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# Sequential processing deficits of reading disabled persons is independent of inter-stimulus interval

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## Abstract

Developmental dyslexia is a language-based learning disability with frequently associated non-linguistic sensory deficits that have been the basis of various perception-based theories. It remains an open question whether the underlying deficit in dyslexia is a low level impairment that causes speech and orthographic perception deficits that in turn impedes higher phonological and reading processes, or a high level impairment that affects both perceptual and reading related skills.

We investigated by means of contrast detection thresholds two low-level theories of developmental dyslexia, the magnocellular and the fast temporal processing hypotheses, as well as a more recent suggestion that dyslexics have difficulties in sequential comparison tasks that can be attributed to a higher-order deficit. It was found that dyslexics had significantly higher thresholds only on a sequential, but not a spatial, detection task, and that this impairment was found to be independent of the inter-stimulus interval. We also found that the poor performance of dyslexics on the temporal task was dependent on the size of the required memory trace of the image rather than on the number of images. Our findings do not support the magnocellular theory and challenge the fast temporal deficit hypothesis. We suggest that dyslexics may have a higher order, dual mechanism impairment. We also discuss the clinical implications of our findings.

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## 1. Introduction

The etiology of developmental dyslexia has been the subject of scientific inquiry for over a century. Because reading is a spatio-temporal process that begins with the decoding of serial visual information, many studies have focused on investigating the various components of visual information processing and of responses to non-orthographic tasks. Lovegrove and Brown (1978), in a series of pioneering, systematic experiments, evaluated low-level visual stimulus processing associated with reading disabilities. Lovegrove et al. found that children with dyslexia have longer visual information store durations to contour orientation (Lovegrove, Billing, & Slaghuis, 1978). They also found that persons with

reading disabilities transfer visual information at a slower rate than age-matched, normally achieving readers (Lovegrove & Brown, 1978), and that these deficits apparently persist into adulthood (Breznitz & Meyler, 2003). Furthermore, they found that persons with reading disabilities are less sensitive at low spatial frequencies, more sensitive at high spatial frequencies (Lovegrove, Heddle, & Slaghuis, 1980; Lovegrove et al., 1982; Martin & Lovegrove, 1984), and less sensitive to temporal frequencies. This difference increases with increasing flicker rate (Martin & Lovegrove, 1987).

These findings, as well as other reports from studies using different research methods including anatomical, behavioral, EEG, and imaging techniques (e.g., Cornelissen & Stein, 1995; Demb, Boynton, Best, & Heeger, 1998; Eden et al., 1996; Livingstone, Rosen, Drislane, & Galaburda, 1991; Schulte-Korne, Bartling, Deimel, & Remschmidt, 2004) have given rise to the “magnocellular theory” (see Stein, 2001 for a recent review). Taken together, these studies

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have given rise to the “magnocellular theory” (see Stein, 2001 for a recent review). This theory focuses on abnormalities of the magnocellular component of the visual system. These abnormalities can be assessed psychophysically by selectively stimulating the magnocellular pathway (Stein & Talcott, 1999).

The primate visual system consists of three subsystems that run parallel from the retinal ganglion cells, through LGN, and back to primary visual cortex (V1). These pathways are characterized by three principal types of cells: parvocellular (P), magnocellular (M) and koniocellular (K). These cells can be distinguished from each other based upon laminar location, morphology, connections and neurochemistry. It has been established that the different cell types respond preferentially to different stimulus characteristics and regarding M and P, these characteristics have been fairly well studied and characterized. The M-cells are known to be more sensitive to moving targets, flicker lights of high temporal frequency, low intensity, low contrast, and low spatial frequency. The P-cells are known to be more sensitive to color, high spatial frequency, and high contrast. Fewer studies have examined K cells, and their properties are not as well understood. A recent study has shown direct projections from LGN to area MT that consists predominantly of K cells, possibly suggesting that they play a role in motion processing (Livingstone & Hubel, 1988; Merigan & Maunsell, 1993; Sincich, Park, Wohlgenuth, & Horton, 2004; Xu, Ichida, Allison, Boyd, & Bonds, 2001).

Tallal (1980) showed that children with dyslexia have difficulty in determining the order of two computer-generated non-speech tones presented at short inter stimulus intervals (8–305 ms), but not at longer intervals (428 ms). Based on these findings, it was suggested that the widely reported phonological deficits of children with reading disabilities (Faust & Sharfstein-Friedman, 2003; Snowling, 1996) are due to auditory deficits in order judgment (Tallal, 1980). In addition, the “fast temporal deficit hypothesis” postulates slower temporal information processing in persons with reading disabilities. The claim that persons with reading disabilities are impaired in rapid temporal information processing was supported by studies of the visual system (Hari, Valta, & Uutela, 1999; Laasonen, Service, & Virsu, 2001; May, Williams, & Dunlap, 1988; Van Ingelghem et al., 2001) and later broadened to the general timing hypothesis postulating that the visual, auditory, vestibular, and motor difficulties found in persons with reading disability are due to a general magnocellular temporal processing deficit (Stein & Walsh, 1997).

However, a growing body of research has questioned the validity of the magnocellular theory (Amitay, Ben-Yehudah, Banai, & Ahissar, 2002; Hutzler, Kronbichler, Jacobs, & Wimmer, 2005; Ramus et al., 2003; Skottun, 2000, 2005; Spinelli et al., 1997; Victor, Conte, Burton, & Nass, 1993). For example, in a study that included two experiments designed to test magnocellular, or transient, functioning, the investigators found that the reading impaired had diminished flicker detection at 10 Hz and reduced contrast

sensitivity at low spatial frequency. However, only a weak correlation was found between flicker detection and contrast sensitivity, suggesting that these variables do not measure the same function (Evans, Drasdo, & Richards, 1994), and thus, as might be expected, although both are M functions, they are probably mediated by different cell populations upstream from the LGN. In another recent study, Keen and Lovegrove (2000) reported evidence that challenges the magnocellular hypothesis. They found that the reading disabled participants did not differ from the control group in tasks that relate to magnocellular processing, such as seeing whole in contrast to parts or processing information coming from peripheral locations on the retina, and in the patterns of responses to variations in the size of the stimulus. However, it was found that the reading disabled participants were slower in processing temporal visual information. It has been hypothesized that these conflicting findings suggest that the magnocellular deficit is not causally related to reading difficulties, yet it might be a correlate of the disorder and perhaps even a biological marker (Vellutino, Fletcher, Snowling, & Scanlon, 2004).

Criticism of the magnocellular theory also focuses on the failure to replicate findings of visual deficits specific to the magnocellular system (Ben-Yehudah, Sackett, Malchi-Ginzberg, & Ahissar, 2001; Johannes, Kussmaul, Munte, & Mangun, 1996), and on the findings that visual impairments have been observed across a wide range of stimuli, not just in those depending on the magnocellular system (Amitay et al., 2002; Farrag, Khedr, & Abel-Naser, 2002; Skottun, 2000).

A relatively new approach that challenges the magnocellular theory claims that persons with reading disabilities have a basic perceptual impairment that may be due to a limited ability to retain and compare perceptual traces across brief time intervals (Ben-Yehudah et al., 2001). Their conclusion was based on a replication of two previous experiments. One experiment that required subjects to make a temporal forced choice found a clear magnocellular-like deficit (Borsting et al., 1996). The other experiment involved a spatial forced choice using simultaneous presentation of stimuli in the upper or lower part of the screen. It was shown that reading disabled persons had similar contrast sensitivity at low spatial frequencies as good readers, indicating no magnocellular deficit (Spinelli et al., 1997). Evidence for deficits in temporal (sequential) tasks, as opposed to spatial (simultaneous) tasks, in reading disabled persons was also reported in two studies: one that examined their performance on a temporal and spatial ‘small dots counted’ task (Eden, Stein, Wood, & Wood, 1995), and one that demonstrated that dyslexics are impaired only in sequential frequency discrimination tasks, but not in spatial frequency discrimination tasks (Ben-Yehudah & Ahissar, 2004).

