

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

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Word count: **5817**

**Abstract** The aim of this study was to use an equivalent noise (EN) 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.

**Keywords:** Development; motion perception; sampling efficiency; internal noise

## 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, 10 et al., 1998; Edwards, et al., 2004), autism (Annaz, 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 20 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, 2014a; Boot, et al., 2012; Elleberg, et al., 2004; Elleberg, et al., 1999; Elleberg, et al., 2003; 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),  
30 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; Elleberg et al., 2004; Elleberg et al., 2003; 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; Bogfjellmo, Bex & Falkenberg,  
2014a, b; Elleberg et al., 2003; Giaschi & Regan, 1997). Elleberg and colleagues (1999)  
found that critical flicker fusion frequency and contrast thresholds for detecting gratings that  
40 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 (Elleberg et al., 2004;  
Elleberg et al., 2003). 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).

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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 modelled 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).  
60 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  
70 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, 2014a), 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  
80 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.

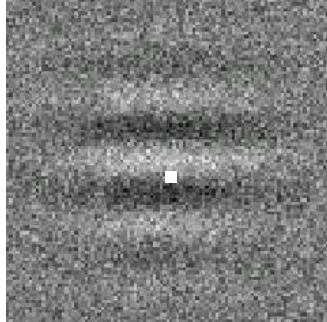
The present study applies an EN model to investigate the limiting mechanisms underlying the development of motion detection and discrimination in typically developing school-aged children. A 1-year follow-up study was performed on a group of children to investigate longitudinal changes in motion detection 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 to 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  $29.3 \pm 4.6$  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  $< 0.1$  logMAR using Glasgow Acuity Cards (GAC score=  $1 - \log\text{MAR}$ ); no strabismus or heterophorias  $< 10 \Delta\text{D}$  (Cover Test); normal history of ophthalmic pathology and birth.



**Figure 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.

### 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, 640x480 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<sup>2</sup>, 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 grey 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 (Figure 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 polar method, and was clipped at  $\pm 2.5$  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  $\mu\text{s deg}^2$ ).

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### 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

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### 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

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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 Equation (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  $\text{y-intercept}/\text{slope}$  (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  $\rho$  between the signals (Simpson, Falkenberg & Manahilov, 2003). For summation, human performance can be described by

$$190 \quad d' = \sqrt{\frac{2kE(1+\rho)}{N_e+N_i}} \quad (3),$$

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

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

200 The actual cross-correlations  $\rho$  between the drifting Gabor signals in this study were 0.77 for 1.0 Hz and 0 for 6.0 Hz. Equations 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).

### 2.1.5 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  
 210 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 Equations 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 Equations 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.

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

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

\*Mean of 15 adults: 29.3 ± 4.6 years

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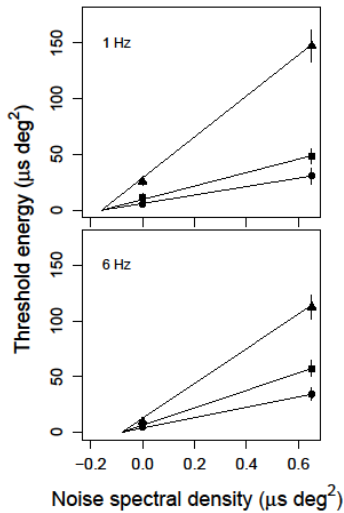
### 3. Results

240 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.

Figure 2 shows ~~that~~ the contrast energy thresholds with and without added noise for adult observers. When noise is added to the stimuli thresholds increase, especially ~~was much higher~~ for direction discrimination, ~~than for detection and summation.~~ 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 fitted by a line. However, the three lines in each panel of Figure 2 were not fitted individually. Instead, ~~aAs~~ 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 confirmed that the data model with a common intercept (internal noise) but different slopes (sampling efficiency) for the three tasks. F for adult observers, ~~model~~ the internal noise is the same for all three tasks ( $F_{1\text{Hz}}(2,132) = 0.051, p = 0.91$ ;  $F_{6\text{Hz}}(2,133) = 0.01, p = 0.97$ ), and a paired t-test showed the internal noise does not vary with speed ( $t(45)=2.1, p >.05$ ). The sampling efficiencies are shown in Figure 3A (diamonds).

