Available online at www.sciencedirect.com
SCIENCE DIRECT®

Vision Research 44 (2004) 2403–2411

Vision Research

www.elsevier.com/locate/visres

Putting order into the development of sensitivity to global motion

D. Ellemberg [a,*], T.L. Lewis [b,c], M. Dirks [b], D. Maurer [b], T. Ledgeway [d]
J.-P. Guillemot [e,f], F. Lepore [f]

[a] McGill Vision Research, Department of Ophthalmology, McGill University, 687 Pine Avenue, West H4-14, Montréal, Québec, Canada H3A 1A1
[b] Department of Psychology, McMaster University, Hamilton, ON, Canada L8S 4K1
[c] Department of Ophthalmology and Vision Sciences, University of Toronto, Toronto, ON, Canada M5S 1A8
[d] School of Psychology, University of Nottingham, Nottingham, N67 2RD, UK
[e] Groupe de Recherche En Neuropsychologie Expérimentale, Université de Montréal, Montréal, Québec, Canada H3C 3P8
[f] Université du Québec a Montréal, Montréal, Québec, Canada H3C 3P8

Received 9 July 2003; received in revised form 28 April 2004

Abstract

We studied differences in the development of sensitivity to first-versus second-order global motion by comparing the motion coherence thresholds of 5-year-olds and adults tested at three speeds (1.5, 6, and $9° s^{-1}$). We used Random–Gabor Kinematograms (RGKs) formed with luminance-modulated (first-order) or contrast-modulated (second-order) concentric Gabor patterns with a sinusoidal spatial frequency of $3c\ deg^{-1}$. To achieve equal visibility, modulation depth was set at 30% for first-order Gabors and at 100% for second-order Gabors. Subjects were 24 adults and 24 5-year-olds. For both first- and second-order global motion, the motion coherence threshold of 5-year-olds was less mature for the slowest speed ($1.5° s^{-1}$) than for the two faster speeds (6 and $9° s^{-1}$). In addition, at the slowest speed, the immaturity was greater for second-order than for first-order global motion. The findings suggest that the extrastriate mechanisms underlying the perception of global motion are different, at least in part, for first- versus second-order signals and for slower versus faster speeds. They also suggest that those separate mechanisms mature at different rates during middle childhood.

Keywords: Visual development; Global motion; Speed processing; First-order motion; Second-order motion; Children; Adults; Random–Gabor kinematograms

1. Introduction

Early stages of motion detection operate over small regions of space. This creates ambiguity about the true direction of motion of an object or display occupying a larger region, ambiguity that is exemplified in the well-known aperture problem (Horn & Schunck, 1981). To determine the overall direction of motion, the outputs of local motion detectors must be integrated over space and time (Smith, Snowden, & Milne, 1994; Williams & Sekuler, 1984). Converging evidence indicates that cells in the primary visual cortex (area VI) signal the direction of motion in local regions of the visual field and that cells in the middle temporal area (i.e., MT), that have much larger receptive fields, integrate those signals over both space and time to give rise to the perception of global motion (Barton, Sharpe, & Raymond, 1995; Maunsell & Newsome, 1987; Maunsell & Van Essen, 1983a; Newsome & Pare, 1988; O'Keefe & Movshon, 1998; Scase, Horsfield, Wilcock, & Karwatowski, 1998; Watamanuik & Sekuler, 1992).

Evidence from non-human primates indicates that neurons in area MT are sensitive to the direction of global motion (Albright, 1984; Maunsell & Van Essen,

---

[*] Corresponding author. Tel.: +1-514-842-1231x34816; fax: +1-514-843-1691.
E-mail address: dave.ellemberg@staff.mcgill.ca (D. Ellemberg).

0042-6989/$ - see front matter © 2004 Elsevier Ltd. All rights reserved.
doi:10.1016/j.visres.2004.05.006

1983b), and that the majority of these neurons become labeled with 2-deoxyglucose during the presentation of global motion stimuli (Born & Tootell, 1992). Area MT also plays a key role in the processing of speed information, whereas the primary visual cortex is involved primarily in the processing of spatial and temporal frequency information (Perrone & Thiele, 2002). For example, Perrone and Thiele (2001) found that the firing of most MT cells is unaffected by changes in spatial or temporal frequency if speed is kept constant.

Psychophysical experiments also indicate that the human visual system has mechanisms that are specifically tuned to speed (Reisbeck & Gegenfurtner, 1999; Schrater & Simoncelli, 1998), although these studies do not distinguish among cortical levels. McKee, Siverman, and Nakayama (1986) found that speed judgments are affected very little by random variations in temporal frequency. Consistent with these findings, speed-tuned mechanisms that operate independently of spatial and temporal frequency mechanisms have been identified with noise masking (Reisbeck & Gegenfurtner, 1999) and adaptation experiments (Schrater & Simoncelli, 1998). Finally, Smith and Edgar (1991) found that temporal frequency discriminations are affected little by random variations in speed. Together the results of these studies point to three separate sets of mechanisms in humans, one tuned to spatial frequency, a second tuned to temporal frequency, and a third tuned to speed.