If the finding of these studies holds that, indeed, persons with dyslexia have a deficit in processing sequential visual information, the question remains open as to the role of inter-stimulus interval (ISI). The relative paucity of information does not provide a clear answer on this issue. On one hand, a previous study that compared contrast detection

thresholds for drifting gratings (spatial frequency of 0.5 cpd and temporal frequency of 10 Hz) in a temporal forced choice task with 500 ms ISI revealed only a marginally significant difference. However, in the longer ISI condition, 1000 ms, the difference became highly significant (Ben-Yehudah et al., 2001). The findings that a longer interval increases the difference of contrast sensitivity between good readers and reading disabled participants can implicate a memory deficit mechanism in reading disabilities (Magnussen, 2000). On the other hand, in an assessment of sequential spatial frequency discrimination in good and poor readers the investigators found inconclusive evidence, but their results were more consistent with greater deficits in processing information in shorter ISIs, a finding that can be explained by a longer attentional dwell time in dyslexia (Ben-Yehudah & Ahissar, 2004).

The above summary shows the extensive research that has been done to explain the wide variety of deficits seen in RD persons. Furthermore, it highlights the need for further research of this issue. The theories that we explore in this study are the “magnocellular deficit theory”, the recent suggestion that the apparently magnocellular findings are actually a manifestation of the task presentation, i.e. the sequential nature of the stimuli in those studies, and the “fast temporal deficit hypothesis”. The present study used four tasks measuring contrast detection thresholds, based on a same–different judgment. In all four tasks the same magnocellular-stimulating stimuli were used. The four tasks were designed to differentially probe the three theories and were thus labeled magno-like tasks, a sequential task and a simultaneous task. The magno-like tasks were used to test the main prediction that persons with reading disabilities (RD) as compared to good readers (GR) are poorer in detecting low contrast stimuli with high temporal frequencies and low spatial frequencies (Merigan & Maunsell, 1990). The sequential paradigm utilized a wide range of Inter-Stimulus Intervals and the simultaneous paradigm systematically examined several presentation durations of the stimuli.

## 2. Methods

### 2.1. Participants

Twenty-seven RD adults (all males; mean age  $25 \pm 2.7$  years) and 31 GR adults (all males; mean age  $26 \pm 3.3$  years) participated in the research. All participants were native Hebrew speakers and naive to the purpose of the study. All participants were tested on the Snellen Visual Acuity test. Participants with visual acuity below normal visual acuity were excluded from the study. The subjects were recruited by placing ads on the university campus and direct mailing utilizing a database from the university center for assisting students diagnosed with learning disabilities. All participants had a minimum of several years of university education. All RD participants had a psycho-educational diagnosis of a developmental reading disability as determined by officially recognized testing agencies and were approved by the university for testing leniencies granted to reading disabled students. The criterion for inclusion in the RD group was a current speed of pseudowords reading score (see below) of at least 1 SD above the control group average. Both of the groups' participants performed within the normal range on the matrices

subtest of the WAIS-III (Wechsler, 1997). Performance on other subtests was not a basis for participants' exclusion. The Bar-Ilan University ethics committee approved the study, and all subjects gave their written informed consent prior to participation in the study.

### 2.2. Psychometric battery and reading related skills tests

The following psychometric tests provided the aptitude and achievement profiles of the subjects.

#### 2.2.1. Cognitive measures

The following subtests are all from Wechsler Adult Intelligence Scale (WAIS-III) (Wechsler, 1997): (i) matrices, (ii) digit span, and (iii) digit symbol. An estimation of Intelligence abilities was derived from the matrices subtest of the WAIS-III that resembles the Raven's Advance Progressive Matrices (APM) which is highly g-loaded (Raven, Raven, & Court, 1998). The digit span and digit symbol coding of the WAIS-III test were used to screen participants for distractibility (Anastopoulos, Spisto, & Maher, 1994). Descriptions of the subtests are below:

- (i) Matrices are an abstract reasoning test that measures analogy skills. The subject is required to figure out visuo-spatial relationships between spatially ordered geometric designs and to find a design that best completes a series by either naming or pointing to a correct item from a list of five options. Points were given for each correct answer based on the standard scoring procedure.
- (ii) Digit span is a task that involves the immediate recall of a verbally presented series of digits. The sequence of digits had to be repeated either in a forward or in a backward fashion, and the score was the maximal span of digits (forward and backward) that could be recalled without errors.
- (iii) Digit Symbol Coding: The subject was presented with a code of matched digits and symbols and was required to fill in the correct symbol for each presented digit as rapidly as possible. The standard score on this task is derived from the number of correctly matched symbols in 2 min.

#### 2.2.2. Reading measures

Hebrew includes both deep and shallow orthographies. In the deep orthography the written Hebrew is pointed (which means that there is a high spelling to sound correspondence) and in the shallow orthography the script is unpointed (which means there is a low spelling to sound correspondence) (Frost, 1994).

The reading tests used were:

Speed of reading lists of single unpointed words (measured in words per minute, WPM) (Shatil, 1995b), pseudowords (pointed) per minute (PWPM) (Shatil, 1995a), and a reading rate of an academic level unpointed text (text speed) (Shatil, 1997a).

A Hebrew version of the conventional Rapid Automatized Naming test (Denckla & Rudel, 1976) that included three subtests: letters (RANletter), symbols (RANsymbol), and a combination of letters, numbers, and symbols (RAS) (Breznitz, 1998). In those tests, the participants were instructed to read 50 items, arranged in pseudorandom order, as accurately and quickly as possible.

#### 2.2.3. Orthographic skills

A test of the written spelling ability of the subject was used. The score was based on the number of spelling errors (Shatil, 1997c).

#### 2.2.4. Phonological awareness

A Hebrew translation of the Spoonerism task (Perin, 1983) was utilized. In this task, after several examples, the participants are presented orally with two words (such as 'King John') and are required to exchange the beginning sound of each word ('Jing Kon'). The score was based on the number of correct answers (Shatil, 1997b).

### 2.2.5. D2 test

Visual attention was assessed with a D2 test, which is a timed test of selective attention (Brickenkamp & Zillmer, 1998). The targets are composed of the letters “d” and “p” with one, two, three, or four dashes arranged either individually or in pairs above or below the letter. The subject is given 20 s to scan each line of text and mark all the “d”s that have two dashes. There are 14 lines of 47 characters each, for a total of 658 items. The measured variables were: (1) the concentration performance (CP). This reflects both the speed and the accuracy of performance and was calculated as the total number of items marked minus omissions minus errors of commission. (2) The fluctuation rate (FR). This measures the consistency of performance across trials and was calculated as the largest number of “d”s marked on one line minus the fewest “d”s marked on a single line.

### 2.3. Stimuli and procedure

The following conditions and procedures were the same in all of the tasks. We used a gabor stimulus in two directions: 45° and 135°. A two-alternative forced choice (2AFC) paradigm was used. The beginning of each trial was demarcated by a tone and a ‘+’ sign that was displayed in the center of the screen in order to direct the subject to fixate the center of the screen. In all trials the subject was informed of a correct answer via a high tone and an incorrect answer with a low tone. Before each experiment the subject had several practice sessions in order to learn and understand the upcoming procedure. In all of the experiments there was no time limit for answering, although the subjects were instructed to respond as rapidly and as accurately as possible. Between trials, the ‘+’ sign was again displayed at the center of the screen. Contrast detection thresholds were assessed in all tasks, except for the perception experiment (see below). Contrast detection was varied in a two-down/one-up adaptive staircase procedure, converging on the value of 71% correct (Levitt, 1971). Contrast was increased by 1 dB following an incorrect response, and decreased by 1 dB following two consecutive correct responses. The stimulus contrast was defined as  $(L_{\max} - L_{\min}) / (L_{\max} + L_{\min})$ , where  $L_{\max}$  and  $L_{\min}$  are the maximum and minimum luminance, respectively (Michelson contrast). Detection thresholds (percentage contrast) were calculated as the average of the last 10 of 13 reversals. All tasks included six ‘catch trials’ (except for the perception experiment) in which the Gabor patch had a permanent high contrast of 50% that was displayed in order to test for errors that did not stem from the difficulty of the perceptual detection. All subjects performed close to 100% on the ‘catch trials’. The viewing distance was 90 cm. The three tasks (described below) were administered to each subject in a random order. The interval between a response and the next trial varied randomly between 1.0 and 1.5 s.