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**Figure 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 Figure 5) show the same pattern of results.

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Children showed the same pattern of results as adults: contrast energy thresholds were much higher for direction discrimination than detection and summation, especially with added levels of noise. Figure 3A shows the sampling efficiency for direction discrimination as a function of age

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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. 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 1Hz 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:

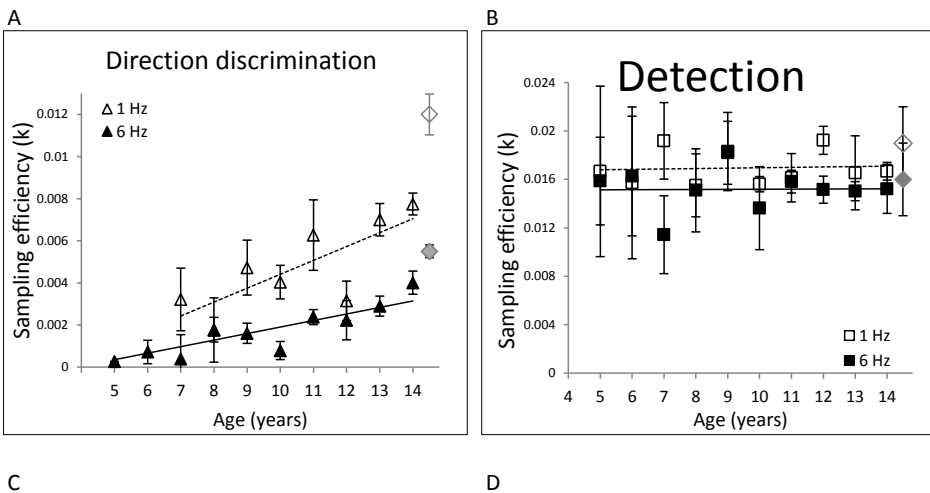
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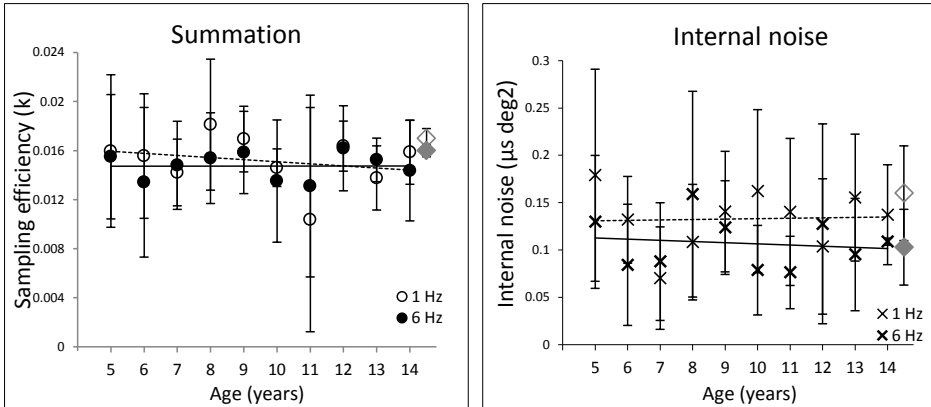
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280  $F(2,85) = 28, p < 0.001$ ). Figure 3 B and C show that sampling efficiency does not change with age or speed for detection ( $F_{1\text{Hz}}(2,78) = 0, p = 0.9, r^2 = 0$ ;  $F_{6\text{Hz}}(2,84) = 0.04, p = 0.8, r^2 = 0.01$ ) or summation  $F_{1\text{Hz}}(2,38) = 0, p = 0.6, r^2 = 0.01$ ;  $F_{6\text{Hz}}(2,39) = 0.06, p = 0.8, r^2 = 0$ ).

