



Selective magnocellular deficits in dyslexia: a “phantom contour” study

Anne J. Sperling^{a,*}, Zhong-lin Lu^b, Franklin R. Manis^b, Mark S. Seidenberg^c

^a Neuroscience Graduate Program, Department of Biological Sciences, University of Southern California, Hedco Neurosciences Building, 3641 Watt Way, Los Angeles, CA 90089-2520, USA

^b Department of Psychology, Seeley G. Mudd Building, University of Southern California, Los Angeles, CA 90089-1061, USA

^c Department of Psychology, University of Wisconsin, Madison, 1202 West Johnson St. Madison, WI 53706, USA

Received 6 November 2001; received in revised form 19 December 2002; accepted 19 December 2002

Abstract

A technique by Rogers-Ramachandran and Ramachandran [Vis. Res. 38 (1998) 71–77] was adapted to evaluate magnocellular (M) and parvocellular (P) visual processing efficiency, with identical task structure, in normal and dyslexic children. A battery of phonological, orthographic and cognitive tasks was administered to assess reading ability and component reading skills in both groups. For the visual processing experiment, children identified shapes created by patterns of dots flickering in counter-phase. The dots were black and white in the M condition, versus isoluminant red and green in the P condition. A staircase procedure determined the children's threshold flicker rate for shape identification. Dyslexics displayed selectively slower visual processing in the M condition but not in the P condition. Across all subjects, performance in the M condition was correlated with measures of orthographic skill, consistent with previous findings linking M processing and orthographic skill. Within the dyslexic group, processing in the M condition was negatively correlated with level of phonological awareness. The results are not consistent with the argument that dyslexics with phonological impairments suffer from deficits across all sensory modalities, as those children with the poorest phonological awareness displayed magnocellular processing well within the normal range.

© 2003 Elsevier Science Ltd. All rights reserved.

Keywords: Dyslexia; Magnocellular; Parvocellular; Visual

1. Introduction

Since the mid-1970s, dyslexia researchers have debated the existence of visual processing deficits in dyslexia specific to what is now known as the magnocellular visual system (Breitmeyer & Ganz, 1976; Cornelissen, Hansen, Hutton, Evangelinou, & Stein, 1998; Dunn & Dunn, 1981; Eden et al., 1996; Slaghuis & Lovegrove, 1984; Stein, 2001; Stein & Walsh, 1997; Tallal, Miller, & Fitch, 1993). At the heart of the debate lies the lack of a causal link between impaired magnocellular processing and the phonological impairments most closely associated with dyslexia. Specifically, no clear explanation exists as to how impaired pronunciation and manipulation of isolated words and non-words, hallmarks of the most common dyslexic phenotype, could be affected by visual magnocellular deficits (Greatrex & Drasdo, 1995; Hayduk, Bruck, & Cavanagh, 1996; Hulme, 1988; Stanovich, 1988). In fact, the very

existence of a selective magnocellular deficit in dyslexia is itself an area of controversy. On the one hand, there is anatomical evidence from autopsies of adult dyslexic brains as well as physiological studies with live subjects to suggest that some dyslexics have abnormal or stunted cortical magnocellular development (Demb, Boynton, & Heeger, 1998; Galaburda, Sherman, Rosen, Aboitiz, & Geschwind, 1992; Jenner, Rosen, & Galaburda, 1999; Livingstone, Rosen, Drislane, & Galaburda, 1991). On the other hand, considerable criticism has arisen from failures to replicate the psychophysical findings (Hayduk et al., 1996; Hulme, 1988; Skottun, 2000). The conflicting results may reflect variability in dyslexic etiology or in subject selection procedures (e.g. selection of children referred to vision clinics). Other methodological concerns exist as well (e.g. the validity of specific measures of contrast sensitivity or motion perception as pure measures of isolated magnocellular function has been questioned) (Greatrex & Drasdo, 1995; Hayduk et al., 1996; Hulme, 1988; Skottun, 2000).

A variety of paradigms have been employed to evaluate magnocellular processing in dyslexics, including flicker fusion rates for sine-wave gratings, velocity discrimination

* Corresponding author. Tel.: +1-213-740-2217; fax: +1-213-740-5687.

E-mail addresses: asperlin@usc.edu (A.J. Sperling), zhonglin@usc.edu (Z.-l. Lu).

judgment, coherent motion perception, contrast sensitivity functions and neuroimaging (Breitmeyer & Ganz, 1976; Cornelissen, Richardson, Mason, Fowler, & Stein, 1995; Cornelissen et al., 1998; Demb et al., 1998; Eden, Stein, Wood, & Wood, 1995; Eden et al., 1996; Livingstone et al., 1991; Slaghuis & Lovegrove, 1984). The degree to which these tasks truly isolate magnocellular processing (as well as the certainty with which parvocellular processing has been evaluated in control conditions) has been repeatedly called into question (Greatrex & Drasdo, 1995; Skottun, 2000). In addition, in many of these studies, little information has been provided concerning the reading abilities of the subjects, although that is starting to change (Cornelissen et al., 1998; Talcott et al., 2000; Witton et al., 1998).

The purpose of this study was to re-evaluate the selective magnocellular-deficit hypothesis and to evaluate the relationship between magnocellular deficit and reading impairment. To accomplish these goals, we first determined the reading profiles of children with and without dyslexia, using a wide variety of reading and cognitive measures. A visual psychophysics paradigm was then used to selectively measure the efficacy of magnocellular- and parvocellular-type processing with identical task structure (Rogers-Ramachandran & Ramachandran, 1998). The combination of extensive reading tests and sensitive visual measures allowed us to evaluate which kinds of reading skills were more closely linked to magnocellular- (or parvocellular-type) processing.

