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Development of sampling efficiency and internal noise in motion detection and discrimination in school-aged children



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ABSTRACT

The aim of this study was to use an equivalent noise paradigm to investigate the development and maturation of motion perception, and how the underlying limitations of sampling efficiency and internal noise effect motion detection and direction discrimination in school-aged children (5–14 years) and adults. Contrast energy thresholds of a 2 c/deg sinusoidal grating drifting at 1.0 or 6.0 Hz were measured as a function of added dynamic noise in three tasks: detection of a drifting grating; detection of the sum of two oppositely drifting gratings and direction discrimination of oppositely drifting gratings. Compared to the ideal observer, in both children and adults, the performance for all tasks was limited by reduced sampling efficiency and internal noise. However, the thresholds for discrimination of motion direction and detection of moving gratings show very different developmental profiles. Motion direction discrimination continues to improve after the age of 14 years due to an increase in sampling efficiency that differs with speed. Motion detection and summation were already mature at the age of 5 years, and internal noise was the same for all tasks. These findings were confirmed in a 1-year follow-up study on a group of children from the initial study. The results support suggestions that the detection of a moving pattern and discriminating motion direction are processed by different systems that may develop at different rates.

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1. Introduction

The ability to perceive motion is a vital and fundamental visual function in humans and several areas in the cerebral cortex are devoted to the analysis of motion. Clinical investigations of vision in children have a tendency to concentrate on visual acuity measurements, and although important, acuity tells us little or nothing about how children perceive the moving world they constantly experience. Although rare, the inability to perceive motion can be severely disabling in everyday life (Zihl, von Cramon, & Mai, 1983). More subtle motion deficits have been in development conditions like amblyopia (Giaschi et al., 1992; Knox, Ledgeway, & Simmers, 2013; Simmers et al., 2003), strabismus (Norcia, 1996), dyslexia (Benassi et al., 2010; Demb et al., 1998; Edwards et al., 2004), autism (Annaz et al., 2010; Koh, Milne, & Dobkins, 2010; Pellicano et al., 2005; Spencer et al., 2000) and cerebral dysfunction (Ahmed & Dutton, 1996; Dutton et al., 2004; Guzzetta et al., 2009; Weinstein et al., 2012). In adults motion perception is impaired in

normal ageing (Bogfjellmo, Bex, & Falkenberg, 2013; Hutchinson et al., 2012), glaucoma (Bullimore, Wood, & Swenson, 1993; Falkenberg & Bex, 2007), multiple sclerosis (Regan, Kothe, & Sharpe, 1991) and Alzheimer's disease (Mapstone, Dickerson, & Duffy, 2008). These disruptions of motion perception suggest that motion perception may be vulnerable in typical visual development, and that reduced sensitivity to motion could be used as an indicator of neurodevelopmental or pathological disorders. To enable the separation of typical and atypical development, it is necessary to understand how normal motion perception develops and matures in childhood.

In typical development, detection of moving patterns and discrimination of motion direction continues to improve during childhood (Armstrong, Maurer, & Lewis, 2009; Bogfjellmo, Bex, & Falkenberg, 2014; Boot et al., 2012; Ellemberg et al., 1999, 2003, 2004; Giaschi & Regan, 1997; Gordon & McCulloch, 1999; Hadad, Maurer, & Lewis, 2011; Hayward et al., 2011; Manning, Aagten-Murphy, & Pellicano, 2012; Meier & Giaschi, 2014; Narasimhan & Giaschi, 2012; Parrish et al., 2005; Schrauf, Wist, & Ehrenstein, 1999). Different aspects of motion perception develop and reach adult levels at different times, ranging from 3 years (Parrish et al., 2005) to 15 years (Schrauf, Wist, & Ehrenstein, 1999),

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depending on the specific psychophysical task and stimulus parameters. Generally, detection of moving patterns develops and matures to adult levels earlier than direction discrimination. Young children show elevated thresholds for detecting global motion coherence (Boot et al., 2012; Ellemberg et al., 2003, 2004; Falkenberg, Dutton, & Simpson, 2010; Gunn et al., 2002; Hadad, Maurer, & Lewis, 2011; Meier & Giaschi, 2014; Narasimhan & Giaschi, 2012), speed discrimination (Ahmed et al., 2005; Hayward et al., 2011; Manning, Aagten-Murphy, & Pellicano, 2012; Narasimhan & Giaschi, 2012; Parrish et al., 2005) and direction discrimination (Armstrong, Maurer, & Lewis, 2009; Ellemberg et al., 2003; Giaschi & Regan, 1997). Ellemberg et al. (1999) found that critical flicker fusion frequency and contrast thresholds for detecting gratings that flickered at high temporal frequencies (20.0 and 30.0 Hz) were mature at 4 years, whereas for 5.0 and 10.0 Hz adult levels were not achieved until 7 years of age. That temporal sensitivity is immature in 5-year-olds was later confirmed by the same group (Ellemberg et al., 2003, 2004). Some studies show that motion coherence thresholds are less mature at slow speeds (Gunn et al., 2002; Hayward et al., 2011; Manning, Aagten-Murphy, & Pellicano, 2012; Meier & Giaschi, 2014; Narasimhan & Giaschi, 2012; Parrish et al., 2005), but have been found to reach adult values by 7–8 years (Giaschi & Regan, 1997; Hayward et al., 2011; Parrish et al., 2005) when speed thresholds are measured. Recently, a rather novel technique of measuring reaction time to fixation showed that the motion processing matured at eight years old (Boot et al., 2012).

While it is evident that motion sensitivity is immature in childhood, the underlying mechanisms and limiting factors in normal development still require elucidation. One approach to studying such limiting factors is through comparing real observer performance to that of an ideal observer. The ideal observer is derived through mathematical statistics (Whalen, 1971) and is completely non-arbitrary. Humans differ in two ways from the ideal observer who uses all the information available (Bennett, Sekuler, & Ozin, 1999; Burgess et al., 1981; Green & Swets, 1966; Legge, Kersten, & Burgess, 1987; Pelli, 1990; Pelli & Farell, 1999). First, real observers behave as though the stimulus contains more noise than it really contains. Their performance can be modeled by assuming that internal noise has been added to the stimulus. Sources of internal noise include random optical, photon and neuronal noise (Barlow, 1978; Pelli, 1990). Second, real observers are inefficient samplers who fail to use all the information delivered in the stimulus. Reduced sampling efficiency can be due to neural factors (cortical immaturities, multiplicative neural noise) in the visual system or cognitive factors such as variable attention or inefficient cross-correlation between the delivered noisy signal and the known signal template (Bennett, Sekuler, & Ozin, 1999; Burgess & Colborne, 1988; Legge, Kersten, & Burgess, 1987). If a fixed signal (“signal known exactly”) is used in an experiment, the ideal strategy is to cross-correlate the stimulus with a template of the signal. An ideal observer will use the true signal as the template, but a real observer will not remember the signal perfectly and hence the template will not be identical to the signal. This is a major cause of sampling inefficiency. Many studies have investigated the limiting factors of human pattern detection and discrimination using the equivalent noise (EN) model (Bennett, Sekuler, & Ozin, 1999; Dakin, Mareschal, & Bex, 2005; Falkenberg & Bex, 2007; Pardhan, 2004; Simpson, Falkenberg, & Manahilov, 2003). The detection and discrimination of moving grating patterns was specifically studied by our group (Simpson, Falkenberg, & Manahilov, 2003) the EN model. The EN model has also recently been applied developmentally to study global motion perception (Bogfjellmo, Bex, & Falkenberg, 2014), where direction discrimination improves in childhood due to improved sampling efficiency. Further, it has been found that both internal noise and sampling efficiency limits

detection and discrimination in older adults (Bennett, Sekuler, & Ozin, 1999; Bogfjellmo, Bex, & Falkenberg, 2013; Falkenberg & Bex, 2007; Pardhan, 2004; Pardhan et al., 1996). In the context of this approach, we can ask whether the immaturity observed in previous developmental studies of motion perception is due to increased levels of internal noise, or to poor sampling efficiency, or both.

The present study applies an EN model to investigate the limiting mechanisms underlying the development of motion detection and discrimination in typically developing school-aged children. A 1-year follow-up study was performed on a group of children to investigate longitudinal changes in motion detection and discrimination. Besides the utility of these data for determining the mechanisms underlying the normal development of motion perception, these data will also be used as a reference for children with developmental disorders (paper in preparation).