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 Figure 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 ( $F_{1\text{Hz}}(1,116) = 0.3, p = 0.6, r^2 = 0$ ;  $F_{6\text{Hz}}(1,126) = 0.4, p = 0.6, r^2 = 0$ ).

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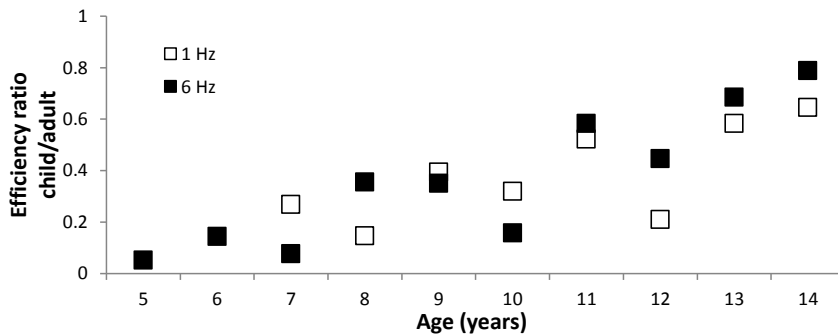




**Figure 3** Mean sampling efficiency estimates for **A**) direction discrimination (triangles); **B**) detection (squares) and **C**) summation (circles) estimated from individual ideal observer fits and plotted as a function of age and speed. Grey diamonds in all panels show the mean adult values. **D**) Mean internal noise estimates for the three tasks combined as a function of age and speed. 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.

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Figure 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 ratio is only ~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.



310 **Figure 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).

#### 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  
320 internal noise on detection and direction discrimination of moving patterns in individual child observers.

##### 4.1. Methods

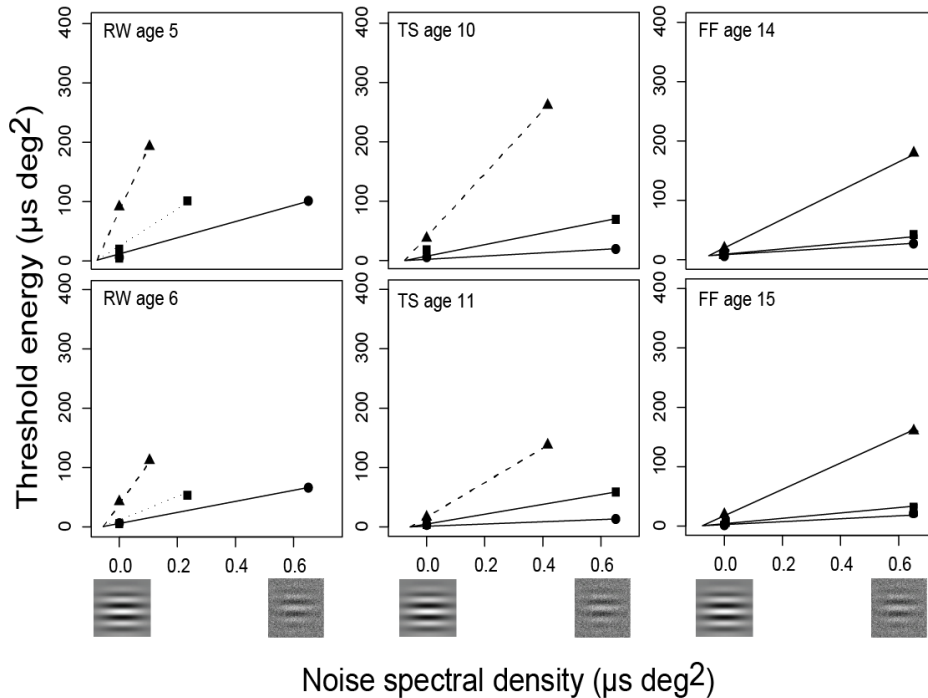
###### 4.1.1. Subjects

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

330 4.1.2. Stimuli, Procedure & 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 Equations 2, 4 and 6 using a four parameter model with a single intercept and different slopes as described above for the adults.





340 **Figure 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.

