Motion and form vision in typical and atypical adult readers

Richard David John Johnston

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List of papers and conference abstracts

Many of the results reported in this thesis have been published either in paper or abstract form.

Papers:

1. **Johnston, R**., Pitchford, N. J., Roach, N. W., & Ledgeway, T. (2017). Visual perception in dyslexia is limited by sub-optimal scale selection. *Scientific Reports*, *7*, 6593.

2. **Johnston, R**., Pitchford, N. J., Roach, N. W., & Ledgeway, T. (2017). Encoding of rapid time-varying information is impaired in poor readers. *Journal of Vision, 17(5),* 1-13.

3. **Johnston, R**., Pitchford, N. J., Roach, N. W., & Ledgeway, T. (2016). Why is the processing of global motion impaired in adults with developmental dyslexia? *Brain and Cognition, 108*, 20-31.

4. **Johnston, R**., Pitchford, N. J., Roach, N. W., & Ledgeway, T. (Under revision). New insights into the role of motion and form vision in neurodevelopmental disorders. *Neuroscience and Biobehavioral Reviews*.

Conference abstracts:

1. **Johnston, R**., Pitchford, N. J., Roach, N. W., & Ledgeway, T. The effects of perceptual uncertainty on global motion and global form detection in developmental dyslexia. *European Conference on Visual Perception, Berlin, Germany, August 2017.*

2. Ledgeway, T., **Johnston, R**., Pitchford, N. J., Roach, N. W. Is spatial scale selection sub-optimal in developmental dyslexia? *European Conference on Visual Perception, Berlin, Germany, August 2017.*

3. **Johnston, R**., Pitchford, N. J., Roach, N. W., & Ledgeway, T. Temporal segmentation of motion and form information in adult poor readers. *Child Vision Research Society, Coleraine, Northern Ireland, June 2017.*

4. **Johnston, R**., Pitchford, N. J., Roach, N. W., & Ledgeway, T. Effects of reading ability on temporal segmentation of motion information. *Applied Vision Association Conference, London, UK, December 2016.*

5. **Johnston, R**., Pitchford, N. J., Roach, N. W., & Ledgeway, T. Scale selection is impaired in developmental dyslexia. *British Congress on*

Optometry and Vision Science, Coleraine, Northern Ireland, September 2016.

6. **Johnston, R**., Pitchford, N. J., Roach, N. W., & Ledgeway, T. (2016). Motion-based segmentation is impaired in adults with developmental dyslexia. *European Conference on Visual Perception, Barcelona, Spain, August 2016.*

7. **Johnston, R**., Ledgeway, T., Pitchford, N. J., Roach, N. W. (2015). Why is the processing of global motion impaired in adult poor readers? *Reading in the Forest, International Workshop on Reading and Dyslexia, Annweiler, Germany, October 2015.*

8. **Johnston, R**., Ledgeway, T., Pitchford, N. J., Roach, N. W. (2015). Visual processing of motion and form by relatively good and poor adult readers. *European Conference on Visual Perception, Liverpool, UK, August 2015.*

9. **Johnston, R**., Ledgeway, T., Pitchford, N. J., Roach, N. W. (2015). What is the underlying nature of the perceptual deficit in adult poor readers? *Applied Vision Association Conference, Nottingham, UK, April 2015.*

Abstract

Poor reading in adults is often associated with developmental dyslexia, especially for adults that have average, or above average, intelligence and no history of ocular ill health, social deprivation, or other learning difficulties. Developmental dyslexia is primarily associated with poor phonological decoding skills, but evidence suggests that there is also a visual perception deficit. In particular, it has been reported that individuals with dyslexia have difficulty integrating local motion, but not local form, cues into a global percept. However, current theories proposed to explain this visual impairment, cannot fully accommodate the perceptual abilities of readers with dyslexia. The aim of this thesis is to investigate the origin of visual impairment in poor readers, including those with dyslexia.

It is unknown if the global motion deficit in readers with dyslexia reflects a difficulty processing motion, temporal information, or integrating local visual cues across multiple (>2) dimensions. To address this issue four diagnostic, global motion and form tasks were administered to a large sample of adult readers. Results showed that generally poor readers, and individuals with dyslexia, had significantly higher coherence thresholds than relatively good readers on a random-dot global motion task, a spatially 1-D global motion task, and a temporally-defined global form task. In contrast, no difference was found on a static global form task. Thus, the visual impairment in developmental dyslexia represents a difficulty integrating cues that change over time, rather than a difficulty processing motion *per se*.

The visual system has to satisfy competing constraints of integrating features that belong to a common object, whilst segmenting those arising from different objects. To explore if the visual deficit in developmental dyslexia extends to spatial segmentation, a motion-based spatial segmentation task and an analogous form task was administered to thirty-eight adult readers. Thresholds were measured for each of a range of segment sizes to characterise task performance. Participants were unable to perform either task when segments were smaller than a spatial resolution (acuity) limit that was independent of reading ability. Thresholds decreased as segment size increased, but for the motion task the rate of improvement was shallower for the poorest readers and the segment size at which performance became asymptotic was larger. Thus, the visual deficit in developmental dyslexia also extends to spatial segmentation when tasks contain time-varying (e.g. motion) information.

To explore why motion-based segmentation is impaired in generally poor readers a biologically-inspired computational model was developed. Simulations showed that even though the size of the motion-boundaries in the image was fixed, and predictable, within a single block of trials relatively poor readers could not utilise this knowledge to select a detection mechanism of the appropriate size (scale) for optimal performance. A prediction of this novel "scale selection hypothesis" is that relatively good readers should exhibit a qualitatively similar pattern of performance to generally poor readers, when scale uncertainty is introduced into the task. This prediction was tested empirically and the results were consistent with the scale selection hypothesis.

Eye movements and fixations are made during reading so the positions of words on the retinae change over time. To encode text effectively, this temporal stream of visual information must be segmented over time, as well as across space, but it is unknown if temporal segmentation is also impaired in developmental dyslexia. To address this issue temporal versions of the spatial segmentation tasks were administered to thirty-eight adult readers. Coherence thresholds were measured at each of a range of oscillation rates (segment durations). Results showed that temporal acuity for both the motion and form tasks were significantly and negatively correlated with reading skill. Thus, generally poor readers have difficulty segmenting temporally changing motion and form cues, particular at the briefest segment durations.

An alternative theory of the origin of visual impairment in developmental dyslexia is the anchoring deficit hypothesis. It proposes that individuals with dyslexia cannot utilise stimulus repetitions to form a perceptual anchor, to reduce memory load when comparing sequential stimuli. This theory has not yet been tested using global motion and form tasks. To address this issue a global motion detection task and an analogous form task were administered to forty-four adult readers. By varying the degree of uncertainty associated with the axis of global motion or orientation, the ability to form a perceptual anchor was manipulated across different blocks of trials. Results showed that reading ability was not significantly associated with performance on the global motion task or the global form task, challenging the anchoring deficit hypothesis.

In summary, the results of this thesis are difficulty to reconcile with previous theories of vision in developmental dyslexia. They show that the visual deficit in generally poor readers and individuals with dyslexia impacts on the ability to both integrate and segment local cues in the image and has at least two distinct components, one spatial and one temporal. That is, 1) a difficulty in selecting the spatial scale optimal for task performance; and 2) a difficulty judging the global direction or orientation of stimuli changing rapidly over time.

Chapter 1[1]

General introduction

1. 1. Reading

Reading is a remarkable cultural invention (Dehaene, 2009). It takes years of extensive practice and training to successfully master the complex transformation of print to speech. Several computational models of reading aloud have been proposed in an attempt to elucidate the architecture of visual word form recognition including the dual route cascade model (Coltheart, Rastle, Perry, Langdon, & Ziegler, 2001). It assumes that reading occurs via two routes: the whole-word lexical route and the sublexical phonological route. The correct pronunciation of irregular words (e.g. chord, placebo, beatify, sidereal) is dependent upon the lexical route, whereas the correct pronunciation of novel words or non-words (e.g. ip, chur, dreker, pelnador) is dependent upon the sublexical phonological route. Several studies have shown that sublexical phonological decoding is a strong predictor of reading ability in children

[1] Parts of this chapter have been included in a larger review on motion and form vision in neurodevelopmental disorders. Citation: Johnston, R., Pitchford, N. J., Roach, N. W., & Ledgeway, T. (Under revision). New insights into the role of motion and form vision in neurodevelopmental disorders. *Neuroscience and Biobehavioral Reviews*.

(Bradley & Bryant, 1983; Wagner & Torgesen, 1987). Thus, it has been associated with developmental dyslexia, especially for individuals who have average or above average intelligence (IQ) and do not have a history of ocular ill health, social deprivation, or other learning difficulties (Rack, Snowling, & Olson, 1992; Ramus et al., 2003; Snowling, 2000; Stanovich, 1988, Stanovich & Siegel, 1994).

1. 2. Developmental dyslexia

Developmental dyslexia is thought to affect approximately 5 to 20% of the population (Shaywitz, 1996) but prevalence rates vary depending on the diagnostic criteria used. As previously mentioned, it is primarily associated with poor sublexical phonological decoding skills. Several studies have shown that both children and adults with dyslexia have a difficulty on cognitive tasks that require the representation, storage, and/or retrieval of speech sounds (Rack et al., 1992; Ramus et al., 2003; Snowling, 2000; Stanovich, 1988, Stanovich & Siegel, 1994). Although the majority of readers with dyslexia exhibit poor phonological decoding skills evidence suggests that they may also have a low-level sensory impairment in the visual domain (Gori & Facoetti, 2014; Gori & Facoetti, 2015; Stein & Kapoula, 2012). This idea is controversial because deficits on visual perception tasks are not found in all readers with dyslexia (Amitay, Ben-Yehudah, Banai, & Ahissar, 2002; Roach, Edwards, & Hogben, 2004; White et al., 2006). A possible explanation for this is that different criteria have been used to diagnose developmental dyslexia across studies.

Definitions of developmental dyslexia are highly controversial. As it is primarily associated with poor phonological decoding skills (Rack et al., 1992; Ramus et al., 2003; Snowling, 2000; Stanovich, 1988, Stanovich & Siegel, 1994) a severe phonological deficit is often taken to be a pertinent characteristic feature of dyslexia. However, it is currently unclear if individuals with poor phonological decoding skills, consistent with the dyslexic profile, can be differentiated from generally poor readers who exhibit impaired

performance on a range of reading tests assessing both sublexical and lexical processing skills. This issue is theoretically important because it speaks directly to the debate as to whether developmental dyslexia is best defined as a distinct type of reading difficulty associated with poor phonological decoding skills or the lower end of a normal distribution of general reading ability (Fletcher, 2009, Siegel, 2006).

1. 3. Theories of vision in developmental dyslexia

As previously mentioned, evidence suggests that readers with dyslexia have a low-level sensory deficit in the visual domain (Gori & Facoetti, 2014; Gori & Facoetti, 2015; Stein & Kapoula, 2012) but the origin of this impairment is currently unclear. Several theories have been proposed to explain the underlying nature of the visual deficit in readers with dyslexia. These include: the magnocellular deficit hypothesis (Galaburda, Sherman, Rosen, Aboitz, & Geschwind, 1985; Galaburda & Livingstone, 1993; Stein, 2001; Stein & Walsh, 1997), the external noise exclusion hypothesis (Sperling, Lu, Manis, & Seidenberg, 2005, 2006), the anchoring deficit hypothesis (Ahissar, 2007), the modified receptive field hypothesis (Grainger, Dufau, & Ziegler, 2016) and the dorsal stream vulnerability hypothesis (Atkinson & Braddick, 2013; Braddick, Atkinson, & Wattam-Bell, 2003; Braddick & Atkinson, 2011). All these theories of vision in developmental dyslexia are critically evaluated in the sections below.

1. 3. 1. The magnocellular deficit hypothesis

Readers with developmental dyslexia are purported to have a selective impairment in the subcortical magnocellular pathway (Galaburda et al., 1985; Galaburda & Livingstone, 1993; Stein, 2001; Stein & Walsh, 1997). In order to fully understand this hypothesis, it is necessary to know a little about the magnocellular and parvocellular pathways.