#### 2.3.1. Perception of spatial orientation in GR and RD

All of the tasks described below require the subject to make a judgment based on spatial orientation detection (same or different judgment for two possible orientation). The objective of this experiment was to eliminate the possibility of differences between the two groups in this capability and to confirm that all subjects understood and could accurately perform the tasks. Previous evidence supports the notion of an equally functioning parvocellular system in RD and GR subjects (Stein & Walsh, 1997) and thus this task was designed to stimulate mainly parvo-cells, i.e., stimuli with high spatial frequency, high contrast, and high luminance (Livingstone & Hubel, 1988; Merigan & Maunsell, 1993). The outcome of this experiment was a measure of spatial frequency thresholds for the Gabor patch. The stimulus was presented on the center of the screen with a mean luminance of 40.5 cd/m<sup>2</sup>. The subjects were asked to push one button if the orientation of the lower part of the Gabor patch pointed to the right and to push a different button if the orientation of the lower part of the Gabor patch pointed to the left. The Gabor patch ( $\sigma = 2^\circ$ ) was displayed for 500 ms with 50% contrast. Contrast detection was varied in a two-down/one-up adaptive staircase procedure, converging on the value of 71% correct (Levitt, 1971). Spatial frequency was increased by 2 dB following an incorrect response, and decreased by 2 dB following two consecutive correct responses.

The results of a *t*-test for independent samples comparing GR and RD groups’ performance revealed that GR and RD did not differ on this experiment,  $t_s < 1$ . This means that in the following tasks if a difference is found between the two groups, it is not due to a difference in orientation perception or a lack of understanding of the task requirements.

#### 2.3.2. M-selective task

This task was designed to examine magnocellular performance. Contrast-detection thresholds of same-different judgment were measured for a 0.5 cpd Gabor patch ( $\sigma = \lambda = 2^\circ$ ). The stimuli were presented on the center of the screen with a low mean luminance of 5.7 cd/m<sup>2</sup>. The subjects were asked to push one button if the orientation of the lower part of the Gabor patch pointed to the right and to push a different button if the orientation of the lower part of the Gabor patch pointed to the left. The Gabor patch was displayed for 500 ms, with a flicker frequency of 10 Hz.

#### 2.3.3. M-selective saccade task

In order to further explore whether there is truly a magnocellular deficit, we added a second component (above that in the ‘M-selective’ task) that is known to be part of the magnocellular functions, i.e., saccadic eye movements (Stein & Talcott, 1999). Despite recent (e.g., Rieckensky, Thiele, Distler, & Hoffmann, 2005) accumulating evidence that under certain condition the P and K pathways contribute to motion detection, this sort of task is still regarded as largely “M-selective”. Contrast-detection thresholds of same-different judgment were measured for a Gabor patch that appeared to jump from side to side. This procedure was repeated twice with different types of temporal variations flicker, which has previously been demonstrated to reveal processing impairments in RD (Martin & Lovegrove, 1987), and rotation, which is known to be processed by medial superior temporal (MST) area in the extrastriate cortex (Tanaka & Saito, 1989), a region that receives input mainly from magno-cells (Merigan & Maunsell, 1993). The three serial Gabor patches in this experiment were not displayed on the center of the screen, but 2° to the left or to the right of the center randomly and it then jumped twice from side to side (right-left-right, or left-right-left). The subjects were asked to follow the jumping Gabor patches and to indicate by means of a button push whether the three displays had the same or different orientations. Each Gabor patch was displayed for 500 ms with a low mean luminance of 5.7 cd/m<sup>2</sup> and had a spatial frequency of 0.5 cpd ( $\sigma = \lambda = 2^\circ$ ). The flicker frequency was 10 Hz and the rotational frequency was 10 Hz with an amplitude of 45°, with the center at either 45° or 135°.

#### 2.3.4. Temporal task

Contrast-detection thresholds of same-different judgments were measured for a series of two flickering Gabor patches that appeared sequentially in the center of the screen. This procedure was repeated in four separate blocks that differed in their ISI. The four different ISIs used were: 30, 500, 1000, 1500 ms. The blocks were presented in a random order. The subjects were asked to indicate by means of a button push whether the two Gabor patches had the same or different orientations. The Gabor patches were each displayed for 500 ms with a low mean luminance of 5.7 cd/m<sup>2</sup> and had a spatial frequency of 0.5 cpd ( $\sigma = \lambda = 2^\circ$ ) with a flicker frequency of 10 Hz.

#### 2.3.5. Spatial task

Two flickering Gabor patches were displayed simultaneously on the screen separated by 5.74°. The three stimulus durations used were 500, 1000 and 2500 ms. This procedure was repeated in three separate blocks that differed in the duration of stimulus presentation and the blocks were presented in random sequence. The subjects were asked to indicate by means of a button push whether the two Gabor patches had the same or different orientations. The spatial frequency of the Gabor patch was 0.5 cpd ( $\sigma = \lambda = 2^\circ$ ) and the flicker frequency was 10 Hz. The Gabor patches were displayed with a low mean luminance of 5.7 cd/m<sup>2</sup>.

### 2.4. Apparatus

All the psychophysical experiments were administered in a dark room and the subjects were given several minutes in which to dark-adapt. We used the VSG2\5 system (Cambridge Research System Ltd., Rochester,

UK) for designing the experiments. The stimuli were displayed on a 21" SONY GDM-F520 Monitor with a frame rate of 170 Hz. The experiments were controlled by and the data analyzed using Matlab (version 7.0). ColorCAL colorimeter was used in order to calibrate the screen (Cambridge Research System Ltd., Rochester, UK). The responses of the participants were recorded by a CB6 response box (Cambridge Research System Ltd., Rochester, UK).

**3. Results**

*3.1. Psychometric results*

Table 1 summarizes the performance of the GR and the RD on the cognitive and reading-related tests along with the corresponding statistical significance.

As can be seen in Table 1, persons with reading disabilities and normal readers did not differ on the mean scaled score of the matrices subtest, typically used to match groups for cognitive abilities. However, as can be seen in Table 1, normally achieving readers performed better than dyslexics on the screening factor for distractibility: digit symbol coding and digit span. In agreement with previous reports, RD were significantly impaired on all reading tests as compared to GR (Pennington, Van Orden, Smith, Green, & Haith, 1990; Ransby & Swanson, 2003). In addition, the RD group was significantly impaired on the concentration performance (CP) as compared to the GR group. There was no significant difference between RD and GR on the fluctuation rate (FR) across trials. Taken as a whole, these findings indicate that, as compared to GR participants, the RD participants had lower concentration ability that probably cannot be accounted for by normal fluctuations in attention.

Table 1  
Performance on psychometrics tests

	GR (n = 31)	RD (n = 27)	t-value	P-value
Age	25.3(2.7)	26.7(3.3)	-1.67	n.s.
<i>Cognitive measures</i>				
Matrices <sup>a</sup>	13.9 (2.3)	13.4 (2.9)	0.77	n.s.
Digit span <sup>a</sup>	11.2 (2.0)	8.7 (2.7)	2.92	0.007
Digit symbol coding <sup>a</sup>	10.7 (2.8)	9.0 (2.5)	4.26	0.001
<i>Reading measures</i>				
WPM speed	125.7 (20.6)	86.8 (23.2)	7.60	0.000
PWPM speed	70.5 (16.8)	52.3 (26.0)	3.67	0.003
Text	72.9 (9.2)	108.0 (29.0)	-6.90	0.000
RAN letter	20.5 (6.0)	24.6 (4.1)	-3.25	0.004
RAN symbols	34.3 (4.5)	46.0 (11.3)	-4.92	0.000
RAS	20.2 (4.4)	27.5 (5.1)	-5.88	0.000
<i>Orthographic</i>				
Spelling	33.4 (3.3)	5.5 (15.6)	-6.99	0.000
<i>Phonological awareness</i>				
Pig Latin	5.5 (5.5)	3.9 (2.3)	3.14	0.002
<i>Attention-d2</i>				
Cp	207.9 (38.6)	168.7 (37)	4.22	0.000
Fr	12.9 (6.4)	11.8 (6.0)	0.63	n.s.

GR = good readers; RD = Reading Disabled Persons; WPM = words per minute; PWPM = pseudowords per minute; Text = oral text reading rate; RAN = rapid automatized naming; RAS = rapid alternating stimuli; CP = concentration performance; FR = fluctuation rate.

<sup>a</sup> Scaled score.

*3.2. Psychophysical measures*

Table 2 summarizes the performance of the RD and the GR groups for all psychophysical tasks, along with the statistical significance.

*3.2.1. Performance on magnocellular tasks*

As shown in Table 2, the RD and GR groups did not differ on the M-selective task. This means that despite using stimuli that were designed to stimulate magno-cells, the two groups did not differ in their contrast thresholds on this task.