2. Experiment 1

2.1. Methods

2.1.1. Subjects

168 children (85 girls) aged 5–14 years took part in the study. The children were divided into 10 groups according to age, 5 years ($n = 15$); 6 years ($n = 11$); 7 years ($n = 17$); 8 years ($n = 20$); 9 years ($n = 22$); 10 years ($n = 20$); 11 years ($n = 19$); 12 years ($n = 17$); 13 years ($n = 14$) and 14 years ($n = 13$). Child observers were recruited from the out-patients department at the Royal Hospital for Sick Children in Glasgow, from children of staff at Glasgow Caledonian University and from visitors at the Glasgow Science Centre. Informed assent was sought from all child observers and parents/guardians gave consent. 15 naive adult observers (age 29.3 ± 4.6 years) from Glasgow Caledonian University also participated with informed consent. Approval to approach children and parents was granted from all of the above institutions and the tenets of the Declaration of Helsinki were followed. Observers wore their current spectacle correction if required. All observers were screened for visual abnormalities by an optometrist (HKF). To be included in the study, observers had to meet the following criteria: VA better than 1.0 Snellen equivalent (0.8 for the 5 year olds) and monocular VA difference $< 0.1 \log \text{MAR}$ using Glasgow Acuity Cards (GAC score = $1 - \log \text{MAR}$); no strabismus or heterophorias $< 10 \Delta D$ (Cover Test); normal history of ophthalmic pathology and birth.

2.1.2. Stimuli

Upward, downward or flickering gratings were generated by a computer with an 8 bit video board and presented on a high resolution monitor (19", Iiyama Vision Master Pro 450, 640×480 pixels) with a refresh rate of 120 Hz. The VGA RGB outputs were combined electronically (Pelli & Zhang, 1991), which gave 12 bits of luminance control, and an optimum palette of 256 luminances (out of 4096) was used. The mean luminance was 30 cd/m^2 , and the display was calibrated with a luminance meter (LS-100; Konica Minolta, Osaka, Japan). The stimulus was viewed binocularly from a head and chin rest 105 cm away in a dimly lit room where the uniform gray background behind the monitor matched the luminance of the display. A central fixation mark was present for the duration of each trial.

The stimulus was a moving or flickering grating with added dynamic noise (Fig. 1), presented within a 5 deg circular window for a total of 333 ms (20 movie frames). The signal grating was a 2 c/deg Gabor patch drifting at 1.0 Hz or 6.0 Hz. The added dynamic Gaussian white noise was generated by a multiply-with-carry generator (Marsaglia, 1994) in combination with the

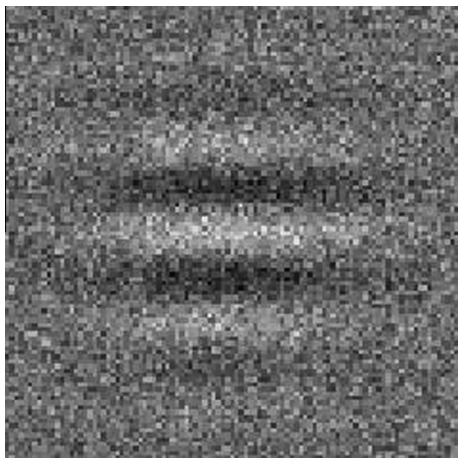


Fig. 1. Illustration of a single frame of the 2 cyc/deg grating stimulus with added noise. On each trial, the observer fixated a central point and reported whether the stimulus contained a moving grating or a blank field (detection task); a counterphase flickering grating or a blank field (summation task) or an upwards or downwards moving grating (discrimination task) in different levels of added noise.

polar method, and was clipped at ± 2.5 standard deviations. The signal contrast of each trial was placed according to a staircase (Levitt, 1971) in steps of 15%, the noise contrast standard deviation was fixed at 0 and 0.25 (corresponding to noise power spectral densities of 0 and $0.65 \mu\text{s deg}^2$). The standard added noise level was 0.25, however some young children were unable to perform the task with this level of noise added. For these observers, the noise standard deviation was reduced until reliable psychometric functions were obtained with contrast standard deviations of 0.2, 0.15 or 0.1 (corresponding to noise power spectral densities of 0.42, 0.23 or $0.1 \mu\text{s deg}^2$).

2.1.3. Procedure

Three tasks were run in random order: detection, summation and discrimination. In the detection task the stimulus was (with equal probability) an upward moving grating or a blank, in the summation task, a counterphase flickering grating (which is the sum of two oppositely drifting gratings) or a blank was presented, and in the discrimination task an upward or downward moving grating was presented with equal probability. After each trial two response boxes appeared outside the stimulus area, representing the two possible stimuli presented (grating or blank for detection and summation, arrows pointing up or down for discrimination). The observers indicated with a mouse click which stimulus had been presented. A happy face appeared after each correct response; no feedback was given for incorrect responses. Child observers were in addition praised and encouraged to maintain focus, interest and attention during the experiment runs. Each observer was given a practice run containing 10 supra-threshold trials highly visible before any data were collected. For each task, contrast thresholds were measured for zero and a non-zero level of added noise (Simpson, Falkenberg, & Manahilov, 2003). Adult observers completed all three tasks at both speeds, whereas child observers completed at least two tasks at one speed in one session. Observers completed at least two runs, and each run terminated after 60 trials.

2.1.4. Equivalent Noise model

Our basic approach was to measure contrast energy thresholds for each task as a function of added noise using an Equivalent Noise model. The EN model exploits the additivity of noise in the stimulus and noise in the visual system, and has proved to be a useful

model of adult performance for various visual tasks (Bennett, Sekuler, & Ozin, 1999; Dakin, Mareschal, & Bex, 2005; Falkenberg & Bex, 2007; Pardhan, 2004; Simpson, Falkenberg, & Manahilov, 2003).

The EN model is an elaboration of the ideal observer. Intuitively, any task becomes harder as noise is added, and ideal observer and human performance is predicted to rise linearly with added noise (Burgess et al., 1981; Najemnik & Geisler, 2005; Pelli, 1990; Pelli & Farell, 1999). The ideal observer uses all the information contained in the stimuli. For the detection task, its performance is limited by the signal energy and external noise. The ideal observer performance for detection is given by the signal energy E and the external noise N_e .

$$d' = \sqrt{\frac{E}{N_e}}$$

Previous studies have shown that real observer performance differs from the ideal in that it is limited by added internal noise N_i and suboptimal sampling efficiency k (Burgess et al., 1981; Green & Swets, 1966; Legge, Kersten, & Burgess, 1987; Pelli, 1990; Pelli & Farell, 1999). Thus the Equivalent Noise model is

$$d' = \sqrt{\frac{kE}{N_e + N_i}} \quad (1)$$

We measure the contrast energy threshold E_t , defined as the energy required for a performance level of $d' = 1$, giving

$$E_t = \frac{N_e + N_i}{k} = \frac{N_e}{k} + \frac{N_i}{k} \quad (2)$$

If external noise power spectral density increases, we predict the energy threshold to increase linearly. N_i and k are estimated by plotting E_t as a function of N_e and fitting a linear regression. The y -intercept for Eq. (2) is N_i/k , and the slope is $1/k$. Therefore we fit a linear regression and estimate k as $1/\text{slope}$, and N_i as $y\text{-intercept}/\text{slope}$ (Legge, Kersten, & Burgess, 1987; Simpson, Falkenberg, & Manahilov, 2003).

For summation and discrimination, the performance of the ideal and EN observer also depends on the actual cross-correlation ρ between the signals (Simpson, Falkenberg, & Manahilov, 2003). For summation, human performance can be described by

$$d' = \sqrt{\frac{2kE(1 + \rho)}{N_e + N_i}} \quad (3)$$

and in terms of thresholds (at $d' = 1$) we have

$$E_t = \frac{N_e + N_i}{2k(1 + \rho)} \quad (4)$$

For discrimination, the performance is given by

$$d' = \sqrt{\frac{2kE(1 - \rho)}{N_e + N_i}} \quad (5)$$

and thresholds are given by

$$E_t = \frac{N_e + N_i}{2k(1 - \rho)} \quad (6)$$

The actual cross-correlations ρ between the drifting Gabor signals in this study were 0.77 for 1.0 Hz and 0 for 6.0 Hz. Eqs. (3)–(6) predict that gratings moving at 1.0 Hz will easily be seen when summed, and poorly discriminated. At 6.0 Hz discrimination will be much easier and summation somewhat harder. For further details of the derivations of the equations see (Simpson, Falkenberg, & Manahilov, 2003; Simpson, Loffler, & Tucha, 2013).