We based our psychophysical test on a paradigm that Rogers-Ramachandran and Ramachandran (1998) developed to evaluate magnocellular and parvocellular processing in adults with normal vision. They created stimuli consisting of two adjacent fields of black and white spots that reversed polarity in counter-phase. At high reversal frequencies, subjects could no longer see the phase contrast of any two adjacent dots; however, they could still perceive “phantom contours” between the fields of dots—that is, they perceived a boundary where the two fields met. At the highest frequencies, the contours could only be seen with black/white dots. The contours disappeared if isoluminant color dots (red/green) were used at that same high frequency. The threshold frequency for red/green dots was significantly slower than that for black/white dots. In addition, perception of the contours was possible with very low contrast black and white dots, and was enhanced by peripheral viewing. Rogers-Ramachandran and Ramachandran suggested that there are distinct processing streams in human vision: a fast system (threshold frequency: 15–17 Hz) that extracts boundaries and contours, and a slower system (threshold frequency: 7 Hz) that determines surface characteristics and color. Consistent with the view that the magnocellular stream operates at higher temporal frequencies than the parvocellular stream (Zeki, 1993; Zihl, von Cramon, & Mai, 1983), Rogers-Ramachandran and Ramachandran concluded that the fast, contour-extracting system was the magnocellular system (or a magnocellular-recipient area)

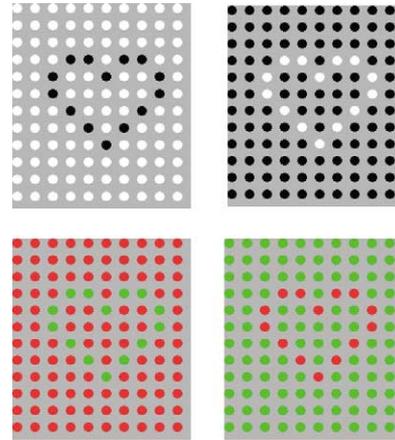


Fig. 1. Counter-phase “heart” dot image used in magnocellular (upper pair) and parvocellular (lower pair) conditions.

whereas the slower system was the parvocellular system (or a parvocellular-recipient area).

Rather than using texture boundaries, as in the Rogers-Ramachandran and Ramachandran paradigm, we created four simple visual shapes—heart, sailboat, rocket, and fish (see Fig. 1 for example), to make the task more interesting to children. In the magnocellular condition, each shape consisted of two flickering black/white images, identical but negatives of each other: black “figure” dots among white “ground” dots; and white “figure” dots among black “ground” dots. In the parvocellular condition, the black/white dots were replaced with isoluminant red/green dots. Isoluminance was determined for each individual child using a minimum-performance calibration procedure.¹ In a given trial, the child had to decide which of the four shapes appeared. We used a staircase procedure to determine the child’s threshold frequency. If dyslexics have a magnocellular-specific deficit, we predicted that they would have lower thresholds for identifying the shapes in the M condition than controls, but comparable thresholds in the P condition. We then considered how the children’s visual processing related to their performance on reading tasks including ones related to phonology.

2. Methods

2.1. Subjects

Children were recruited from two local middle school systems (Long Beach, CA and Los Angeles, CA). We obtained written, informed consent from both the parents and the children themselves. Nineteen children were assigned to the dyslexic group (mean age: 12:5) and an equal number

¹ The calibration is a major improvement on the original Rogers-Ramachandran and Ramachandran paradigm, in that it guaranteed true isoluminance in the red/green condition.

to the control group (mean age: 12:4) and the age difference was not significant (Student's *t*-test, $P > 0.95$). One child in the control group was not run in the parvocellular condition, due to red/green colorblindness. Rigid criteria were imposed for inclusion in the dyslexic group. Inclusion required standardized scores at least one standard deviation below the mean on a test of general reading ability, the Woodcock Reading Mastery Test—Word Identification sub-test, with standard scores within or above a standard deviation of the mean on measures of general cognitive ability, either the Peabody Picture Vocabulary Test—Revised (PPVT-R) or the Visual Closure sub-test of the Woodcock–Johnson Revised Cognitive Abilities Test (Dunn & Dunn, 1981; Woodcock & Johnson, 1989). Controls had to have Woodcock Word Identification, PPVT-R and Woodcock–Johnson Visual Closure scores at or above the dyslexic cut-off scores on these tests (see Table 1 for summary).

2.2. Additional reading tests

Subjects' phonological and orthographic skills were assessed using four additional tests. To determine phonological skill, subjects read aloud from a list of 75 non-words, and deleted phonemes from 25 aurally presented words and 15 non-words (Phoneme Deletion; for a full description of these two tests, see (Joanisse, Manis, Keating, & Seidenberg, 2000; Manis et al., 1999). To determine orthographic skill, subjects read aloud from a list of 65 exception

words, and we administered a two-alternative forced-choice orthographic decision task (Orthographic Choice). The task requires subjects to choose rapidly between a correctly spelled word and a pseudo-homophone (e.g. soap/sope). Half the list was comprised of target words with regular spellings, and half with exceptional (irregular) spellings. Finally, we also administered selections from the Gray Oral Reading Tests, third edition (GORT III) (Wiederholt & Bryant, 1992), to determine passage reading accuracy, rate, and comprehension. The timed test evaluates both phonological awareness and general reading ability.