The inability of some experiments to find magnocellular deficits has been attributed to the fact that these deficits are subtle, and that the magnocellular system is not all or none (Stein & Walsh, 1997). The suggestion is thus that in order to search for magnocellular impairments in dyslexia one incorporate in the stimulus as many facets as possible that are unique to the magno system. We added to the second task jumping targets that would engage the saccadic eye movement system, which receives its input and some control from the magnocellular system (Schiller & Lee, 1994).

An analysis of variance (ANOVA) for repeated measures conducted on contrast-detection thresholds on the M-selective saccade task with group (RD/GR) as a between-subject variable and type of temporal frequencies (flicker/rotation) as a within-subject variable, revealed a significant effect only for type of temporal frequencies,  $F(1, 56) = 15.80, p < 0.01$  ( $M = 2.66$  and  $M = 2.33$  for flicker and rotation, respectively). No significant effects were found for both group,  $F(1, 56) = 3.15, p = 0.08$  and Group  $\times$  Type of Temporal Frequencies interaction,  $F(1, 56) = 0.33, p > 0.10$ , indicating that RD's and GR's thresholds do not seem to differ significantly, despite using various conditions similar to previous studies that

Table 2  
Performance on psychophysical tasks

Visual tasks	GR	RD	P-value
<i>M-selective task</i>			
M-selective	2.4 (0.5)	2.5 (0.8)	0.700 <sup>a</sup>
<i>M-selective and saccades task</i>			
Flicker	2.5 (0.6)	2.8 (0.8)	0.081 <sup>b</sup>
Rotation	2.2 (0.4)	2.4 (0.8)	
<i>Temporal task</i>			
30	2.8 (0.6)	3.5 (1.4)	0.04 <sup>b</sup>
500	2.7 (0.4)	3.0 (0.8)	
1000	2.7 (0.7)	3.5 (1.3)	
1500	2.6 (0.4)	3.2 (1.4)	
2500	2.6 (0.4)	3.2 (1.4)	
<i>Spatial task</i>			
500	2.2 (0.4)	2.2 (0.5)	0.12 <sup>b</sup>
1000	2.2 (0.4)	2.3 (0.5)	
1500	2.2 (0.4)	2.2 (0.5)	
2500	1.9 (0.5)	2.2 (0.5)	

GR good readers; RD reading disabled persons.

<sup>a</sup> P-value two-sample t-tests.

<sup>b</sup> P-value of the group effect in a repeated measure ANOVA for group (GR versus RD) by condition.

revealed magnocellular impairments in persons with reading disabilities.

### 3.2.2. Performance on temporal and spatial tasks

An analysis of variance (ANOVA) for repeated measures conducted on contrast-detection thresholds on the temporal task, with group (GR/RD) as a between-subject variable and ISI (30, 500, 1000, 1500 ms) as a within-subject variable, revealed a significant effect only for group,  $F(1, 54) = 4.45$ ,  $p < 0.05$ , with higher thresholds for the RD group ( $M = 3.10$ ) than for the GR group ( $M = 2.75$ ). No significant effects were found for both ISI,  $F(3, 52) = 2.70$ ,  $p > 0.05$ , and Group  $\times$  ISI interaction,  $F(3, 52) = 1.16$ ,  $p > 0.05$ .

A two-way analysis of variance (ANOVA) for repeated measures conducted on contrast-detection thresholds on the spatial task with presentation duration (500, 1000, 2500 ms) as within-subjects effect and group as between-subjects effect, revealed a significant effect of the presentation duration  $F(2, 53) = 4.98$ ,  $p = 0.01$ . No significant effects emerged for both group,  $F(1, 54) = 2.49$ ,  $p > 0.1$  and Group  $\times$  Presentation Duration interaction  $F < 1$  effects. These findings, that indicate poor performance of visual stimuli comparison of the RD group on temporal tasks but not on spatial tasks, are in agreement with previous findings (Ben-Yehudah & Ahissar, 2004; Ben-Yehudah et al., 2001; Eden et al., 1995). Fig. 1A shows the performance of GR and RD groups on the temporal task for each of the ISI conditions and on the spatial task for each presentation duration. Fig. 1B presents the mean threshold for each group (GR versus RD) and for each presentation type (sequential versus simultaneous).

### 3.2.3. Strategy used for temporal and spatial tasks

Previous studies that have investigated the performance of persons with reading disabilities on sequential and simultaneous discrimination tasks found no correlation between the performance of the control group on those two tasks (Ben-Yehudah & Ahissar, 2004). Their interpretation was that good readers adopt different strategies when comparing gratings presented simultaneously versus sequentially. However, in the dyslexic group, they found correlations between the performance on simultaneous versus sequential tasks for some of the sequential ISIs. Although the results were not completely consistent, they suggested that persons with dyslexia might use a different discrimination strategy only at the longest interval. We tested whether the two groups (GR and RD) perform equally when a detection task with same-different judgment is required. If they do, we would suggest that this points to a subtle behavioral difference. Good readers use different strategies for simultaneous versus sequential tasks, whereas persons with reading disabilities changing their strategy only for sequential tasks with longer intervals. Furthermore, we propose that this behavioral difference is independent of the type of task (i.e., detection, discrimination, etc.). Such evidence may indicate a constant strategy difference between good readers and

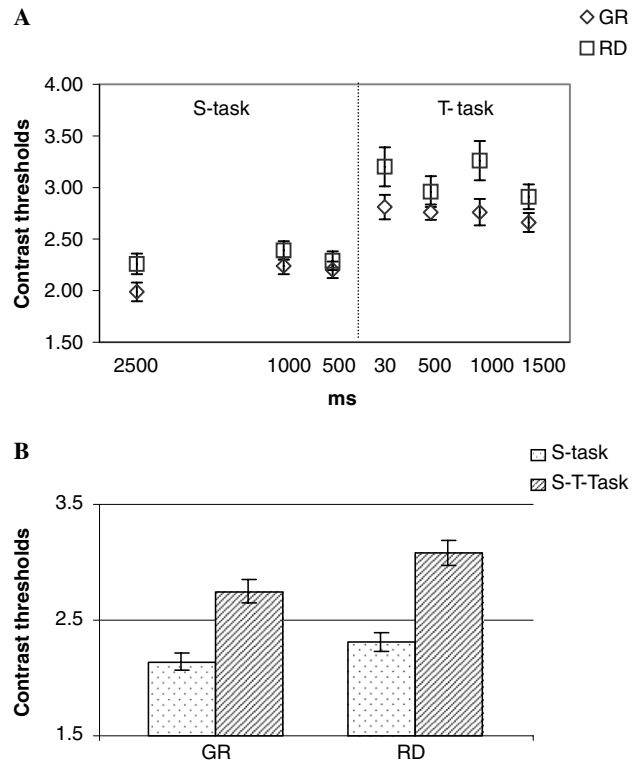


Fig. 1. The contrast detection thresholds (mean  $\pm$  SEM) of each group on the spatial and temporal tasks. (A) The contrast thresholds of each group under all conditions. (B) The mean contrast thresholds of each group on each task. GR = good readers; RD = reading disabled persons; S-task = spatial task; T-task = temporal task.

persons with reading disabilities on the performance of temporal forced choice tasks.

Table 3 presents separate Pearson correlations between the spatial condition with presentation duration of 500 ms and the four temporal conditions (30, 500, 1000 and 1500 ms) for GR and RD participants. As shown in Table 3, whereas for the GR group, the spatial condition correlated only with one temporal condition (1000 ISI), for the RD group, performance on the spatial condition highly correlated with three out of the four temporal conditions (i.e., for the 30, 500, 1000 ISIs). The similarity between Ben-Yehudah and Ahissar's (2004) findings and those of the present study suggest that as opposed to GR who change strategies depending on the nature (spatial versus temporal)

Table 3

Pearson's correlations between contrast detection thresholds on the spatial task and the temporal task

	ISI (ms)			
	30	500	1000	1500
GR	0.25	0.33	0.41*	0.23
RD	0.56**	0.60**	0.61**	0.35

GR = good readers; RD = reading disabled persons. The correlation coefficient is indicated.

\*  $P$  (significant correlations)  $< 0.05$ .

\*\*  $P$  (significant correlations)  $< 0.01$ .

Table 4  
Pearson's correlations between mean contrast detection thresholds on spatial and temporal tasks and scores on cognitive tests

	Temporal task		Spatial task	
	GR	RD	GR	RD
Digit span	−0.33	−0.42*	−0.07	−0.34
D2-CP	−0.33	0.16	−0.06	0.21
D2-FR	0.28	0.06	0.11	0.27

GR = good readers; RD = reading disabled persons; CP = concentration performance; FR = fluctuation rate. The correlation coefficient is indicated.