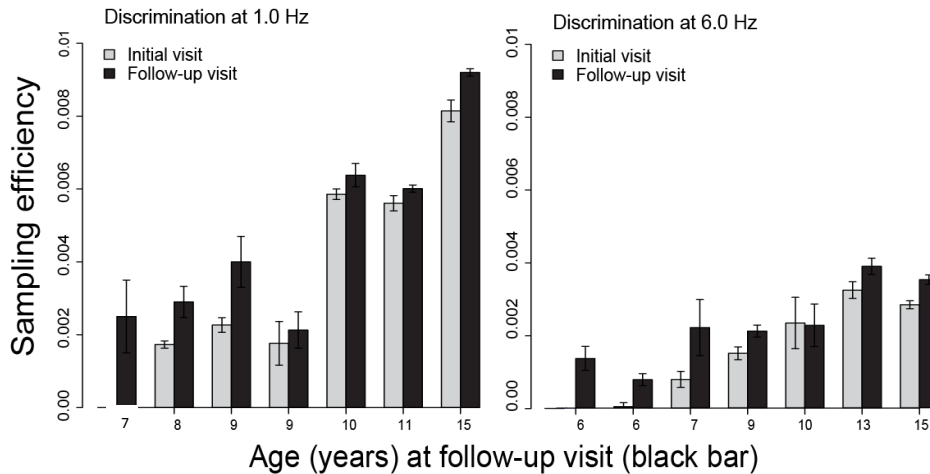
### 5. Results

350 Figure 5 shows the contrast energy thresholds for detection, summation and discrimination of  
~~gratings moving at 6.0 Hz and 1.0 Hz~~ 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 Figure 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). Figure 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. ~~This confirms that there is an increase in sampling efficiency with age.~~

Commented [h4]: Moved to end of section



**Figure 6** The improvement in sampling efficiency between the initial visit (grey 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 grey and black bars show one observer, error bars show +/-1 SE.

360

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

370

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 found in ~~confirm the results from the initial~~ 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 and reduced sampling efficiency (Bennett, Sekuler & Ozin, 1999; Bogfjellmo, Bex & Falkenberg, 2013, 2014a; 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 and colleagues (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, in line with (Bogfjellmo, Bex & Falkenberg, 2014a). 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.

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I would leave them, since many people go straight from abstract to Discussion. Redundancy is good

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, 2014a). 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, ~~and~~ 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., 2012; Kiorpes et al., 2003), 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.

440 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 & Movhson, 2004; 450 Salzman, Britten & Newsome, 1990) and pattern orientation direction (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 Equations 4 and 6). It is not clear why using two motion

**Commented [h6]:** It seems to me that observers only use the combined directions (flicker) to perform the detection, and not the filters tuned to the two delivered directions.

Could this be because the judgement is based on outputs after MT where both directions will be pooled? Whereas if the judgement was made from the V1 output, individual directions might be used?

Kind of what happens with perception of plaids, where you get activation of MT for the perceived direction, whereas V1 responds to the actual stimulus directions???

Not sure if this is relevant or true, but it might explain why humans do not perform as the ideal observer, and that detection of the sum of two gratings is very good compared to discrimination???

I think this is very good idea and you should incorporate it

460 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. ~~The observers task in the summation task, the  
observer is required to detect whether the perceived stimulus is a “flicker” flickering or  
a blank patcher nothing, so another interpretation would be that observers use one motion  
spatiotemporal filters 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 of motion  
(i.e. flicker) and not the individual components of the pattern (i.e. sum of upward and downward  
moving gratings), indicates that the template matching may occur in higher visual cortex, after  
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 ~~motion~~ matures earlier than the ability  
to discriminate the direction of pattern motion, ~~which is what we find~~. 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).

480 That motion detection and discrimination have different developmental trajectories is consistent  
with other studies (Annaz, 2010; Elleberg et al., 2004; Elleberg et al., 1999; Elleberg et al.,  
2003; 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 at 7-8 years when measuring minimum

**Commented [h7]:** I have tried to write something of the different results of summation and discrimination as in previous comment. Not sure if it is clear, so please edit and shorten.