2.2. Statistical analysis

The individual raw data from at least two repetitions were combined and a psychometric function was fitted to each observer's yes/no data by the method of maximum likelihood estimation (Geyer, 2003; Hall, 1968). Contrast threshold energies ($d' = 1$) were calculated from the psychometric function, with and without noise, for each observer and task. The contrast energies and cross-correlations of the stimuli were calculated numerically using the actual stimulus sequences. We pooled the contrast thresholds for adults as everyone performed all the tasks at both speeds, and we estimated internal noise and sampling efficiency using Eqs. (2), (4), and (6). For these pooled data we used a likelihood ratio test (Faraway, 2004) to investigate the goodness of fit of a full six parameter model having separate slopes and intercepts for each task compared with the simpler four parameter model with a single intercept that we have previously shown to best describe these tasks (Simpson, Falkenberg, & Manahilov, 2003). As most children only performed two tasks at one speed, the internal noise and sampling efficiencies were calculated from individual contrast threshold energies for each level of noise and task using Eqs. (2), (4), and (6). Least squares estimates and analysis of variance (ANOVA) were used to determine the differences in internal noise and sampling efficiency with age and task.

For sampling efficiency and internal noise to be calculated, contrast thresholds for two noise levels (zero and non-zero) are necessary. Some of the youngest children were unable to perform the direction discrimination task (5–7 years $n = 22$, 7–9 years $n = 5$) or detection task (5–6 years $n = 3$) with any level of noise added to the stimuli. Data from these children were not included in the analysis, and explains why sampling efficiency for 1.0 Hz is only estimated for children over the age of 7.

3. Results

Table 1 shows the mean contrast energy thresholds as a function of age, task and speed for the no added noise condition. Even for noiseless stimuli, direction discrimination is harder than detection and discrimination, especially for 1.0 Hz. Further, it can be seen that only direction discrimination improves with age. By adding noise to the stimuli, using the Equivalent Noise paradigm, we can determine what causes this improvement. Fig. 2 shows the contrast energy thresholds with and without added noise for adult observers. When noise is added to the stimuli thresholds increase, especially for direction discrimination. The Equivalent Noise model says that energy thresholds rise linearly with external noise level, and thus for each condition (detection of a moving grating, detection of the sum of two oppositely moving gratings, or discrimination of a pair of oppositely moving gratings) the data can be

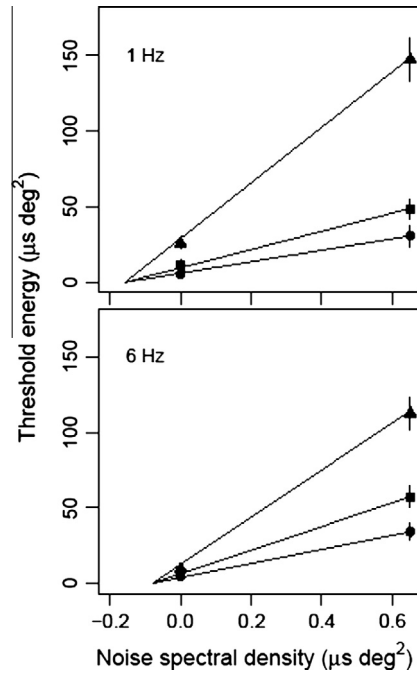


Fig. 2. The average adult contrast energy threshold for detecting an upwards drifting grating (squares), detecting the sum of an upwards and downwards drifting grating (circles) and for discriminating an upwards from a downwards drifting grating (triangles) as a function of power spectral density of the added Gaussian white noise. Each point is the average of 15 adults, and error bars show 95% confidence intervals. Lines show the least squares fits of the ideal observer model with a common x-intercept (internal noise) but different slopes (sampling efficiencies) for each task. Child observers (see Fig. 5) show the same pattern of results.

fitted by a line. However, the three lines in each panel of Fig. 2 were not fitted individually. Instead, as in our previous study (Simpson, Falkenberg, & Manahilov, 2003), a likelihood ratio test (Faraway, 2004) was conducted which showed that the data were well described by a model having a common intercept (internal noise) but different slopes (sampling efficiency) for the three tasks. For adult observers, the internal noise is the same for all three tasks ($F_{1Hz}(2, 132) = 0.051, p = 0.91$; $F_{6Hz}(2, 133) = 0.01, p = 0.97$), and a paired t -test showed the internal noise does not vary with speed ($t(45) = 2.1, p > .05$). The adult sampling efficiencies and internal noise are shown in Fig. 3 (diamonds).

Fig. 3A shows the sampling efficiency for direction discrimination as a function of age for gratings drifting at speeds of 1.0 and 6.0 Hz. Error bars show 95% confidence intervals, and the fitted lines are the linear regression fits estimated by least squares on the data from individual observers.

Table 1
Contrast energy thresholds (mean \pm 1 SE) with no added noise to the stimuli, as a function of age, task and speed.

Age (years)	Contrast energy thresholds ($\mu\text{s deg}^2$) with no added noise										Adult ^a
	5	6	7	8	9	10	11	12	13	14	
<i>Disc</i>											
1 Hz	–	–	42 \pm 12	52 \pm 28	36 \pm 19	36 \pm 12	29 \pm 17	44 \pm 13	33 \pm 9	32 \pm 6	26 \pm 7
6 Hz	98 \pm 9	53 \pm 8	21 \pm 9	26 \pm 16	22 \pm 7	20 \pm 13	21 \pm 4	16 \pm 12	18 \pm 6	14 \pm 4	10 \pm 2
<i>Sum</i>											
1 Hz	12 \pm 8	8 \pm 5	6 \pm 11	9 \pm 11	8 \pm 11	7 \pm 11	5 \pm 11	6 \pm 11	6 \pm 11	8 \pm 11	6 \pm 2
6 Hz	12 \pm 4	3 \pm 11	5 \pm 11	3 \pm 11	11 \pm 11	4 \pm 11	4 \pm 11	6 \pm 11	3 \pm 11	5 \pm 11	5 \pm 2
<i>Up</i>											
1 Hz	10 \pm 6	7 \pm 7	8 \pm 3	11 \pm 5	15 \pm 10	13 \pm 11	6 \pm 6	13 \pm 3	10 \pm 6	11 \pm 5	11 \pm 2
6 Hz	12 \pm 6	10 \pm 5	19 \pm 11	9 \pm 10	12 \pm 9	4 \pm 3	8 \pm 4	10 \pm 2	6 \pm 4	7 \pm 3	6 \pm 3

^a Mean of 15 adults: 29.3 \pm 4.6 years.