To detect cues to motion, the visual system must decode either changes in luminance or in other stimulus properties such as contrast or texture (Badcock & Derrington, 1985; Cavanagh & Mather, 1989; Chubb & Sperling, 1988, 1989). The perception of motion based on variations in luminance is known as first-order motion. The perception of motion based only on variations in other stimulus properties, such as texture or contrast, is known as second-order motion. Several lines of evidence suggest that, in the early stages of motion processing, first- and second-order motion are analysed by different signal processing mechanisms. For example, human adults cannot integrate alternating frames containing first- and second-order local motion into an unambiguous motion percept (Legdeway & Smith, 1994), and their sensitivity to first- or second-order local motion is not affected by adaptation to motion of the other type (Nishida, Ledgeway, & Edwards, 1997). Further, neurons in areas 17 and 18 of the cat typically have different spatial frequency tuning for first- versus second-order gratings (Mareschal & Baker, 1998, 1999; Zhu & Baker, 1993). However, it still remains controversial whether, in area MT, first- and second-order motion continue to be processed by different neural mechanisms (Wilson, Ferrara, & Yo, 1992). The finding that most neurons in monkey area MT respond to both first- and second-order stimuli is taken as evidence for a single motion pathway that integrates both first- and second-order cues to motion (Albright, 1992; also see Wilson et al., 1992). Moreover, Edwards and Babcock (1995) found that the detection of coherent motion was impaired when first-order noise was added to the second-order signal, indicating at least some level of integration. On the other hand, some findings have been taken as evidence for the separate processing of first- and second-order motion even at the level of MT. Specifically, humans do not integrate alternating frames containing first- and second-order global motion into an unambiguous percept of motion (Mather & West, 1993), and their detection of coherent motion is not affected when second-order noise is added to the first-order signal (Edwards & Babcock, 1995).

The development of the mechanisms for the computation of speed is still largely unknown. Studies of infants indicate that sensitivity to slower speeds develops later than sensitivity to faster speeds (Aslin & Shea, 1990; Bertenthal & Bradbury, 1992; Dannemiller & Freedland, 1989; Dobkins & Teller, 1996). Even at five years of age, speed affects children's sensitivity to direction of motion under some conditions. Whereas their sensitivity to the direction of a moving first-order grating is nearly adult-like, regardless of whether it is moving at 1.5 or $6° \mathrm{s}^{-1}$, their sensitivity to the direction of a moving second-order grating is much less mature at the faster than at the slower speed (Ellemberg et al., 2003). However, those studies used stimuli designed to measure sensitivity to local motion, rather than the integration of local motion signals into a global percept to compute overall direction and speed.

A comparison across two studies suggests that the extrastriate mechanisms specialized for global motion develop at different rates for different speeds. Using random dot kinematograms that drifted at $5° \mathrm{s}^{-1}$, Atkinson et al. (1999) found that 5-year-olds' coherence thresholds for global motion are worse than those of adults by a factor of 2.5. In contrast, we presented dots that drifted much faster (at a speed of $18° \mathrm{s}^{-1}$) and found that 6-year-olds' coherence thresholds are adult-like (Ellemberg, Lewis, Maurer, Brar, & Brent, 2002). One possibility is that there is rapid development between 5 and 6 years of age. Alternatively, the developmental pattern may vary for different speeds. Both studies used random dot kinematograms that did not separate first- from second-order cues to motion. No previous study has tested whether the developmental pattern varies for different types of global motion (viz., first- versus second-order global motion), as is known to be true for local motion (Ellemberg et al., 2003).

The purpose of the present study was to investigate differences in the development of sensitivity for global motion as a function of speed and of motion type (first-order or second-order). We compared coherence thresholds for 5-year-olds and adults tested at three speeds, using limited lifetime random Gabor kinematograms that contained either first- or second-order cues to motion. We computed coherence thresholds for 5-year-olds and adults measured at three speeds, using limited lifetime random Gabors formed from first- or second-order cues, a percentage of which moved coherently on each trial.

2. Methods

2.1. Observers

A group of 24 adults (18–23 years) and 24 5-year-olds (±3 months) participated in the experiment. To be included in the study, all subjects, including those from the pilot study (see below), had to meet our criteria on a visual screening examination. Adults had a linear letter acuity (Lighthouse Visual Acuity Chart) of at least 20/20 in each eye without optical correction, worse acuity with a +3 dioptre add (to rule out hypermetropia of greater than 3 dioptres), fusion at near on the Worth four dot test, and stereoacuity of at least 40 arc sec on the Titmus test. The 5-year-olds met the same criteria except that they were required to have a visual acuity of at least 20/25 when tested with the Good Lite Crowding cards.

2.2. Apparatus and stimuli

An Apple Macintosh G3 generated the motion stimuli on a Sony Trinitron Multiscan 200 GS computer monitor. Pixel resolution was 1024 by 768 pixels with a refresh rate of 75 Hz. The stimuli were produced by means of a linearized subset of grey values. Mean screen luminance was maintained at 35 cd m^{-2}.

Studies of global motion typically use random dot kinematograms that contain first- or second-order cues to motion and are spatially and temporally broad-band. Instead we used Gabors, which were narrow-band, and which were defined by either first-order or second-order cues (see Fig. 1 for details). The internal sinusoidal structure was concentric and not striped, so that orientation could not be used as a cue to the direction of motion. We call these new stimuli circular Random–Gabor Kinematograms or RGKs.

The Gabor micropatterns were composed of concentric sine-wave gratings multiplied by a Gaussian function in the horizontal (x) and vertical (y) dimensions.[1] Each Gabor had a standard deviation of 0.24 deg. and was truncated at two standard deviations. The first-order (luminance-modulated) stimulus was created by adding the micropatterns to a spatially two-dimensional, binary, random noise carrier (see Fig. 1, left panel). The resulting image contained an array of patches, within each of which the mean luminance of the noise varied according to the Gabor waveform (an example of the stimulus is presented in Fig. 2a).