1. 3. 1. 1. The magnocellular and parvocellular pathways

Evidence suggests that anatomically distinct and functionally independent visual pathways can be discerned in a subcortical part of the primate brain called the lateral geniculate nucleus (LGN) (Livingstone & Hubel, 1988; Merigan & Maunsell, 1993; Zeki & Shipp, 1988). The two major subdivisions are the magnocellular and parvocellular pathways. A third koniocellular pathway has also been identified but its precise functional role is yet to be fully elucidated (Casagrande, 1994; Hendry & Yoshioka, 1994; Hendry & Reid, 2000; Kaas, Heurta, Weber, & Harting, 1978). Magnocellular cells reside in the two ventral layers of the LGN. They are thought to play a key role in the processing of relatively low spatial frequency stimuli, containing coarse scale details, which change rapidly over time (Derrington & Lennie, 1984; Schiller & Malpeli, 1978). In addition, magnocellular cells are principally sensitive to achromatic stimuli and mediate visual perception at relatively low scotopic and mesopic luminance levels (Lee, Smith, Pokorny, & Kremers, 1997; Purpura, Kaplan, & Shapley, 1988). They also respond preferentially to temporal transients produced by abrupt stimulus onsets and offsets (Derrington & Lennie, 1984; Kaplan & Shapley, 1988; but see Levitt, Schumer, Sherman, Spear, & Movshon, 2001). In contrast, parvocellular cells reside in the four dorsal layers of the LGN. They have been implicated in the processing of relatively high spatial frequency stimuli, containing fine scale details, which either remain static or change very slowly over time (Derrington & Lennie, 1984; Schiller & Malpeli, 1978). In addition, parvocellular cells are principally sensitive to chromatic stimuli and mediate visual perception at relatively high

photopic luminance levels (Lee et al., 1997; Purpura et al., 1988). They also respond preferentially to stimuli that do not contain stimulus transients (Derrington & Lennie, 1984; Kaplan & Shapley, 1982; but see Levitt et al., 2001). Elucidating the spatial and temporal frequencies at which visual processing switches from the magnocellular pathway to the parvocellular pathway is not trivial and a topic of much debate (Skottun, 2000). The magnocellular deficit hypothesis predicts that readers with developmental dyslexia should exhibit reduced contrast sensitivity for stimuli of relatively low spatial (≤2c/deg) and high temporal frequency (≥10Hz) (Galaburda et al., 1985; Galaburda & Livingstone, 1993; Stein, 2001; Stein & Walsh, 1997).

1. 3. 1. 2. Studies using static gratings

Lovegrove, Bowling, Badcock and Blackwood (1980) were amongst the first to investigate the magnocellular deficit hypothesis. To do so, they administered a contrast sensitivity task to ten children with developmental dyslexia (mean age = 14 years) who had an average reading age 5 years below that predicted by their chronological age on the Neale Analysis of Reading ability (NARA) (Neale, 1966). In this standardised reading test, participants are asked to read aloud a series of short passages containing regular and irregular words of increasing difficulty. The performance of the group of readers with dyslexia was compared to that of ten relatively good readers (mean age = 14 years) matched for both chronological age and non-verbal IQ. The visual stimuli comprised static sinusoidal gratings (2, 4, 12 and 16c/deg) that were presented at each of a range of durations between 40 and 1000ms. To determine the

minimum contrast needed for reliable task performance, a single-interval, forced-choice procedure (1IFC) was employed. On each trial, participants had to judge whether or not a sinusoidal grating had appeared and contrast sensitivity was measured. Results showed that readers with dyslexia had lower overall contrast sensitivity than relatively good readers at all durations tested (Figure 1). In addition, a significant reader group by spatial frequency interaction was found when the duration of the stimuli ranged from 150 to 500ms. Readers with dyslexia had lower contrast sensitivity than relatively good readers when the spatial frequency of the gratings was 4 and 12c/deg but the difference in contrast sensitivity between the two reader groups was much smaller at the lowest spatial frequency tested. These findings challenge the magnocellular deficit hypothesis, as it predicts that contrast sensitivity in readers with dyslexia should have been impaired to a greater extent when the spatial frequency of the gratings was 2c/deg. They are difficult to interpret because post hoc tests (e.g. independent samples t-tests or non-parametric equivalents) were not conducted to determine the spatial frequencies at which readers with dyslexia exhibited lower contrast sensitivity than relatively good readers.

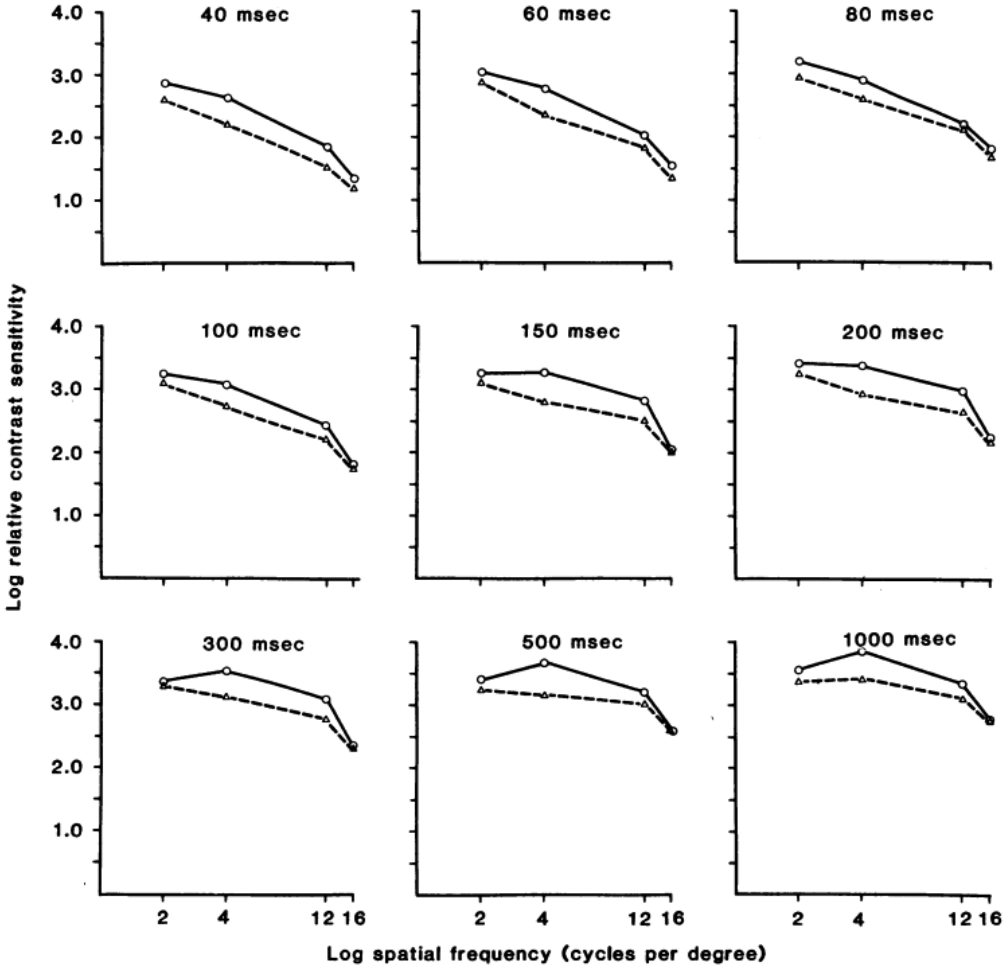


Figure 1. Graphs showing contrast sensitivity as a function of spatial frequency (i.e. contrast sensitivity functions) for static gratings at each of a range of durations (40 to 1000ms) in readers with developmental dyslexia (open triangles; dashed line) and relatively good readers (open circles; solid line). Adapted from Lovegrove et al. (1980).

Lovegrove et al. (1982, Experiment 1) argued that magnocellular deficits might be more apparent in slightly younger children with dyslexia than those who took part in their previous study, as the mechanisms underlying spatial vision may still be maturing in these individuals (Lovegrove et al. 1980). To explore this issue, a contrast sensitivity task was administered to five children with developmental dyslexia (mean age = 12.5 years) who had an average reading age 3 years below that predicted by their chronological age on the NARA (Neale, 1966). The performance of this group of readers with dyslexia was compared to that of five relatively good readers (mean age = 12.25 years) matched for non-verbal IQ who scored within 1 standard deviation (SD) of the normalised mean on the same reading test. The visual stimuli consisted of static sinusoidal gratings (2, 4, 8 and 12c/deg) that were presented at each of a range of durations between 40 and 1000ms. A high contrast stimulus was presented at the beginning of each trial and participants had to manually adjust its contrast until the grating could no longer be seen. Results showed that overall contrast sensitivity did not differ across readers with dyslexia and relatively good readers at any of the durations tested (Figure 2). However, a significant reader group by spatial frequency interaction was found when the duration of the stimuli ranged from 40 to 1000ms. Readers with dyslexia had lower contrast sensitivity than relatively good readers when the spatial frequency of the gratings was 2c/deg but post hoc tests were not carried out to determine if these between-group differences were statistically significant. This coupled with the fact that contrast sensitivity was measured using the method of adjustment means that strong conclusions about the magnocellular deficit hypothesis cannot be made. The subjective nature of the method of adjustment

means that it is impossible to determine the response criterion participants were using to perform the task (Graham, 1989). A further criticism of the study by Lovegrove et al. (1982, Experiment 1) concerns the fact that contrast sensitivity is now known to reach adult levels by approximately eight years of age (Ellemberg, Lewis, Liu, & Maurer, 1999; Jeon, Maurer, & Lewis, 2014). Thus, it would have been fully developed in all participants tested. Further research is needed to explore the possibility that magnocellular deficits only arise in readers with dyslexia when the mechanisms underlying spatial vision are still maturing.

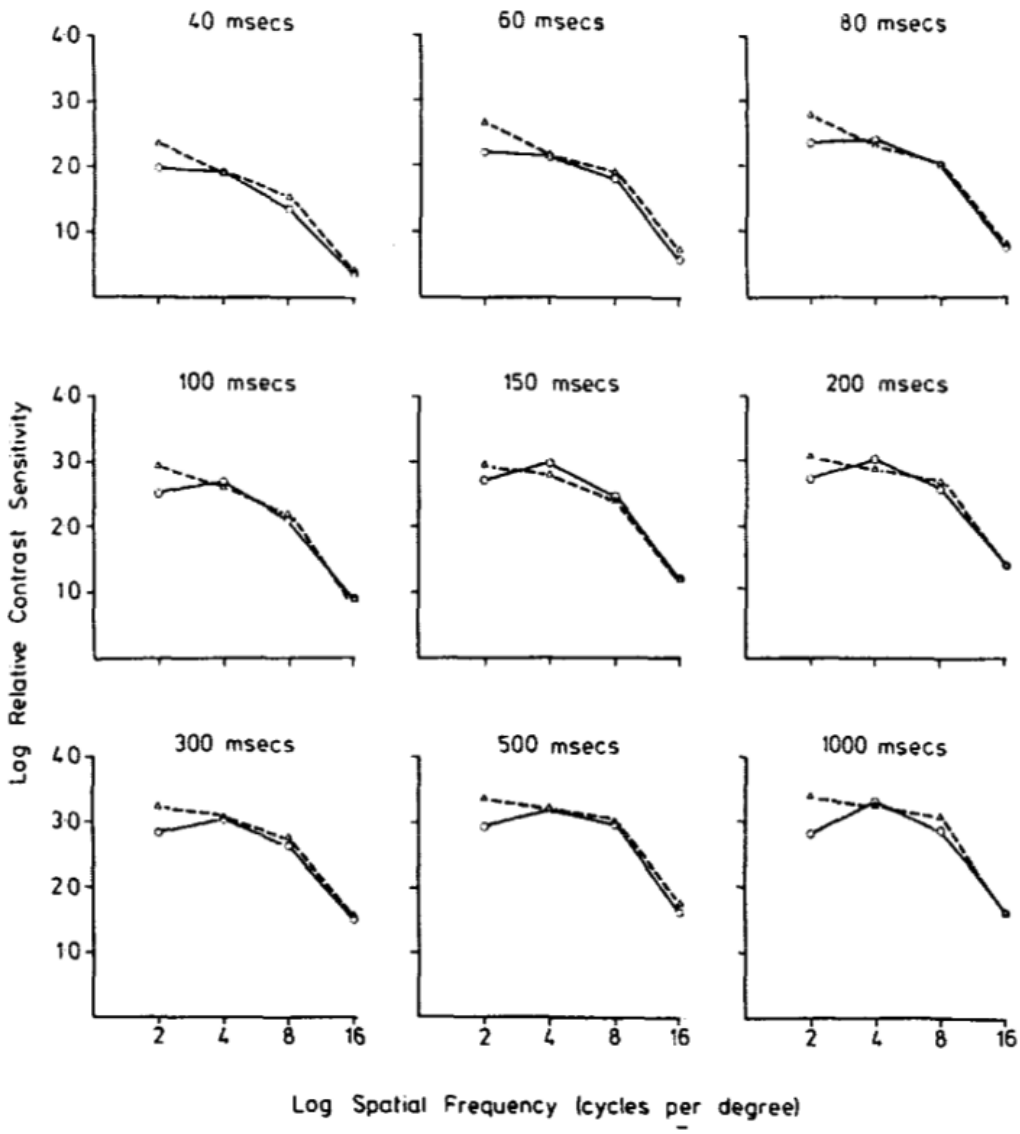


Figure 2. Graphs showing contrast sensitivity functions for static gratings at each of a range of durations (40 to 1000ms) in readers with developmental dyslexia (solid line; open circles) and relatively good readers (dashed line; open triangles). Adapted from Lovegrove et al. (1982, Experiment 1).

