

## The Effect of Displacement on Sensitivity to First- and Second-Order Global Motion in 5-year-olds and Adults

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### Abstract

We compared the development of sensitivity to first- *versus* second-order global motion in 5-year-olds ( $n = 24$ ) and adults ( $n = 24$ ) tested at three displacements (0.1, 0.5 and 1.0°). Sensitivity was measured with Random–Gabor Kinematograms (RGKs) formed with luminance-modulated (first-order) or contrast-modulated (second-order) concentric Gabor patterns. Five-year-olds were less sensitive than adults to the direction of both first- and second-order global motion at every displacement tested. In addition, the immaturity was smallest at the smallest displacement, which required the least spatial integration, and smaller for first-order than for second-order global motion at the middle displacement. The findings suggest that the development of sensitivity to global motion is limited by the development of spatial integration and by different rates of development of sensitivity to first- *versus* second-order signals.

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### Keywords

Visual development, global motion, displacement, first-order motion, second-order motion, children, adults, Random–Gabor kinematograms

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## 1. Introduction

Accumulating evidence suggests that the primary visual cortex and several extrastriate areas are involved in the processing of visual motion. Specifically, early stages of motion detection in the primary visual cortex operate over relatively small regions of space and signal the direction of motion in local regions of the visual field (Horn and Schunck, 1981; Smith *et al.*, 1994; Williams and Sekuler, 1984). To determine the overall (global) direction of motion, the outputs of local motion detectors are then integrated over space and time, a process that is likely to be mediated by neurons in the middle temporal area (i.e., area MT/V5). This gives rise to the perception of global motion (Maunsell and Newsome, 1987; Maunsell and Van Essen, 1983; Newsome and Pare, 1988; O'Keefe and Movshon, 1998; Scase *et al.*, 1998).

For both local and global motion, there is considerable evidence that motion is processed, at least in part, by two or more distinct processing streams. One stream or mechanism is responsible for extracting motion signalled by luminance cues (first-order motion) and another is responsible for processing motion signalled by image attributes other than luminance, such as texture (second-order motion), in which there is no change in mean luminance (Badcock and Derrington, 1985; Cavanagh and Mather, 1989; Chubb and Sperling, 1988; Dumoulin *et al.*, 2003; Ellemberg *et al.*, 2003a; Vaina *et al.*, 2000; Zhou and Baker, 1993). Although it has been suggested that the outputs of the separate first- and second-order motion encoding mechanisms are integrated in area MT, an area of the extrastriate visual cortex that processes global motion (Wilson *et al.*, 1992), we and others have provided evidence suggesting some degree of separability between the signal processing mechanisms of first- versus second-order global motion (Ashida *et al.*, 2007; Edwards and Badcock, 1995; Ellemberg *et al.*, 2004a; Mather and West, 1993).

Converging evidence also suggests that for global motion processing, displacement and speed exert independent influences (Kiorpes and Movshon, 2004; Vaina *et al.*, 2005; Wattam-Bell, 1992). In fact, findings from several studies suggest that spatial displacement is likely to be a much more important determinant of sensitivity to global motion than is speed (Baker and Braddick, 1985; Braddick *et al.*, 2003; Kiorpes and Movshon, 2004). For example, a recent behavioural study in monkeys found that, throughout development and for a wide range of speeds (0.8 to 40°/s) and displacements (2 to 50 min), the discrimination of the direction of global motion was highly dependent on dot displacement but essentially independent of speed (Kiorpes and Movshon, 2004).