\*  $P$  (significant correlations) < 0.05.

of the task, the RD group modifies its strategy only when there is long ISI.

#### 3.2.4. Correlations between cognitive skills and performance on temporal and spatial tasks

In the temporal task the detection and comparison between two stimuli separated in time involves memory and attention mechanisms (Lakha & Wright, 2004). It has been suggested that the poor performance of persons with reading disabilities on temporal tasks may be due to impairments on one or both of these mechanisms (Ben-Yehudah & Ahissar, 2004; Hari & Renvall, 2001). We were interested in investigating whether the poor performance of persons with reading disabilities on the temporal task (and not on the spatial task) correlates with their poor performance on the d2 test (which reflects attention ability) and digit span test (which reflects memory skills). Table 4 presents Pearson correlations between the mean thresholds of the spatial and temporal tasks and the performance on the two cognitive tests. Whereas for good readers, no correlations were found between the performance on the spatial and temporal tasks and the performance on the cognitive tests, for persons with reading disabilities, a correlation was found only between the temporal task and the performance on the digit span test.

Note that we cannot conclude from these findings which mechanism is impaired in persons with reading disabilities that could be the cause of their poor performance on temporal tasks, because in the d2 test we measured only some of the attentional parameters (concentration and fluctuation). Also, the digit span is a verbal working memory test that is not necessarily related to the performance on the temporal task that was used which involves visual working memory (Magnussen, 2000).

## 4. Discussion

### 4.1. Summary of the results

We found no evidence for magnocellular impairments in the reading disabled participants as a group, despite using several conditions that specifically stimulate the magnocellular pathway. Our design was based on the assumption that the visual magnocellular impairments in most dyslexic

persons are mild, and that the transient system deficits are not manifested in an all or none fashion (Stein, Talcott, & Walsh, 2000; Stein & Walsh, 1997). However, from our study alone, which tested group performance as a whole and did not focus on individual performance, one cannot conclude that the magnocellular system is not impaired and is not the cause for reading difficulties in a subgroup of persons with reading disabilities. Our findings are consistent with those of other studies that failed to confirm the magnocellular theory (Amitay et al., 2002; Hutzler et al., 2005; Ramus et al., 2003; Skottun, 2000, 2005; Spinelli et al., 1997; Victor et al., 1993).

We found that persons with reading disabilities have significantly higher thresholds on a sequential detection task when a same–different judgment is requested. This significant difference between persons with reading disabilities and good readers was found to be independent of the ISI (in a range of durations from tens of milliseconds up to more than a second). No difference was found between the two groups on the same detection procedure (with a same–different judgment) in the spatial presentation. The findings challenge the fast temporal deficit hypothesis and will be discussed below. However, they support previous findings (Ben-Yehudah & Ahissar, 2004) that whereas good readers change the comparison strategy they use for spatial versus temporal tasks, persons with reading disabilities seem to change their comparison strategy only for temporal tasks with long ISIs (1500 ms).

The findings for the M-selective saccade task are the most interesting. This task was the original design for investigating magnocellular impairments. We hypothesized that persons with reading disabilities, as compared to good readers, will show poor performance if they suffer from magnocellular deficits. However, this task has a sequential presentation condition with same–different judgments, and it differs from the temporal task (with ISI of 500 ms) on only two components. First, in the M-selective and saccades task the stimuli were not presented on the center of the screen as in the temporal task. Secondly, a sequence of three stimuli was presented in the M-selective and saccades task instead of sequence of two stimuli in the temporal task.

These findings can be explained by two fundamental differences between the M-selective saccades task and the temporal task. In order to further explain these differences, we will call one orientation direction of the stimuli “a” and the other orientation direction “b”. The M-selective saccade task could take on two forms: a-a-b or a-b-a. When the sequential stimuli order is a-a-b, the second occurrence of “a” reinforces the memory trace of the image in perceptual or short-term memory and the comparison of a-a-b (as in the M-selective saccades task) is thus easier than an a-b comparison (as in the temporal task). When the sequential stimuli order is a-b-a the subject is faced with two change detections as opposed to the single change detection in the comparison of a-b (as in the temporal task) and thus the M-selective saccades task is again easier than the temporal task.

#### 4.2. Temporal deficits in dyslexia

Evidence for temporal processing deficits in the reading disabled population has been accumulated from different studies that evaluated sensory information processing. Lovegrove demonstrated that reading disabled children had significantly longer durations of visual information store and that their rate of transfer of information was significantly slower than that of controls (Lovegrove & Brown, 1978). Tallal showed that children with dyslexia have difficulty in determining the order of two computer-generated non-speech tones presented at short inter stimulus intervals but not at longer intervals (Tallal, 1980). Her group later suggested that persons with language-based learning impairment have a pervasive, pansensory/motor deficit, which impedes their ability to perceive or produce rapidly successive information within a tightly delineated time window of tens of ms (see Tallal, Miller, & Fitch, 1993 for review). This claim of a slower sensory processing in RD was also supported by studies that evaluated reading disabled response time in visual and auditory tasks (Ram-Tsur, Faust, Caspi, & Zivotofsky, 2005; Sigmundsson, 2005; Temple et al., 2000).

We demonstrated in the present study that temporal detection deficits in the visual domain in persons with reading disabilities are independent of the ISI in the range of tens of millisecond to more than a second. The findings that temporal deficits continue to exist even for intervals longer than a second are consistent with previous findings that persons with reading disabilities show impairments on sequential spatial discrimination tasks (Ben-Yehudah & Ahissar, 2004).

Based on the findings presented here, we suggest two possible explanations for the suggestion that RD have a deficit in rapid sequential processing of visual information. The first is that the fast temporal deficit hypothesis is correct, but it is not limited only to fast temporal presentations of, i.e., short inter-stimulus intervals (around tens of ms, as defined by Tallal et al., 1993), but rather can be applied to a wider range of ISI's, maybe up to several seconds. In light of the large body of evidence indicating deficits only for short intervals (usually between tens to hundreds of milliseconds) in children and adults with reading disabilities (Hari & Kiesila, 1996; Hari & Renvall, 2001; Laasonen et al., 2001, Laasonen, Service, & Virsu, 2002; Laasonen, Tomma-Halme, Lahti-Nuutila, Service, & Virsu, 2000; Rutkowski, Crewther, & Crewther, 2003), we assume that there might be an impaired mechanism limited only to rapid temporal presentations. Thus, based on our as well as on other recent evidence (Ben-Yehudah & Ahissar, 2004) for the low performance of persons with reading disabilities on temporal forced choice tasks with longer ISI's, we suggest a dual mechanism for the impairment that underlies the deficits found in persons with reading disabilities on temporal tasks in both shorter and longer intervals.

#### 4.3. Neurobiological mechanisms underlying impairments in temporal tasks with short intervals in persons with reading disabilities

A possible explanation for the perceptual deficits that persons with reading disabilities show in temporal tasks with short intervals could be an impairment in their attention mechanism. Attention deficits in persons with reading disabilities can be caused by sluggish performance in shifting attention due to specific difficulties in disengaging attention (Hari, Renvall, & Tanskanen, 2001; Hari et al., 1999).

The suggestion that attentional impairment plays a significant role in dyslexia is not new, although unlike some previous work (Cheng, Eysel, & Vidyasagar, 2004; Vidyasagar, 2001), we are not necessarily suggesting a link to the magnocellular deficit hypothesis. Those authors demonstrated that the magnocellular pathway is important for serial search tasks in which an "attentional spotlight" is used to scan the objects. They further explained that the early selection of spatial locations of objects via an attentional spotlight is crucial for reading, and that this can explain why a magnocellular deficit could cause dyslexia (Cheng et al., 2004; Vidyasagar, 2001; Vidyasagar, 2004). However, recently Vidyasagar's whole edifice came under attack due to several problems (Skottun & Skoyles, 2006).

In a study that examined psychophysical temporal order judgment and line motion illusion tasks, it was found that, when compared to a control group, the reading disabled participants showed slower processing of stimuli in the left than the right visual hemifield. The authors suggested that this was due to a left-sided 'minineglect' that can be caused by minor right parietal lobe dysfunction in dyslexia (Hari et al., 2001). A similar left-sided 'minineglect' has also been found in children with attention deficit -hyperactivity disorder (ADHD) (Sheppard, Bradshaw, Mattingley, & Lee, 1999). Indeed, a significant co-morbidity has been suggested between reading disabilities and ADHD (Willcutt, Pennington, Olson, Chhabildas, & Hulslander, 2005).