Several studies in the general population have shown that overall contrast sensitivity is reduced when stimuli are presented at oblique as opposed to cardinal orientations (Appelle, 1972; Campbell, Kulikowski, & Levinson, 1966; Furmanski & Engel, 2000; but see Wilson, Loffler, Wilkinson, & Thistlethwaite, 2001). It has been suggested that this oblique effect may partially result from environmental factors such as learning to read (Mayer, 1977). This raises the possibility that contrast sensitivity at oblique as opposed to cardinal orientations may be impaired in readers with dyslexia and relatively good readers. To investigate this issue Lovegrove et al. (1982, Experiment 2) carried out a second experiment in which a contrast sensitivity task was administered to fourteen children with developmental dyslexia (mean age = 12.6 years) who had an average reading age 4 years and 1 month below that predicted by their chronological age on the NARA (Neale, 1966). The performance of this group of readers with dyslexia was compared to that of fourteen relatively good readers (mean age = 12.6 years) matched for both chronological age and non-verbal IQ who scored within 1SD of the normalised mean on the same reading test. The static gratings were identical to those used in their previous study (Lovegrove at al., 1982, Experiment 1) except the stimuli were oriented either vertically or obliquely, 45º counter-clockwise of vertical. A 1IFC procedure was used to measure contrast sensitivity in which participants had to judge whether or not a grating had appeared on each trial. Results showed that overall contrast sensitivity did not differ across readers with dyslexia and relatively good readers (Figure 3) but a significant reader group by spatial frequency interaction was found. Readers with dyslexia had lower contrast sensitivity than relatively good readers when the spatial

frequency of the gratings was 2c/deg regardless of whether the stimuli were oriented vertically or obliquely. However, the error bars used to provide a measure of variability in the data overlapped considerably. This suggests that the between-group differences may not have been statistically significant. In addition, no three-way interaction between reader group, spatial frequency, and stimulus orientation was found. These results challenge the magnocellular deficit hypothesis, as readers with dyslexia did not exhibit impaired performance at relatively low spatial frequencies. It is unclear why relatively good readers had lower contrast sensitivity than readers with dyslexia when the spatial frequency of the gratings was 12c/deg.

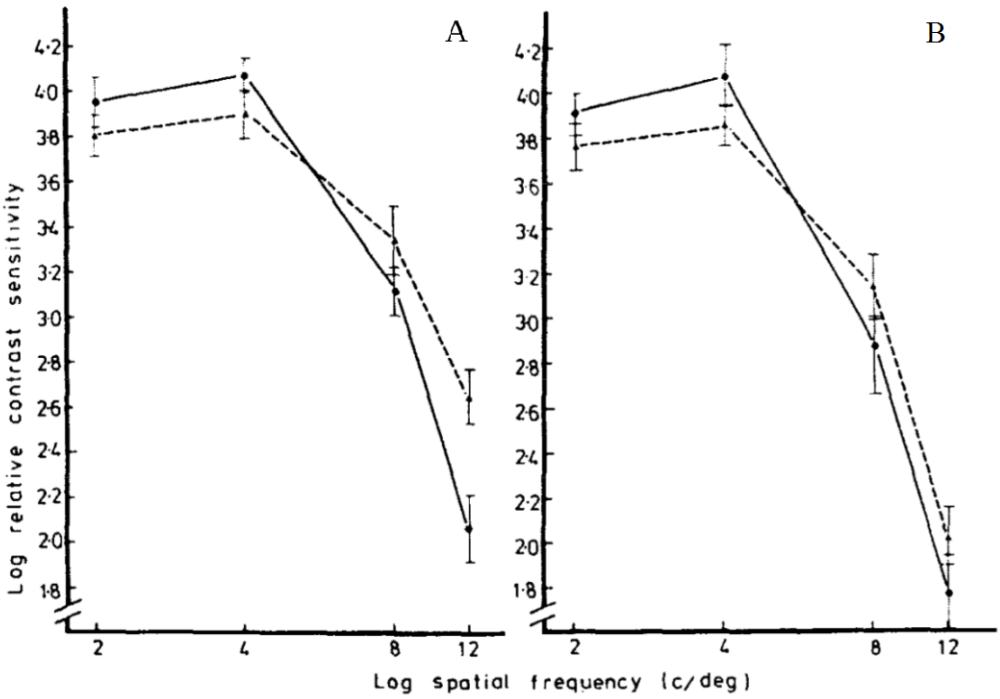


Figure 3. Graphs showing contrast sensitivity functions for static gratings in readers with developmental dyslexia (dashed line) and relatively good readers (solid line) when the visual stimuli were oriented either vertically (A) or obliquely, 45º counter-clockwise of vertical (B). Adapted from Lovegrove et al. (1982, Experiment 2).

Evidence suggests that overall contrast sensitivity for static gratings in the general population improves when the field size of the stimulus is increased, presumably because additional visual information becomes available (Hoekstra, van der Goot, van den Brink, & Bilsen, 1974; Howell & Hess, 1978; Rovamo, Luntinen, & Näsänen, 1993; Savoy & McCann, 1975). To explore if readers with dyslexia are able to utilise this additional information to improve performance Martin and Lovegrove (1984, Experiment 1) administered a contrast sensitivity task to fourteen readers with developmental dyslexia (mean age = 12.11 years) who had an average reading age 4 years and 1 month below that predicted by their chronological age on the NARA (Neale, 1966). The performance of this group of readers with dyslexia was compared to that of fourteen relatively good readers (mean age = 12.11 years) matched for both chronological age and non-verbal IQ who had a reading age no less than 1 year and 6 months below that predicted by their chronological age on the same test. The stimuli consisted of static sinusoidal gratings (1, 2, 4, 8 and 12c/deg) presented in a circular display window with a diameter that subtended either 2 or 8º of visual angle (Table 1). To determine the minimum contrast needed for reliable task performance, a two-interval, forced-choice procedure (2IFC) was employed. On each trial, participants had to judge whether the stimulus appeared in the first or second temporal interval and contrast sensitivity was measured. Results showed that overall contrast sensitivity did not differ across readers with dyslexia and relatively good readers (Figure 4). However, a significant reader group by spatial frequency interaction was found. Readers with dyslexia had lower contrast sensitivity than relatively good readers at spatial frequencies ≤2c/deg regardless of whether the stimuli subtended 2 or 8º

of visual angle. The three-way interaction between reader group, spatial frequency, and stimulus size was not statistically significant. Although these results might appear to support the magnocellular deficit hypothesis strong conclusions cannot be made because post hoc tests were not conducted to determine the spatial frequencies at which readers with dyslexia exhibited impaired task performance.

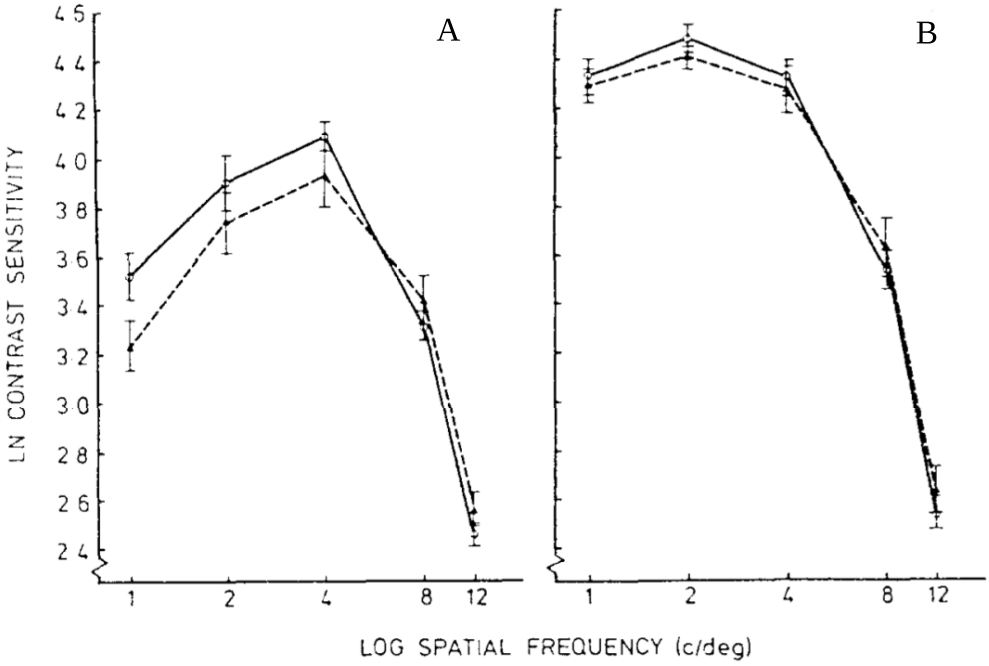


Figure 4. Graphs showing contrast sensitivity functions for static gratings in readers with dyslexia (dashed line) and relatively good readers (solid line) when the diameter of stimuli subtended either 2º (A) or 8º (B) of visual angle. Adapted from Martin and Lovegrove (1984, Experiment 1).

Evidence suggests that magnocellular cells mediate visual perception at relatively low scotopic and mesopic luminance levels, whilst parvocellular cells mediate visual perception at relatively high photopic luminance levels (Lee et al., 1997; Purpura et al., 1988). This raises the possibility that the mean luminance of the display upon which the stimuli are presented could influence contrast sensitivity for static gratings in readers with dyslexia. To investigate whether or not this is the case Martin and Lovegrove (1984, Experiment 2) conducted a second experiment in which a contrast sensitivity task was administered to the same fourteen readers with developmental dyslexia (mean age = 12.11 years) and fourteen relatively good readers (mean age = 12.11 years) matched for both chronological age and non-verbal IQ. The task and visual stimuli were identical to those used in their previous study (Martin & Lovegrove, 1984, Experiment 1) except the mean luminance of the display was set to either 3.42 or 102.74cd/m^2 (Table 1). Results showed that overall contrast sensitivity did not differ across readers with dyslexia and relatively good readers (Figure 5). However, a significant reader group by spatial frequency interaction was found. Readers with dyslexia had lower contrast sensitivity than relatively good readers at spatial frequencies ≤2c/deg regardless of whether the luminance of the display was 3.42 or 102.74cd/m^2. In addition, the three-way interaction between reader group, spatial frequency, and display luminance was statistically significant. Readers with dyslexia had lower contrast sensitivity than relatively good readers at 4c/deg when the luminance of the display was 3.42cd/m^2 but not when it was 102.74cd/m^2. Although these results suggest that contrast sensitivity for static gratings is impaired to a greater extent at relatively low luminance levels in readers with

dyslexia one cannot rule out the possibility that the three-way interaction arose because readers with dyslexia performed better than relatively good readers at 12c/deg when the luminance of the display was 3.42cd/m^2 but not when it was 102.74cd/m^2.

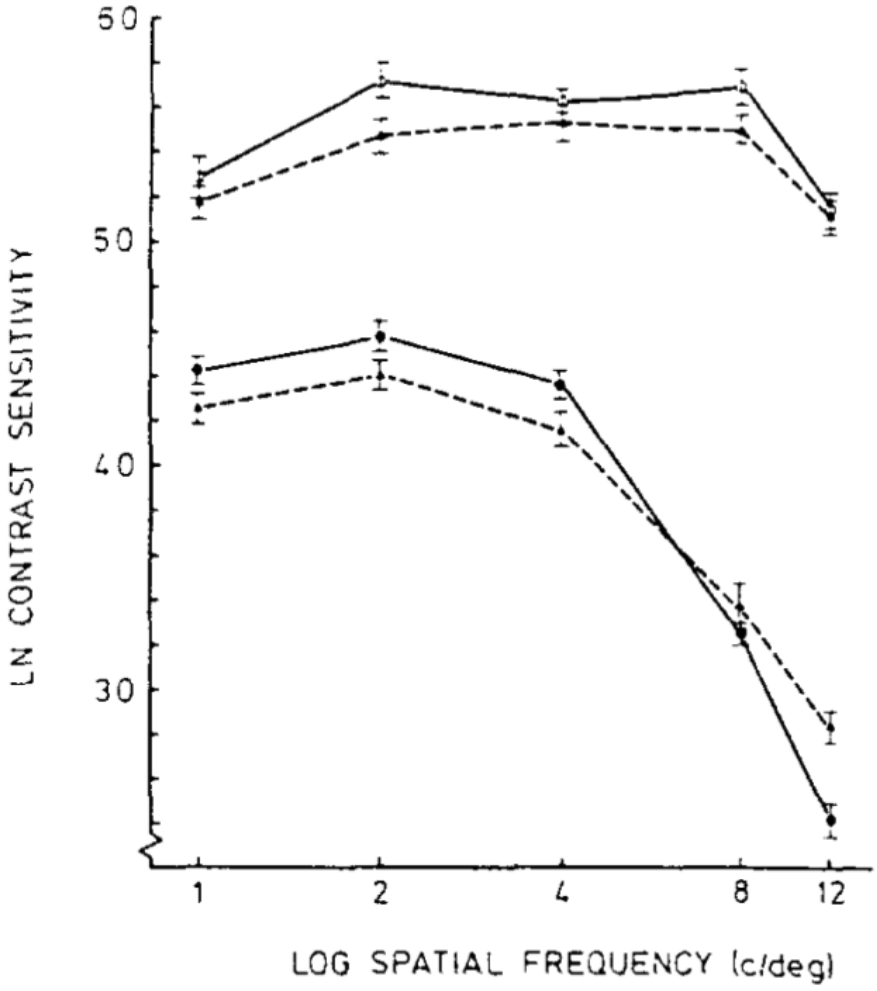


Figure 5. Graphs showing contrast sensitivity functions for readers with developmental dyslexia (dashed line) and relatively good readers (solid line) when the mean luminance level of the display was either 3.42 (bottom half of the figure) or 102.74cd/m^2 (top half of the figure). Adapted from Martin and Lovegrove (1984, Experiment 2).