2.3. Visual stimuli

The experiment was run on a Macintosh G4 computer with a Radius Thunder color graphics card installed to allow greater color resolution (10 bits per gun). Stimuli were displayed on an Apple Multiple Scan 720 monitor. All trials were conducted in darkened rooms. The monitor was also shielded with a black cardboard hood to minimize remaining ambient light. The phantom contour experiment was programmed using Matlab 5.2, with Psychtoolbox extensions (Brainard, 1997). In both the magnocellular and parvocellular conditions (M/P, respectively), the background was the same gray (12.7 cd/m²) and the dots were of the same cone contrast (9%) in DKL color space (Derrington, Krauskopf, & Lennie, 1984). The low luminance of the background gray level was chosen to minimize contrast and luminance, so as to maximize magnocellular response (Demb, Boynton, & Heeger, 1997).

2.4. Procedure

The experiment was split into two–three 45–60 min sessions. Children were either tested in their schools, during regular school hours, or in a lab room at the University of Southern California after regular school hours. In a few cases, the reading skill section of the experiment was administered at the children's homes. Children were allowed breaks whenever necessary. The reading skill section lasted between 75 and 90 min. The phantom contour experiment required 20–30 min. Subjects were given an opportunity to adapt to the darkness of the room while performing a non-reading verbal task (Phoneme Deletion). In addition, subjects were familiarized with pictures of the dot images prior to the start of the experiment.

The magnocellular and parvocellular conditions were run in separate blocks, with the magnocellular condition first.² On each trial, one of the four shapes (made of two flickering images) was shown to the subject. At a subject's threshold, although the phase of individual dots cannot be

Table 1
Mean standardized scores of reading and non-reading ability

	Dyslexics (<i>N</i> = 19) (S.E.)	Controls (<i>N</i> = 19) (S.E.)
<i>General reading ability</i>		
Woodcock Word Identification (percentile)	10.2 (1.5)	65.9 (4.0)***
Grade equivalent	4.3 (0.13)	9.0 (0.57)***
GORT III		
Accuracy	7.8 (1.2)	15.8 (1.1)***
Comprehension	13.8 (0.73)	16.6 (0.74)*
Rate	7.4 (1.1)	18.3 (1.2)***
<i>General cognitive ability</i>		
Visual Closure sub-test	102.6 (2.8)	103.5 (2.4)
Peabody Picture Vocabulary Test—Revised	89.7 (3.3)	106.3 (4.6)**
<i>Phonological awareness</i>		
Non-word reading	32.1 (3.2)	59.2 (1.5)***
Phoneme Deletion—words	14.9 (1.1)	20.4 (0.88)***
Non-words	7.4 (0.76)	11.6 (0.75)***
<i>Orthographic skills</i>		
Exception word reading	53.4 (1.1)	64.4 (1.8)***
Orthographic Choice accuracy (%)		
Overall	86 (1.3)	94 (1.2)***
Regulars only	89 (1.5)	96 (0.87)***
Exceptions only	82 (1.7)	91 (1.9)***

* $P < 0.02$.

** $P < 0.01$.

*** $P < 0.001$.

² We found in pilot studies that the black/white version of the task was easier than the red/green condition. Furthermore, we wanted to control for the effects of boredom and inattentiveness during the long 60-trial black/white run. Thus, we administered this version first.

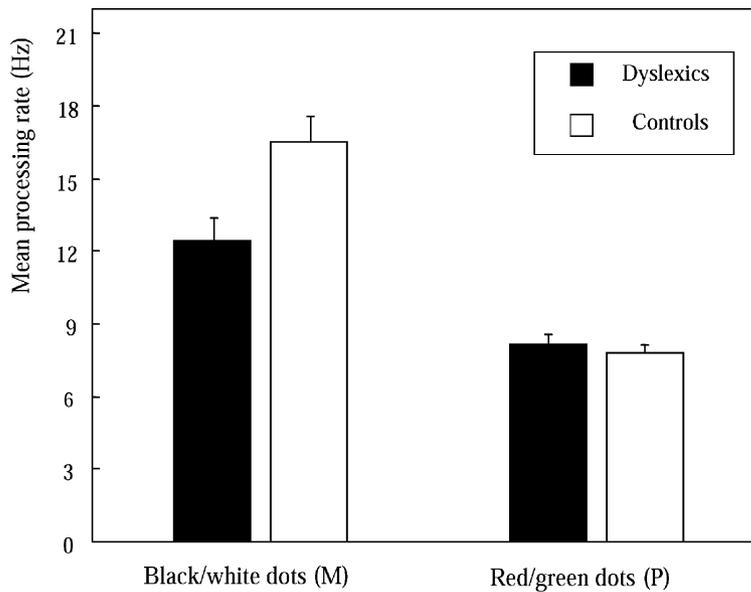


Fig. 2. Magnocellular (M) and parvocellular (P) thresholds for dyslexic and control subjects.

distinguished, a “phantom contour” of the shape can be correctly identified approximately 71% of the time. The subject reported verbally which of the four shapes appeared. The experimenter typed a key for each response and the computer provided auditory feedback for each correct response. A two-up/one-down staircase was used to measure the flicker rate at which the subject could perform the task at 71% correct. The magnocellular condition had 60 trials.