The attentional deficits can also be explained by parietal lobe dysfunction. Thus, other findings that implicate hypofunction of the parietal lobe support the claim that such a dysfunction exists in persons with reading disabilities. For example, in performing visual search tasks, persons with reading disabilities tend to show longer response times (Eskenazi & Diamond, 1983), impaired accuracy (Casco & Prunetti, 1996; Vidyasagar & Pammer, 1999) and a tendency not to focus visual attention as well as normal readers, due to the diffused distribution of visual processing resources (Facoetti, Paganoni, & Lorusso, 2000). It has been shown that a serial search strongly activates posterior parietal cortex on the same area that was engaged by successive shifts of spatial attention (Corbetta, Shulman, Miezin, & Petersen, 1995), and that search speed is slowed by transcranial magnetic stimulation of the right parietal cortex (Ashbridge, Walsh, & Cowey, 1997).



Another possible explanation for the impaired sequential processing in short ISI is offered by the cerebellar hypothesis that postulates that dyslexia is caused by cerebellar deficits (See Nicolson, Fawcett, & Dean, 2001 for a recent review). There is evidence that children with dyslexia are slower in the automatic temporal skills, a phenomenon known to be related to cerebellar functioning (Nicolson & Fawcett, 1993; Overly, Nicolson, Fawcett, & Clarke, 2003). It has also been shown that cerebellar damage can cause deficits in attention and working memory (Malm et al., 1998; Ravizza et al., 2005) and that it can cause dyslexic-like symptoms during reading (Moretti, Bava, Torre, Antonello, & Cazzato, 2002).

#### 4.4. Neurobiological impairments in persons with reading disabilities in temporal tasks with long intervals

In the same–different task, observers examine a pair of items and determine whether they match (same) or do not match (different). This process is based on low order functioning of perceptual retention mechanisms (Magnussen, 2000), and on higher order functioning of comparison mechanisms that compare stimuli that are retained in working memory (Baddeley, 1986, 1997). Working memory can be divided into separate components for the storage of visual and verbal materials (Baddeley, 1978, 1992). Within the visual modality, working memory can be divided into a high-capacity sensory memory and a relatively limited-capacity short-term memory (Phillips, 1974).

It has been suggested that persons with reading disabilities have working memory impairments in the visual and auditory domains (Gang & Siegel, 2002; Reiter, Tucha, & Lange, 2005). Neuroanatomical studies have shown that the reduced short-term memory in children with neurodevelopment disorders is due to parietal bank morphology which is related to the coding and storage of phonological material, and to the presence of an extra gyrus in the parietal region which is associated with reduced phonological working memory (Kibby et al., 2004). A genetic study revealed, from a genome scan with 320 markers, a novel dominant locus linked to dyslexia in the pericentromeric region of chromosome 3. This chromosome is associated with deficits in mechanisms involved in the reading process, namely phonological awareness, rapid naming, and verbal short term memory (Nopola-Hemmi et al., 2001).

In the current study we found that in persons with reading disabilities, the temporal task (with same–different judgment) was correlated with verbal working memory. Similar results have been reported in a sequential spatial frequency discrimination task (Ben-Yehudah & Ahissar, 2004).

#### 4.5. Implications of temporal processing impairments in reading

We are thus suggesting that two impaired mechanisms can explain the deficits in temporal processing in RD subjects. One mechanism is the attentional component, which

mainly explains the processing deficits in short ISIs, and the other mechanism is the working memory component, which explains the deficits on temporal tasks with longer ISIs.

The consequences of impairments in speed of processing, attributed mainly to temporal tasks with short ISIs, can lead to slower information processing in general and to disproportionate “asynchrony” between speed of processing in the visual versus the auditory system. It was suggested that such an excessive “asynchrony” in the speed of processing of the two systems may be one of the underlying causes of dyslexics’ impaired reading skills (Breznitz & Meyler, 2003; Breznitz & Misra, 2003). Furthermore, The Double Deficit Hypothesis suggests that children with both speed and phonology problems have the most severe reading problems (Wolf & Bowers, 1999). A study that measured the speed of brain waves using EEG evoked potentials in order to see whether the problem lies in registering the tone (sensory) or in categorizing it as high/low, found that children with a reading disability were characterized by slowed central auditory information processing (Fawcett et al., 1993). In educational terms, this means that children with dyslexia need more time to read a familiar word (Van der Leij & Van Daal, 1999) and that this may lead to a strategy of trying to process large chunks of letters during reading, rather than breaking the word down phonologically in order to read unfamiliar words (Nicolson et al., 2001). This strategy may put heavy demands on working memory, that has been suggested to be impaired (see above) in persons with reading disabilities, and thus could limit the number of new words that can be tackled.

## 5. Conclusions

Our results show that persons with reading disabilities have difficulties in performing a temporal task that involves a same–different judgment of two stimuli. In contrast, no differences between RD and GR were found in same–different judgments for simultaneous spatial displays. We also found that the poor performance in the temporal task depended on the size of the required memory trace of the image, rather than the number of the images. Our findings are consistent with those of previous studies that challenge but do not definitively refute the magnocellular hypothesis. Moreover, we question the merit of the fast temporal deficit hypothesis as a lone explanation. We suggest instead a dual mechanism hypothesis to account for the deficits found in sequential comparisons over a wide range of ISIs. Future research should use more stimuli and longer ISIs to study the performance of persons with reading disabilities in sequential tasks. In addition, the correlation in this population between poor performance on temporal tasks involving visual and auditory memory and attention tests should also be further explored.