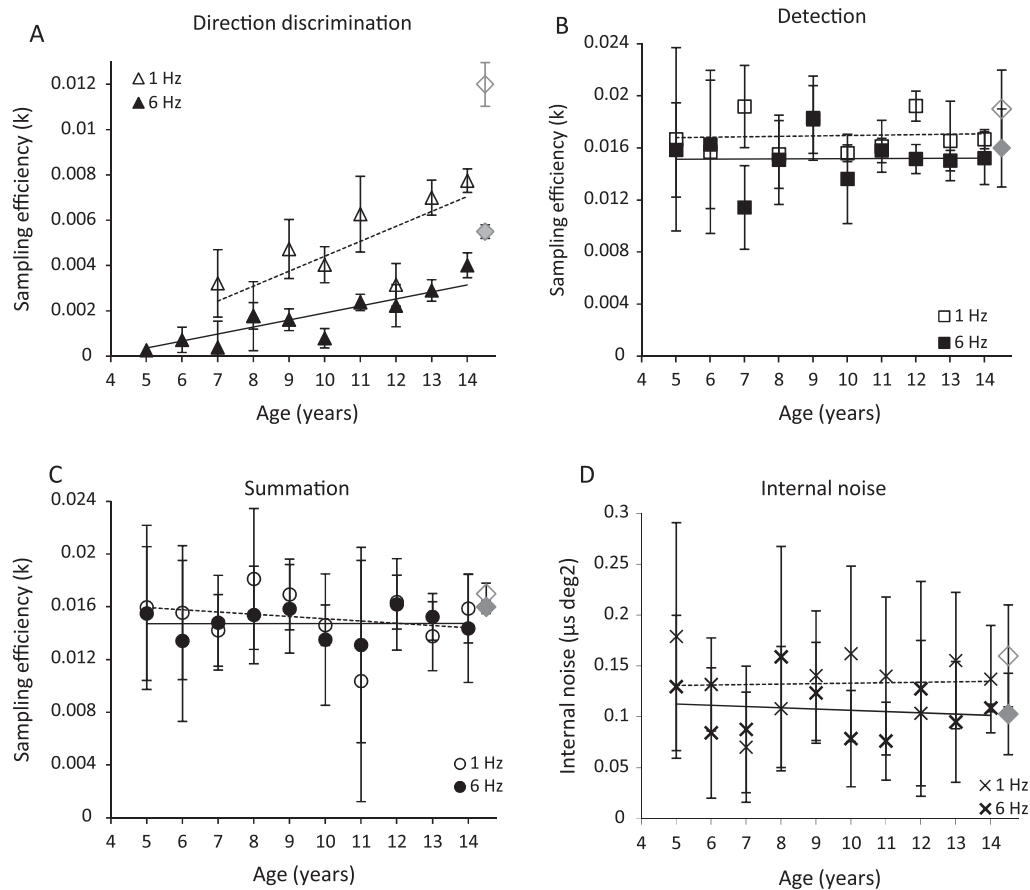


Fig. 3. Mean sampling efficiency estimates for (A) direction discrimination (triangles); (B) detection (squares) and (C) summation (circles) estimated from individual ideal observer fits and plotted as a function of age and speed. Gray diamonds in all panels show the mean adult values. Open symbols represent the mean values at 1.0 Hz, and solid symbols the mean values at 6.0 Hz. Error bars show 95% confidence intervals, the fitted lines are the linear regression fits estimated by least squares. At 1.0 Hz the sampling efficiency for discrimination could not be estimated before 7 years of age.

It is apparent from the slopes that sampling efficiency improve with age for both speeds (linear regression: $F_{1\text{Hz}}(1,40) = 32$, $p < 0.001$, adjusted $r^2 = 0.54$; $F_{6\text{Hz}}(1,45) = 57$, $p < 0.001$, adjusted $r^2 = 0.79$) and that the function for the 1 Hz grating was steeper than that of the 6 Hz grating (likelihood ratio test, $p < 0.001$). This means that sampling efficiency improves more rapidly during development for the slower speed pattern than it does for the faster pattern. The intercepts for the two fitted functions are not significantly different. It can also be seen that the sampling efficiency for 1.0 Hz is higher than for 6.0 Hz across the age range (ANOVA: $F(2,85) = 28$, $p < 0.001$). Fig. 3B and C shows that sampling efficiency does not change with age or speed for detection ($F_{1\text{Hz}}(2,78) = 0$, $p = 0.9$, $r^2 = 0$; $F_{6\text{Hz}}(2,84) = 0.04$, $p = 0.8$, $r^2 = 0.01$) or summation ($F_{1\text{Hz}}(2,38) = 0$, $p = 0.6$, $r^2 = 0.01$; $F_{6\text{Hz}}(2,39) = 0.06$, $p = 0.8$, $r^2 = 0$).

The internal noise does not differ with development or task (unbalanced ANOVA; $F_{1\text{Hz}}(3,114) = 1.2$, $p = 0.31$; $F_{6\text{Hz}}(3,124) = 1.1$, $p = 0.34$), and Fig. 3D shows the mean internal noise with 95% confidence levels for each age group for 1.0 and 6.0 Hz. The fitted lines are the linear regression fits estimated by least squares, and it can be seen that internal noise does not change with age as both lines are flat ($F_{1\text{Hz}}(1,116) = 0.3$, $p = 0.6$, $r^2 = 0$; $F_{6\text{Hz}}(1,126) = 0.4$, $p = 0.6$, $r^2 = 0$).

Fig. 4 shows the efficiency ratio of children compared to adults for direction discrimination. Young children are extremely inefficient compared to adults for both speeds. The sampling efficiency improves in childhood, but even at 14 years of age, the efficiency

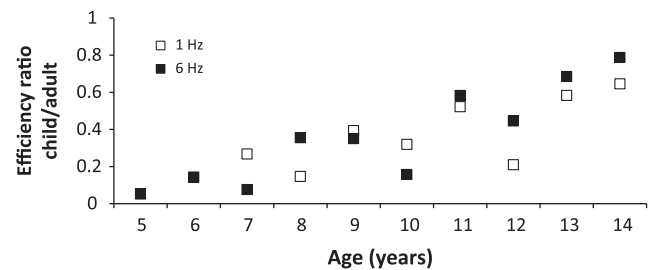


Fig. 4. Relative efficiency ratios of children compared to adults for direction discrimination. For each year, the ratio of child sampling efficiency relative to the adult sampling efficiency is plotted for speeds of 1.0 (open squares) and 6.0 Hz (solid squares).

ratio is only $\sim 2/3$ compared to adults. In contrast, for detection and summation there are no significant differences with age. The relative efficiency ratios are close to one across all age groups, meaning that for detecting a moving pattern, children are as efficient as adults.

4. Follow-up experiment

Experiment 1 showed that motion direction discrimination continues to improve after the age of 14 years due to an increase in sampling efficiency, whereas the detection of a moving pattern is already mature at the age of 5 years. However, only a few children

were able to perform all three tasks (discrimination, detection and summation). A 1-year follow-up experiment was performed on these children to further investigate the development of sampling efficiency and internal noise on detection and direction discrimination of moving patterns in individual child observers.

4.1. Methods

4.1.1. Subjects

14 of the children who performed all three tasks in the initial Experiment 1 took part in a follow-up experiment 12 ± 2 months after the first visit. The same inclusion criteria as in Experiment 1 were applied, and all participated with informed consent.

4.1.2. Stimuli, procedure and analysis

The stimuli were the same as in the initial Experiment 1. The signal contrast was controlled by a staircase procedure and the noise contrast was fixed between 0 and 0.25. The three tasks were the same as in the initial Experiment 1: detection of an upward drifting grating, detection of a counterphase flickering grating, and the discrimination of an upward or downward drifting grating. All children performed all three tasks at either 1.0 Hz ($n = 7$) or 6.0 Hz ($n = 7$), and sampling efficiency and internal noise were calculated using Eqs. (2), (4), and (6) using a four parameter model with a single intercept and different slopes as described above for the adults.

5. Results

Fig. 5 shows the contrast energy thresholds for detection, summation and discrimination of as a function of added noise for three observers at the initial Experiment 1 (top panels) and the Follow-up experiment (bottom panels). The lines show the least square fits

of the ideal observer model (Eqs. (2), (4), and (6)). It can be seen that the pattern of results is the same as for adults in Fig. 2; the slope for direction discrimination is much steeper than for detection and summation. It can also be seen that for direction discrimination there is an improvement in performance for at the 1-year follow-up (shallower slopes, bottom panels).

Fig. 6 shows the individual improvement in sampling efficiency between the initial Experiment 1 and the 1 year follow-up experiment as a function of age for 1.0 and 6.0 Hz. For direction discrimination, a repeated measures ANOVA showed a significant main effect for speed ($F(1,13) = 34.9$, $p < 0.01$), and age ($F(1,13) = 30.3$, $p < 0.01$) and a significant interaction between age and speed ($F(1,13) = 14$, $p < 0.01$). There was also a significant improvement between the initial Experiment 1 and the follow-up experiment ($F(1,13) = 31.8$, $p < 0.01$), but no interaction effects with age ($p > 0.25$).

Linear regression analysis confirmed that there is an improvement in sampling efficiency for direction discrimination with age for 1.0 Hz ($F(1,12) = 103$, $p < 0.01$, $r^2 = 0.89$) and 6.0 Hz ($F(1,12) = 60$, $p < 0.01$, $r^2 = 0.81$). For detection and summation, the sampling efficiency and internal noise did not change with age, speed or between visits (repeated measures ANOVA; all $p > 0.08$). The results confirm that sampling efficiency increases with age as in Experiment 1.