The second-order (contrast-modulated) Gabor was created by multiplying the micropatterns with the random noise carrier.[2] The construction of these stimuli is described in the right panel of Fig. 1. The resulting image contained an array of patches, within each of which the mean contrast of the noise varied according to the Gabor waveform. This produced Gabor micropatterns in which average luminance was the same across the high and the low contrast regions of the Gabor (an example of the stimulus is presented in Fig. 2b).

Therefore, for both the first- and second-order RGKs, the Gabors consisted of static two-dimensional random noise (referred to as the carrier), the luminance of which was binary. Each noise element subtended 2×2 arc min, and was assigned independently with a probability of 50% to be either 'light' or 'dark'.

The first- and second-order stimuli each consisted of 80 Gabors moving against a background of random noise, with a limited lifetime for the direction of motion. Just like the Gabors, the background consisted of binary light and dark pixels. At a viewing distance of 57 cm, the stimulus display subtended 20 by 20 degrees of visual angle.

Coherence thresholds were measured for Gabors that moved at speeds of 1.5, 6, and $9° s^{-1}$. The jump size or displacement of each Gabor between frames was held constant at 0.24°, and the duration of each trial was 1.5 s. In order to vary speed while keeping displacement constant, we varied lifetime of the images for each speed. We chose to manipulate lifetime, in order to keep speed constant across the three speed conditions. Just like the commonly used random-dot-kinematogrames, the overall direction of motion in RGKs cannot be determined with local motion detectors. The direction of motion in which each Gabor moves is limited in time so that after a given lifetime, a new group of Gabors, determined randomly, move in the signal direction and the remaining Gabors move in random directions. Thus, it

---

[1] The first-order Gabor is represented by the following equation:

$$L_{(x,y)} = L_0[1 + \exp[-(x^2 + y^2)/2\delta^2]C_g \cos(2\pi\sqrt{(x^2 + y^2)}/\lambda) + C_n N_{rnd}] \quad (1)$$

where L_0 is the mean luminance of the pattern, δ is the standard deviation of the Gaussian (0.24°), C_g is the modulation depth of the internal sinusoid, λ is the sinusoidal spatial wavelength (3c deg^{-1}) and C_n is the contrast of the noise carrier N_{rnd} (chosen to be either −1 or +1 with probability 0.5).

[2] The second-order Gabor is represented by the following equation:

$$L_{(x,y)} = L_0[1 + (1 + \exp[-(x^2 + y^2)/2\delta^2]C_g \times \cos(2\pi\sqrt{x^2 + y^2}/\lambda))C_n N_{rnd}] \quad (2)$$

where L_0, δ, C_g, λ, C_n and N_{rnd} refer to the same parameters as Eq. (1).