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## References

- Amitay, S., Ben-Yehudah, G., Banai, K., & Ahissar, M. (2002). Disabled readers suffer from visual and auditory impairments but not from a specific magnocellular deficit. *Brain*, *125*, 2272–2285.
- Anastopoulos, A., Spisto, M., & Maher, M. (1994). WISC-III Freedom from Distractibility factor: its utility in identifying children with attention deficit hyperactivity disorder. *Psychological Assessment*, *6*, 368–371.
- Ashbridge, E., Walsh, V., & Cowey, A. (1997). Temporal aspects of visual search studied by transcranial magnetic stimulation. *Neuropsychologia*, *35*, 1121–1131.
- Baddeley, A. (1978). The trouble with levels: a reexamination of Craik and Lockhart's framework for memory research. *Psychological Review*, *85*, 139–152.
- Baddeley, A. (1986). *Working memory*. Oxford: Clarendon.
- Baddeley, A. (1992). Working memory. *Science*, *255*, 556–559.
- Baddeley, A. (1997). *Human memory: Theory and practice* (Revised ed.). Hove: Psychology Press.
- Ben-Yehudah, G., & Ahissar, M. (2004). Sequential spatial frequency discrimination is consistently impaired among adult dyslexics. *Vision Research*, *44*, 1047–1063.
- Ben-Yehudah, G., Sackett, E., Malchi-Ginzberg, L., & Ahissar, M. (2001). Impaired temporal contrast sensitivity in dyslexics is specific to return and compare paradigms. *Brain*, *124*, 1381–1395.
- Borsting, E., Ridder, W., Dudeck, K., Kelley, C., Matsui, L., & Motoyama, J. (1996). The presence of a magnocellular defect depends on the type of dyslexia. *Vision Research*, *36*, 1047–1053.
- Breznitz, Z. (1998). Rapid automatized naming. Unpublished test. Haifa University, Haifa.
- Breznitz, Z., & Meyler, A. (2003). Speed of lower-level auditory and visual processing as a basic factor in dyslexia: electrophysiological evidence. *Brain and Language*, *85*, 166–184.
- Breznitz, Z., & Misra, M. (2003). Speed of processing of the visual-orthographic and auditory-phonological systems in adult dyslexics: the contribution of “asynchrony” to word recognition deficits. *Brain and Language*, *85*, 486–502.
- Brickenkamp, R., & Zillmer, E. (1998). *The d2 test of attention*. Seattle: Hogrefe & Huber Publishers.
- Casco, C., & Prunetti, E. (1996). Visual search of good and poor readers: effects with targets having single and combined features. *Perceptual and Motor Skills*, *82*, 1155–1167.
- Cheng, A., Eysel, U. T., & Vidyasagar, T. R. (2004). The role of the magnocellular pathway in serial deployment of visual attention. *The European Journal of Neuroscience*, *20*, 2188–2192.
- Corbetta, M., Shulman, G. L., Miezin, F. M., & Petersen, S. E. (1995). Superior parietal cortex activation during spatial attention shifts and visual feature conjunction. *Science*, *270*, 802–805.
- Cornelissen, P., & Stein, J. (1995). Contrast sensitivity and coherent motion in dyslexics. *Vision Research*, *35*, 1483–1494.
- Demb, J., Boynton, G., Best, M., & Heeger, D. (1998). Psychophysical evidence for a magnocellular pathway deficit in dyslexia. *Vision Research*, *38*, 1555–1559.
- Denckla, M., & Rudel, R. (1976). Rapid “automatized” naming (RAN): dyslexia differentiated from other learning disabilities. *Neuropsychologia*, *14*, 471–479.
- Eden, G., Stein, J., Wood, H., & Wood, F. (1995). Temporal and spatial processing in reading disabled and normal children. *Cortex*, *31*, 451–468.
- Eden, G., VanMeter, J., Rumsey, J., Maisog, J., Woods, R., & Zeffiro, T. (1996). Abnormal processing of visual motion in dyslexia revealed by functional brain imaging. *Nature*, *382*, 66–69.
- Eskenazi, B., & Diamond, S. P. (1983). Visual exploration of non-verbal material by dyslexic children. *Cortex*, *19*, 353–370.
- Evans, B., Drasdo, N., & Richards, I. (1994). An investigation of some sensory and refractive visual factors in dyslexia. *Vision Research*, *34*, 1913–1926.
- Facoetti, A., Paganoni, P., & Lorusso, M. L. (2000). The spatial distribution of visual attention in developmental dyslexia. *Experimental Brain Research*, *132*, 531–538.
- Farrag, A., Khedr, E., & Abel-Naser, W. (2002). Impaired parvocellular pathway in dyslexic children. *European Journal of Neurology*, *9*, 359–363.
- Faust, M., & Sharfstein-Friedman, S. (2003). Naming difficulties in adolescents with dyslexia: application of the tip-of-the-tongue paradigm. *Brain and Cognition*, *53*, 211–217.
- Fawcett, A., Chattopadhyay, A., Kandler, R., Jarratt, J., Nicolson, R., & Proctor, M. (1993). Event-related potentials and dyslexia. *Annals of the New York Academy of Sciences*, *682*, 342–345.
- Frost, R. (1994). Prelexical and postlexical strategies in reading: evidence from a deep and a shallow orthography. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *20*, 116–129.
- Gang, M., & Siegel, L. (2002). Sound-symbol learning in children with dyslexia. *Journal of Learning Disabilities*, *35*, 137–157.
- Hari, R., & Kiesila, P. (1996). Deficit of temporal auditory processing in dyslexic adults. *Neuroscience Letter*, *205*(2), 138–140.
- Hari, R., & Renvall, H. (2001). Impaired processing of rapid stimulus sequences in dyslexia. *Trends in Cognitive Sciences*, *5*, 525–532.
- Hari, R., Renvall, H., & Tanskanen, T. (2001). Left minineglect in dyslexic adults. *Brain*, *124*, 1373–1380.
- Hari, R., Valta, M., & Uutela, K. (1999). Prolonged attentional dwell time in dyslexic adults. *Neuroscience Letter*, *271*, 202–204.
- Hutzler, F., Kronbichler, M., Jacobs, A., & Wimmer, H. (2005). Perhaps correlational but not causal No effect of dyslexic readers' magnocellular system on their eye movements during reading. *Neuropsychologia*, *19* published online.
- Johannes, S., Kussmaul, C., Munte, T., & Mangun, G. (1996). Developmental dyslexia: passive visual stimulation provides no evidence for a magnocellular processing defect. *Neuropsychologia*, *34*, 1123–1127.
- Keen, A., & Lovegrove, W. (2000). Transient deficit hypothesis and dyslexia: examination of whole-parts relationship, retinal sensitivity, and spatial and temporal frequencies. *Vision Research*, *40*, 705–715.
- Kibby, M., Kroese, J., Morgan, A., Hiemenz, J., Cohen, M., & Hynd, G. (2004). The relationship between perisylvian morphology and verbal short-term memory functioning in children with neurodevelopmental disorders. *Brain and Language*, *89*, 122–135.
- Laasonen, M., Service, E., & Virsu, V. (2001). Temporal order and processing acuity of visual, auditory, and tactile perception in developmentally dyslexic young adults. *Cognitive, Affective and Behavioral Neuroscience*, *1*, 394–410.
- Laasonen, M., Service, E., & Virsu, V. (2002). Crossmodal temporal order and processing acuity in developmentally dyslexic young adults. *Brain and Language*, *80*, 340–354.
- Laasonen, M., Tomma-Halme, J., Lahti-Nuutila, P., Service, E., & Virsu, V. (2000). Rate of information segregation in developmentally dyslexic children. *Brain and Language*, *75*, 66–81.
- Lakha, L., & Wright, M. (2004). Capacity limitations of visual memory in two-interval comparison of Gabor arrays. *Vision Research*, *44*, 1707–1716.
- Levitt, H. (1971). Transformed up-down methods in psychoacoustics. *The Journal of the Acoustical Society of America*, *49*, 467–477.