6. Discussion

The present study applied an Equivalent Noise model to investigate how sampling efficiency and internal noise limit the ability to detect moving and flickering grating patterns and to discriminate motion direction in typically developing school-aged children. In line with other studies using an EN model, we find that motion sensitivity in children and adults is limited by both internal noise

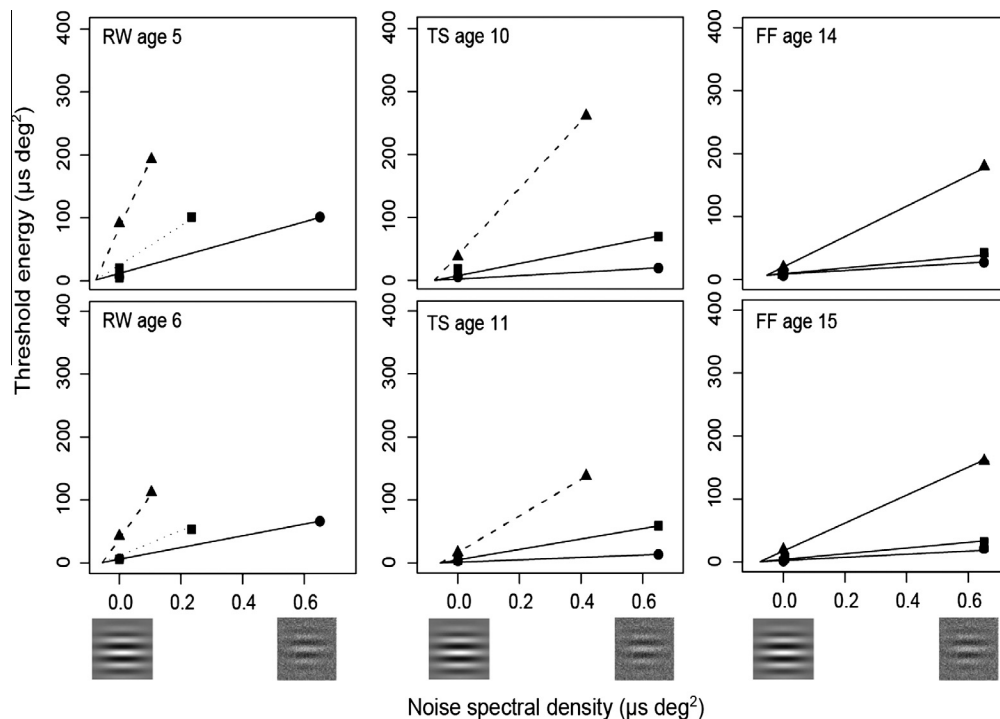


Fig. 5. The contrast energy threshold for detecting an upwards drifting grating (squares), detecting the sum of an upwards and downwards drifting grating (circles) and for discriminating an upwards from a downwards drifting grating (triangles) as a function of power spectral density of the added Gaussian white noise for three typical observers. The gratings were drifting at 6.0 Hz (RW, FF) and 1.0 Hz (TS). The top panels show the results from the initial Experiment 1, and the bottom panels show the results from the Follow-up experiment 1 year later. Lines show the least squares fits of the ideal observer model (Eqs. (2), (4), and (6)) with a common x-intercept (internal noise) but different slopes (sampling efficiencies) for each task.

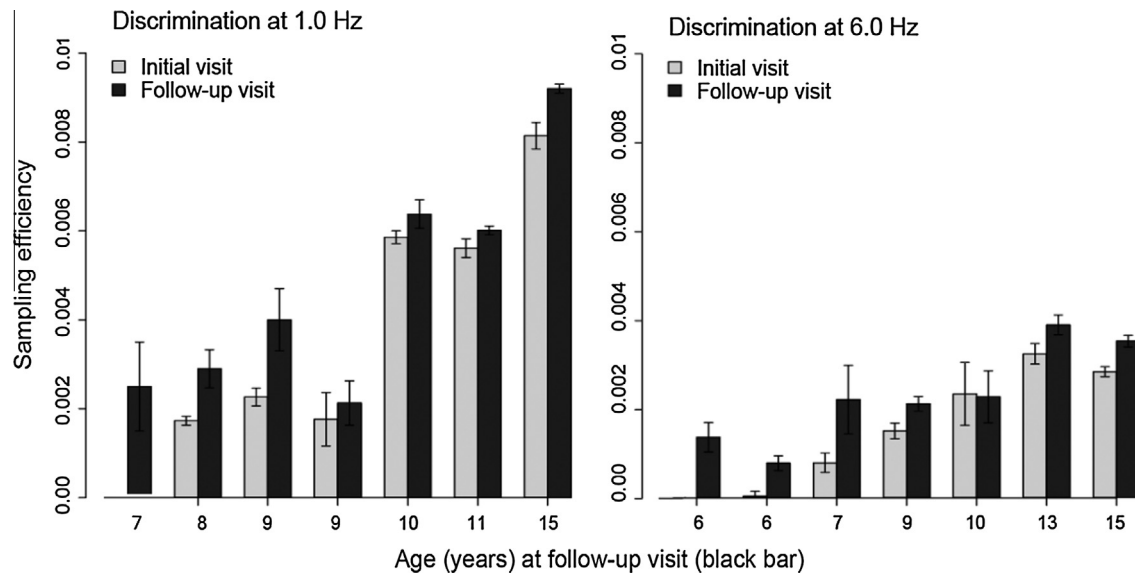


Fig. 6. The improvement in sampling efficiency between the initial visit (gray bars) and 1 year follow-up visit for direction discrimination as a function of age at the follow-up visit for 1.0 Hz and 6.0 Hz. Each pair of gray and black bars show one observer, error bars show ± 1 SE.

and reduced sampling efficiency (Bennett, Sekuler, & Ozin, 1999; Bogfjellmo, Bex, & Falkenberg, 2013, 2014; Burgess et al., 1981; Falkenberg & Bex, 2007; Huang et al., 2007; Kersten, Hess, & Plant, 1988; Legge, Kersten, & Burgess, 1987; Pardhan, 2004; Pardhan et al., 1996; Simpson, Falkenberg, & Manahilov, 2003). Here we show that the ability to discriminate the directions of two moving gratings develops gradually and is still immature at 14 years. This means that young children need a higher signal contrast to correctly discriminate the direction of motion. In contrast, the ability to detect a moving or flickering grating becomes adult-like by 5 years. Further, we show that the lower performance in direction discrimination of moving gratings can be attributed to reduced sampling efficiency, but not any greater internal noise in children compared to adults. This is in agreement with (Bogfjellmo, Bex, & Falkenberg, 2014) who investigated direction discrimination of global motion perception in children aged 5–17 years.

This study shows that internal noise is the same across age, task and speed. Changes to optical factors that increase light scatter, reduce retinal illumination or cause optical defocus, will raise internal noise in the visual system, and limit processing of fine details. As the spatial frequency in this study was 2 c/deg, and that refractive status and accommodation are mature by the age of 4 years (Banks & Crowell, 1993; Howland, 1993), optical factors is unlikely to be the reason for the internal noise. Another reason could be a variability in placement of the observer's criterion, or inconsistent decision-making by the observer (Bennett, Sekuler, & Ozin, 1999; Burgess & Colborne, 1988; Legge, Kersten, & Burgess, 1987). However, a more likely source is intrinsic neural noise present in the central nervous system (Kiorpes et al., 2003; Pelli, 1990; Skoczenski & Norcia, 1998). Whatever the cause, the internal noise is the same in children and adults.

The main limiting factor in direction discrimination of grating patterns in childhood is poor sampling efficiency. We recently showed this to be the case for global motion discrimination also (Bogfjellmo, Bex, & Falkenberg, 2014). Reduced sampling efficiency means children are unable to use all the information in the stimuli to aid performance, and is related to neural factors (cortical immaturities, multiplicative neural noise) in the visual system, or cognitive factors such as variable attention or mismatched cross-correlation between the delivered noisy signal and the

known signal template (Bennett, Sekuler, & Ozin, 1999; Bosking & Maunsell, 2011; Burgess & Colborne, 1988; Casco et al., 2012; Legge, Kersten, & Burgess, 1987). It is known that the visual cortex continues to develop well into the second decade. Synaptic pruning, myelination of axons, cortical thinning and GABAergic signaling mechanisms occurring in adolescence (Gogtay et al., 2004; Huttenlocher, 1990; Mitchell & Neville, 2004; Pinto et al., 2010; Shaw et al., 2008) may alone or in combination, improve template matching by narrowing of direction selective bandwidths, and explain why sampling efficiency for direction discrimination continues to improve in school aged children. This is supported by studies in macaque monkeys, where development of contrast sensitivity is contributed to maturation of cortical visual processing (sampling efficiency), rather than retinal processing (internal noise) (Kiorpes et al., 2003, 2012), and that directional sensitive bandwidths of V1 neurons in narrows with age (Hatta et al., 1998). Reduced sampling efficiency has also been attributed to neural loss within the ageing visual system, although exactly how or where these neural changes occur is still not clear (Bogfjellmo, Bex, & Falkenberg, 2013; Falkenberg & Bex, 2007).