Little is known about developmental changes in the effects of displacement on the perception of motion in humans. In contrast, several studies have looked at developmental changes in the effects of speed. For example, for first-order local motion, sensitivity to slower speeds (less than 2°/s) develops later than sensitivity to faster speeds, whereas for second-order local motion, it is sensitivity to faster speeds that develops more slowly (Aslin and Shea, 1990; Bertenthal and Bradbury, 1992; Ellemberg *et al.*, 2003b). In a recent study, we found a differ-

ent developmental pattern for global motion (Elleberg *et al.*, 2004a). We used Random–Gabor Kinematograms (RGKs) composed of either luminance-modulated or contrast-modulated concentric Gabor patterns to compare the development of first- and second-order global motion perception at three speeds (1.5, 6 and 9°/s). Displacement was held constant at 0.24° and variations in speed were achieved by varying the temporal offset (delay) between successive updates of the position of each Gabor. Although 5-year-olds' thresholds were not mature in any condition for either first- or second-order global motion, the motion coherence threshold was less mature for the slowest than for the two faster speeds. In addition, at the slowest speed, the immaturity was greater for second-order than for first-order global motion. The findings suggest that speed has different effects on the extrastriate mechanisms underlying the perception of global motion than it does on the earlier mechanisms underlying the perception of local motion.

The goal of the present study was to gain a better understanding of the effect of spatial displacement on sensitivity to first- and second-order global motion. This was done by investigating differences in the development of sensitivity for global motion as a function of displacement (by holding speed constant) and of motion type (first-order or second-order). Specifically, we compared global motion coherence thresholds for 5-year-olds and adults tested at three displacements. We used limited lifetime random Gabor kinematograms that contained either first- or second-order cues to motion, like those used in our previous study of the influence of speed on sensitivity to global motion (Elleberg *et al.*, 2004a). We chose a constant speed of 1.5°/s because, in our previous study, we found that the differences across conditions and age were largest at this speed.