In order to ensure that the red/green dots were truly isoluminant in the parvocellular condition, a “minimum performance” calibration procedure was used for each individual subject, to find the “true” isoluminant point for the subject (Lu & Sperling, 2001). Subjects ran five blocks of at least 20 trials of the parvocellular condition (with the experimenter either adding luminance to the red dots while subtracting an equal amount of luminance from the green dots—or the reverse—producing luminance contrast that ranged from -3 to $+3\%$). Using the same staircase procedure, the added-luminance version that produced the minimum performance was identified as the true isoluminant version. Subjects then re-ran the staircase procedure at this calibrated level, and the overall threshold frequency was computed using both the calibration trial and the “new” staircase trials. Data from the non-isoluminant calibration trials was not used in any further analyses.

3. Results

Table 1 illustrates the subjects’ scores on the reading and general cognitive measures. The dyslexics were significantly worse than controls on the phonological awareness, phonological decoding and orthographic measures, and were read-

ing well below grade level ($P < 0.001$). The pattern is typical of phonological dyslexia (Gottardo, Stanovich, & Siegel, 1996; Liberman & Shankweiler, 1985; Manis, Seidenberg, Doi, McBride-Chang, & Petersen, 1996; Stanovich, 1988; Wagner & Torgensen, 1987). On the general cognitive tests, however (Visual Closure and Peabody Picture Vocabulary), they scored within or above a standard deviation of the mean, thereby displaying the classic reading–IQ discrepancy in dyslexia.

The average threshold frequency for shape identification in the magnocellular condition was 12.4 Hz for dyslexics (S.E. = 0.86) and 16.5 Hz for controls (S.E. = 0.86) (see Fig. 2). The difference between the two groups was significant (Student’s t -test, $P < 0.01$).³ The scores for the parvocellular condition were 8.2 Hz for dyslexics (S.E. = 0.41) and 7.8 Hz for controls (S.E. = 0.37), and this difference was not significant ($P > 0.25$). In both groups the magnocellular threshold was faster than the parvocellular threshold (paired-samples t -test, $P < 0.001$). Performance on the M condition was not significantly correlated with performance on the P condition ($P > 0.25$).

Across the entire sample, log of threshold frequency in the M condition was significantly correlated with standardized score on the general word reading ability test (Woodcock Word Identification: Pearson correlation, 0.44, $P < 0.006$). Log of threshold frequency M condition was also significantly correlated with d' on the Orthographic Choice task.

³ Although control subjects scored significantly higher on Peabody Picture Vocabulary than dyslexic subjects, this measure was not found to be correlated with either of the visual measures ($P > 0.25$), nor did this difference affect the significance level of the visual findings ($F(2, 37) = 5.592$, $P > 0.25$; i.e. the significance of the difference in the M condition remained the same, $P < 0.01$).

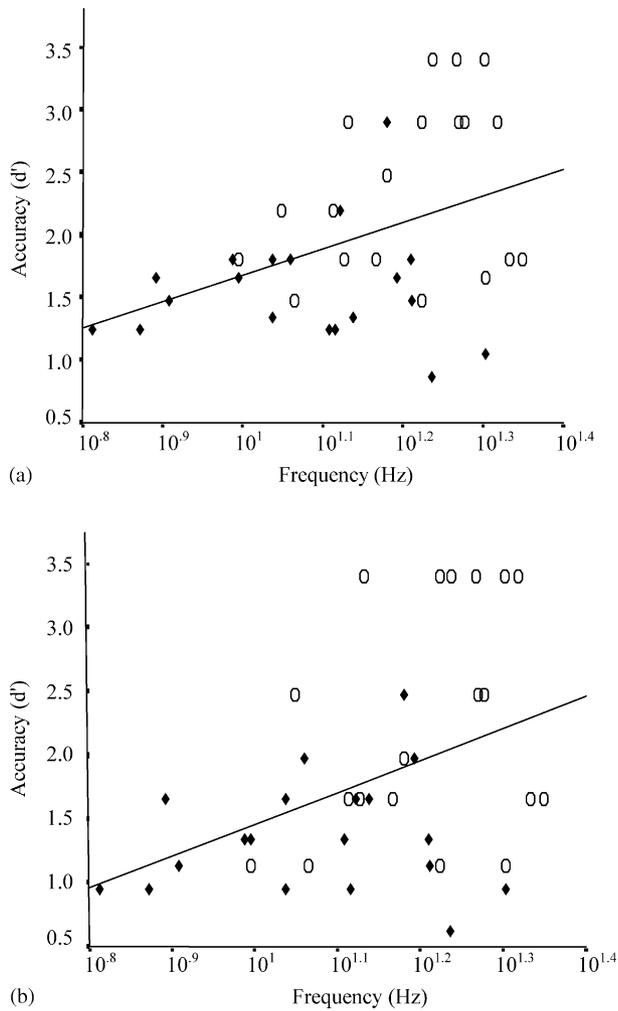


Fig. 3. (a) Overall Orthographic Choice accuracy vs. threshold frequency in M condition (dyslexics: diamonds; controls: circles). (b) Accuracy on exceptions words only vs. threshold frequency in M condition (dyslexics: diamonds; controls: circles).