One possible cause of the poor efficiency is the templates used to accomplish the discrimination or detection. The ideal observer computes the cross-correlation of the stimulus with templates of the known signals. The template producing the larger cross-correlation is judged as indicating the direction of motion in the stimulus. Real observers, and especially young children, do not have a perfect memory for the signal which they are trying to discriminate or detect, and so have imperfect templates. This leads to loss of information and reduced sampling efficiency. For discrimination, the observers need to cross-correlate the received stimulus with two templates of the upward and downward moving grating. The very low efficiency suggests that discrimination is a difficult task for the visual system, and that children's ability to form two mental templates of two relatively similar signals is immature in adolescence. For detection, the observers only need to use one template of the upward moving grating. Our data suggest that the ability to perform coarse template matching necessary for detection is easier for the visual system and already adult like by the age of five.

It could be argued that cognitive factors such as improvements in ability to maintain attention or consistent criteria underlie the improvements in sampling efficiency that we observe. However,

if non-visual factors are involved with changes in efficiency, one would expect changes in efficiency for all tasks, which were run in random order to minimize such effects. Yet only direction discrimination shows developmental changes. This suggests that development is likely due to maturation of cortical processes and improved ability to cross-correlate and template match noisy signals. A related idea is that sampling efficiency is poor for direction discrimination among children because this task is cognitively complex compared to detection. The cognitive complexity of the task does not seem a plausible explanation of poor child performance, since young infants and monkeys are able to discriminate motion direction (Banton, Dobkins, & Bertenthal, 2001; Dobkins & Teller, 1996; Hall-Haro & Kiorpes, 2008; Kiorpes & Movshon, 2004; Salzman, Britten, & Newsome, 1990) and pattern orientation (Bornstein, Krinsky, & Benasich, 1986). In addition, such an explanation does not say why sampling efficiency rather than internal noise is primarily affected.

The different developmental patterns for detection of a sum of two patterns (flicker) and for discriminating the direction of two patterns is surprising because both of these tasks require motion filters tuned to each of the two directions. The only difference between the tasks is how the outputs of the filters are used (see Eqs. (4) and (6)). It is not clear why using two motion filter outputs for discrimination is more difficult than it is for summation. Perhaps it is due to the requirement of labeled lines for each motion direction quite late in the process leading to a discrimination response, and that pooling motion filter outputs can happen at an early stage when making a summation response. According to that interpretation, this ability to keep motion filter outputs separate matures over time. In the summation task, the observer is required to detect whether the presented stimulus is a flickering or a blank patch, so another interpretation would be that observers use one spatiotemporal filter tuned to the combined directions (flicker) to perform the detection, and not two separate filters tuned to the two delivered directions in the stimuli. Thus, observers only need one template to perform the cross-correlation, and performance will be better than for discrimination. That observers make judgments on the whole spatiotemporal pattern (flicker) and not the individual components of the pattern (sum of upward and downward moving gratings), indicates that the template matching may occur in or after area MT, where neurons combine component motion from V1 and show strong pattern selectivity (Heeger, Simoncelli, & Movshon, 1996; Rust et al., 2006). If this is true, then the ability to detect the presence of a spatiotemporal pattern matures earlier than the ability to discriminate the direction of pattern motion. This explanation is supported by studies showing that human infants are able to detect plaid pattern motion measuring optokinetic nystagmus (Dobkins et al., 2004), and that direction discrimination of plaid pattern motion in monkeys develops late in contrast to motion detection of a single grating who were adultlike already in infants monkeys (Hall-Haro & Kiorpes, 2008).

That motion detection and discrimination have different developmental trajectories is consistent with other studies (Annaz et al., 2010; Ellemberg et al., 1999, 2003, 2004; Gunn et al., 2002; Koh, Milne, & Dobkins, 2010; Parrish et al., 2005; Pellicano et al., 2005; Schrauf, Wist, & Ehrenstein, 1999; Spencer et al., 2000) using different methods. Although some find that detection of motion-defined form (dynamic vision) reaches adult values somewhat later (7–16 years) than in the present study. In some respects, these motion defined form tasks are more a discrimination task. In one study children had to identify a letter (Giaschi & Regan, 1997) or shape (Parrish et al., 2005) comprising moving pixels, and in another two studies the gap in a Landolt C had to be located (Schrauf, Wist, & Ehrenstein, 1999), or the location of the signal dots defined by motion coherence determined (Gunn et al., 2002). In this context, the age at which adult levels are attained

accords with the present study. Support for the concept that the mechanisms for simple motion detection are mature by 5 years, as found in the present study, is found in a developmental VEP study in children, where no change in VEP motion thresholds in children was found over the age of 5 years (Gordon & McCulloch, 1999). Direction discrimination of moving signals has been found in other studies to be immature at 5 years of age, in global motion tasks (Narasimhan & Giaschi, 2012) and depending on temporal frequency (Ellemberg et al., 2003, 2004; Giaschi & Regan, 1997; Meier & Giaschi, 2014). Temporal contrast sensitivity has been found to become adult like by the age of 7 years (Ellemberg et al., 1999), slightly earlier than in the present study, probably due to longer and variable presentation times with greater signal energies.

That direction discrimination differs with temporal frequency is consistent with other studies (Bogfjellmo, Bex, & Falkenberg, 2014; Ellemberg et al., 1999, 2003). Ellemberg et al. (1999) found that sensitivity was greater at lower temporal frequencies (5.0 Hz) than higher (30.0 Hz). This is comparable to the higher efficiency at 1.0 Hz found in the present study. In contrast, we recently showed that for global motion discrimination, sensitivity is higher for higher speeds in development (Bogfjellmo, Bex, & Falkenberg, 2014). The main reason for the different results is that the present study compares human observers to an ideal observer. The ideal observer model predicts that discrimination is better for 6.0 Hz compared to 1.0 Hz. However observers behave as though the stimuli are the same, and the calculated sampling efficiency for 6.0 Hz is thus very low. This suggests that the visual system uses mismatched motion filters spatiotemporal templates tuned to low temporal frequencies (Simpson, Falkenberg, & Manahilov, 2003). Although the absolute sampling efficiency is higher for 1.0 Hz, the differences between child and adult observers are smaller for 6.0 Hz than for 1.0 Hz. Further, the contrast energy thresholds without added noise are better for 6.0 Hz than 1.0 Hz, consistent with (Ahmed et al., 2005; Bogfjellmo, Bex, & Falkenberg, 2014; Manning, Aagten-Murphy, & Pellicano, 2012). In adults it is well known that contrast sensitivity changes with temporal frequency (Anderson & Burr, 1985; Burr & Ross, 1982). One would expect a more sluggish system in children (Kiorpes et al., 2012), consistent with the loss of efficiency seen in this paper.

The degree of mismatch may decrease over development, causing improved sampling efficiency with maturation. The different slopes for direction discrimination also suggest that the rate of development differs for the two temporal frequencies. This supports ideas that different neural mechanisms process low and high speeds, and that these mechanisms develop independently (Ahmed et al., 2005; Aslin & Shea, 1990; Bogfjellmo, Bex, & Falkenberg, 2014; Dobkins & Teller, 1996; Edwards, Badcock, & Smith, 1998; Manning, Aagten-Murphy, & Pellicano, 2012).

7. Conclusion

The detection of the presence of moving patterns and discrimination of the direction of motion is limited by both internal noise and reduced sampling efficiency, but the two abilities have quite different developmental profiles. Whereas direction discrimination is still not mature at 14 years of age, simple detection is already mature at 5 years. Using an Equivalent Noise model we showed that the improvement in performance with age for direction discrimination is due to an increase in sampling efficiency with no significant change in internal noise. The different rates of development for detection and direction discrimination suggest that these two tasks are processed by different mechanisms that have different maturation periods.

Disclosure

None.