## 2. Methods

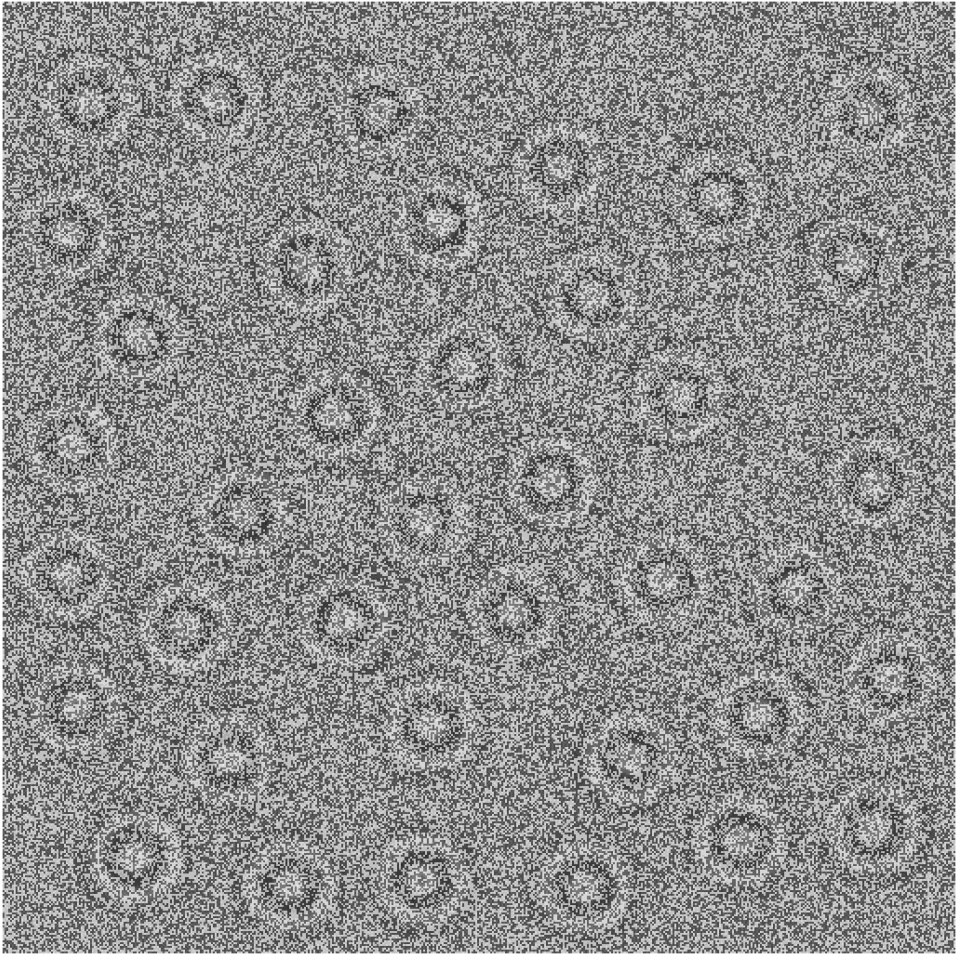
### 2.1. Observers

The participants were 24 adults (18–28 years) and 24 5-year-olds ( $\pm 3$  months). To be included in the study, all subjects had to meet our criteria on a visual screening examination, the details of which are presented elsewhere (Elleberg *et al.*, 2004a).

### 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<sup>2</sup>.

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 (for details see Elleberg *et al.*, 2004a, Fig. 1). The internal sinusoidal structure was concentric so that orientation could not be used as

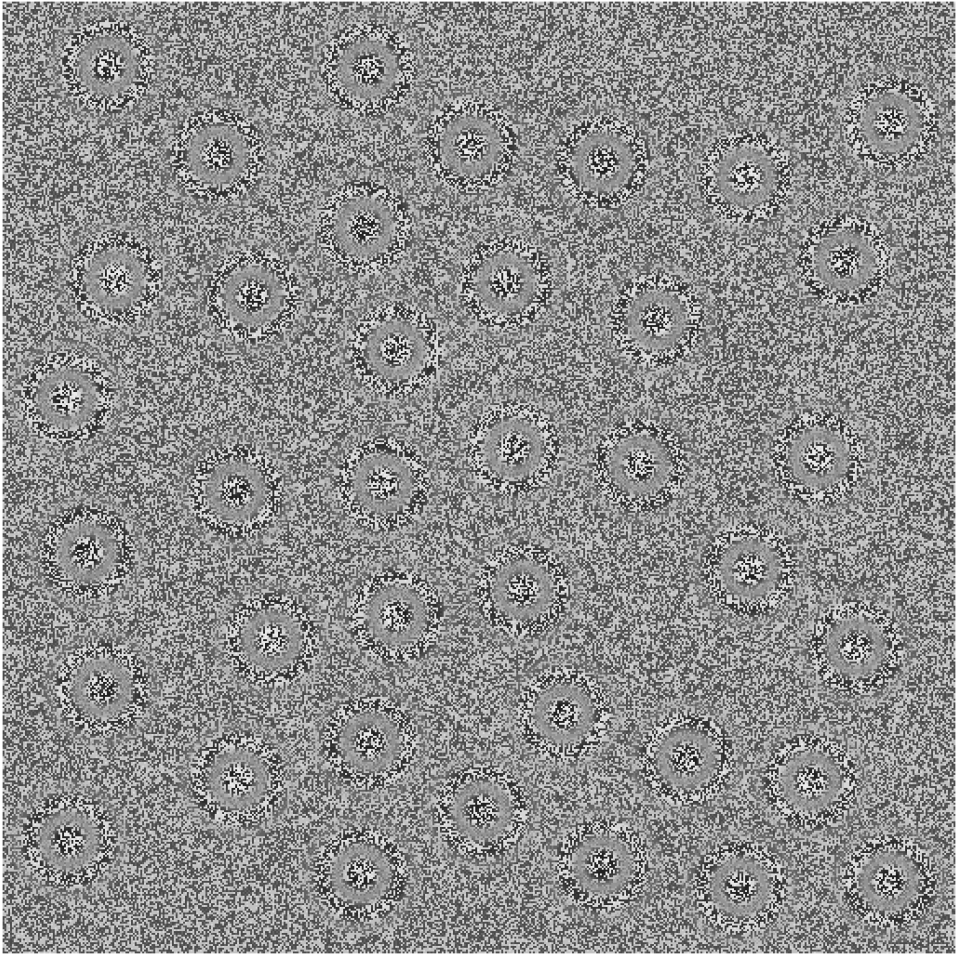


(a)

**Figure 1.** 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  $0.24^\circ$  and an internal sinusoidal spatial frequency of  $3 \text{ c deg}^{-1}$ . 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.

a cue to the direction of motion. We call these new stimuli circular Random–Gabor Kinematograms or RGKs.