Overall score and exception-words-only score (d' calculated from percent correct) were both significantly correlated with threshold frequency in the M condition (d' versus log of frequency: overall: Pearson correlation, 0.41, $P < 0.01$; exception words: Pearson correlation, 0.41, $P < 0.011$), but not d' for regular words-only ($P > 0.10$) (see Fig. 3). The correlations were only present when the subject groups were combined; no correlation was found between threshold frequency and Orthographic Choice scores when either the dyslexic group or the control group was considered separately ($P > 0.25$). For the sample as a whole, no additional correlation was found between any of the other reading measures, including all tests of phonological processing, and either magnocellular or parvocellular processing ($P > 0.25$).

Analyses of the dyslexics only showed non-word reading score was negatively correlated with the log of threshold frequency during the M condition (Pearson correlation, -0.46 , $P < 0.05$). Further comparisons involved splitting the dyslexic group into those with threshold frequencies

Table 2
Comparison of reading scores within the dyslexic group

	Low-M ($N = 9$) (S.E.)	Hi-M ($N = 10$) (S.E.)
M condition threshold (Hz)	9.2 (0.59)	15.3 (0.72)***
P condition threshold (Hz)	7.0 (0.44)	9.2 (0.45)**
Woodcock Word Identification (percentile)	11.0 (2.3)	9.5 (2.0)
Grade equivalent	4.4 (0.20)	4.2 (0.17)
GORT III		
Accuracy	10.1 (1.4)	5.7 (1.6) ^a
Comprehension	14.1 (0.96)	13.6 (1.1)
Rate	9.7 (1.7)	5.4 (1.2) ^a
Visual Closure sub-test	101.9 (4.2)	103.3 (3.8)
Peabody Picture Vocabulary Test—Revised	87.9 (4.6)	91.4 (4.9)
Non-word reading	40.1 (4.1)	24.9 (3.7)*
Phoneme Deletion—words	16.9 (0.72)	13.2 (1.8)
Non-words	8.9 (0.90)	6.1 (1.1) ^a
Exception word reading	56.1 (2.6)	51.0 (2.4)
Orthographic Choice accuracy (%)		
Overall	86 (1.2)	85 (2.4)
Regulars only	90 (0.96)	88 (2.8)
Exceptions only	82 (2.1)	83 (2.8)

^a $P < 0.06$.
* $P < 0.02$.
** $P < 0.002$.
*** $P < 0.001$.

more than one standard deviation below the mean of the control group in the M condition, and those scoring within the control range. Nine children comprised the former group (low-M), and ten the latter group (hi-M) (see Table 2). Analyses revealed that the low-M group was significantly better at non-word reading than the hi-M group (Student's t -test, $P < 0.02$). Specifically, the former group had a mean of 40/70 correct versus 25/70 correct for the latter group. We note, however, that although the low-M children were better at non-word reading, and thus less impaired, they were still significantly worse than controls ($P < 0.001$). In addition, comparisons of another measure of phonological processing, Phoneme Deletion (non-words), as well as of GORT accuracy and rate, revealed similar trends ($P < 0.06$ in all three instances). Although the dyslexics in the low-M group had significantly lower threshold frequencies in the P condition than the dyslexics in the hi-M group (low-M: 7.0 Hz; hi-M: 9.2 Hz, $P < 0.002$), their threshold frequencies in the P condition were still not significantly different from those in the control group ($P > 0.22$). None of the cognitive or verbal measures correlated with threshold frequency in the P condition ($P > 0.25$). The low- and hi-M groups did not have significantly different Orthographic Choice scores ($P > 0.25$; see Table 2).

Within the control group, none of the phonological, orthographic, or cognitive measures were correlated with threshold frequency for either the M or P conditions ($P > 0.25$).

4. Discussion

Using rigorous criteria, we segregated our subjects into dyslexic and control groups and evaluated their phonological and orthographic abilities across a wide range of measures. The phantom contour results replicate Rogers-Ramachandran and Ramachandran's original findings, demonstrating the existence of two visual processing streams. In both groups of children, the magnocellular stream, which functions with luminance cues, operated significantly faster than the parvocellular stream, which makes use of surface color cues. An important methodological advantage of the paradigm is that it enabled us to selectively and equally evaluate both magnocellular and parvocellular processing. The only difference between the M and P conditions is a change of the visual stimuli from black and white to red and green. The identical task structure is crucial to claims of selective magnocellular-type deficits in dyslexia.

The results are consistent with previous studies that have claimed that only a portion of dyslexic individuals has some form of magnocellular deficit (Borsting et al., 1996; Spinelli et al., 1997; Talcott et al., 2000; Witton et al., 1998). Nearly half of the children (9/19) in the dyslexic group had black/white thresholds more than one standard deviation below the control group mean. The crucial question is, given the evidence that some children have this type of deficit, how does it relate to their reading? The study revealed that general reading ability (as indexed by the standardized Woodcock Word Identification test) was indeed correlated with magnocellular-type processing. The study of a wide array of phonological, orthographic, and cognitive ability measures allowed us to isolate the specific reading factor correlated with magnocellular-type processing: orthographic ability. The finding is in agreement with a growing line of research linking orthographic, and not phonological, ability with magnocellular-type processing (Talcott et al., 2000; Witton et al., 1998).

The finding that there was no difference between the dyslexics and the controls in the parvocellular condition is perhaps as important as the finding of a significant difference between the two groups in the magnocellular condition. The combination of both these results is what allows us to conclude that dyslexics have *selective* magnocellular deficits. Our study stands in contrast to many others in the literature which did not properly control as rigorously for the parvocellular conditions (Borsting et al., 1996; Cornelissen et al., 1995, 1998; Eden et al., 1995, 1996; Livingstone et al., 1991; Skottun, 2000; Spinelli et al., 1997; Talcott et al., 2000; Witton et al., 1998).