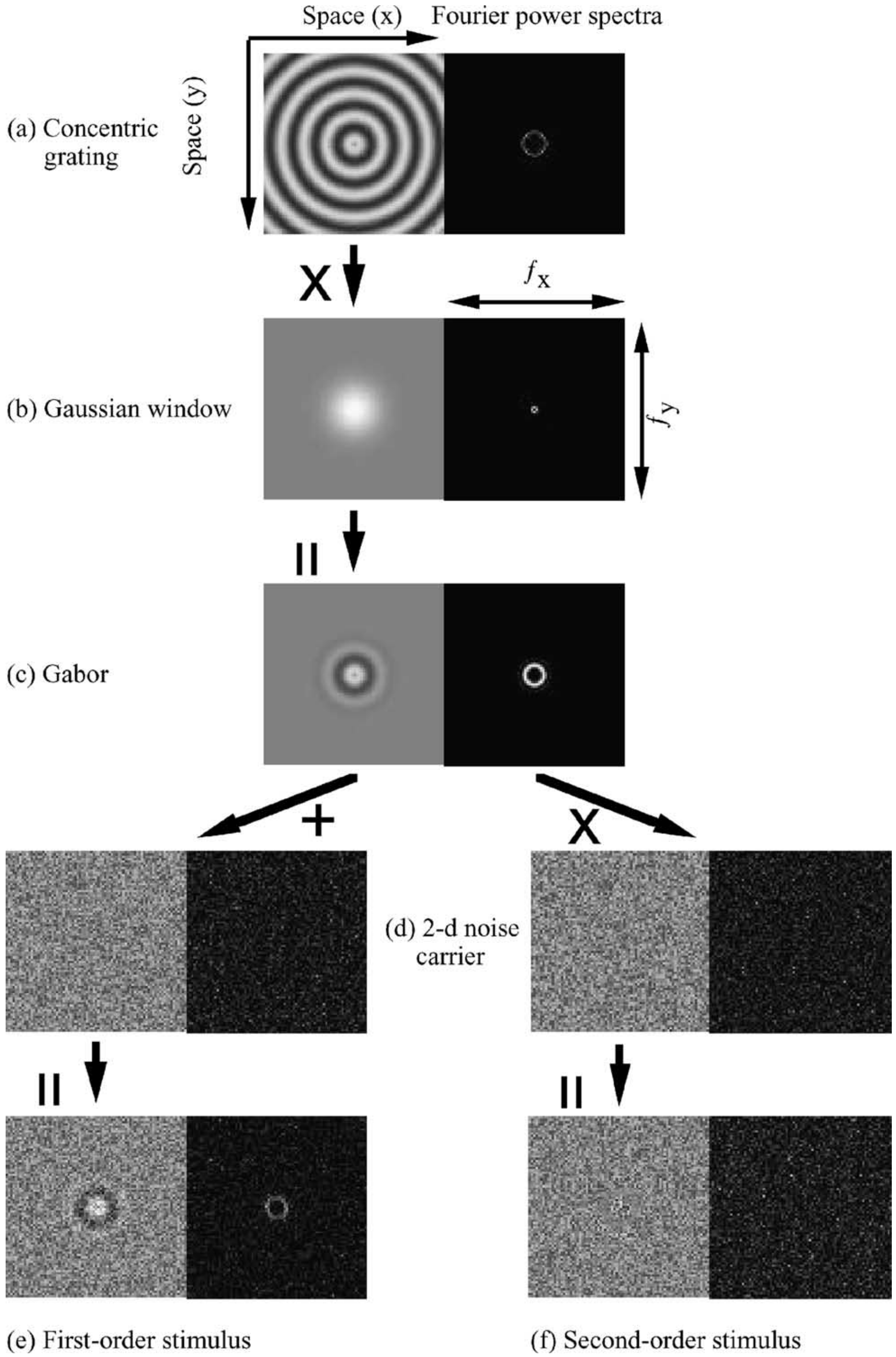

Fig. 1. Space–space (x–y) plots demonstrating the construction of a single first-order (luminance-defined) and second-order (contrast-defined) Gabor patch analogous to those used in the actual experiments. To the right of each image is a power spectrum, computed by applying a Fast Fourier Transform to the 128×128 pixel array representing that image. The power spectrum represents the power (amplitude squared) at each spatial frequency and orientation, with brighter values indicating greater power. For clarity the d.c. components were omitted and the intensity values were scaled to cover the available range of brightness. Panel (a) shows a concentric sinusoidal grating pattern. Its spectrum is both spatially narrowband and effectively isotopic in orientation (as indicated by the circular locus of power about the origin). Multiplying the concentric grating with a 2-d Gaussian window (b) results in a Gabor patch (c) that has power at all orientations. However, that power is still confined to a relatively narrow range of spatial frequencies (indicated by the circular 'donut' region in the Fourier spectrum). The Gabor patch was then either added to, or multiplied with, a spatially 2-d noise carrier (d) to create a first-order stimulus (e) or a second-order stimulus (f). Although the first-order image shown in (e) is spectrally broadband (due to the numerous Fourier components contributed by the noise carrier), the dominant power is still centered on a relatively limited range of spatial frequencies that span all possible orientations. Second-order stimuli (f) also exhibit the same properties when their spectral characteristics are considered in the contrast, rather than the luminance, domain.

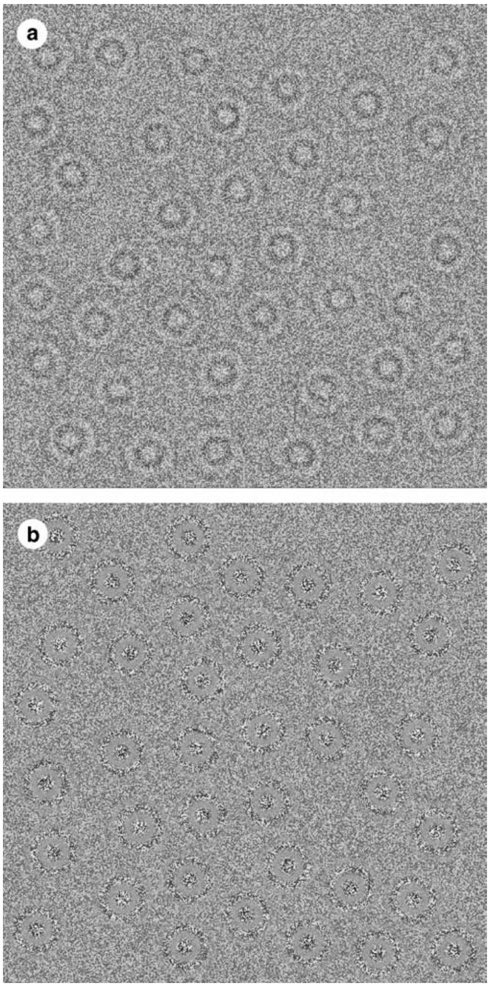

Fig. 2. Example of the stimulus configuration for (a) the first-order (luminance modulated) RGKs and (b) the second-order (contrast modulated) RGKs. The modulation depth of the first- and second-order RGKs were 30% and 100%, respectively. In the study, each Gabor had a vertical and horizontal space constant (standard deviation of the Gaussian) of 0.24° and an internal sinusoidal spatial frequency of 3c $\deg^{-1}$. In the schematic, the space constant and the modulation depth of the Gabors were modified in order to improve the visibility of the stimuli when static.

is not possible to determine the direction of the entire pattern by following a single dot, but rather this configuration requires the integration of local signals over a larger summation field.

2.3. Procedure

The procedure was explained and written consent was obtained from the parents of the children and from the adults who participated. The experimental protocol was approved by the Committee on the Ethics of Research on Human Subjects, McMaster University. Participants viewed the screen binocularly from a distance of 57 cm with their chin in a chin rest and were instructed to fixate a central mark (a cross) that was present throughout the procedure. Parents sat in the testing room out of their child's sight and were asked to remain silent during testing.