References

- Ahmed, M., & Dutton, G. N. (1996). Cognitive visual dysfunction in a child with cerebral damage. *Developmental Medicine and Child Neurology*, 38(8), 736–739.
- Ahmed, I. J., Lewis, T. L., Ellemberg, D., & Maurer, D. (2005). Discrimination of speed in 5-year-olds and adults: Are children up to speed? *Vision Research*, 45(16), 2129–2135.
- Anderson, S. J., & Burr, D. C. (1985). Spatial and temporal selectivity of the human motion detection system. *Vision Research*, 25(8), 1147–1154.
- Annaz, D., Remington, A., Milne, E., Coleman, M., Campbell, R., Thomas, M. S. C., et al. (2010). Development of motion processing in children with autism. *Developmental Science*, 13(6), 826–838.
- Armstrong, V., Maurer, D., & Lewis, T. L. (2009). Sensitivity to first- and second-order motion and form in children and adults. *Vision Research*, 49(23), 2774–2781.
- Aslin, R. N., & Shea, S. L. (1990). Velocity thresholds in human infants: Implications for the perception of motion. *Developmental Psychology*, 26, 589–598.
- Banks, M. S., & Crowell, J. A. (1993). Front-end limitations to infant spatial vision: Examination of two analyses. In K. Simons (Ed.), *Early visual development, normal and abnormal* (pp. 91–116). New York: Oxford University Press.
- Banton, T., Dobkins, K., & Bertenthal, B. I. (2001). Infant direction discrimination thresholds. *Vision Research*, 41(8), 1049–1056.
- Barlow, H. (1978). The efficiency of detecting changes of density in random dot patterns. *Vision Research*, 18, 637–650.
- Benassi, M., Simonelli, L., Giovagnoli, S., & Bolzani, R. (2010). Coherence motion perception in developmental dyslexia: A meta-analysis of behavioral studies. *Dyslexia*, 16(4), 341–357.
- Bennett, P. J., Sekuler, A. B., & Ozin, L. (1999). Effects of aging on calculation efficiency and equivalent noise. *Journal of the Optical Society of America A: Optics, Image Science, and Vision*, 16(3), 654–668.
- Bogfjellmo, L.-G., Bex, P. J., & Falkenberg, H. K. (2013). Reduction in direction discrimination with age and slow speed is due to both increased internal noise and reduced sampling efficiency. *Investigative Ophthalmology & Visual Science*, 54(8), 5204–5210.
- Bogfjellmo, L.-G., Bex, P. J., & Falkenberg, H. K. (2014). The development of global motion discrimination in school aged children. *Journal of Vision*, 14(2).
- Boot, F. H., Pel, J. J., Evenhuis, H. M., & van der Steen, J. (2012). Quantification of visual orienting responses to coherent form and motion in typically developing children aged 0–12 years. *Investigative Ophthalmology & Visual Science*, 53(6), 2708–2714.
- Bornstein, M. H., Krinsky, S. J., & Benasich, A. A. (1986). Fine orientation discrimination and shape constancy in young infants. *Journal of Experimental Child Psychology*, 41(1), 49–60.
- Bosking, W. H., & Maunsell, J. H. (2011). Effects of stimulus direction on the correlation between behavior and single units in area MT during a motion detection task. *Journal of Neuroscience*, 31(22), 8230–8238.
- Bullimore, M. A., Wood, J. M., & Swenson, K. (1993). Motion perception in glaucoma. *Investigative Ophthalmology & Visual Science*, 34(13), 3526–3533.
- Burgess, A. E., & Colborne, B. (1988). Visual signal detection. IV. Observer inconsistency. *Journal of the Optical Society of America A*, 5(4), 617–627.
- Burgess, A. E., Wagner, R. F., Jennings, R. J., & Barlow, H. B. (1981). Efficiency of human visual signal discrimination. *Science*, 214, 93–94.
- Burr, D. C., & Ross, J. (1982). Contrast sensitivity at high velocities. *Vision Research*, 22(4), 479–484.
- Casco, C., Robol, V., Grassi, M., & Venturini, C. (2012). Positional noise in Landolt-C stimuli reduces spatial resolution: A study with younger and older observers. *Vision Research*, 67, 37–43.
- Dakin, S. C., Mareschal, I., & Bex, P. J. (2005). Local and global limitations on direction integration assessed using equivalent noise analysis. *Vision Research*, 45(24), 3027–3049.
- Demb, J. B., Boynton, G. M., Best, M., & Heeger, D. J. (1998). Psychophysical evidence for a magnocellular pathway deficit in dyslexia. *Vision Research*, 38(11), 1555–1559.
- Dobkins, K. R., Fine, I., Hsueh, A. C., & Vitten, C. (2004). Pattern motion integration in infants. *Journal of Vision*, 4(3), 144–155.
- Dobkins, K. R., & Teller, D. Y. (1996). Infant contrast detectors are selective for direction of motion. *Vision Research*, 36(2), 281–294.
- Dutton, G. N., Saaed, A., Fahad, B., Fraser, R., McDaid, G., McDade, J., et al. (2004). Association of binocular lower visual field impairment, impaired simultaneous perception, disordered visually guided motion and inaccurate saccades in children with cerebral visual dysfunction – A retrospective observational study. *Eye*, 18(1), 27–34.
- Edwards, M., Badcock, D. R., & Smith, A. T. (1998). Independent speed-tuned global-motion systems. *Vision Research*, 38(11), 1573–1580.
- Edwards, V. T., Giaschi, D. E., Dougherty, R. F., Edgell, D., Bjornson, B. H., Lyons, C., et al. (2004). Psychophysical indexes of temporal processing abnormalities in children with developmental dyslexia. *Developmental Neuropsychology*, 25(3), 321–354.
- Ellemberg, D., Lewis, T. L., Dirks, M., Maurer, D., Ledgeway, T., Guillemot, J. P., et al. (2004). Putting order into the development of sensitivity to global motion. *Vision Research*, 44(20), 2403–2411.
- Ellemberg, D., Lewis, T. L., Liu, C. H., & Maurer, D. (1999). Development of spatial and temporal vision during childhood. *Vision Research*, 39(14), 2325–2333.
- Ellemberg, D., Lewis, T. L., Meghji, K. S., 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(5), 419–428.
- Falkenberg, H. K., & Bex, P. J. (2007). Sources of motion-sensitivity loss in glaucoma. *Investigative Ophthalmology & Visual Science*, 48(6), 2913–2921.
- Falkenberg, H. K., Dutton, G. N., & Simpson, W. A. (2010). Does motion discrimination sensitivity in children aged 5–14 years improve after 1 year? *Investigative Ophthalmology & Visual Science*, 51(5), 1839–.
- Faraway, J. (2004). *Linear regression models with R*. Boca Raton, FL: Chapman & Hall/CRC.
- Geyer, C. (2003). *Maximum likelihood in R*. <<http://www.stat.umn.edu/geyer/5931/mle/mle.pdf>>.
- Giaschi, D., & Regan, D. (1997). Development of motion-defined figure-ground segregation in preschool and older children, using a letter-identification task. *Optometry and Vision Science*, 74(9), 761–767.
- Giaschi, D. E., Regan, D., Kraft, S. P., & Hong, X. H. (1992). Defective processing of motion-defined form in the fellow eye of patients with unilateral amblyopia. *Investigative Ophthalmology & Visual Science*, 33(8), 2483–2489.
- Gogtay, N., Giedd, J. N., Lusk, L., Hayashi, K. M., Greenstein, D., Vaituzis, A. C., et al. (2004). Dynamic mapping of human cortical development during childhood through early adulthood. *Proceedings of the National Academy of Sciences of the United States of America*, 101(21), 8174–8179.
- Gordon, G., & McCulloch, D. (1999). A VEP investigation of parallel visual pathway development in primary school age children. *Documenta Ophthalmologica*, 99, 1–10.
- Green, D. M., & Swets, J. A. (1966). *Signal detection theory and psychophysics*. New York: John Wiley and Sons.
- Gunn, A., Cory, E., Atkinson, J., Braddick, O., Wattam-Bell, J., Guzzetta, A., et al. (2002). Dorsal and ventral stream sensitivity in normal development and hemiplegia. *NeuroReport*, 13(6), 843–847.
- Guzzetta, A., Tinelli, F., Del Viva, M. M., Bancalè, A., Arrighi, R., Pascale, R. R., et al. (2009). Motion perception in preterm children: Role of prematurity and brain damage. *NeuroReport*, 20(15), 1339–1343.
- Hadad, B. S., Maurer, D., & Lewis, T. L. (2011). Long trajectory for the development of sensitivity to global and biological motion. *Developmental Science*, 14(6), 1330–1339.
- Hall, J. L. (1968). Maximum-likelihood sequential procedure for estimation of psychometric functions. *Journal of the Acoustical Society of America*, 44, 370.
- Hall-Haro, C., & Kiorpes, L. (2008). Normal development of pattern motion sensitivity in macaque monkeys. *Visual Neuroscience*, 25(5–6), 675–684.
- Hatta, S., Kumagami, T., Qian, J., Thornton, M., Smith, E. L., 3rd, & Chino, Y. M. (1998). Nasotemporal directional bias of V1 neurons in young infant monkeys. *Investigative Ophthalmology & Visual Science*, 39(12), 2259–2267.
- Hayward, J., Truong, G., Partanen, M., & Giaschi, D. (2011). Effects of speed, age, and amblyopia on the perception of motion-defined form. *Vision Research*, 51(20), 2216–2223.
- Heeger, D. J., Simoncelli, E. P., & Movshon, J. A. (1996). Computational models of cortical visual processing. *Proceedings of the National Academy of Sciences*, 93(2), 623–627.
- Howland, H. C. (1993). Early refractive development. In K. Simons (Ed.), *Early visual development, normal and abnormal* (pp. 5–38). New York: Oxford University Press.
- Huang, C., Tao, L., Zhou, Y., & Lu, Z. L. (2007). Treated amblyopes remain deficient in spatial vision: A contrast sensitivity and external noise study. *Vision Research*, 47(1), 22–34.
- Hutchinson, C. V., Arena, A., Allen, H. A., & Ledgeway, T. (2012). Psychophysical correlates of global motion processing in the aging visual system: A critical review. *Neuroscience & Biobehavioral Reviews*, 36(4), 1266–1272.
- Huttenlocher, P. R. (1990). Morphometric study of human cerebral cortex development. *Neuropsychologia*, 28(6), 517–527.
- Kersten, D., Hess, R. F., & Plant, G. T. (1988). Assessing contrast sensitivity behind cloudy media. *Clinical Vision & Science*, 2, 143–158.
- Kiorpes, L., & Movshon, J. A. (2004). Development of sensitivity to visual motion in macaque monkeys. *Visual Neuroscience*, 21(06), 851–859.
- Kiorpes, L., Price, T., Hall-Haro, C., & Movshon, J. A. (2012). Development of sensitivity to global form and motion in macaque monkeys (*Macaca nemestrina*). *Vision Research*, 63, 34–42.
- Kiorpes, L., Tang, C., Hawken, M. J., & Movshon, J. A. (2003). Ideal observer analysis of the development of spatial contrast sensitivity in macaque monkeys. *Journal of Vision*, 3(10), 630–641.
- Knox, P. J., Ledgeway, T., & Simmers, A. J. (2013). The effects of spatial offset, temporal offset and image speed on sensitivity to global motion in human amblyopia. *Vision Research*, 86C, 59–65.
- Koh, H. C., Milne, E., & Dobkins, K. (2010). Contrast sensitivity for motion detection and direction discrimination in adolescents with autism spectrum disorders and their siblings. *Neuropsychologia*, 48(14), 4046–4056.
- Legge, G. E., Kersten, D., & Burgess, A. E. (1987). Contrast discrimination in noise. *Journal of the Optical Society of America A: Optics, Image Science, and Vision*, 4(2), 391–404.
- Levitt, H. (1971). Transformed up-down methods in psychoacoustics. *The Journal of the Acoustical Society of America*, 49(Suppl. 2), 467+.
- Manning, C., Aagten-Murphy, D., & Pellicano, E. (2012). The development of speed discrimination abilities. *Vision Research*, 70, 27–33.