- Livingstone, M., & Hubel, D. (1988). Segregation of form, color, movement, and depth: anatomy, physiology, and perception. *Science*, *240*, 740–749.
- Livingstone, M., Rosen, G., Drislane, F., & Galaburda, A. (1991). Physiological and anatomical evidence for a magnocellular defect in developmental dyslexia. *Proceedings of the National Academy of Sciences of the USA*, *88*, 7943–7947.
- Lovegrove, W., Billing, G., & Slaghuis, W. (1978). Processing of visual contour orientation information in normal and disabled reading children. *Cortex*, *14*, 268–278.
- Lovegrove, W., & Brown, B. (1978). Developmental of information processing in normal and disabled readers. *Perceptual and Motor Skills*, *46*, 1047–1054.
- Lovegrove, W., Heddle, M., & Slaghuis, W. (1980). Reading disability: spatial frequency specific deficits in visual information store. *Neuropsychologia*, *18*, 111–115.
- Lovegrove, W., Martin, F., Bowling, A., Blackwood, M., Badcock, D., & Paxton, S. (1982). Contrast sensitivity functions and specific reading disability. *Neuropsychologia*, *20*, 309–315.
- Magnussen, S. (2000). Low-level memory processes in vision. *Trends in Neurosciences*, *23*, 247–251.
- Malm, J., Kristensen, B., Karlsson, T., Carlberg, B., Fagerlund, M., & Olsson, T. (1998). Cognitive impairment in young adults with infratentorial infarcts. *Neurology*, *51*, 433–440.
- Martin, F., & Lovegrove, W. (1984). The effects of field size and luminance on contrast sensitivity differences between specifically reading disabled and normal children. *Neuropsychologia*, *22*, 73–77.
- Martin, F., & Lovegrove, W. (1987). Flicker contrast sensitivity in normal and specifically disabled readers. *Perception*, *16*, 215–221.
- May, J., Williams, M., & Dunlap, W. (1988). Temporal order judgements in good and poor readers. *Neuropsychologia*, *26*, 917–924.
- Merigan, W., & Maunsell, J. (1990). Macaque vision after magnocellular lateral geniculate lesions. *Visual Neuroscience*, *5*, 347–352.
- Merigan, W., & Maunsell, J. (1993). How parallel are the primate visual pathways? *Annual Review of Neuroscience*, *16*, 369–402.
- Moretti, R., Bava, A., Torre, P., Antonello, R., & Cazzato, G. (2002). Reading errors in patients with cerebellar vermis lesions. *Journal of Neurology*, *249*, 461–468.
- Nicolson, R., & Fawcett, A. (1993). Children with dyslexia automatize temporal skills more slowly. *Annals of the New York Academy of Sciences*, *682*, 390–392.
- Nicolson, R., Fawcett, A., & Dean, P. (2001). Developmental dyslexia: the cerebellar deficit hypothesis. *Trends in Neurosciences*, *24*, 508–511.
- Nopola-Hemmi, J., Myllyluoma, B., Haltia, T., Taipale, M., Ollikainen, V., Ahonen, T., Voutilainen, A., Kere, J., & Widen, E. (2001). A dominant gene for developmental dyslexia on chromosome 3. *Journal of Medical Genetics*, *38*, 658–664.
- Overy, K., Nicolson, R., Fawcett, A., & Clarke, E. (2003). Dyslexia and music: measuring musical timing skills. *Dyslexia*, *9*, 18–36.
- Pennington, B., Van Orden, G., Smith, S., Green, P., & Haith, M. (1990). Phonological processing skills and deficits in adult dyslexics. *Child Development*, *61*, 1753–1778.
- Perin, D. (1983). Perin spoonerism task. *British Journal of Psychology*, *74*, 129–144.
- Phillips, W. (1974). On the distinction between sensory storage and short-term visual memory. *Perception and Psychophysics*, *16*, 283–290.
- Ram-Tsur, R., Faust, M., Caspi, A., & Zivotofsky, A. Z. (2005). Evidence for visuomotor deficits in developmental dyslexia: application of the double-step paradigm. *Theoretical and Experimental Neuropsychology (TENNET)*, Montreal.
- Ramus, F., Rosen, S., Dakin, S., Day, B., Castellote, J., White, S., et al. (2003). Theories of developmental dyslexia: insights from a multiple case study of dyslexic adults. *Brain*, *126*, 841–865.
- Ransby, M., & Swanson, H. (2003). Reading comprehension skills of young adults with childhood diagnoses of dyslexia. *Journal of Learning Disabilities*, *36*, 538–555.
- Raven, J., Raven, J., & Court, J. (1998). *Manual for Raven's progressive matrices and vocabulary scales*. Oxford: Oxford Psychologists Press, Ltd.
- Ravizza, S., McCormick, C., Schlerf, J., Justus, T., Ivry, R., & Fiez, J. (2005). Cerebellar damage produces selective deficits in verbal working memory. *Brain* published online.
- Reiter, A., Tucha, O., & Lange, K. W. (2005). Executive functions in children with dyslexia. *Dyslexia*, *11*, 116–131.
- Rieckens, I., Thiele, A., Distler, C., & Hoffmann, K. P. (2005). Chromatic sensitivity of neurons in area MT of the anaesthetized macaque monkey compared to human motion perception. *Experimental Brain Research*, *167*, 504–525.
- Rutkowski, J., Crewther, D., & Crewther, S. (2003). Change detection is impaired in children with dyslexia. *Journal of Vision*, *3*, 95–105.
- Schiller, P., & Lee, K. (1994). The effects of lateral geniculate nucleus, area V4, and middle temporal (MT) lesions on visually guided eye movements. *Visual Neuroscience*, *11*, 229–241.
- Schulte-Korne, G., Bartling, J., Deimel, W., & Remschmidt, H. (2004). Visual evoked potential elicited by coherently moving dots in dyslexic children. *Neuroscience Letter*, *357*, 207–210.
- Shatil, E. (1995a). One-minute test for pseudowords. Unpublished test. Haifa: University of Haifa.
- Shatil, E. (1995b). One-minute test for words. Unpublished test. Haifa: University of Haifa.
- Shatil, E. (1997a). Text reading. Unpublished test. Haifa: Haifa University.
- Shatil, E. (1997b). Phonological processing. Unpublished test. Haifa: Haifa University.
- Shatil, E. (1997c). Spelling test. Unpublished test. Haifa: Haifa University.
- Sheppard, D., Bradshaw, J., Mattingly, J., & Lee, P. (1999). Effects of stimulant medication on the lateralisation of line bisection judgements of children with attention deficit hyperactivity disorder. *Journal of Neurology, Neurosurgery, and Psychiatry*, *66*, 57–63.
- Sigmundsson, H. (2005). Do visual processing deficits cause problem on response time task for dyslexics? *Brain and Cognition*, *58*, 213–216.
- Sincich, L. C., Park, K. F., Wohlgenuth, M. J., & Horton, J. C. (2004). Bypassing V1: a direct geniculate input to area MT. *Nature Neuroscience*, *7*, 1123–1128.
- Skottun, B. (2000). The magnocellular deficit theory of dyslexia: the evidence from contrast sensitivity. *Vision Research*, *40*, 111–127.
- Skottun, B. (2005). Magnocellular reading and dyslexia. *Vision Research*, *45*, 133–134.
- Skottun, B., & Skoyles, J. (2006). Attention, reading and dyslexia. *Clinical & Experimental Optometry*, *89*, 241–245.
- Snowling, M. J. (1996). Dyslexia: a hundred years on. *British Medical Journal*, *313*, 1096–1097.
- Spinelli, D., Angelelli, P., De Luca, M., Di Pace, E., Judica, A., & Zoccolotti, P. (1997). Developmental surface dyslexia is not associated with deficits in the transient visual system. *Neuroreport*, *8*, 1807–1812.
- Stein, J. (2001). The magnocellular theory of developmental dyslexia. *Dyslexia*, *7*, 12–36.
- Stein, J., & Talcott, J. (1999). Impaired neuronal timing in developmental dyslexia – the magnocellular hypothesis. *Dyslexia*, *5*, 59–77.
- Stein, J., Talcott, J., & Walsh, V. (2000). Controversy about the visual magnocellular deficit in developmental dyslexics. *Trends in Cognitive Sciences*, *4*, 209–211.
- Stein, J., & Walsh, V. (1997). To see but not to read; the magnocellular theory of dyslexia. *Trends in Neurosciences*, *20*, 147–152.
- Tallal, P. (1980). Auditory temporal perception, phonics, and reading disabilities in children. *Brain and Language*, *9*(2), 182–198.
- Tallal, P., Miller, S., & Fitch, R. (1993). A case for the preeminence of temporal processing. *Ann. NY Acad. Sci.*, *682*, 27–47.
- Tanaka, K., & Saito, H. (1989). Analysis of motion of the visual field by direction, expansion/contraction, and rotation cells clustered in the dorsal part of the medial superior temporal area of the macaque monkey. *Journal of Neurophysiology*, *62*, 626–641.
- Temple, E., Poldrack, R., Protopapas, A., Nagarajan, S., Salz, T., Tallal, P., Merzenich, M., & Gabrieli, J. (2000). Disruption of the neural response to rapid acoustic stimuli in dyslexia: evidence from functional MRI. *Proceedings of the National Academy of Sciences of the USA*, *97*, 13907–13912.

- Van der Leij, A., & Van Daal, V. (1999). Automatization aspects of dyslexia: speed limitations in word identification, sensitivity to increasing task demands, and orthographic compensation. *Journal of Learning Disabilities, 32*, 417–428.
- Van Ingelghem, M., van Wieringen, A., Wouters, J., Vandenbussche, E., Onghena, P., & Ghesquiere, P. (2001). Psychophysical evidence for a general temporal processing deficit in children with dyslexia. *Neuroreport, 12*, 3603–3607.
- Vellutino, F., Fletcher, J., Snowling, M., & Scanlon, D. (2004). Specific reading disability (dyslexia): what have we learned in the past four decades? *Journal of Child Psychology and Psychiatry, and Allied Disciplines, 45*, 2–40.
- Victor, J., Conte, M., Burton, L., & Nass, R. (1993). Visual evoked potentials in dyslexics and normals: failure to find a difference in transient or steady-state responses. *Visual Neuroscience, 10*, 939–946.
- Vidyasagar, T. R. (2001). From attentional gating in macaque primary visual cortex to dyslexia in humans. *Progress in Brain Research, 134*, 297–312.
- Vidyasagar, T. R. (2004). Neural underpinnings of dyslexia as a disorder of visuo-spatial attention. *Clinical and Experimental Optometry, 87*, 4–10.
- Vidyasagar, T. R., & Pammer, K. (1999). Impaired visual search in dyslexia relates to the role of the magnocellular pathway in attention. *Neuroreport, 10*, 1283–1287.
- Wechsler, D. (1997). *WAIS-III: Administration and scoring manual: Wechsler adult intelligence scale* (3rd ed.). San Antonio: Psychological Corporation.
- Willcutt, E., Pennington, B., Olson, R., Chhabildas, N., & Hulslander, J. (2005). Neuropsychological analyses of comorbidity between reading disability and attention deficit hyperactivity disorder: in search of the common deficit. *Developmental Neuropsychology, 27*, 35–78.
- Wolf, M., & Bowers, P. (1999). The “Double-Deficit Hypothesis” for the developmental dyslexias. *Journal of Educational Psychology, 91*, 1–24.
- Xu, X., Ichida, J. M., Allison, J. D., Boyd, J. D., & Bonds, A. B. (2001). A comparison of koniocellular, magnocellular and parvocellular receptive field properties in the lateral geniculate nucleus of the owl monkey (*Aotus trivirgatus*). *The Journal of Physiology, 531*, 203–218.