Coherence thresholds were measured using limited lifetime Random–Gabor Kinematograms. The subjects' task on each trial was to say whether the global direction of motion was up or down. The percentage of "signal" Gabors moving up or down varied across trials by a 2-down, 1-up staircase (Levitt, 1971). The remaining percentage of "noise" Gabors on each trial moved randomly. The threshold was defined as the percentage of Gabors moving in the same direction for 71% correct performance and was obtained by averaging the results from the last six reversals of the staircase. More specifically, the experimenter told the 5-year-olds: "You will see a grey cloud filled with raindrops on the computer screen. Your job is to tell me if the raindrops are moving up (experimenter points up) or down (experimenter points down)." The experimenter watched the subjects to ensure that they maintained central fixation, provided regular reminders to do so, and began trials only when the subjects were looking at the fixation cross in the middle of the screen. To familiarize them with the RGKs, the participants experienced four demonstration trials, two with each type of motion, one with upward motion and one with downward motion. Then, to ensure that the subjects understood the task, criterion trials were presented. To pass criterion, subjects had to achieve two correct judgements at 100% coherence and two correct judgements at 50% coherence on four consecutive trials. The subjects were given three chances to achieve criterion, and all met this criterion. After passing the criterion, the subjects received a practice run that consisted of an entire staircase, that matched the type of motion (i.e., first-order or second-order) on which they would be tested first. The experimenter was aware of the direction of motion on each trial and, when the subjects committed an error, provided feedback.

Test of thresholds. Each subject was tested on six thresholds consisting of first- and second-order global motion, each at three speeds (1.5, 6, and 9°s^{-1}). The procedure for measuring each threshold was identical to that for the practice run except that the experimenter was unaware of the direction of motion on each trial and no feedback was provided. Subjects indicated their answer by providing a verbal response and/or by pointing up or down. The experimenter keyed in those responses. Regardless of their response, children were praised periodically and were reminded to watch carefully. All adults completed testing in one session. The 5-year-olds were tested during two separate one-hour sittings, both of which were completed within the specified age range. Half the subjects were tested first on RGKs formed from first-order Gabors, whilst the remaining subjects were tested first on RGKs formed from second-order Gabors.

Within each type of motion, the three speeds were presented in random order. The procedure for the type of motion tested second was identical except that the criterion and practice phases were omitted.

2.4. Pilot studies to equate the visibility of the two types of motion

We conducted a series of pilot experiments to determine the modulation depths of the first- and second-order Gabors that make them equally perceptible for judgements of global motion. We tested 12 adults (mean age = 20.7 years) and 12 5-years-olds (±3 months) in order to determine the range of amplitude modulation of the first- and second-order Gabors that produce maximum performance (i.e., lowest coherence thresholds) on the Global motion task, for each of the conditions to be tested. Specifically, using the same procedures and stimuli described above, we measured coherence thresholds using first- and second-order RGKs that had different levels of modulation depth. We found that coherence threshold decreased with increasing modulation depth, for each condition, to reach asymptote at a given depth modulation. For first-order RGKs at all three speeds and at both ages, thresholds were best and consistent within subject (within a factor of 2) when modulation depth was above about 30% (20–40%, depending on the subject). For second-order RGKs at all three speeds and both ages, thresholds were best and consistent within subject only when modulation depth was above 90% for 5-year-olds and 60% for adults.

For the main experiment, we chose a modulation depth of 30% for first-order motion and 100% for second-order motion. Both values were within the range of best performance for both 5-year-olds and adults, and hence ensured that subjects would not have performed better had we chosen different values. Their appropriateness was confirmed with 6 adults who were asked to match the visibility of a first- and second-order Gabors moving at each of the three speeds. Those subjects reported that a first-order Gabor at 30% modulation depth was equal in perceptibility to a second-order Gabor at 100% modulation depth.

2.5. Data analysis

For each of the conditions, we replaced deviant scores using Kirk's (1989) outlier procedure. Specifically, each coherence threshold was converted to a Z-score using the group mean and standard deviation for that condition. Z-scores greater than +2.5 or less than −2.5 were replaced with the original group mean for that condition. Nine data points were replaced: six from three of the 5-year-olds and one from each of three adults. The maximum number of data points eliminated from the same condition was two. All further analyses used the revised data sets.

The data were analysed by a 3-way mixed analysis of variance (ANOVA). The ANOVA had one between-subjects factor of age with two levels (5-year-olds, adults), a within-subjects factor of speed with three levels (1.5, 6, and $9° s^{-1}$), and a within-subjects factor of type of motion with two levels (first-order, second-order). The significant 3-way interaction was analysed further with separate 2-way ANOVAs for each type of motion, in which each ANOVA had a between-subjects factor of age and a within-subjects factor of speed. Analyses of simple effects were used to analyse all significant 2-way interactions.

3. Results

Fig. 3 shows coherence thresholds for 5-year-olds (circles) and adults (squares) for first-order (solid symbols) and second-order (open symbols) RGKs at each of the three speeds.

The 3-way ANOVA revealed an interaction amongst age, type of motion, and speed, $F_{2,92} = 5.02$ ($p < 0.01$). The other significant effects were interactions between age and motion type, $F_{1,46} = 6.80$ ($p < 0.02$), age and speed $F_{1,46} = 27.93$ ($p < 0.0001$), motion type and speed, $F_{1,46} = 9.46$ ($p < 0.01$), a main effect of age, $F_{1,46} = 31.44$, ($p < 0.01$), a main effect of motion type, $F_{1,46} = 9.19$ ($p < 0.01$), and a main effect of speed, $F_{1,46} = 44.55$ ($p < 0.01$).