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.



(b)

**Figure 1.** (Continued.)

The Gabor micropatterns were composed of concentric sine-wave gratings multiplied by a Gaussian function in the horizontal ( $x$ ) and vertical ( $y$ ) dimensions. The first-order Gabor is represented by the following equation:

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

where  $L_o$  is the mean luminance of the pattern,  $\delta$  is the standard deviation of the Gaussian ( $0.24^\circ$ ),  $C_g$  is the modulation depth of the internal sinusoid,  $\lambda$  is the sinusoidal spatial wavelength ( $3 \text{ c deg}^{-1}$ ) and  $C_n$  is the contrast of the noise carrier  $N_{\text{rnd}}$  (chosen to be either  $-1$  or  $+1$  with probability 0.5).

Each Gabor had a standard deviation of  $0.24^\circ$  and was truncated at  $\pm 2$  standard deviations. The first-order (luminance-modulated) stimulus was created by adding the micropatterns to a spatially two-dimensional, binary, random noise carrier. The

resulting image contained an array of patches, within each of which the mean luminance of the noise varied according to the Gabor waveform (Fig. 1(a)).

The second-order (contrast-modulated) Gabor was created by multiplying the micropatterns with the random noise carrier, and it is represented by the following equation:

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

where  $L_o$ ,  $\delta$ ,  $C_g$ ,  $\lambda$ ,  $C_n$  and  $N_{\text{rnd}}$  refer to the same parameters as equation (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 (Fig. 1(b)).

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 was composed of a single screen pixel (subtending 2.2 arc min) and was assigned independently with a probability of 50% to be either ‘light’ or ‘dark’.

Coherence thresholds were measured for Gabors that moved at a constant speed of 1.5°/s. We tested three displacements: 0.1°, 0.5° and 1.0°. To vary Gabor displacement across conditions and keep speed constant at 1.5°/s, we varied the temporal offset (delay) between successive updates of the positions of the Gabors. For the displacement of 0.1°, the temporal offset was 66.6 ms (5 frames); for the displacement of 0.5°, temporal offset was 333 ms (25 frames); and for the displacement of 1.0°, temporal offset was 666.6 ms (50 frames). If the position of a Gabor exceeded the display area it was redrawn in a new, random location within the display area, before resuming its motion. On any given trial, a proportion of the Gabors (signal) moved in the same direction either upwards or downwards, whilst the remaining Gabors (noise) moved in random directions. These noise Gabors were replaced randomly by another direction of motion, chosen from the 360° range, but importantly they had exactly the same magnitude of spatial displacement and speed as the signal Gabors. Trial duration was set at 1.5 s.

Just like the commonly used random-dot-kinematograms, 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 on each positional update, an individual Gabor is randomly assigned to be either a signal Gabor or a noise Gabor with a probability that is determined by the global motion coherence level. Thus, it is not possible to determine the direction of the entire pattern by following a single Gabor (except, of course, when the coherence level approaches 100%), 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 McMaster Research Ethics Board. 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.

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 in random directions. 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.

#### 2.3.1. Test of Thresholds

Each subject was tested on six thresholds consisting of first- and second-order global motion, each at three displacements (0.1, 0.5 or 1.0°). 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. The procedure for the type of motion tested after the first test staircase was identical except that the criterion and practice phases were omitted.

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 displacements were presented in random order.