In the studies cited so far participants either had to adjust the contrast of a grating or judge whether or not a grating had appeared (Lovegrove et al., 1980, 1982; Martin & Lovegrove, 1984). The magnocellular deficit hypothesis predicts that readers with dyslexia should also exhibit lower contrast sensitivity than relatively good readers when tasked with discriminating the orientation of relatively low spatial frequency gratings. To investigate this issue Cornelissen, Richardson, Mason, Fowler and Stein (1995) administered a contrast sensitivity task to fourteen children with dyslexia (mean age = 9.88 years) who had a reading age at least 2SD below that predicted by their chronological age and full-scale IQ on the British Ability Scales (BAS) Reading Test (Elliott, Murray, & Pearson, 1979). In this standardised measure of reading ability, participants are asked to read aloud ninety regular and irregular words of increasing difficulty. The performance of the group of readers with dyslexia was compared to that of fourteen relatively good readers (mean age = 9.68 years) matched for full-scale IQ who had a reading age greater than that predicted by their chronological age on the same test. The visual stimuli comprised static sinusoidal gratings (0.5, 1.5, 3 and 6c/deg) and a 1IFC procedure was used to measure contrast sensitivity. On each trial, participants had to judge the orientation of the stimulus (horizontal, vertical, 45º counter-clockwise of vertical, 45º clockwise of vertical). Results showed that overall contrast sensitivity did not differ across readers with dyslexia and relatively good readers. In addition, no significant reader group by spatial frequency interaction was found. These results demonstrate that contrast sensitivity for discriminating the orientation of static gratings is not impaired in readers with dyslexia but the visual stimuli were presented on a display with a relatively

high luminance level of 112cd/m^2 (Table 1). This could have confounded their results as previous research has shown that contrast sensitivity for static gratings in readers with dyslexia may be impaired to a greater extent at relatively low luminance levels (Martin & Lovegrove, 1984, Experiment 2).

Recent work has highlighted a lack of reproducibility in the neurosciences (Button et al., 2013; Duas-Mallet, Button, Boraud, Gonon, & Munafò, 2017; Loannidis, 2005). A major factor contributing to this problem is small sample size, which reduces statistical power and decreases the probability that a significant between-group difference represents a genuine effect. Sample size was relatively small in the research cited so far. To address this issue, Evans, Drasdo and Richards (1994) administered a contrast sensitivity task to thirty-nine children with developmental dyslexia (mean age not specified) who had an average reading age 1 year and 4 months below that predicted by their chronological age on the NARA (Neale, 1966). The performance of this group of readers with dyslexia was compared to that of forty-three relatively good readers (mean age not specified) matched for full-scale IQ who scored within 1SD of the normalised mean on the Mill Hill Vocabulary Scale (Raven, 1958). In this standardised psychometric test, participants are asked to choose the correct synonym for a word from a list of six different alternatives. The visual stimuli comprised static sinusoidal gratings (1, 2, 4, 8 and 12c/deg) and a 1IFC procedure was used to measure contrast sensitivity. On each trial, participants had to judge whether the grating was orientated vertically, 45º counter-clockwise of vertical or 45º clockwise of vertical. Results showed that overall contrast sensitivity was lower in readers with dyslexia than relatively good

readers. In addition, a significant reader group by spatial frequency interaction was found. To determine the spatial frequencies at which readers with dyslexia exhibited impaired task performance contrast sensitivity ratios were calculated. Ratios of contrast sensitivity at the lowest (1c/deg) and highest spatial frequency (12c/deg) were significantly smaller in readers with dyslexia than relatively good readers. Although these results tentatively support the magnocellular deficit hypothesis, Evans et al. (1994) did not conduct the appropriate statistical analyses to explore the significant reader group by spatial frequency interaction. Thus, it is unclear if readers with dyslexia exhibited impaired performance in comparison to relatively good readers at the lowest spatial frequencies tested.

Evidence suggests that the magnocellular pathway is more sensitive than the parvocellular pathway to the temporal transients produced by abrupt stimulus onsets and offsets (Derrington & Lennie, 1984; Kaplan & Shapley, 1982; but see Levitt et al., 2001). If readers with dyslexia have a selective deficit in the magnocellular pathway they should exhibit significantly lower contrast sensitivity than relatively good readers for abruptly presented, low spatial frequency gratings but not high spatial frequency gratings. No significant group difference would be expected for gratings in which the contrast is smoothly ramped on and then off, over the time course of each trial, irrespective of spatial frequency. To investigate this hypothesis Gross-Glenn et al. (1995) administered a contrast sensitivity task to twenty-one readers with developmental dyslexia (mean age = 39 years) who had a reading age at least 1.5SD below that predicted by their full-scale IQ on either the Gray Oral

Reading Test (GORT) (Gray, 1967) or the Wide Range Achievement Test (WRAT) (Jastak & Wilkinson, 1984). In the GORT, participants are asked to read aloud a series of passages containing regular and irregular words of increasing difficulty, whereas in the WRAT, participants are asked to read aloud seventy-four regular words of increasing difficulty. The performance of the group of readers with dyslexia was compared to that of twenty-five relatively good readers (mean age = 38 years) matched for full-scale IQ who scored within 1SD of the normalised mean on the GORT (Gray, 1967) and the WRAT (Jastak & Wilkinson, 1984). The visual stimuli consisted of static sinusoidal gratings (0.6, 4 and 12c/deg). In the smoothly ramped condition, stimulus contrast increased linearly for 500ms, remained constant for 500ms, and decreased linearly for 500ms. In the unramped condition, the gratings were presented abruptly for each of a range of durations between 17 and 1088ms. A 2IFC procedure was used to measure contrast sensitivity in which participants had to judge whether the stimulus appeared in the first or second temporal interval. Results showed that overall contrast sensitivity did not differ across readers with dyslexia and relatively good readers in the ramped condition. However, a different pattern emerged in the unramped condition. Contrast sensitivity was significantly lower in readers with dyslexia but only when the spatial frequency of the gratings was 12c/deg and stimulus duration was relatively short (17 and 102ms). These results are difficult to reconcile with the magnocellular deficit hypothesis as no significant group difference was found at the lowest spatial frequencies tested. They support previous research showing that contrast sensitivity for static gratings in readers with dyslexia is dependent upon stimulus duration (Lovegrove et al. 1980) suggesting that

some form of temporal processing impairment might be contributing to the difficulties readers with dyslexia experience. Gross-Glen et al. (1995) were able to compare temporal summation across readers with dyslexia and relatively good readers because contrast sensitivity for static gratings in the ramped condition was measured as a function of stimulus duration. Temporal summation data are typically fitted with two straight lines (Figure 6). The first line has a slope of 1 when plotted on log-log axes because the product of stimulus contrast and duration is constant, a phenomenon first discovered by Bloch (1885). Evidence suggests that Bloch's law holds for ~50ms after which a second line with a much shallower slope has to be fitted to the data (Breitmeyer & Ganz, 1977; Gorea & Tyler, 1986; Legge, 1978). To explore if temporal summation differs across readers with dyslexia and relatively good readers Gross-Glen et al. (1995) fitted two lines to each participant's data. Results showed that the critical duration (i.e. the duration at which Bloch's law breaks down) was significantly longer in readers with developmental dyslexia than relatively good readers but only when the spatial frequency of the gratings was 12c/deg. These findings demonstrate that readers with dyslexia integrate incoming visual information over a longer period of time than relatively good readers However, an unresolved issue is whether or not the critical duration is larger in readers with dyslexia in comparison to relatively good readers across a range of spatial frequencies because Gross-Glen et al. (1995) only measured contrast sensitivity for gratings of 0.6 and 12c/deg. The fitting procedure used to determine the critical duration could also be improved upon in future research. Recent work has shown that the manual estimation method used by Gross-Glen et al. (1995) yields more variable results than iterative two-phase

regression analysis, which determines the critical duration automatically via the fitting procedure rather than arbitrarily by eye (Mulholland, Redmond, Garway-Heath, Zlatkova, & Anderson, 2015).

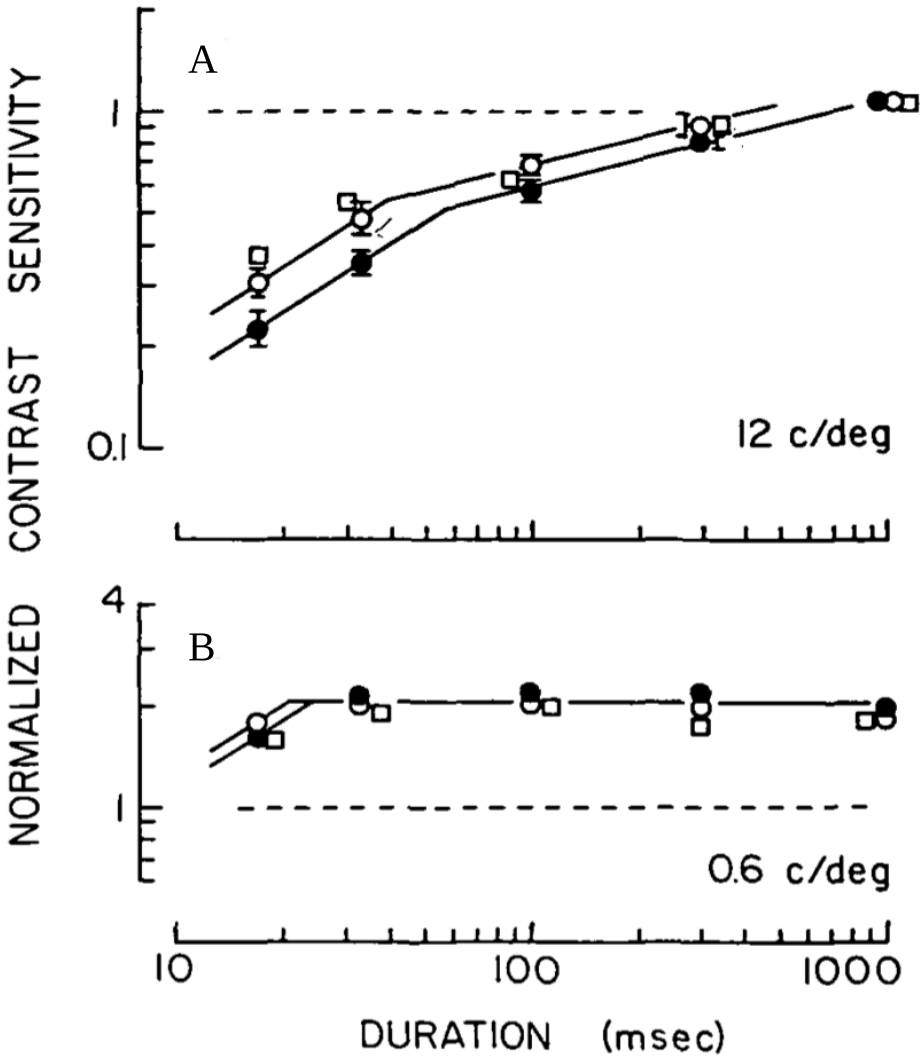


Figure 6. Graphs showing contrast sensitivity at 12c/deg (A) and 0.6c/deg (B) as a function of stimulus duration for readers with developmental dyslexia (solid circles) and relatively good readers (open circles and squares). A function comprising two straight lines was fitted to the data by eye to estimate the critical duration (i.e. the point at which Bloch's law breaks down). Error bars represent ±1 SEM. Adapted from Gross-Glen et al. (1995).

1. 3. 1. 3. Studies using other types of visual stimuli

Skottun (2000) questioned why so many studies have used static gratings to investigate the magnocellular deficit hypothesis when neurophysiological research in non-human primates has shown that a selective magnocellular deficit should only manifest as reduced contrast sensitivity for stimuli of low spatial (≤ 2c/deg) and high temporal frequency (≥ 10Hz) (Merigan, Byrne, & Maunsell, 1991; Merigan, Katz, & Maunsell, 1991; Merigan & Maunsell, 1993). To explore if such a pattern of impairment is found in readers with dyslexia Martin and Lovegrove (1987, Experiment 1) administered a contrast sensitivity task to fifteen readers with developmental dyslexia (mean age = 13.8 years) who had a reading age at least 5 years and 6 months below that predicted by their chronological age on the NARA (Neale, 1966). The performance of this group of readers with dyslexia was compared to that of fifteen relatively good readers (mean age = 13.7 years) who had a reading age greater than that predicted by their chronological age on the same test. The visual stimuli were sinusoidal gratings (2c/deg) that reversed phase at each of a range of temporal frequencies between 5 and 25Hz. A 2IFC procedure was used to measure contrast sensitivity in which participants had to judge whether the grating appeared in the first or second temporal interval. Results showed that overall contrast sensitivity was lower in readers with dyslexia than relatively good readers. In addition, a significant reader group by temporal frequency interaction was found. Readers with dyslexia had lower contrast sensitivity than relatively good readers but only when the temporal frequency of the flickering gratings ranged from 10 to 25Hz. These results support the

magnocellular deficit hypothesis but, as Martin and Lovegrove (1984, Experiment 1) only tested performance at one spatial frequency, it is unclear if readers with dyslexia also exhibit impaired contrast sensitivity for counterphase gratings when the spatial frequency of the stimuli is ≥2c/deg. Such a deficit would not be indicative of magnocellular impairment but rather a difficulty processing rapidly changing visual input.