To evaluate the 3-way interaction further, we conducted 2-way ANOVAs comparing age to speed for each of the two types of motion. The 2-way ANOVA for first-order motion revealed a significant interaction between age and speed, $F_{1,92} = 17.77$ ($p < 0.001$), a main effect of age, $F_{1,46} = 24.03$ ($p < 0.001$), and a main effect

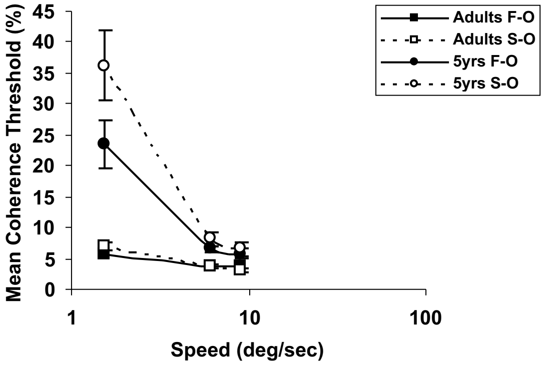

Fig. 3. Mean coherence thresholds (±1 SE) for adults (circles) and 5-year-olds (squares) for first-order RGKs (solid symbols) and second-order RGKs (open symbols) at each of the three speeds (1.5, 6, and $9° s^{-1}$).

of speed, $F_{2,46} = 26.80$ ($p < 0.001$). An analysis of simple effects on the interaction revealed that 5-year-olds' thresholds were worse than those of adults for each of the three speeds. Inspection of Fig. 3 shows that the interaction arose because, compared to adults, the 5-year-olds thresholds were much worse (5 times) at the slowest speed compared to the two faster speeds.

The 2-way ANOVA for second-order motion also revealed a significant interaction between age and speed, $F_{1,92} = 24.57$ ($p < 0.001$), a main effect of age, $F_{1,46} = 27.51$ ($p < 0.001$), and a main effect of speed, $F_{2,46} = 40.53$ ($p < 0.001$). An analysis of simple effects on the interaction revealed that 5-year-olds' thresholds were worse than those of adults for each of the three speeds. Again, inspection of Fig. 2 shows that compared to adults, the 5-year-olds thresholds were much worse (6 times) at the slowest speed compared to the two faster speeds. Inspection of Fig. 3 also indicates that at the slowest speed ($1.5° \mathrm{s}^{-1}$), 5-year-olds' thresholds were even worse for second-order than for first-order motion and that the adults' thresholds were equally good for the two types of motion.

4. Discussion

We found that 5-year-olds were immature both for first- and second-order global motion at every speed. The extent of the immaturity varied with condition: it was larger for the slowest speed than for the two faster speeds and it was especially large for second-order motion at the slowest speed (see Fig. 3). These findings indicate that the extrastriate mechanisms that integrate local motion cues over time and across space to produce the perception of global motion are still immature at 5-years of age, and that, these mechanisms mature more slowly for slower speeds and under some conditions, for second-order global motion.

Non-visual factors, such as differences between the 5-year-olds and the adults in attention, criterion, or eye movements may have contributed to some of the age differences in performance, but are unlikely to account for the overall pattern of results. All tasks measured thresholds; yet the children's performance was more mature for some conditions than for others. For example, 5-year-olds were less than two times worse than adults at the faster speeds (6 and $9° \mathrm{s}^{-1}$), compared to five times worse than adults at the slowest speed ($1.5° \mathrm{s}^{-1}$). At the slowest speed, the 5-year-olds were also more mature for first-order global motion than for second-order global motion. Further, this differential performance cannot be explained by differences in adult sensitivity because adults' coherence thresholds did not differ for the three speeds and the two types of motion (see Fig. 3). Rather, the differential elevation of threshold in the 5-year-olds is likely to be related to motion-sensitive mechanisms that develop more slowly for slower speeds and for second-order global motion.

Recent findings by Scott-Samuel and Georgeson (1999) suggest that when temporal frequency (spatial frequency × speed) is above 7.5 Hz, first-order artefacts may be introduced into the perception of second-order motion. This could potentially pose a problem in our study because the Gabors that moved at speeds of 6 and $9° \mathrm{s}^{-1}$ had nominal temporal frequencies of 18 and 27 Hz respectively (i.e., because the internal spatial frequency of the Gabors was 3c deg^{-1}). However, because the spatial frequency of the second-order contrast modulation used by Scott-Samuel and Georgeson (1999) was fixed at 0.6c deg^{-1}, it is entirely possible that the presence of first-order artefacts is dependent on image speed rather than drift temporal frequency. If this is indeed the case then such artefacts are non-existent unless the image speed exceeds $12.5° \mathrm{s}^{-1}$ (a value much greater than the maximum speed used in the present study). More importantly, Smith and Ledgeway (1997) found no such artefacts when the carrier consisted of high spatial frequency random noise dots instead of amplitude modulated gratings with a high contrast like those used by Scott-Samuel and Georgeson. Because the carrier for our stimuli consisted of small random noise dots (each composed of a single screen pixel subtending 2×2 arc min), and there was no luminance variation within each noise dot, it is unlikely that our second-order stimuli contained any such first-order artefacts. Nonetheless, this concern cannot account for 5-year-olds' greater immaturity for first-order motion at the slowest speed than at the two faster speeds, nor for their even larger immaturity for second-order motion, at least at the slowest speed.