#### 2.4. Pilot Studies to Equate the Visibility of the Two Types of Motion

In a previous study, where we first introduced these stimuli (Ellemberg *et al.*, 2004a), 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-year-olds ( $\pm 3$  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 first-order RGKs, thresholds were best and consistent within subject (within a factor of 2) when the modulation depth was above about 30% (20–40%, depending on the subject). For second-order RGKs, thresholds were best and consistent within subject only when modulation depth was above 90% for 5-year-olds and 60% for adults. Therefore, for the main experiment, we chose a modulation depth of 30% for first-order motion and 100% for second-order motion, the same values as those used in our study of sensitivity to global motion at different speeds (Ellemberg *et al.*, 2004a). Both values are 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.

#### 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. Seven data points were replaced: one from each of three 5-year-olds and four 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 displacement with three levels (0.1, 0.5 and 1.0°), 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 displacement, in which each ANOVA had a between-subjects factor of age and a within-subjects factor of motion type. Analyses of simple effects were used to analyse all significant 2-way interactions.

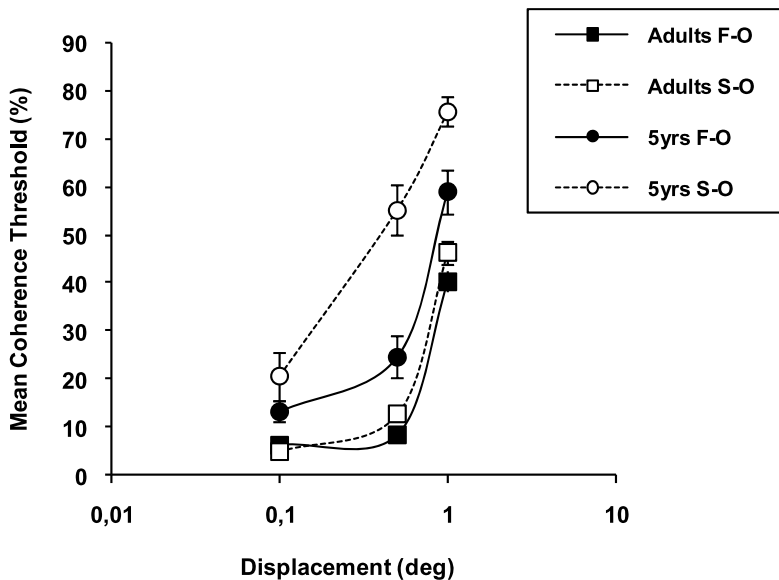


### 3. Results

Figure 2 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 displacements. The 3-way ANOVA revealed an interaction amongst age, type of motion, and displacement,  $F_{2,92} = 5.89$  ( $p < 0.01$ ),  $\eta_p^2 = 0.123$ . All other 2-way and 1-way effects were significant ( $ps < 0.02$ ).

The 3-way interaction was evaluated by conducting 2-way ANOVAs comparing age to type of motion for each of the three displacements. For the smallest displacement ( $0.1^\circ$ ), there was a main effect of age,  $F_{1,46} = 17.79$  ( $p < 0.01$ ),  $\eta_p^2 = 0.258$ , indicating that adults had lower thresholds than 5-year-olds. However, there was no main effect of motion type,  $F_{1,46} = 1.83$  ( $p > 0.10$ ), and no significant interaction between age and motion type,  $F_{1,46} = 1.47$  ( $p > 0.10$ ), indicating that 5-year-olds' thresholds are equally reduced for first-order and second-order motion at this displacement.