Our results have implications for current theories of dyslexia. First, the results support the idea that there is a magnocellular deficit in some dyslexic children which affects orthographic processing. The basis for this deficit is unknown. One possibility is that it reflects the low end of a normal distribution of magnocellular processing abilities, rather than a developmental anomaly, but this needs to be

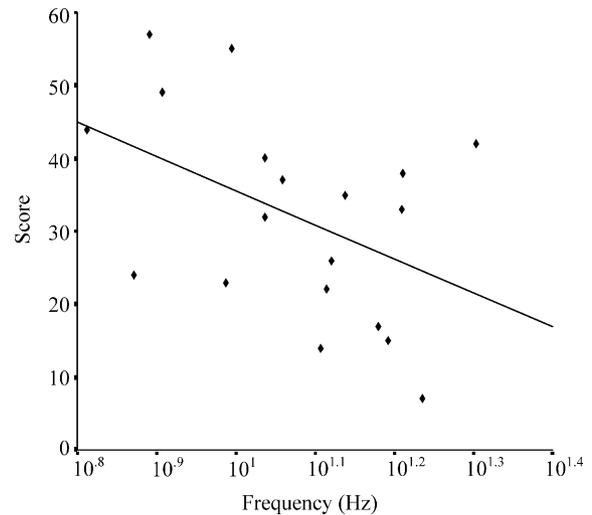


Fig. 4. Plot of threshold frequency in M condition vs. non-word reading scores.

examined further. These children will have more difficulty encoding and remembering orthographic information, as indexed by the Orthographic Choice task. The capacity is also relevant to reading exception words, such as PINT or HAVE. The child has to remember these particular configurations of letters in order to associate them with irregular pronunciations (Fig. 4).

The findings are consistent with the suggestion from several recent studies that some dyslexics exhibit motion perception deficits. There is evidence, from fMRI studies, that the visual pathways and especially the dorsal motion area MT/V5 are less activated in dyslexics during motion perception tasks (Demb et al., 1997, 1998; Eden et al., 1996) but see (Kinsey, 2002) for conflicting findings). As dorsal motion areas receive input largely from the magnocellular system (Zeki, 1993; Zihl et al., 1983), coherent motion perception had been used in prior studies as a test of magnocellular processing. In some cases, researchers have found correlations between motion perception and general reading ability or single-word reading (Cornelissen et al., 1995, 1998; Eden et al., 1996). Studies conducted by Talcott et al. (2000) and Witton et al. (1998) have been among those to suggest that it is orthographic skill specifically—not phonological awareness—that is correlated with coherent motion perception ability (Talcott et al., 2000; Witton et al., 1998). In these newer studies, the research groups have used the terms “dynamic” and “temporal”, rather than “magnocellular”, to characterize what could be the core visual deficit in motion perception—it stems from an inability to process information that changes rapidly over the course of time. There may be good reasons to shift away from the term “magnocellular” when discussing coherent motion perception. The assumption that coherent motion is processed by magnocellular-recipient areas only—without parvocellular input—is controversial, and may be an over-generalization of the role of the magnocellular stream

(Croner & Albright, 1999; Lu & Sperling, 2001; Schiller & Malpeli, 1978). Experiments that evaluate both magnocellular and parvocellular processing with the same task structure, such as the current study, would better support claims of selective magnocellular deficits in dyslexia.

We gave our own subjects the same type of orthographic skill test used by Talcott et al. (2000) and Witton et al. (1998) (Orthographic Choice), and found strong, positive relationships with phantom contour perception. The correlations lend further support to observations linking M-type processing and orthographic skill. In particular, exception-word choice, which requires subjects to focus more specifically on orthography and ignore phonology than regular-word choice does, was most strongly and selectively correlated with magnocellular processing efficiency. Determining whether magnocellular processing exerts a direct influence on orthographic skill requires further analyses of specific skills required for Orthographic Choice tasks. Although our findings agree with those of Talcott et al. (2000) and Witton et al. (1998), the degree to and specificity with which our different tasks (phantom contour perception and coherent motion perception) tap magnocellular processing are quite different. Additional reading measures could help highlight the relationship between orthographic skill and magnocellular processing.

A second implication of the findings concerns the pan-sensory deficit hypothesis (Stein, 2001; Stein & Walsh, 1997; Tallal et al., 1993). According to this hypothesis, dyslexics have a congenital pan-sensory deficit in processing rapidly changing stimuli, owing to deficits in global magnocellular-type processing (Stein, 2001; Stein & Walsh, 1997; Tallal et al., 1993). The deficit could explain the phonological deficit in dyslexics, since often the difference between two similar phonemes is based upon small, rapid changes in formant frequencies, and magno-type cells, which likely exist in auditory as well as visual modalities, respond to rapid, transient stimulus patterns. A child with difficulty processing these critical rapid changes could be further hindered in the ability to learn the vital grapheme-phoneme correspondences involved in early reading. Proponents assert that the reported visual magnocellular deficits could be the result of a single, underlying congenital abnormality that affects all magno-cells, including the auditory ones; by extension, all forms of rapid temporal processing, including phonological decoding, would be affected (Eden et al., 1996; Stein, 2001; Tallal et al., 1993). Therefore, a potential prediction of the theory would be that individuals who are more severely impaired in phonological processing would display more severe processing deficits across all sensory modalities, including vision and audition. Although we only evaluated processing in a single modality, vision, we thoroughly evaluated phonological processing, and our results are not consistent with this prediction. Indeed, the relationship we obtained for phonological skill and magnocellular processing was in the opposite direction. The dyslexics with the slowest processing efficiencies had

better phonological skills, as judged by their performance on tests of non-word reading, paragraph-reading accuracy, and Phoneme Deletion tasks, than dyslexics with faster processing efficiencies (see Table 2).