I think that the two Dobkins references supports that detection and summation can be adultlike, whereas discrimination is not.

OK I have edited

~~speed thresholds (Giaschi & Regan, 1997; Parrish et al., 2005). In contrast, for coherence thresholds mature levels develop by 10-16 years (Gunn et al., 2002; Schrauf, Wist & Ehrenstein, 1999).~~ In some respects, these motion defined form tasks are more a

490 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 (Ellemborg et al., 2004; Ellemborg et al., 2003; Giaschi & Regan, 1997; Meier & Giaschi, 2014). Temporal contrast sensitivity has been found to become adult like by the age of 500 7 years (Ellemborg 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, 2014a; Ellemborg et al., 1999; Ellemborg et al., 2003)).~~

~~Although there is improvement with development, even adults show low sampling efficiency for direction discrimination.~~ Ellemborg and colleagues (1999) found that sensitivity was greater at lower temporal frequencies (5.0 Hz) than higher (30.0 Hz). This is comparable ~~with to~~ the higher 510 ~~sampling efficiency found at 1.0 Hz compared to 6.0 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, 2014a). 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~~

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ok

Commented [h9]: This section is about the different findings with speed. In contrast to global motion, we find that efficiency is lower for faster speed.

I have tried to write this short and clear, but not sure I managed.

Feel free to edit, I think the reason we find a difference is 1) we have gratings  
2) we compare to ideal observer

520 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, 2014a; 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 (Aslin & Shea, 1990; Dobkins & Teller, 1996 (Ahmed et al., 2005; Aslin & Shea, 1990; Bogfjellmo, Bex & Falkenberg, 2014a; Dobkins & Teller, 1996; Edwards, Badcock & Smith, 1998; Manning, Aagten-Murphy & Pellicano, 2012) .

## 7. Conclusion

540 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. Although there is improvement with development, even adults show low sampling efficiency for direction discrimination. Observers are especially inefficient with fast moving patterns; they behave as

Commented [h10]: Feel free to shorten the conclusion



though the stimuli are much more similar to one another than they really are. This may be because the visual system uses mismatched motion filters tuned to low speeds, and the filters gradually improves during development. 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. ~~The Equivalent Noise discrimination test may have potential clinical value in the investigation of neuro-developmental disorders, and is currently under study in our group.~~

**Commented [h11]:** To shorten it may be possible to remove this section –it is not about development, but generally about human observers.

ok to remove

**Commented [h12]:** Removed –not necessary? But nice to include as I want to write up the patient data as well

And then people might look for it☺

ok

## References

- 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.
- Ahmed, M., & Dutton, G.N. (1996). Cognitive visual dysfunction in a child with cerebral damage. *Developmental medicine and child neurology*, 38 (8), 736-739.
- 560 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., Swettenham, J. (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.
- 570 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.
- 580 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. (2014a). The development of global motion discrimination in school aged children. *Journal of Vision*, 14 (2)
- Bogfjellmo, L.-G., Bex, P.J., & Falkenberg, H.K. (2014b). Sensitivity to global motion patterns with low contrast. *Manuscript submitted for publication*,
- 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.
- 590 Bornstein, M.H., Krinsky, S.J., & Benasich, A.A. (1986). Fine orientation discrimination and shape constancy in young infants. *J Exp Child Psychol*, 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. *J Neurosci*, 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.
- 600 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 Res*, 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. *J Vis*, 4 (3), 144-155.
- 610 Dobkins, K.R., & Teller, D.Y. (1996). Infant contrast detectors are selective for direction of motion. *Vision Research*, 36 (2), 281-294.