To explore contrast sensitivity for counterphase gratings across a wide range of spatial frequencies Martin and Lovegrove (1987, Experiment 2) conducted a second experiment in which a contrast sensitivity task was administered to the same fifteen readers with developmental dyslexia (mean age = 13.8 years) and fifteen relatively good readers (mean age = 13.7 years). The task and visual stimuli were identical to those used previously (Martin & Lovegrove, 1987, Experiment 2) except the temporal frequency of the flickering gratings was held constant at 20Hz, whilst spatial frequency was varied between 1 and 12c/deg. Results showed that readers with dyslexia had significantly lower contrast sensitivity than relatively good readers across all spatial frequencies tested (Figure 7). The extent to which they were impaired increased as the spatial frequency of gratings increased. These results demonstrate that overall contrast sensitivity for stimuli changing rapidly over time is lower in readers with dyslexia than relatively good readers. However, they challenge the magnocellular deficit hypothesis, as readers with dyslexia exhibited impaired performance across a wide range of spatial frequencies.

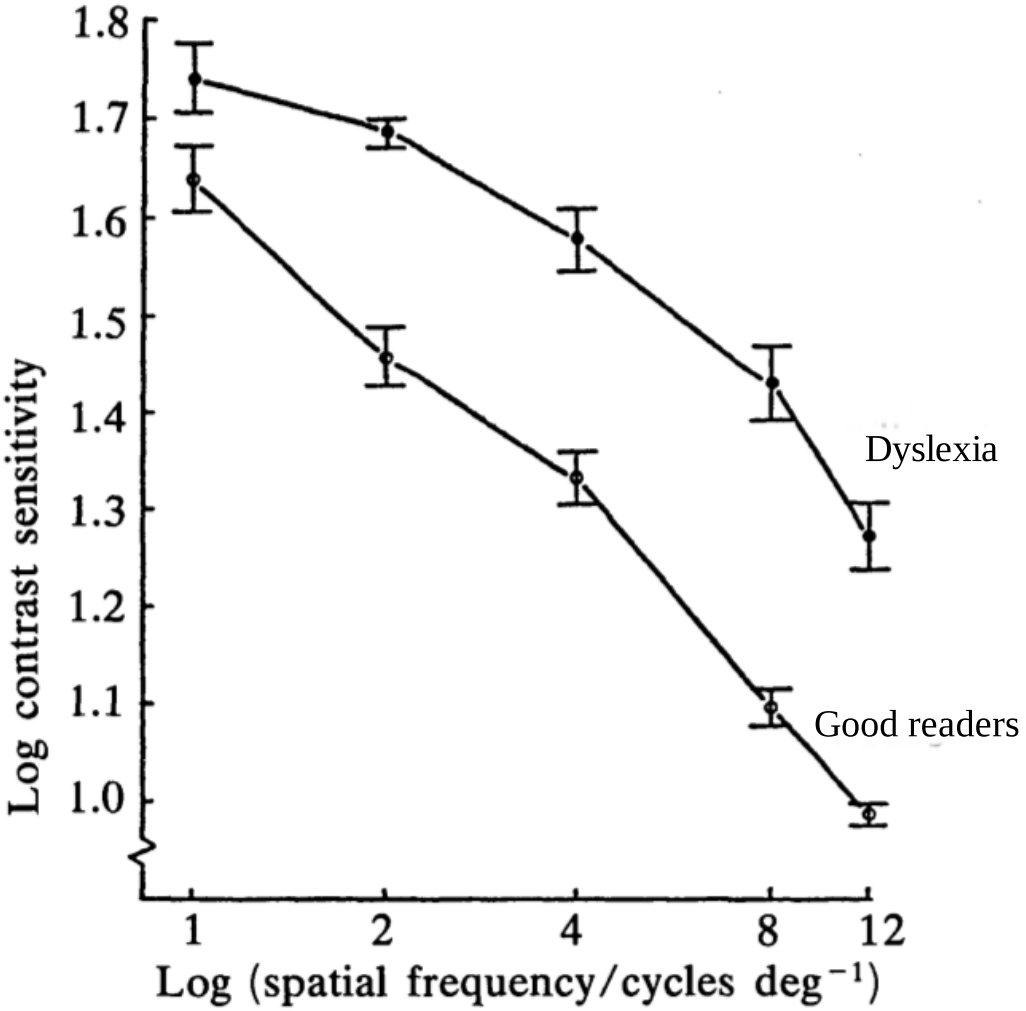


Figure 7. Graphs showing contrast sensitivity for counterphase flickering gratings as a function of spatial frequency for readers with developmental dyslexia (bottom line) and relatively good readers (top line). Adapted from Martin and Lovegrove (1987, Experiment 2).

In the study by Martin and Lovegrove (1987) participants had to judge whether or not a grating had appeared on each trial. However, the magnocellular deficit hypothesis predicts that readers with dyslexia should also exhibit lower contrast sensitivity than relatively good readers when tasked with discriminating the orientation of low spatial frequency counterphase gratings flickering at relatively high temporal frequencies. To explore whether or not this is the case Cornelissen et al. (1995) administered a contrast sensitivity task to fourteen children with dyslexia (mean age = 9.88 years) who had a reading age at least 2SD below that predicted by their chronological age and full-scale IQ on the BAS Reading Test (Elliott, Murray, & Pearson, 1979). The performance of this group of readers with dyslexia was compared to that of fourteen relatively good readers (mean age = 9.68 years) matched for full-scale IQ who had a reading age greater than that predicted by their chronological age on the same test. The visual stimuli comprised sinusoidal gratings (0.5, 1.5, 3 and 6c/deg) that reversed phase at a rate of 20Hz. A 1IFC procedure was used to measure contrast sensitivity in which participants had to judge the orientation of the stimulus (horizontal, vertical, 45º counter-clockwise of vertical, 45º clockwise of vertical). Results showed that overall contrast sensitivity did not differ across readers with dyslexia and relatively good readers. In addition, no significant reader group by spatial frequency interaction was found. These results demonstrate that contrast sensitivity for discriminating the orientation of counterphase gratings is not impaired in readers with dyslexia but the display upon which the stimuli were presented had a relatively high luminance level of 112cd/m^2 (Table 1). Evidence suggests that contrast sensitivity for static gratings is impaired to a greater extent in

readers with dyslexia at relatively low luminance levels (Martin & Lovegrove, 1984, Experiment 2). Further research is needed to explore if contrast sensitivity for counterphase gratings in readers with dyslexia is strongly influenced by the overall display luminance, as appears to be the case for static gratings (see section 1. 3. 1. 2.). An alternative explanation for the discrepancy between Cornelissen et al. (1995) and Martin and Lovegrove (1987) is that different psychophysical procedures were used to measure contrast sensitivity (Table 1). In the study by Cornelissen et al. (1995) a 1IFC procedure was used, whereas Martin and Lovegrove (1987) used a 2IFC procedure that necessitated comparisons across sequentially presented stimuli separated by a 500ms inter-stimulus-interval (ISI).

Impaired contrast sensitivity in readers with dyslexia on 2IFC tasks requiring comparisons across sequentially presented stimuli could reflect the known impairment with short-term memory (Ramus et al., 2003). To explore this possibility Ben-Yehudah, Sackett, Malchi-Ginzber and Ahissar (2001) administered a contrast sensitivity task to thirty-eight readers with developmental dyslexia (mean age = 22.3 years) and forty relatively good readers (mean age = 22.5 years). Although participants in the dyslexia group were recruited solely on the basis of a documented history of reading difficulties they performed significantly worse than relatively good readers on several measures of phonological decoding and whole-word lexical processing. The visual stimuli were sinusoidal gratings (0.5c/deg) that reversed phase at each of a range of temporal frequencies between 5 and 25Hz. Perceptual memory load was varied across two experimental conditions. In the “t-flicker”

condition, contrast sensitivity was measured using a 2IFC procedure in which participants had to judge whether the grating appeared in the first or second temporal interval. In the "s-flicker" condition, contrast sensitivity was measured using a 1IFC procedure in which participants had to judge whether the grating appeared in the upper or lower half of the display. Results showed that readers with dyslexia had lower overall contrast sensitivity than relatively good readers when the 2IFC procedure was used to measure contrast sensitivity but not when the 1IFC procedure was employed. These findings cannot be readily interpreted within the framework of the magnocellular deficit hypothesis. Ben-Yehudah et al. (2001) argued that readers with dyslexia have difficulty on sensory tasks in which comparisons have to be made across sequentially presented stimuli but there were subtle differences between the t-flicker and s-flicker conditions. For example, the size of the counterphase gratings was larger and stimulus duration was longer in the t-flicker condition than the s-flicker condition (Table 1). Thus, it remains a possibility that some of the differences found between the two reader groups arose, at least in part, because of differences in the stimulus parameters (size and duration) used in the two experimental conditions rather than the memory demands of the tasks *per se*.

The results of Ben-Yehudah et al. (2001) do not corroborate other research that used 1IFC procedures to measure contrast sensitivity for counterphase gratings in readers with dyslexia. For example, Felmingham and Jakobson (1995) administered a contrast sensitivity task to nine readers with developmental dyslexia (mean age = 10.9 years) who had a reading age at least 2 years below

that predicted by their chronological age on the WRAT (Jastak & Wilkinson, 1984). The performance of this group of readers with dyslexia was compared to that of nine relatively good readers (mean age = 10.6 years) matched for full-scale IQ who scored within 1SD of the normalised mean on the same reading test. The visual stimuli comprised sinusoidal gratings of 2c/deg that reversed phase at each of a range of temporal frequencies between 5 and 25Hz. A 1IFC procedure was used to measure contrast sensitivity in which participants had to judge whether the stimulus appeared in the upper or lower half of the display. Thus, it was identical to the s-flicker condition in the study by Ben-Yehudah et al. (2001). Results showed that overall contrast sensitivity was lower in readers with dyslexia than relatively good readers. In addition, a reader group by spatial frequency interaction was found. Readers with dyslexia had significantly lower contrast sensitivity than relatively good readers but only when the temporal frequency of the stimuli was between 15 and 25Hz. These results demonstrate that overall contrast sensitivity for counterphase gratings is impaired, in at least some readers with developmental dyslexia, irrespective of whether 1IFC or 2IFC procedures are used to measure contrast sensitivity (Martin & Lovegrove, 1987).

A key question is whether or not contrast sensitivity for other types of rapidly changing stimuli is impaired in readers with dyslexia. To investigate this issue Borsting et al. (1996) administered a contrast sensitivity task to seventeen adults with developmental dyslexia (mean age not specified) who reported significant difficulties with reading and spelling during childhood. The performance of this group of readers with dyslexia was compared to that of

seventeen relatively good readers (mean age not specified) who had no history of reading problems. The visual stimuli comprised moving sinusoidal gratings (0.5, 1, 2, 4, 8 and 12c/deg) that drifted at a temporal frequency of 1 or 10Hz. A 2IFC procedure was used to measure contrast sensitivity in which participants had to judge whether the moving stimulus appeared in the first or second temporal interval. Results showed that overall contrast sensitivity did not differ significantly across readers with dyslexia and relatively good readers when the gratings drifted at 1Hz but a different pattern emerged when they drifted at 10Hz. Overall contrast sensitivity was lower in readers with dyslexia than relatively good readers (Figure 8). A series of post hoc t-tests revealed that readers with dyslexia had significantly lower contrast sensitivity than relatively good readers at spatial frequencies ≤2c/deg. These findings support previous research showing that contrast sensitivity for rapidly changing stimuli is impaired in readers with dyslexia (Felmingham & Jakobson, 1995; Martin & Lovegrove, 1987) but strong conclusions about the magnocellular deficit hypothesis cannot be made because Borsting et al. (1996) did not specify if a significant reader group by spatial frequency interaction was found.

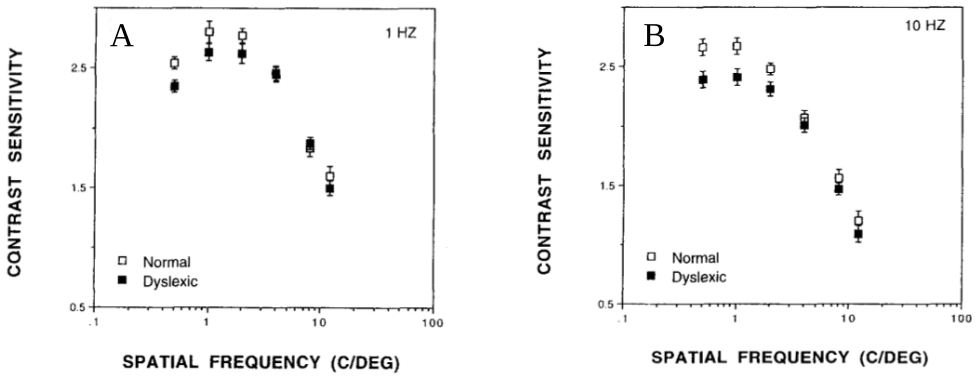


Figure 8. Graphs showing contrast sensitivity for gratings drifting at 1Hz (A) and 10Hz (B) in readers with developmental dyslexia (solid squares) and relatively good readers (open squares). Adapted from Borsting et al. (1996).