- Mapstone, M., Dickerson, K., & Duffy, C. J. (2008). Distinct mechanisms of impairment in cognitive ageing and Alzheimer's disease. *Brain*, *131*(Pt 6), 1618–1629.
- Marsaglia, G. (1994). *Yet another rng.* (p. Posted to internet newsgroup sci.stat.math).
- Meier, K., & Giaschi, D. (2014). The maturation of global motion perception depends on the spatial and temporal offsets of the stimulus. *Vision Research*, *95*, 61–67.
- Mitchell, T. V., & Neville, H. J. (2004). Asynchronies in the development of electrophysiological responses to motion and color. *Journal of Cognitive Neuroscience*, *16*(8), 1363–1374.
- Najemnik, J., & Geisler, W. S. (2005). Optimal eye movement strategies in visual search. *Nature*, *434*(7031), 387–391.
- Narasimhan, S., & Giaschi, D. (2012). The effect of dot speed and density on the development of global motion perception. *Vision Research*, *62*, 102–107.
- Norcia, A. M. (1996). Abnormal motion processing and binocularity: Infantile esotropia as a model system for effects of early interruptions of binocularity. *Eye*, *10*(Pt 2), 259–265.
- Pardhan, S. (2004). Contrast sensitivity loss with aging: Sampling efficiency and equivalent noise at different spatial frequencies. *Journal of the Optical Society of America A: Optics, Image Science, and Vision*, *21*(2), 169–175.
- Pardhan, S., Gilchrist, J., Elliott, D. B., & Beh, G. K. (1996). A comparison of sampling efficiency and internal noise level in young and old subjects. *Vision Research*, *36*(11), 1641–1648.
- Parrish, E. E., Giaschi, D. E., Boden, C., & Dougherty, R. (2005). The maturation of form and motion perception in school age children. *Vision Research*, *45*(7), 827–837.
- Pelli, D. G. (1990). The quantum efficiency of vision. In *Vision coding and efficiency* (pp. 3–24). Cambridge: Cambridge University Press.
- Pelli, D. G., & Farell, B. (1999). Why use noise? *Journal of the Optical Society of America A: Optics, Image Science, and Vision*, *16*(3), 647–653.
- Pelli, D. G., & Zhang, L. (1991). Accurate control of contrast on microcomputer displays. *Vision Research*, *31*(7–8), 1337–1350.
- Pellicano, E., Gibson, L., Maybery, M., Durkin, K., & Badcock, D. R. (2005). Abnormal global processing along the dorsal visual pathway in autism: A possible mechanism for weak visuospatial coherence? *Neuropsychologia*, *43*(7), 1044–1053.
- Pinto, J. G., Hornby, K. R., Jones, D. G., & Murphy, K. M. (2010). Developmental changes in GABAergic mechanisms in human visual cortex across the lifespan. *Frontiers in Cellular Neuroscience*, *4*, 16.
- Regan, D., Kothe, A. C., & Sharpe, J. A. (1991). Recognition of motion-defined shapes in patients with multiple sclerosis and optic neuritis. *Brain*, *114*(Pt 3), 1129–1155.
- Rust, N. C., Mante, V., Simoncelli, E. P., & Movshon, J. A. (2006). How MT cells analyze the motion of visual patterns. *Nature Neuroscience*, *9*(11), 1421–1431.
- Salzman, C. D., Britten, K. H., & Newsome, W. T. (1990). Cortical microstimulation influences perceptual judgements of motion direction. *Nature*, *346*(6280), 174–177.
- Schrauf, M., Wist, E. R., & Ehrenstein, W. H. (1999). Development of dynamic vision based on motion contrast. *Experimental Brain Research*, *124*(4), 469–473.
- Shaw, P., Kabani, N. J., Lerch, J. P., Eckstrand, K., Lenroot, R., Gogtay, N., et al. (2008). Neurodevelopmental trajectories of the human cerebral cortex. *Journal of Neuroscience*, *28*(14), 3586–3594.
- Simmers, A. J., Ledgeway, T., Hess, R. F., & McGraw, P. V. (2003). Deficits to global motion processing in human amblyopia. *Vision Research*, *43*(6), 729–738.
- Simpson, W. A., Falkenberg, H. K., & Manahilov, V. (2003). Sampling efficiency and internal noise for motion detection, discrimination, and summation. *Vision Research*, *43*(20), 2125–2132.
- Simpson, W. A., Loffler, G., & Tucha, L. (2013). Cross-correlation in face discrimination. *Vision Research*, *76*, 60–67.
- Skoczenski, A. M., & Norcia, A. M. (1998). Neural noise limitations on infant visual sensitivity. *Nature*, *391*(6668), 697–700.
- Spencer, J., O'Brien, J., Riggs, K., Braddick, O., Atkinson, J., & Wattam-Bell, J. (2000). Motion processing in autism: Evidence for a dorsal stream deficiency. *NeuroReport*, *11*(12), 2765–2767.
- Weinstein, J. M., Gilmore, R. O., Shaikh, S. M., Kunselman, A. R., Trescher, W. V., Tashima, L. M., et al. (2012). Defective motion processing in children with cerebral visual impairment due to periventricular white matter damage. *Developmental Medicine and Child Neurology*, *54*(7), e1–8.
- Whalen, A. D. (1971). *Detection of signals in noise*. New York: Academic Press.
- Zihl, J., von Cramon, D., & Mai, N. (1983). Selective disturbance of movement vision after bilateral brain damage. *Brain*, *106*(Pt 2), 313–340.