The 2-way ANOVA for the middle displacement ( $0.5^\circ$ ) revealed a significant interaction between age and motion type,  $F_{1,46} = 39.32$  ( $p < 0.001$ ),  $\eta_p^2 = 0.481$ , a main effect of age,  $F_{1,46} = 54.20$  ( $p < 0.001$ ),  $\eta_p^2 = 0.534$ , and a main effect of motion type,  $F_{1,46} = 61.78$  ( $p < 0.001$ ),  $\eta_p^2 = 0.583$ . An analysis of simple effects on the interaction revealed that 5-year-olds were worse than adults for both first- and second-order global motion (simple effects,  $p < 0.01$ ), and their thresholds were significantly higher for second-order than for first-order motion (simple



**Figure 2.** Mean coherence thresholds ( $\pm 1$  SE) for adults (squares) and 5-year-olds (circles) for first-order (F-O, solid symbols) and second-order (S-O, open symbols) Random-Gabor Kinematograms at each of the three displacements ( $0.1$ ,  $0.5$  and  $1.0^\circ$ ).

effects,  $p < 0.01$ ). Adult thresholds were equally good for both types of motion (simple effects,  $p > 0.10$ ). Therefore, at the displacement of  $0.5^\circ$ , 5-year-olds' sensitivity is significantly worse than that of adults for both first- and second-order motion, with even greater reductions for second-order motion.

For the largest displacement ( $1.0^\circ$ ) there was a main effect of age,  $F_{1,46} = 45.42$  ( $p < 0.001$ ),  $\eta_p^2 = 0.517$ , and a main effect of motion type,  $F_{1,46} = 14.48$  ( $p < 0.001$ ),  $\eta_p^2 = 0.225$ . The results of the analysis indicate that 5-year-olds had higher thresholds than adults for both first- and second-order global motion, and that 5-year-olds as well as adults were significantly better for first-order motion than for second-order motion. The interaction between age and motion type was not significant ( $p > 0.10$ ).

As indicated previously, the results of the 3-way ANOVA also showed a main effect of displacement. An exploratory set of Dunnett *post-hoc* analyses were conducted for each age group to localise the origin of this significant effect. For adults, there was no significant difference between the thresholds for the two smallest displacements ( $p > 0.10$ ), but both were significantly better than the threshold of the widest displacement of  $1.0^\circ$  ( $p < 0.01$ ). In contrast, 5-year-olds' thresholds were significantly different at each of the three displacements. The thresholds at the displacement of  $0.1^\circ$  were significantly better than those at  $0.5$  and  $1.0^\circ$ , and the results at  $0.5^\circ$  were significantly better than those at  $1.0^\circ$  ( $ps < 0.05$ ). Therefore, increasing displacement from  $0.1$  to  $0.5^\circ$  has a deleterious effect on the perception of global motion in children but not in adults, indicating that adults can tolerate larger shifts in displacement than can children, especially at the largest displacements.

#### 4. Discussion

Five-year-olds were immature for both first- and second-order global motion at every displacement tested. Further, children were generally more immature for second-order global motion than for first-order global motion (see Fig. 2), an effect that was significant at the middle displacement (i.e.,  $0.5^\circ$ ). These findings indicate that the extrastriate mechanisms that integrate local motion cues across space to produce the perception of global motion are still immature at 5-years of age, and that, under some conditions, these mechanisms mature more slowly for second-order than for first-order global motion.

It is unlikely that non-visual factors such as differences in attention, criterion, or eye movements account for the overall pattern of results of the 5-year-olds. First, all tasks measured thresholds and the children's performance was more mature for some conditions than for others. Specifically, for first- and second-order motion at a displacement of  $0.1$ , their thresholds were close to adult-like, whereas their thresholds based on the same staircase for other conditions (i.e., second-order motion at displacements of  $0.5$  and  $1.0$ ), were much poorer than those of adults. Those differences are likely to reflect different patterns of development of motion mechanisms, rather than non-visual factors. Second, by age 5, children perform as well as

adults on some psychophysical tasks that have performance demands like those in the present study, namely, tasks that use two-alternative forced-choice procedures to measure thresholds. For example, studies of sensitivity to the direction of local motion indicate that detection thresholds of 5-year-olds are nearly adult-like for first-order (luminance-defined) stripes moving at 1.5 or 6°/s and for second-order (contrast-defined) stripes moving at 1.5°/s (Elleberg *et al.*, 2003b). Moreover, sensitivity to the direction of global motion tested with random dot kinematograms is mature under at least some testing conditions as early as 3 years of age (Parrish *et al.*, 2005). Therefore, the differential pattern of thresholds in the 5-year-olds is likely to be related to mechanisms for processing global motion that develop more quickly for the smallest displacement and for first-order motion (see Fig. 2).