Borsting et al. (1996) showed that contrast sensitivity for drifting gratings is impaired in readers with dyslexia at relatively high temporal frequencies. However, a key question is whether performance on other visual tasks containing stimuli that are changing rapidly over time is impaired in developmental dyslexia. To explore if readers with dyslexia have difficulty judging the speed of drifting gratings Demb, Boynton, Best and Heeger (1998a) administered a speed discrimination task to five readers with developmental dyslexia (mean age = 22.2 years) and five relatively good readers (mean age = 26.8 years). Although participants in the dyslexia group had an average score within 1SD of the normalised mean on the WRAT (Jastak & Wilkinson, 1984) they did perform significantly worse than relatively good readers. The visual stimuli comprised drifting sinusoidal gratings (0.4c/deg). Two gratings were presented sequentially on each trial. One stimulus moved at a speed of 20.8°/s, whilst the speed of the other stimulus was varied. A 2IFC procedure was used to measure speed discrimination thresholds in which participants had to judge whether the grating presented in the first or second temporal interval moved at a faster speed. Results showed that speed discrimination thresholds were significantly higher in readers with dyslexia than relatively good readers. In addition, scores on the Word Attack subtest of the Woodcock-Johnson III (Woodcock-Johnson, McGrew, & Mather, 2001) were significantly and negatively correlated with speed discrimination thresholds across the entire sample. In this standardised measure of reading ability, participants are required to read aloud non-words of increasing difficulty. These findings support a large body of research showing that readers with dyslexia have difficulty processing visual stimuli that are changing rapidly over time

(Borsting et al., 1996; Felmingham & Jakobson, 1995; Martin & Lovegrove, 1987, Experiment 2) but the neural underpinnings of this deficit are equivocal.

A difficulty processing rapidly changing visual input might manifest as decreased neural activity in visual cortex. To explore whether or not this is the case in dyslexia Demb, Boynton and Heeger (1998b) carried out an additional experiment in which the same five readers with developmental dyslexia (mean age = 22.2 years) and five relatively good readers (mean age = 26.8 years) viewed drifting gratings inside a magnetic resonance imaging (MRI) scanner. Results showed that the bi-lateral, blood-oxygen-level-dependent (BOLD) response in V1 was significantly lower in readers with dyslexia than relatively good readers. A similar pattern was found in hMT - the human homologue of monkey V5/MT (Born & Bradley, 2005; Zeki, 2015). Directionally selective cells in this part of the brain have larger receptive fields than their V1 counterparts and for this reason are thought to provide a global (overall) representation of object motion (Dubner & Zeki, 1971; Gattas & Gross, 1981; Albright & Desimone, 1987). It was argued by Demb et al. (1998b) that their results support the magnocellular deficit hypothesis because V5/MT receives input that can be traced back to the magnocellular layers of the LGN (Livingstone & Hubel, 1998; Maunsell & van Essen, 1987; Zeki & Shipp, 1987). This was the major view for many years but more recent research in non-human primates points to a mixing of magnocellular and parvocellular signals in V1 (Nassi & Callaway, 2009; Sincich & Horton, 2005; Vidyasagar, Kulikowski, Lipnicki, & Dreher, 2002). Thus, it seems unlikely that BOLD

response in V5/MT can provide a reliable index of magnocellular function, which therefore challenges the conclusions of Demb et al. (1998b).

1. 3. 1. 4. Sublexical vs. lexical processing

Developmental dyslexia is primarily associated with poor sublexical phonological decoding skills (see section 1. 2.) but it is possible that impaired contrast sensitivity for rapidly changing stimuli might be more strongly related to some components underlying reading skill than others. To investigate this issue Borsting et al. (1996) administered the Adult Dyslexia Test (Griffin, Christenson, & Walton, 1990) and identified from their original sample nine individuals for whom whole-word lexical processing skills were specifically impaired (mean age = 36 years) and nine individuals for whom both whole-word lexical processing skills and phonological decoding skills were impaired (mean age = 35 years). The performance of these two groups of poor readers was compared to that of nine relatively good readers (mean age = 35 years). Results showed that overall contrast sensitivity was similar across the three reader groups when the gratings drifted at 1Hz but when they drifted at 10Hz overall contrast sensitivity differed significantly across the three reader groups. There was some evidence to suggest that individuals for whom both whole-word lexical processing skills and phonological decoding skills were impaired had lower contrast sensitivity than relatively good readers when the spatial frequency of the gratings was ≤2c/deg. These results suggest that contrast sensitivity for stimuli changing rapidly over time is only impaired in generally poor readers who have a deficit with both phonological decoding and whole-

word lexical processing but further research is needed to investigate the reliability of this finding because the reader group by spatial frequency interaction was not statistically significant.

A further limitation of the study by Borsting et al. (1996) is that they did not identify a group of individuals for whom sublexical phonological decoding skills were specifically impaired, consistent with the dyslexic profile (Rack et al., 1992; Ramus et al., 2003; Snowling, 2000; Stanovich, 1988, Stanovich & Siegel, 1994). To address this issue Slaghuis and Ryan (1999) used the Adult Dyslexia Test (Griffin, Christenson, & Walton, 1990) to identify five individuals for whom whole-word lexical processing skills were specifically impaired, three individuals for whom phonological decoding skills were specifically impaired, and seven individuals for whom both whole-word lexical processing skills and phonological decoding skills were impaired. A contrast sensitivity task was then administered. The visual stimuli comprised sinusoidal gratings (0.5, 2, 4 and 8c/deg) that reversed phase at each of a range of temporal frequencies between 4 and 16Hz. A 2IFC procedure was used to measure contrast sensitivity in which participants had to judge whether the stimulus appeared in the first or second temporal interval. Results showed that overall contrast sensitivity differed significantly across the four reader groups. Several two- and three-way interactions were also found. Post hoc tests revealed that individuals for whom both whole-word lexical processing skills and phonological decoding skills were impaired had lower contrast sensitivity than relatively good readers at spatial frequencies ≤2c/deg when the gratings flickered at 4Hz and 8Hz. No significant group differences were found when

the gratings flickered at 16Hz. These results support those of Borsting et al. (1996) as they show that contrast sensitivity for stimuli changing rapidly over time is only impaired in generally poor readers who have a deficit with both phonological decoding and whole-word lexical processing. However, sample size was small, which questions the reliability of these findings. A lack of statistical power might also explain why contrast sensitivity did not differ significantly across the four reader groups when the temporal frequency of the gratings was 16Hz (Button et al., 2013; Duas-Mallet et al., 2005; Loannidis, 2005).

The results of Borsting et al. (1996) and Slaghuis and Ryan (1999) are theoretically important because they speak directly to the debate as to whether dyslexia is best-defined as the lower end of a normal distribution of reading ability or a distinct type of reading difficulty associated with poor phonological decoding skills (Fletcher, 2009, Siegel, 2006). Taken together, they suggest that impaired contrast sensitivity for stimuli changing rapidly over time is only impaired in generally poor readers who have a deficit with both phonological decoding and whole-word lexical processing. Crucially, individuals with a specific phonological deficit, consistent with the dyslexic profile, did not exhibit impaired task performance. Although these results suggest that the performance of generally poor readers and individuals with dyslexia differs on low-level visual perception tasks strong conclusions cannot be made because sample size was very small in both studies. This issue will be systematically addressed in Chapter 3.

1. 3. 1. 5. Orthographic regularity

Most of the studies cited so far investigated the magnocellular deficit hypothesis in native English speakers (Table 1). However, it is possible that contrast sensitivity for rapidly changing stimuli might be influenced by orthographic regularity. Evidence suggests that children who learn to read in more regular orthographies such as German, which are characterised by more consistent grapheme to phoneme mappings, are more reliant upon sublexical processing than children who learn to read in less regular orthographies such as English (Landerl, Wimmer, & Frith, 1997; Seymour, Aro, & Erskine, 2003; Wimmer & Goswami, 1994). Reading via the sublexical route requires serial letter-by-letter decoding (Coltheart et al., 2001). This implies that contrast sensitivity for rapidly changing stimuli might not be impaired in dyslexic readers of regular orthographies as they presumably have more experience processing temporal information than dyslexic readers of English. To investigate this issue Walther-Müller (1995, Experiment 1) administered a contrast sensitivity task to seventeen German-speaking readers with developmental dyslexia (mean age = 10.29 years) who scored at least 1.5SD below the normalised mean on a German oral reading test called the "Zurcher Lesetest" (Linder & Grissemann, 1980). The performance of this group of readers with dyslexia was compared to that of seventeen relatively good readers (mean age = 10.37 years) who were also native German speakers. Both reader groups were matched for full-scale IQ. The visual stimuli comprised sinusoidal gratings of either 1 or 12c/deg that reversed phase at a rate of 16.8Hz. A 2IFC procedure was used to measure contrast sensitivity in which

participants had to judge whether the stimulus appeared in the first or second temporal interval. Results showed that overall contrast sensitivity was similar across readers with dyslexia and relatively good readers. In addition, no significant reader group by spatial frequency interaction was found. These findings suggest that contrast sensitivity for rapidly changing stimuli is only impaired in dyslexic readers of more irregular orthographies such as English but further research is needed to confirm whether or not this the case. Several studies have shown that contrast sensitivity for rapidly changing stimuli is impaired in some dyslexic readers of Italian, which is a more regular orthography than English (Cicchini et al., 2015; Morrone et al., 2011).

1. 3. 1. 6. Ocular dominance

Another issue that has an important bearing on contrast sensitivity in readers with dyslexia is the visual phenomenon of ocular dominance. Approximately 65% of readers with dyslexia have unstable ocular dominance, which manifests as a difficulty combing retinal input with ocular motor signals about eye position (Stein & Fowler, 1981, 1982, 1985). It is possible that contrast sensitivity for rapidly changing stimuli might be impaired to a greater extent in this subgroup of readers with dyslexia. To explore whether or not this is the case Mason, Cornelissen, Fowler and Stein (1993) administered a contrast sensitivity task to twenty-two readers with developmental dyslexia who had a reading age at least 2SD below that predicted by their chronological age and full-scale IQ on the BAS Reading Test (Elliott, Murray, & Pearson, 1979). Eleven relatively good readers (mean age = 9.33 years) who had a reading age

greater than that predicted by their chronological age on the same test also took part in the experiment. The Dunlop Test (Stein & Fowler, 1981, 1982, 1985) was also given to assess stability of ocular dominance. From it, eleven dyslexic readers with stable ocular dominance (mean age = 9 years) and eleven dyslexic readers with unstable ocular dominance (mean age = 8.83 years) were identified. Stability of ocular dominance was not impaired in any of the relatively good readers. The visual stimuli comprised sinusoidal gratings (0.5, 1.5, 3 and 6c/deg) that reversed phase at a temporal frequency of 20Hz. A 1IFC procedure was used to measure contrast sensitivity in which participants had to judge the orientation (horizontal, vertical, 45º counter-clockwise of vertical, 45º clockwise of vertical) of the stimulus. Results showed that both groups of dyslexic readers had lower overall contrast sensitivity than relatively good readers but dyslexic readers with unstable ocular dominance were impaired to a greater extent than dyslexic readers with stable ocular dominance. No significant reader group by spatial frequency interaction was found. These results suggest that contrast sensitivity for rapidly changing stimuli in readers with dyslexia is particularly impaired in those with unstable ocular dominance. However, it is important to note that both groups of readers with dyslexia did not exhibit a pattern of impairment that is indicative of a selective magnocellular deficit as impaired contrast sensitivity was not restricted to the lowest spatial frequencies tested.