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- Dutton, G.N., Saaed, A., Fahad, B., Fraser, R., McDaid, G., McDade, J., Mackintosh, A., Rane, T., & Spowart, K. (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 Res*, *38* (11), 1573-1580.
- Edwards, V.T., Giaschi, D.E., Dougherty, R.F., Edgell, D., Bjornson, B.H., Lyons, C., & Douglas, R.M. (2004). Psychophysical indexes of temporal processing abnormalities in children with developmental dyslexia. *Dev Neuropsychol*, *25* (3), 321-354.
- 620 Ellemberg, D., Lewis, T.L., Dirks, M., Maurer, D., Ledgeway, T., Guillemot, J.P., & Lepore, F. (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 & Vision Science*, *48* (6), 2913-2921.
- 630 Falkenberg, H.K., Dutton, G.N., & Simpson, W.A. (2010). Does Motion Discrimination Sensitivity in Children Aged 5-14 Years Improve After 1 Year? *Invest. Ophthalmol. Vis. Sci.*, *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.
- 640 Gogtay, N., Giedd, J.N., Lusk, L., Hayashi, K.M., Greenstein, D., Vaituzis, A.C., Nugent, T.F., Herman, D.H., Clasen, L.S., Toga, A.W., Rapoport, J.L., & Thompson, P.M. (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. *Doc Ophthalmol*, *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., & Cioni, G. (2002). Dorsal and ventral stream sensitivity in normal development and hemiplegia. *Neuroreport*, *13* (6), 843-847.
- 650 Guzzetta, A., Tinelli, F., Del Viva, M.M., Bancalè, A., Arrighi, R., Pascale, R.R., & Cioni, G. (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-Haro, C., & Kiorpes, L. (2008). Normal development of pattern motion sensitivity in macaque monkeys. *Vis Neurosci*, *25* (5-6), 675-684.
- Hall, J.L. (1968). Maximum-likelihood sequential procedure for estimation of psychometric functions. *Journal of the Acoustical Society of America*, *44*, 370.
- 660 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. *Invest Ophthalmol Vis Sci*, *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.
- 670 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.

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- 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.
- 680 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 Res*, 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 Res*, 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.
- 690 Legge, G.E., Kersten, D., & Burgess, A.E. (1987). Contrast discrimination in noise. *J Opt Soc Am A*, 4 (2), 391-404.
- Levitt, H. (1971). Transformed up-down methods in psychoacoustics. *J Acoust Soc Am*, 49 (2), Suppl 2:467+.
- Manning, C., Aagten-Murphy, D., & Pellicano, E. (2012). The development of speed discrimination abilities. *Vision Res*, 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 Res*, 95, 61-67.
- 700 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 (0), 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. *J Opt Soc Am A Opt Image Sci Vis*, 21 (2), 169-175.
- 710 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 Res*, 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 Res*, 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? *J Opt Soc Am A Opt Image Sci Vis*, 16 (3), 647-653.
- Pelli, D.G., & Zhang, L. (1991). Accurate control of contrast on microcomputer displays. *Vision Research*, 31 (7-8), 1337-1350.
- 720 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. *Front Cell Neurosci*, 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. *Nat Neurosci*, 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.
- 730 Schrauf, M., Wist, E.R., & Ehrenstein, W.H. (1999). Development of dynamic vision based on motion contrast. *Experimental Brain Research*, 124 (4), 469-473.

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- Shaw, P., Kabani, N.J., Lerch, J.P., Eckstrand, K., Lenroot, R., Gogtay, N., Greenstein, D., Clasen, L., Evans, A., Rapoport, J.L., Giedd, J.N., & Wise, S.P. (2008). Neurodevelopmental trajectories of the human cerebral cortex. *J Neurosci*, 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 Res*, 43 (20), 2125-2132.
- Simpson, W.A., Loffler, G., & Tucha, L. (2013). Cross-correlation in face discrimination. *Vision Res*, 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., Boltz, M.E., McAuliffe, M.B., Cheung, A., & Fesi, J.D. (2012). Defective motion processing in children with cerebral visual impairment due to periventricular white matter damage. *Dev Med Child Neurol*, 54 (7), e1-8.
- Whalen, A.D. (1971). *Detection of signals in noise*. (New York: Academic Press.
- 750 Zihl, J., von Cramon, D., & Mai, N. (1983). Selective disturbance of movement vision after bilateral brain damage. *Brain*, 106 (Pt 2), 313-340.