Another consideration in interpreting the data comes from the findings by Scott-Samuel and Georgeson (1999) suggesting that when temporal frequency (spatial frequency  $\times$  speed) is above 7.5 Hz, first-order artifacts may be introduced into the perception of second-order motion. Further, with small pixels in static noise, the display is vulnerable to adjacent pixel nonlinearity (Klein *et al.*, 1996). This does not seem to pose a problem in our study given our pattern of results and because the Gabors moved at a speed of 1.5°/s and had an internal spatial frequency of 3 c deg<sup>-1</sup>. Thus, they had a nominal temporal frequency of 4.5 Hz. Moreover, Smith and Ledgeway (1997) found no such artifacts when the carrier consisted of high spatial frequency random noise dots like the ones used in the present study. Therefore, 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 is no luminance variation within each noise dot, it is unlikely that our second-order stimuli contained any first-order artifacts (see also Ledgeway and Hutchinson, 2005, 2006).

Inspection of Fig. 2 indicates that immaturities ranged from 5-year-olds being 1.8 times worse than adults at the smallest displacement (0.1°) for first-order motion to being 5.8 times worse than adults at the middle displacement (0.5°) for second-order motion. These results are comparable to what we previously found for sensitivity to global motion as a function of speed, with displacement held constant at 0.24° (Elleberg *et al.*, 2004a). Immaturities ranged from 5-year-olds being 1.5 times worse than adults at the fastest speed (9°/s) for first-order motion to being 5.3 times worse than adults at the slowest speed (1.5°/s) for second-order motion. This impact of both displacement and speed on the development of human global motion perception disagrees with Kiorpes and Movshon (2004) who found that motion sensitivity of Macaque monkeys is more dependent on dot displacement than on dot speed during development. However, the algorithm used by Kiorpes and Movshon to specify the motion of the noise dots in their displays was subtly different from that used in the current study. In the study of Kiorpes and Movshon, if a dot was assigned to be a noise dot on any given displacement, it was simply replaced by a new dot drawn at a random location within the display area. Thus noise dots effectively had both random directions and random speeds. However, in the present study, signal and noise Gabors had identical jump sizes (and speeds) on

each image update, but the noise Gabors simply moved in random directions. Pilly and Seitz (2009) have recently shown that these two different rules for assigning the motion of noise elements (termed ‘white noise’ and ‘Brownian motion’, respectively) can have a marked effect on performance on global motion tasks, at least in human adults. Generally, observers are best at estimating the global motion direction of stimuli derived using the Brownian motion algorithm used in the present study and they suggested that this may be explicable in terms of the spatiotemporal displacement tuning characteristics of extrastriate motion areas. It is possible that these methodological differences lead to different outcomes.

Our findings indicate that for 5-year-olds, the perception of second-order global motion is more immature than the perception of first-order global motion and this is most marked at the intermediate displacement of  $0.5^\circ$ . These findings complement our previous results showing that, compared to first-order global motion, 5-year-olds are especially immature for second-order global motion at slower speeds (Elleberg *et al.*, 2004a). Computational modeling supported by psychophysical and electrophysiological data suggests that the detection of second-order motion requires at least two additional processing steps that are subsequent to a first stage linear filter in the primary visual cortex (Baker, 1999; Chubb and Sperling, 1988, 1989; Wilson *et al.*, 1992). This is supported by VEP findings of slower latencies ( $\sim 50$  ms) to second-order motion onset compared to first-order motion onset (Elleberg *et al.*, 2003a). The additional processing necessary for the extraction of second-order motion may be responsible for the greater immaturities we found for second-order motion at the intermediate displacement.