For first- and second-order global motion, the difference between the 5-year-old and adult thresholds is 3 times larger at the slower speed ($1.5° \mathrm{s}^{-1}$) than at the two faster speeds (6 and $9° \mathrm{s}^{-1}$). Although there is some evidence (e.g., Seiffert & Cavanagh, 1999) using sinusoidal gratings that positional mechanisms could limit motion discrimination under some conditions for both first- and second-order motion, this does not appear to be the case when modulation depth (e.g., contrast) or speed is high. Further, there is independent evidence from adults that global-motion extraction, at least for first-order stimuli, occurs within two independent speed tuned systems—one sensitive to 'high' speeds and the other to 'low' speeds (Edwards, Badcock, & Smith, 1998). Thus, our results suggest that children have greater immaturities for global motion carried by the system sensitive to 'slowly' moving dots than the system sensitive to faster moving dots.

The present findings differ from the pattern we found previously for sensitivity to the direction of local motion at two of these speeds (1.5 and $6° \mathrm{s}^{-1}$). For direction of first-order local motion, 5-year-olds are nearly adult-like at both the slower and faster speeds, whilst for second-order local motion, they are especially immature at the faster speed and nearly adult-like at the slower one (Ellemberg et al., 2003). Together these results suggest that the speed-tuned mechanisms for local versus global motion undergo different patterns of developmental change, with those that have been identified in area MT for global motion (Perrone & Thiele, 2001) likely maturing more rapidly for faster speeds compared to slower speeds.

The comparison between the present study and our previous study on first-versus second-order local motion (Ellemberg et al., 2003) indicates that in 5-year-olds, sensitivity to the direction of global motion is less mature than sensitivity to the direction of local motion. For the first-order stimuli, 5-year-olds were about 9 times less sensitive for global than for local motion at $1.5° s^{-1}$ and 15 times less sensitive at $6° s^{-1}$. For second-order stimuli, 5-year-olds were 10 times less sensitive for global than for local motion at $1.5° s^{-1}$ and 2 times less sensitive at $6° s^{-1}$. (Note that in these comparisons, we are comparing the size of the gap between 5-year-olds and adults for local versus global motion, not making direct comparisons between different thresholds obtained from the 5-year-olds). These results suggest that, at least for the motion pathway, aspects of vision mediated by structures higher in the neuronal hierarchy develop more slowly. However, it is not clear whether this is a general developmental principle. Therefore, more evidence in needed to determine whether development is also slower beyond the primary visual cortex for other aspects of visual processing.

The findings from the present study indicate that first- and second-order global motion are processed, at least in part, by different mechanisms in the extrastriate areas that pool local motion signals to give rise to the percept of global motion. This conclusion is supported by the greater immaturites in the 5-year-olds' sensitivity to second-order than to first-order global motion at $1.5° s^{-1}$. Overall, our findings agree with those from previous psychophysical studies that indicate some degree of separability between the signal processing mechanisms of first- versus second-order global motion (Edwards & Babcock, 1995; Mather & West, 1993). Our findings are inconsistent with a straightforward interpretation of a mathematically and theoretically driven model proposed by Wilson et al. (1992), that the outputs of separate first- and second-order motion pathways are fully integrated (in a strictly equivalent manner) at the level of the extrastriate visual cortex (area MT) that processes global motion.

5. Conclusions

The present findings indicate that the extrastriate mechanisms that integrate local motion cues over time and across space to produce the perception of global motion are still immature at 5-years of age. Both for first- and second-order global motion, these mechanisms mature more slowly for slower than for faster speeds. Further, at the slowest speed, sensitivity to second-order global motion matures less rapidly than sensitivity to first-order global motion.

Acknowledgments

This research was supported by a Canadian Institutes of Health Research grant (MOP 36430) to Daphne Maurer, a Canada Research Chair to Franco Lepore, an NSERC grant to Franco Lepore and to Jean-Paul Guillemot, and by a FCAR team grant to Franco Lepore and Jean-Paul Guillemot. Dave Ellemberg was supported by the E.A. Baker award (MRC).

References

Albright, T. D. (1984). Direction and orientation selectivity of neurons in visual area MT of the macaque. *Journal of Neurophysiology, 52*, 1106–1130.

Albright, T. D. (1992). Form-cue invariant motion processing in primate visual cortex. *Science, 255*, 1141–1143.

Aslin, R. N., & Shea, S. L. (1990). Velocity thresholds in human infants: Implications for the perception of motion. *Developmental Psychology, 26*, 589–598.

Atkinson, J., Braddick, O., Lin, M. H., Curran, W., Guzzetta, A., & Cioni, G. (1999). Form and motion coherence: Is there dorsal stream vulnerability in development. *Investigative Ophthalmology and Visual Science, Supplement 2079*, S395.

Badcock, D. R., & Derrington, A. M. (1985). Detection the displacement of periodic patterns. *Vision Research, 25*, 1253–1258.

Barton, J. J. S., Sharpe, J. A., & Raymond, J. E. (1995). Retinotopic and direction defects in motion discrimination in human with cerebral lesions. *Annual Review of Neurology, 37*, 665–675.

Bertenthal, B. I., & Bradbury, A. (1992). Infants' detection of shearing motion in random-dot displays. *Developmental Psychology, 28*, 1056–1066.

Born, R. T., & Tootell, B. H. (1992). Segregation of global and local motion processing in primate middle temporal visual area. *Nature, 357*, 497–499.

Cavanagh, P., & Mather, G. (1989). Motion: the long and short of it. *Spatial Vision, 4*, 103–129.