The unexpectedly negative relationship which we found between magnocellular-type processing and phonological awareness is difficult to interpret at the time of this writing. Could magnocellular deficits reduce the severity of phonological deficits? An unlikely conclusion, and moreover, though the children with low scores in the M condition were better at non-word reading, they were still significantly worse than controls. The children, like dyslexics in general, did have obvious phonological deficits, however mild. Alternatively, the magnocellular-processing deficit may be an indirect, correlated symptom, whose functional significance, as regards phonological processing, remains unknown.

5. Conclusions

Over the last decade, a number of researchers have examined the variability in phonological and orthographic deficits within the dyslexic population (Castles & Coltheart, 1993; Joanisse et al., 2000; Manis et al., 1996, 1997, 1999). Studies by Castles and Coltheart (1993) and Manis et al. (1996) have produced classification schemes which differentiate those dyslexics with primarily phonological deficits (*phonological dyslexia*), those with primarily orthographic deficits and milder phonological deficits (*surface* (Castles & Coltheart, 1993) or *delay-type dyslexia* (Manis et al., 1996)), as well as those with both deficits (*mixed dyslexia*). Considering the complexity inherent in language and reading, it is possible that different congenital, neuronal deficits underlie the various subtypes, and even a single subtype, and could be differentially linked to visual or auditory deficits. The dyslexics in our study all fit into the most common of the subtypes, phonological dyslexia. Future investigations of the relationship between dyslexia and magnocellular processing would clearly benefit from the inclusion of all subtypes of dyslexia, especially those with primarily orthographic deficits. A few studies have in fact begun to take these steps (Borsting et al., 1996; Witton et al., 1998).

In conclusion, we combined a large number of reading measures, to carefully characterize the reading abilities of both dyslexic and normal readers, with an experimental paradigm that provides an equal evaluation of both magnocellular- and parvocellular-type processing. We found evidence for a link between selective magnocellular-type processing and general reading ability, and in particular, orthographic skill.

Acknowledgements

This work was supported by a LAS Merit Fellowship from USC to A. Sperling and NICHD grant HD29891 to F. Manis. We thank the administrators, teachers, parents and students

of the Long Beach Unified School District for their support of and participation in this study. We also thank Luis Lesmes for technical assistance, Caroline Bailey and Laura Gillies for help with subject testing, and two anonymous reviewers for constructive comments.