1. 3. 1. 7. Genotypic variation

Contrast sensitivity for rapidly changing visual stimuli in readers with dyslexia might be mediated by genetic variation as evidence suggests that one in ten readers with dyslexia have a deletion on intron 2 of the *DCDC2* gene (Meng et al., 2005, 2011; Powers et al., 2011; Schumacher et al., 2007). To explore whether or not this is the case Cicchini, Marino, Mascheretti, Perani and Morrone (2015) administered a contrast sensitivity task to twenty-one readers with developmental dyslexia who scored at least 2SD below the normalised mean on the MT Reading Test (Cornoldi & Colpo, 1995; Sartori, Job, & Tressoldi, 1995). In this standardised measure of reading ability, participants are required to read aloud real Italian words and non-words of increasing difficulty. Eight relatively good readers (mean age = 18.7) also took part in the experiment. All participants were genotyped to determine if they had a deletion on the *DCDC2* gene. Eleven of the dyslexic readers had the genetic deletion (mean age = 17.7 years), whilst the other ten dyslexic readers and all eight relatively good readers did not have the genetic deletion (mean age = 16.7 years). The visual stimuli comprised sinusoidal gratings (0.5 to 4c/deg) that drifted at 8Hz. A 1IFC procedure was used to measure contrast sensitivity in which participants had judge the direction of the stimulus (upwards vs. downwards). Results showed that overall contrast sensitivity was significantly lower in dyslexic readers who had the genetic deletion on *DCDC2* than dyslexic readers who did not have the genetic deletion. Interestingly, the extent of impairment in dyslexic readers with the genetic deletion was larger when the spatial frequency of the gratings was 4c/deg in comparison to when it was 0.5c/deg. A series of computational analyses that decomposed the moving stimuli into their spatial and temporal frequency components suggested that the

underlying nature of the visual deficit in this subgroup of readers with dyslexia might reflect spatial under-sampling. This would induce aliasing (artefacts) but only at relatively high spatial frequencies, consistent with the pattern of impairment observed in dyslexic readers with the deletion of *DCDC2*. Cicchini et al. (2015) argued that genotypic variation might explain discrepancies across studies that have investigated contrast sensitivity for rapidly changing stimuli in readers with dyslexia. However, it is important to note that dyslexic readers without the genetic deletion had significantly lower contrast sensitivity than relatively good readers without the genetic deletion when the spatial frequency of the stimuli was 4c/deg. This suggests that factors other than genotypic variation are contributing to the inter-subject variability in contrast sensitivity for rapidly changing stimuli in readers with dyslexia.

An interesting question is whether or not contrast sensitivity for stimuli changing rapidly over time in developmental dyslexia is related to microstructural changes in the brain. Several studies have shown that *DCDC2* plays a key role in neuronal migration and white matter organisation *in utero* (Burbridge et al., 2008; Galaburda et al., 2006; Meng et al., 2005). To explore this issue Morrone et al. (2011) administered a contrast sensitivity task to ten dyslexic readers (mean age not specified) who had a genetic deletion on the *DCDC2* gene. The visual stimuli consisted of sinusoidal gratings that drifted at a temporal frequency of 8Hz. A 1IFC procedure was used to measure contrast sensitivity in which participants had judge the direction of the stimulus (upwards vs. downwards). Participants also underwent diffusion tensor imaging (DTI), in an MRI scanner, to measure fractional anisotropy (FA). FA

is a value ranging from zero to unity that reflects the direction of water diffusion in the brain (Alexander, Lee, Lazar, & Field, 2007). A value of zero is indicative of isotropic diffusion in a random direction, whereas a value of one is indicative of anisotropic diffusion in a single direction. Thus, FA is thought to assess fibre density, fibre organisation, axon diameter and the degree of myelination (Beaulieu, 2002; Jones, Knösche, & Turner, 2013). Results showed that contrast sensitivity was significantly and positively correlated with FA values at two locations in close proximity to hMT. These findings suggest that impaired contrast sensitivity for stimuli changing rapidly over time is in some way related to microscopic anomalies in extrastriate brain regions. However, a major limitation of the study by Morrone et al. (2011) is that it lacked a control group. For this reason, further research is needed to determine if a similar relationship is found in readers with dyslexia who do not have a genetic deletion on *DCDC2* and relatively good readers.

Study	Matching criteria	Orthography	Age (years)		Stimulus parameters			Procedure	Impaired overall CS	CS only impaired at SF ≤2c/deg	CS only impaired at TF ≥10Hz
			Dyslexic	Good	Duration (ms)	Diameter (°)	Luminance (cd/m^2)				
Static gratings											
Cornelissen et al. (1995)	FSIQ	English	9.88	9.68	1000	8	112	1IFC	No	No	--
Evans et al. (1994)	NVIQ	English	--	--	--	2.5	10.3	1IFC	Yes	--	--
Gross – Glen et al. (1994)	FSIQ	English	39	38	17-1088	--	105	2IFC	No	No	--
Lovegrove et al. (1980)	NVIQ	English	14	14	40-1000	2	2.2	1IFC	No	No	--
Lovegrove et al. (1982, Exp. 1)	NVIQ	English	12.5	12.25	40-1000	3.5	1.5	MOA	No	--	--
Lovegrove et al. (1982, Exp. 2)	NVIQ	English	12.6	12.6	500	4	10.3	1IFC	No	--	--
Martin & Lovegrove (1984, Exp. 1)	NVIQ	English	12.11	12.11	350	2 or 8	10.3	2IFC	No	--	--

Martin & Lovegrove (1984, Exp. 2)	NVIQ	English	12.11	12.11	350	4	3.42 & 102.74	2IFC	No	--	--
Counterphase flickering gratings											
Ben-Yehudah et al. (2001)	NVIQ	Hebrew	22.3	22.5	1000 or 2000	2.5 or 12.5	15.3	1IFC & 2IFC	Yes	Yes	Yes
Cornelissen et al. (1995)	FSIQ	English	9.88	9.68	1000	8	112	1IFC	No	No	No
Felmingham & Jakobson (1995)	FSIQ	English	10.9	10.9	500	3.25	6	1IFC	Yes	Yes	Yes
Martin & Lovegrove (1987, Exp. 1)	--	English	13.8	13.7	500	4	11	2IFC	Yes	Yes	Yes
Martin & Lovegrove (1987, Exp. 2)	--	English	13.8	13.7	500	4	11	2IFC	Yes	No	Yes
Walther-Müller (1995)	FSIQ	German	10.29	10.36	500	2	9.16	2IFC	No	No	No

Drifting gratings											
Cicchini et al. (2015)	None	Italian	16.7-17.7	19.7	150	2	30	1IFC	Yes	Yes	No
Demb et al. (1998a)	--	English	22.2	26.8	--	5	5	2IFC	--	--	--
Borsting et al. (1996)	--	English	35-36	35	500	--	22.3	2IFC	Yes	--	--
Morrone et al. (2011)	--	Italian	--	--	--	--	--	1IFC	--	Yes	--

Table 1. A summary of research that used static, counterphase and drifting gratings to explore the magnocellular deficit hypothesis. CS = contrast sensitivity; SF = spatial frequency; FSIQ = full-scale IQ; NVIQ = non-verbal IQ; 1IFC = single-interval, forced-choice; 2IFC = two-interval, forced-choice.

1. 3. 2. The external noise exclusion hypothesis

Effective reading requires letters within words and words within text to be isolated from noise or clutter. An alternative theory that has been proposed to explain the origin of the visual impairment in developmental dyslexia is the external noise exclusion hypothesis. This framework predicts that readers with dyslexia should exhibit impaired performance on visual tasks necessitating the segregation of a signal and external noise. To investigate the external noise exclusion hypothesis Sperling et al. (2005) administered a contrast sensitivity task to twenty-eight readers with developmental dyslexia (mean age = 12.2 years) who scored at least 0.67SD below the normalised mean on either the Word Identification or the Word Attack subtests of the Woodcock Reading Mastery Test (WRMT) (Woodcock, 1987). In the Word Identification subtest, participants are asked to read aloud regular and irregular words of increasing difficulty, whereas in the Word Attack subtest they are asked to read aloud non-words of increasing difficulty. Performance on the contrast sensitivity task was compared across the group of readers with dyslexia and twenty-seven relatively good readers (mean age = 11.2 years) who scored above the normalised mean on the same tests. The visual stimuli comprised static gratings (8c/deg) and counterphase gratings (2c/deg) that reversed phase at a rate of 15Hz (Figure 9AB). A 2IFC procedure was used to measure contrast sensitivity in which participants had to judge whether the grating appeared in the first or second temporal interval. The gratings were either presented on a uniform grey background (‘no noise’) or were embedded in a static random checkerboard pattern (‘high noise’) (Figure 9C). The external noise exclusion

hypothesis predicts that readers with dyslexia should exhibit lower contrast sensitivity then relatively good readers for static and counterphase gratings in the high noise condition but not the no noise condition. However, if readers with dyslexia have difficulty processing visual stimuli that are changing rapidly over time (see section 1. 3. 1.) they should exhibit lower contrast sensitivity than relatively good readers for counterphase gratings but not static gratings regardless of whether the stimuli are embedded in the random checkerboard pattern or presented on a uniform grey background. Results showed that contrast sensitivity was significantly lower in readers with dyslexia than relatively good readers for static and counterphase gratings in the high noise condition but no significant group differences were found in the no noise condition. These results suggest that the origin of visual impairment in developmental dyslexia may reflect a general difficulty on visual tasks necessitating the segregation of a signal and external noise.

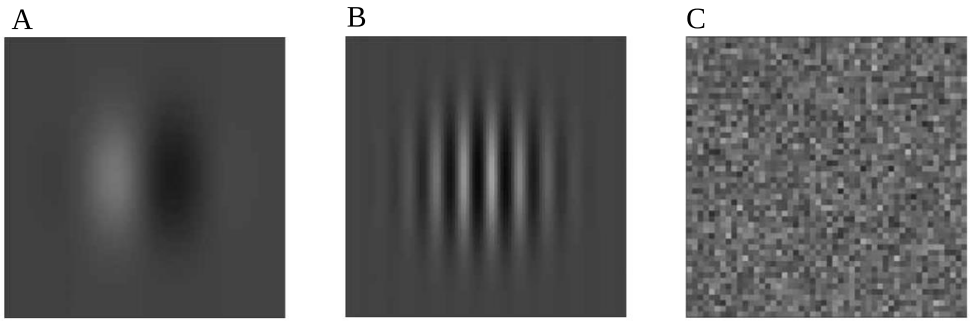


Figure 9. Schematic illustration of the visual stimuli used in the study by Sperling et al. (2005). Counterphase gratings of 2c/deg that reversed phase at a rate of 15Hz (A) and static gratings of 8c/deg (B) were either presented on a uniform grey back or were embedded in a static, random checkerboard pattern (C). Adapted from Sperling et al. (2005).

Several studies have shown that the effects of visual crowding are larger in readers with dyslexia than relatively good readers (Gori & Facoetti, 2015; but see Doron, Herzog, Manassi, & Ahissar, 2015). If this is the case, readers with dyslexia should exhibit impaired contrast sensitivity for stimuli that are presented in clutter regardless of whether they are embedded in static external noise or presented on a uniform grey background. To investigate the external noise exclusion hypothesis Martelli et al. (2009, Experiment 1) administered a letter identification task to five children with developmental dyslexia (mean age not specified) who scored at least 2SD below the normalised mean on the MT Reading test (Cornoldi & Colpo, 1995; Sartori, Job, & Tressoldi, 1995). This standardised reading test provides a measure of speeded reading and comprises real Italian words and non-word of increasing difficulty. The performance of the group of readers with dyslexia was compared to that of five relatively good readers (mean age not specified). The stimuli consisted of single letters and ten-letter, Italian words that were presented in the fovea for 200ms. They were either embedded in a static random checkerboard pattern or presented on a uniform grey background. A 1IFC procedure was used to measure contrast sensitivity in which participants had to identify the isolated single letter or the central letter of the ten-letter word. Results showed that readers with dyslexia had significantly lower contrast sensitivity than relatively good readers but only when the stimuli comprised ten-letter words. This occurred regardless of whether they were embedded in external noise or were presented on a uniform grey background. Although these findings cast doubt on the external noise exclusion hypothesis sample size was relatively small in the study by Martelli et al. (2009). Small sample size has been identified as a

major contributing factor to the lack of reproducibility in the neurosciences (Button et al., 2013; Duas-Mallet et al., 2017; Loannidis, 2005; Loannidis, 2005) and low statistical power could provide an alternative explanation for the pattern of results found in readers with dyslexia. In addition, the mean age of reader groups was not specified. Several studies in the general population have shown that the effects of visual crowding are larger in the fovea and parafovea of children under the age of eight (Atkinson, Anker, Evans, Hall, & Pimm-Smith, 1988; Farzin, Rivera, & Whitney, 2010; Jeon, Hamid, Maurer, & Lewis, 2010). The developmental trajectory of visual crowding in readers with dyslexia is equivocal, which makes it a promising area for future research.

1. 3. 3. The anchoring deficit hypothesis

Evidence suggests that readers with dyslexia have difficulty on 2IFC tasks in which comparisons have to be made across sequentially presented stimuli (Ben-Yehudah et al., 2001; but see Felmingham & Jakobson, 1995). The anchoring deficit hypothesis has been proposed to explain why such a deficit might arise and was originally formulated to explain performance on auditory discrimination tasks. It assumes that readers with dyslexia cannot utilise stimulus repetitions to reduce perceptual memory load.