Chubb, C., & Sperling, G. (1988). Drift-balanced random stimuli: a general basis for studying non-Fourier motion perception. *Journal of the Optical Society of America A, 5*, 1986–2007.

Chubb, C., & Sperling, G. (1989). Two motion perception mechanisms revealed through distance-driven reversal of apparent motion. *Proceedings of the National Academy of Scenes of the USA, 86*, 2985–2989.

Dannemiller, J. L., & Freedland, R. L. (1989). The detection of slow stimulus movement in 2- to 5-month-olds. *Journal of Experimental Child Psychology, 47*, 337–355.

Dobkins, K. R., & Teller, D. Y. (1996). Infant contrast detectors are selective for direction discrimination. *Vision Research, 36*, 281–294.

Edwards, M., & Badcock, D. R. (1995). No interaction between first- and second-order motion pathways. *Vision Research, 35*, 2589–2602.

Edwards, M., Badcock, D. R., & Smith, A. T. (1998). Independent speed-tuned global-motion systems. *Vision Research, 38*, 1573–1580.

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.

Ellemberg, D., Lewis, T. L., Medhji, K., Maurer, D., Guillemot, J-P., & Lepore, F. (2003). Comparison of sensitivity to first- and second-order local motion in 5-year-olds and adults. *Spatial Vision, 16*, 419–428.

Horn, B. K. P., & Schunck, B. G. (1981). Determining optical flow. *Artificial Intelligence, 17*, 185–203.

Kirk, R. E. (1989). *Statistics: An introduction*. Orlando, FL: Holt, Rinehart, and Winston.

Legdeway, T., & Smith, A. T. (1994). Evidence for separate motion-detecting mechanisms for first and second order motion in human vision. *Vision Research, 34*, 2727–2740.

Levitt, H. J. (1971). Transformed up down methods in psychoacoustics. *Journal of the Acoustic Society of America, 49*, 467–477.

Mareschal, I., & Baker, C. L. (1998). Temporal and spatial responses to second-order stimuli in cat area 18. *Journal of Neurophysiology, 80*, 2811–2873.

Mareschal, I., & Baker, C. L. (1999). Cortical processing of second-order motion. *Visual Neuroscience, 16*, 527–540.

Mather, G., & West, S. (1993). Evidence for second-order motion detectors. *Vision Research, 33*, 1109–1112.

Maunsell, J. H. R., & Newsome, W. T. (1987). Visual processing in monkey extrastriate cortex. *Annual Review of Neuroscience, 10*, 363–401.

Maunsell, J. H. R., & Van Essen, D. C. (1983a). Functional properties of neurons in middle temporal visual area of the macaque monkey: I. Selectivity for stimulus direction, speed and orientation. *Journal of Neurophysiology, 49*, 1127–1147.

Maunsell, J. H. R., & Van Essen, D. C. (1983b). Functional properties of neurons in middle temporal visual area of the macaque monkey: II. Binocular interactions and sensitivity to binocular disparity. *Journal of Neurophysiology, 49*, 1148–1167.

McKee, S. P., Siverman, G. H., & Nakayama, K. (1986). Precise velocity discrimination despite random variations in temporal frequency and contrast. *Vision Research, 26*, 609–616.

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

Nishida, S., Ledgeway, T., & Edwards, M. (1997). Dual multiple scale processing for motion in the human visual system. *Vision Research, 37*, 2685–2698.

O'Keefe, L. P., & Movshon, A. J. (1998). Processing of first- and second-order motion signals by neurons in area MT of the macaque monkey. *Visual Neuroscience, 15*, 305–317.

Perrone, J. A, & Thiele, A. (2001). Speed skills: measuring the visual speed analyzing properties of primate MT neurons. *Nature Neuroscience, 4*, 526–532.

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

Reisbeck, H. R., & Gegenfurtner, K. R. (1999). Velocity tuning mechanisms in human motion perception. *Vision Research, 39*, 3267–3285.

Scase, M. O., Horsfield, M. A., Wilcock, D. J., & Karwatowski, W. S. S. (1998). Brain activation by random dot kinematograms of varying coherence: A fMRI study. *Investigative Ophthalmology and Visual Science, Supplement 39*, S1130.

Schrater, P. R., & Simoncelli, E. P. (1998). Local velocity representation: evidence from motion adaptation. *Vision Research, 38*, 3899–3912.

Scott-Samuel, N. E., & Georgeson, M. A. (1999). Does early non-linearity account for second-order motion? *Vision Research, 39*, 2853–2865.

Seiffert, A. E., & Cavanagh, P. (1999). Position-based motion perception for color and texture stimuli: effects of contrast and speed. *Vision Research, 39*, 4172–4185.

Smith, A. T., & Edgar, O. K. (1991). Antagonistic comparison of temporal frequency filter outputs as a basis for speed perception. *Vision Research, 34*, 253–265.

Smith, A. T., & Ledgeway, T. (1997). Separate detection of moving luminance and contrast modulations: fact or artifact. *Vision Research, 37*, 45–62.

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.

Watamanuik, S. N. J., & Sekuler, R. (1992). Temporal and spatial integration in dynamic random-dot stimuli. *Vision Research, 32*, 2341–2347.

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

Wilson, H. R., Ferrara, V. P., & Yo, C. (1992). A Psychophysically motivated model for two-dimensional motion perception. *Visual Neuroscience, 9*, 79–97.

Zhu, Y.-X., & Baker, C. L. (1993). A processing stream in mammalian visual cortex neurons for non-Fourier responses. *Science, 261*, 98–101.