Overall, our results point to a key role of spatial integration in sensitivity to global motion at larger displacements. In adults, coherence thresholds increased as displacement increased from  $0.5$  to  $1.0^\circ$ , but not as displacement increased from  $0.1$  to  $0.5^\circ$ . This is the same pattern as reported in previous psychophysical studies of human and nonhuman primates (Mather and West, 1993; Newsome and Pare, 1988). Further, we found that adults’ global motion sensitivity is no different for first- and second-order global motion at each displacement, except at the largest displacement ( $1.0^\circ$ ), where adults’ perception of second-order global motion is poorer. Mather and West (1993), who measured the effects of displacement on coherence thresholds for first- and second-order random dot kinematograms, reported worse performance for second-order motion at all displacements between  $0.4$  and  $0.6^\circ$ . However, it is difficult to draw conclusions from their findings because their sample was too small ( $n = 3$ ) to provide any statistical verification of their results. Our finding of higher coherence thresholds for second-order motion only at the largest displacement in adults is consistent with findings that spatial integration is poorer for second-order than for first-order information (Elleberg *et al.*, 2004b; Hess *et al.*, 2000). An alternative explanation for the steep increase in coherence threshold at the largest displacement is a putative change from first- to third-order processing (or attentional tracking) or the need to temporally integrate over a smaller number of frames for this displacement (i.e., less redundancy to promote temporal integration).

The first alternative is supported by evidence that first-order motion processing breaks down at large displacements, and that beyond this point motion detection could be mediated by third-order processes (Lu and Sperling, 2001). However, the parallel increase in threshold found for the second-order motion condition argues against this point. The second point is inconsistent with our finding that the greatest immaturities were found for the middle displacement. It seems more likely that the effects of displacement observed in the current study reflect limits on spatial integration.

Similarly, inspection of Fig. 2 suggests the influence of spatial integration abilities on the results for 5-year-olds: for first- and second-order global motion, 5-year-olds were nearly 2 times less mature at the two largest displacements ( $0.5$  and  $1.0^\circ$ ) compared to the smallest displacement ( $0.1^\circ$ ). This is consistent with previous findings in infants that the maximum displacement yielding a perception of coherent motion increases with age (Wattam-Bell, 1992). This also agrees with evidence of protracted development of sensitivity to larger displacements in monkeys (Kiorpes and Movshon, 2004). Together, these findings suggest that the slow development of sensitivity to global motion reflects, at least in part, protracted development of spatial integration, an ability that is known to continue to improve even after 14 years of age (Kovacs, 2000).

The findings for displacement in adults can help to explain why children were especially immature for second-order motion at the intermediate displacement but not for the smaller or larger displacements. Recall that in adults, coherence thresholds increased as displacement increased from  $0.5$  to  $1.0^\circ$  and sensitivity was poorer for second-order than for first-order global motion only at the largest displacement. The same pattern was found in 5-year-olds at the largest displacement (higher thresholds for second-order global motion), a finding that could reflect the same influence of motion type on spatial integration, with generally poorer spatial integration leading to elevated thresholds at the largest displacement for both first- and second-order motion in children. This could explain why at the smallest displacement — where not as much spatial integration is required — 5-year-olds are least immature and equally so for first- and second-order motion.

In adults, the increase in displacement from the smallest to the intermediate value had no effect on coherence thresholds. That is, adults' thresholds for the intermediate displacement were not limited by the additional spatial integration required. However, children's thresholds increased from the lowest to the intermediate displacement for first-order motion, a result suggesting that immature spatial integration limited their performance. In addition, their thresholds increased even more for second-order motion than for first-order motion, as would be expected if the mechanisms mediating sensitivity to second-order motion mature more slowly than those mediating sensitivity to first-order motion. Overall, the results suggest that the extrastriate mechanisms underlying the perception of global motion are different for first- *versus* second-order motion at least at some displacements, just as they

are at some speeds for first- versus second-order global motion (Elleberg *et al.*, 2004a) and for first- versus second-order local motion (Elleberg *et al.*, 2003b).

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