (0.75 dots/deg² and 4 dots/deg², respectively). The current pattern of results, however, cannot completely account for the discrepancies across previous studies because we found coherence thresholds in 5–6 year olds to be immature in every condition.

Even though the slow, dense condition in the present study closely matches the Parrish et al. (2005) stimulus, child thresholds were slightly lower and adult thresholds were higher in the previous study. Other differences between these two studies include the stimulus duration (400 versus 854 ms) and the direction of motion (left-right versus up-down). The lower child thresholds in the previous study could have resulted from the longer stimulus duration and easier up-down direction discrimination, but it is not clear why this combination would produce higher coherence thresholds in adults. This will require further investigation. It should also be pointed out, that previous results with the sparse, fast stimulus (0.75 dots/deg², 18 deg/s) have varied considerably across studies as well (Ellemberg et al., 2002; Hadad, Maurer, & Lewis, 2011; MacKay et al., 2005; Taylor et al., 2009).



Fig. 2. Motion coherence thresholds for each age group as a function of dot density and dot speed. Error bars represent one standard error of the mean. Lower threshold values correspond to better performance on the global motion direction-discrimination task.

 Table 1

 Threshold elevation for the children compared to adults.

Density	Threshold elevations	
	Slow speed (1 deg/s)	Fast speed (4 deg/s)
30 dots/deg ²	4.6 ×	3.7×
15 dots/deg ²	4.9 ×	4.3×
1 dot/deg ²	6.2 ×	4.4 imes

4.1. Effect of speed on global motion development

Our results suggest that global motion perception for fast motion appears to be better developed than for slow motion in 5– 6 year old children; this is consistent with the results of previous research (Lewis & Maurer, 2005). The different development rates result in different sensitive periods, resulting in slow speed mechanisms that are more susceptible to disruption by visual developmental disorders such as amblyopia (Hayward et al., 2011; Kiorpes, Tang, & Movshon, 2006; Schor & Levi, 1980a, 1980b; Simmers et al., 2003; Steinman, Levi, & McKee, 1988), and fast speed mechanisms that are less vulnerable to developmental deficits (Ellemberg et al., 2002).

Our recent findings of faster maturation for motion-defined form at fast speeds relative to slow speeds (Hayward et al., 2011) were interpreted as supporting the idea of separate processing systems for fast and slow motion (Burr, Fiorentini, & Morrone, 1998; Edwards, Badcock, & Smith, 1998; Gegenfurtner & Hawken, 1995; Gorea, Papathomas, & Kovacs, 1993; Hawken, Gegenfurtner, & Tang, 1994; Heinrich et al., 2004; Khuu & Badcock, 2002; Van de Grind et al., 2001; Van der Smagt, Verstraten, & Van de Grind, 1999; Verstraten, Van der Smagt, & Van de Grind, 1998). The 'slow' system is hypothesized to be active at speeds below 3 deg/s and the 'fast' system becomes more involved as speeds increase, to an upper limit of approximately 80 deg/s (Burr, Fiorentini, & Morrone, 1998; Khuu & Badcock, 2002; Van de Grind et al., 2001). It has even been suggested that these slow and fast motion systems correspond to the ventral and dorsal cortical streams, respectively (Gegenfurtner & Hawken, 1996; Thompson, Brooks, & Hammett, 2006). According to this view, our results could be attributed to slower maturation and longer vulnerability of the ventral stream rather than the dorsal stream. Previous evidence about which pathway matures first is inconsistent (Bachevalier, Hagger, & Mishkin, 1991; Distler et al., 1996; Kovacs et al., 1999; Mitchell & Neville, 2004).

4.2. Effect of dot density on global motion development

The ability to perceive global motion depends on spatial integration of local motion signals (Smith, Snowden, & Milne, 1994; Williams & Sekuler, 1984). The capacity to spatially integrate local motion signals develops slowly (Kiorpes & Movshon, 2004; Wattam-Bell, 1994). Consequently the development of global motion is limited by the development of spatial integration (Ellemberg, Allen, & Hess, 2004; Ellemberg et al., 2010). It is possible that the increased coherence thresholds for the children as density decreased, is related to the protracted development of spatial integration, specifically the area over which integration is possible. A coherence threshold is determined by spatial integration area of the motion signals and its rate of temporal change; as long as all the signal dots remain within the spatial integration area the thresholds will be constant, but once the signal dots exceed the spatial integration area, thresholds will increase proportionally (Ledgeway, McGraw, & Simmers, 2011; Watamaniuk & Sekuler, 1992). The integration area covers a shorter spatial range in children than in adults (Kovacs et al., 1999), and continues to develop even after 14 years of age (Kovacs, 2000).

5. Clinical implications

Previous studies of clinical populations such as pre-term children (Atkinson & Braddick, 2007; MacKay et al., 2005; Taylor et al., 2009) or adults with schizophrenia (Chen et al., 2003) and dyslexia (Talcott et al., 2000) have shown marked deficits in global motion processing. Our results, however, caution against generalizing these deficits to other speeds and densities based on only a single measurement at a specific combination of speed and density. For example, robust deficits in global motion perception have been reported in amblyopia using sparse displays (0.44 dots/deg²; Simmers et al., 2003) but only minimal deficits have been found using dense displays (32 dots/deg²; Ho et al., 2005, 2006). We suggest that global motion perception reaches adult functional levels more quickly for dense displays than for sparse displays and that the mechanisms processing sparse displays are more susceptible to disruption by visual developmental disorders such as amblyopia. The global motion deficit in amblyopia may arise from abnormal pooling of local motion signals due to increased spatial uncertainty, restricted range of spatial integration mechanisms (Levi, Whitaker, & Provost, 2009) as well as disruption of mechanisms in the extrastriate visual cortex. It is conceivable that the sparse displays are more sensitive to these deficits, leading to robust global motion deficits at sparse densities.

6. Conclusions

We have shown that while adult coherence thresholds remain relatively unaffected by stimulus parameters, both speed and density have a significant effect on thresholds for children. At age 6, global motion is less mature for slow than fast speeds and particularly for sparse relative to higher densities. The maturation discrepancies across previous studies are at least partially accounted for by the effect of dot density. Our results advocate the importance of exploring a range of stimulus parameters (in terms of dot speed and density) to fully characterize the nature of the global motion deficits in amblyopia.

Acknowledgments

This study was funded by NSERC Grant 194526 to D. Giaschi. The authors wish to thank Jennifer Fong, Ryan Lo and Houman Rashidian for assistance with data collection.

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