References

- Borsting, E., Ridder, W. H., 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 [see comments].
- Brainard, D. H. (1997). The psychophysics toolbox. *Spatial Vision*, *10*, 433–436.
- Breitmeyer, B. G., & Ganz, L. (1976). Implications of sustained and transient channels for theories of visual pattern masking, saccadic suppression, and information processing. *Psychological Review*, *83*, 1–36.
- Castles, A., & Coltheart, M. (1993). Varieties of developmental dyslexia. *Cognition*, *47*, 149–180.
- Cornelissen, P. L., Hansen, P., Hutton, J., Evangelinou, V., & Stein, J. (1998). Magnocellular visual function and children's single word reading. *Vision Research*, *38*, 471–482.
- Cornelissen, P., Richardson, A., Mason, A., Fowler, S., & Stein, J. (1995). Contrast sensitivity and coherent motion detection measured at photopic luminance levels in dyslexics and controls. *Vision Research*, *35*, 1483–1494.
- Croner, L. J., & Albright, T. D. (1999). Seeing the big picture: Integration of image cues in the primate visual system. *Neuron*, *24*, 777–789.
- Demb, J. B., Boynton, G. M., & Heeger, D. J. (1997). Brain activity in visual cortex predicts individual differences in reading performance. *Proceedings of the National Academy of Sciences of the United States America*, *94*, 13363–13366.
- Demb, J. B., Boynton, G. M., & Heeger, D. J. (1998). Functional magnetic resonance imaging of early visual pathways in dyslexia. *Journal of Neuroscience*, *18*, 6939–6951.
- Derrington, A. M., Krauskopf, J., & Lennie, P. (1984). Chromatic mechanisms in lateral geniculate nucleus of macaque. *Journal of Physiology*, *357*, 241–265.
- Dunn, L. M., & Dunn, L. M. (1981). *Peabody picture vocabulary test—revised*. Circle Pines, MD: American Guidance Service.
- Eden, G. F., Stein, J. F., Wood, H. M., & Wood, F. B. (1995). Temporal and spatial processing in reading disabled and normal children. *Cortex*, *31*, 451–468.
- Eden, G. F., 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 [see comments].
- Galaburda, A. M., Sherman, G. F., Rosen, G. D., Aboitiz, F., & Geschwind, N. (1992). Developmental dyslexia: Four consecutive patients with cortical abnormalities. *Annals of Neurology*, *49*, 527–534.
- Gottardo, A., Stanovich, K. E., & Siegel, L. S. (1996). The relationships between phonological sensitivity, syntactic processing, and verbal working memory in the reading performance of third-grade children. *Journal of Experimental Child Psychology*, *63*, 563–582.
- Greatrex, J. C., & Drasdo, N. (1995). The magnocellular deficit hypothesis in dyslexia: A review of reported evidence. *Ophthalmic and Physiological Optics*, *15*, 501–506.
- Hayduk, S., Bruck, M., & Cavanagh, P. (1996). Low-level visual processing skills of adults and children with dyslexia. *Cognitive Neuropsychology*, *13*, 975–1015.
- Hulme, C. (1988). The implausibility of low-level visual deficits as a cause of children's reading difficulties. *Cognitive Neuropsychology*, *5*, 369–374.
- Jenner, A. R., Rosen, G. D., & Galaburda, A. M. (1999). Neuronal asymmetries in primary visual cortex of dyslexic and nondyslexic brains. *Annals of Neurology*, *46*, 189–196.
- Joanisse, M. F., Manis, F. R., Keating, P., & Seidenberg, M. S. (2000). Language deficits in dyslexic children: Speech perception, phonology and morphology. *Journal of Experimental Child Psychology*, *77*, 30–60.
- Kinsey, K. (2002, April). Motion discrimination in dyslexic and normal readers. In *Poster session presented at the annual meeting of the Cognitive Neuroscience Society*, San Francisco, CA.
- Lieberman, I. Y., & Shankweiler, D. (1985). Phonology and the problems of learning to read and write. *Remedial and Special Education*, *6*, 8–17.
- Livingstone, M. S., Rosen, G. D., Drislane, F. W., & Galaburda, A. M. (1991). Physiological and anatomical evidence for a magnocellular defect in developmental dyslexia. *Proceedings of the National Academy of Sciences of the United States America*, *88*, 7943–7947.
- Lu, Z. L., & Sperling, G. (2001). Sensitive calibration and measurement procedures based on the amplification principle in motion perception. *Vision Research*, *41*, 2355–2374.
- Manis, F. R., McBride-Chang, C., Seidenberg, M. S., Keating, P., Doi, L. M., Munson, B., & Petersen, A. (1997). Are speech perception deficits associated with developmental dyslexia? *Journal of Experimental Child Psychology*, *66*, 211–235.
- Manis, F. R., Seidenberg, M. S., Doi, L. M., McBride-Chang, C., & Petersen, A. (1996). On the bases of two subtypes of developmental dyslexia [corrected]. *Cognition*, *58*, 157–195.
- Manis, F. R., Seidenberg, M. S., Stallings, L., Joanisse, M., Bailey, C., Freedman, L., Curtin, S., & Keating, P. (1999). Development of dyslexic subgroups: A 1-year follow up. *Annals of Dyslexia*, *49*, 105–134.
- Rogers-Ramachandran, D. C., & Ramachandran, V. S. (1998). Psychophysical evidence for boundary and surface systems in human vision. *Vision Research*, *38*, 71–77.
- Schiller, P. H., & Malpeli, J. G. (1978). Function specialization of the lateral geniculate nucleus laminae of the rhesus monkey. *Journal of Neurophysiology*, *41*, 788–797.
- Skottun, B. C. (2000). The magnocellular deficit theory of dyslexia: The evidence from contrast sensitivity. *Vision Research*, *40*, 111–127.
- Slaghuis, W. L., & Lovegrove, W. (1984). Flicker masking of spatial-frequency-dependent visible persistence and specific reading disability. *Perception*, *13*, 527–534.
- 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.
- Stanovich, K. E. (1988). The right and wrong places to look for the cognitive locus of reading disability. *Annals of Dyslexia*, *38*, 154–177.
- Stein, J. (2001). The magnocellular theory of developmental dyslexia. *Dyslexia*, *7*, 12–36.
- Stein, J., & Walsh, V. (1997). To see but not to read the magnocellular theory of dyslexia. *Trends in Neuroscience*, *20*, 147–152.
- Talcott, J. B., Witton, C., McLean, M. F., Hansen, P. C., Rees, A., Green, G. G. R., & Stein, J. F. (2000). Dynamic sensory sensitivity and children's word decoding skills. *Proceedings of the National Academy of Sciences of the United States America*, *97*, 2952–2957.
- Tallal, P., Miller, S., & Fitch, R. H. (1993). Neurobiological basis of speech: A case for the preeminence of temporal processing. *Annals of the New York Academy of Science*, *682*, 27–47.
- Wagner, R. K., & Torgesen, J. K. (1987). The nature of phonological processing and its causal role in the acquisition of reading skills. *Psychological Bulletin*, *101*, 192–212.
- Wiederholt, J. L., & Bryant, B. R. (1992). *Gray oral reading tests* (3rd ed.). Austin, TX: Pro-Ed.
- Witton, C., Talcott, J., Hansen, P., Richardson, P., Griffiths, T., Rees, A., Stein, J., & Green, G. (1998). Sensitivity to dynamic auditory and visual stimuli predicts non-word reading ability in both dyslexic and normal readers. *Current Biology*, *8*, 791–797.
- Woodcock, R. W., & Johnson, M. B. (1989). *Woodcock-Johnson tests of cognitive ability—revised*. Allen, TX: DLM Teaching Resources.
- Zeki, S. (1993). *A vision of the brain*. Boston: Blackwell Scientific Publications.
- Zihl, J., von Cramon, D., & Mai, N. (1983). Selective disturbance of movement vision after bilateral brain damage. *Brain*, *106*, 313–340.