1. 3. 3. 1. Studies in the auditory domain

To investigate the anchoring deficit hypothesis, Ahissar, Lubin, Putter-Katz and Banai (2006) administered an auditory task to nineteen readers with

developmental dyslexia (mean age = 13.3 years) and twelve relatively good readers (mean age = 12 years) matched for non-verbal IQ. Participants in the dyslexia group scored at least 1.5SD below the mean of the group of relatively good readers on a measure of phonological decoding ability (Banai & Ahissar, 2006). Two tones were presented sequentially on each trial. The frequency of the test tone was always higher than the frequency of the reference tone. In the 'standard' condition, the frequency of the reference tone remained fixed, whereas in the 'no standard' condition it spanned a broad frequency range. Hence, a perceptual anchor could be formed in the standard but not the no standard condition to reduce the load of online retention (Harris, 1948). A 2IFC procedure was used to measure auditory discrimination thresholds in which participants had to judge whether the stimulus in the first or second temporal interval had a higher frequency. Results showed that thresholds were similar across readers with dyslexia and relatively good readers in the no standard condition. However, a different pattern emerged in the standard condition as readers with dyslexia had significantly higher auditory discrimination thresholds than relatively good readers. These findings demonstrate that readers with dyslexia may not be able to effectively utilise stimulus repetitions to reduce perceptual memory load on 2IFC tasks in which comparisons have to made across sequentially presented stimuli. This could explain why readers with dyslexia in Ben-Yehudah et al. (2006) only exhibited lower contrast sensitivity for counterphase flickering gratings than relatively good readers in the s-flicker but not the t-flicker conditions (see section 1. 3. 1. 3.).

The nature of 2IFC tasks means that perceptual memory load is higher for the stimulus presented in the first temporal interval, as it needs to be retained until the stimulus in the second temporal interval has been presented. Raviv, Ahissar and Loewenstein (2012) showed that prior statistics (i.e. accumulated knowledge about the central tendency of the stimulus set) could be used to ease the load of online retention on 2IFC tasks in which comparisons have to be made across sequentially presented stimuli. They found that participants do not compare the first and second stimulus as asked to do so. Instead, the second stimulus is compared to a weighted average of the stimulus in the first temporal interval and a memory trace of stimuli that have been presented on previous trials. To investigate if this process is impaired in readers with dyslexia Jaffe-Dax, Raviv, Jacoby, Loewenstein and Ahissar (2015) administered an auditory discrimination task to fourteen readers with developmental dyslexia and fourteen relatively good readers matched for non-verbal IQ (mean age of the entire sample = 25.4 years). Participants in the dyslexia group scored at least 0.3SD below the mean of the control group on a measure of phonological decoding ability (Banai & Ahissar, 2006). Two tones were presented sequentially on each trial. A 2IFC procedure was used to measure auditory discrimination thresholds in which participants had to judge whether the stimulus presented in the first or second temporal interval had a higher frequency. The difference in frequency between the two tones was varied so that the stimulus in either the first or second temporal interval was closer to the mean frequency of previous trials. It was hypothesised that performance should improve on 'bias+' trials in which the frequency of the first stimulus was closer to the mean frequency of previous trials than the frequency of the second

stimulus. However, performance should worsen on 'bias-' trials in which the frequency of the second stimulus was closer to the mean frequency of previous trials than the frequency of the first stimulus. Results showed that thresholds were lower in readers with developmental dyslexia and relatively good readers when the frequency of the first stimulus was closer to the mean of previous trials than the frequency of the second stimulus. However, the difference between bias+ and bias- trials was significantly smaller in readers with dyslexia than relatively good readers. These findings extend those of Ahissar et al. (2006) and offer further support for the anchoring deficit hypothesis.

The P2 component of the event related potential (ERP) may be indicative of a mechanism that can be used to reduce the load of online retention on 2IFC tasks. Several studies have shown that its amplitude increases when auditory stimuli are presented repeatedly (Tremblay, Kraus, McGee, Ponton, & Otis, 2001; Tremblay, Inoue, McClannahan, & Ross, 2010; Ross & Tremblay, 2009). In the auditory discrimination task used by Jaffe-Dax et al. (2015) the amplitude of the P2 component in response to the first tone should be larger on bias+ than bias- trials because its frequency is contracted towards the mean (Ravi et al., 2012). If readers with dyslexia are unable to incorporate prior knowledge about stimulus statics to reduce perceptual memory load on 2IFC tasks no significant difference in P2 amplitude in response to the first tone would be expected between bias+ and bias- trials. To explore this prediction Jaffe-Dax et al. (2015) conduced a second experiment in which the stimuli from their auditory discrimination task were presented passively to the same fourteen readers with developmental dyslexia and fourteen relatively good

readers (mean age of the entire sample = 25.4 years) matched for non-verbal IQ. Results showed that the amplitude of the P2 component of the ERP was larger in bias+ than bias- trials but only in relatively good readers and not readers with dyslexia. These findings further support the anchoring deficit hypothesis as they show that the mechanisms used to track stimulus statistics are impaired in developmental dyslexia.

1. 3. 3. 2. Studies in the visual domain

An important issue is whether a general difficulty incorporating prior knowledge about stimulus statistics in readers with dyslexia transcends the auditory and visual domains. To address this issue Jaffe-Dax, Lieder, Biron and Ahissar (2016) administered a spatial frequency discrimination task to thirty-three readers with developmental dyslexia (age = 24.4 years) who scored at least 2SD below the normalised mean on a measure of phonological decoding ability (Deutsch & Bentin, 1996). The performance of this group of readers with dyslexia was compared to that of forty relatively good readers (age = 23.4 years) matched for non-verbal IQ. Two sinusoidal gratings were presented sequentially on each trial. The difference in spatial frequency between the two gratings was varied in an analogous manner to the auditory tones in the study by Jaffe-Dax et al. (2015). A 2IFC procedure was used to measure spatial frequency discrimination thresholds in which participants had to judge whether the stimulus presented in the first or second temporal interval had a higher spatial frequency. The anchoring deficit hypothesis predicts that performance should improve on 'bias+' trials in which the spatial frequency of

the first stimulus was closer to the mean frequency of previous trials than the spatial frequency of the second stimulus and worsen on 'bias-' trials in which the spatial frequency of the second stimulus is closer to the mean frequency of previous trials than the first stimulus. Results showed that thresholds were lower in readers with dyslexia and relatively good readers when the spatial frequency of the first stimulus was closer to the mean frequency of previous trials than the spatial frequency of the second stimulus. However, the difference between bias+ and bias- trials was significantly smaller in readers with dyslexia than relatively good readers. These findings point to a general difficulty incorporating prior knowledge about stimulus statistics in readers with dyslexia that transcends the auditory and visual domains. The anchoring deficit hypothesis has received considerable support (Ahissar et al., 2006; Ahissar, 2007; Jaffe-Dax et al., 2015, 2016) but it cannot readily explain deficits on 1IFC tasks in which perceptual memory load is relatively low and comparisons do not have to be made across sequentially presented stimuli (Cichini et al., 2015; Felmingham & Jakobson, 1995; Morrone et al., 2011).

1. 3. 4. The modified receptive field hypothesis

An alternative theory that has been proposed to explain the origin of visual impairment in readers with dyslexia is the modified receptive field hypothesis (Grainger et al., 2016). This framework is inspired by computational models of reading (Dehaene, Cohen, Sigman, & Vinckier, 2005; Grainger & van Heuven, 2003; Whitney, 2001) and proposes that the spatial extent or 'receptive field size' of putative letter (but not object) detectors in visual cortex decreases

during reading acquisition to combat the effects of crowding and inter-letter interference (Grainger, Tydgat, & Isselé, 2010; Tydgat & Grainger, 2009). Several neurophysiological studies have also confirmed that the receptive field size of neurons in extrastriate visual areas is dynamic rather than hard-wired, consistent with the modified receptive field hypothesis (Cox et al., 2013; Womelsdorf, Anton-Erxleben, Pieper, & Treue, 2006; Womelsdorf, Anton-Erxleben, & Treue, 2008; Treue & Martinez-Trujillo, 2012). The modified receptive field hypothesis is also supported by human neuroimaging and psychophysical studies showing that learning to read plays a major role in the development of the human visual system (Dehaene et al., 2010; Dehaene et al., 2015; Szwed et al., 2011; Szwed et al., 2012). Presumably, readers with dyslexia are less likely to reap the benefits associated with reading acquisition during early childhood than relatively good readers, which raises the possibility that they might have larger receptive fields than relatively good readers. Although the modified receptive field hypothesis has not yet been tested empirically a direct prediction of this framework is that the effects of visual crowding should be significantly larger in readers with developmental dyslexia than relatively good readers but only for visual stimuli comprising letters or words. Research exploring visual crowding in developmental dyslexia is outlined below.

Visual crowding places a fundamental limit on visual perception. It is characterised by an inability to identify objects when they are closely surrounded by other visual stimuli (Levi, 2008; Pelli, 2008; Whitney & Levi, 2011). Bouma and Legein (1977) were amongst the first to investigate visual

crowding in readers with dyslexia. To do so, they administered a letter identification task to twenty readers with developmental dyslexia (age range = 10 to 14 years) who had a reading age up to 5 years below that predicted by their chronological age on the Tanghe reading test (Tanghe, 1971). In this standardised measure of reading ability, participants are asked to read aloud regular and irregular words as well as sentences of increasingly difficulty. The performance of the group of readers with dyslexia was compared to that of twenty relatively good readers (age range = 9 to 13 years). The visual stimuli comprised letters that were presented in the fovea or at an eccentricity of 1°. They either appeared in isolation or were flanked by two other letters. A 1IFC procedure was employed in which participants had to identify the isolated or flanked letters and the number of letters identified correctly was measured. Results showed that performance on the task was similar across readers with dyslexia and relatively good readers when isolated letters were presented in the fovea and at an eccentricity of 1°. However, a different pattern emerged when the stimuli consisted of flanked letters. Readers with dyslexia performed significantly worse than relatively good readers when the stimuli were presented in the fovea and when they were presented at an eccentricity of 1°. These results support the modified receptive field hypothesis as they point to larger effects of visual crowding in readers with dyslexia than relatively good readers regardless of the whether the stimuli are presented in the fovea or the parafovea. Several studies in the general population have shown that the effects of visual crowding are typically non-existent or very small in the fovea of adults but not children (Levi, Klein, & Hariharan, 2002; Norgett & Siderov, 2014; Toet & Levi, 1992; Strasburger, Harvey, & Rentschler, 1991)

The modified receptive field hypothesis predicts that the effects of visual crowding should be larger in readers with dyslexia irrespective of whether the stimuli comprise flanked letters or whole-words. Spinelli, De Luca, Judica and Zoccolotti (2002, Experiment 1) administered a word identification task to twenty-two readers with developmental dyslexia (mean age = 12.7 years) who had an average standard score 3.3SD below the normalised mean on the MT reading test (Cornoldi & Colpo, 1995; Sartori, Job, & Tressoldi, 1995). The performance of this group of readers with dyslexia was compared to that of ninety-seven relatively good readers (mean age = 12.3 years) who had an average score within 1SD of the normalised mean on the same test. The visual stimuli comprised pairs of Italian, five-letter words that were presented sequentially in the fovea. A 2IFC procedure was used to measure reaction time. On each trial, participants had to judge whether the word presented in the second temporal interval matched the word presented in the first temporal interval. The word presented in the second temporal interval either appeared in isolation or was closely surrounded by other words. Results showed that reaction times were significantly slower in readers with dyslexia than relatively good readers when the words presented in the second temporal interval were closely surrounded by other words in comparison to when they were presented in isolation. These findings provide further support for the modified receptive field hypothesis as they demonstrate that the effects of crowding are larger in developmental dyslexia regardless of whether the visual stimuli consist of flanked letters or whole words.

A further prediction of the modified receptive field hypothesis is that visual crowding should only be impaired in readers with dyslexia for stimuli comprising letters and words but not objects and symbols as the spatial extent of putative letter detectors but not object detectors is assumed to decrease during reading acquisition (Grainger et al., 2010; Tydgat & Grainger, 2009). In the study by Spinelli et al. (2002, Experiment 2) a second experiment was conducted in which a similar task was administered to the same twenty-two readers with developmental dyslexia (mean age = 12.7 years) and ninety-seven relatively good readers (mean age = 12.3 years). The visual stimuli comprised symbol-strings (e.g. λ♯∧□÷) instead of real, five-letter, Italian words. On each trial, participants had to judge whether the string presented in the second temporal interval matched the string presented in the first temporal interval and reaction time was measured. The string presented in the second temporal interval either appeared in isolation or was closely surrounded by other string. Results showed that reaction times were significantly slower in readers with dyslexia than relatively good readers when the strings presented in the second temporal interval were closely surrounded by other strings in comparison to when they were presented in isolation. These findings are difficult to reconcile with the modified receptive field hypothesis as it assumes that the receptive field size of neurons involved in visual word form recognition but not object recognition decreases during reading acquisition (Grainger et al., 2010; Tydgat & Grainger, 2009).

The extent of visual crowding in the general population is strongly influenced by the distance between neighbouring elements. Research has shown that it

breaks down when stimuli are separated by a 'critical spacing' that scales with eccentricity (Bouma, 1970; Martelli, Majaj, & Pelli, 2005; Pelli, Levi, & Chung, 2004; Strasburger et al., 1991; Toet & Levi, 1992). This raises the possibility that increasing the distance between individual letters in words might increase reading speed in some readers with dyslexia. To investigate this hypothesis Spinelli et al. (2002, Experiment 3) conducted a third experiment in which a word identification task was administered to twenty-seven readers with developmental dyslexia (mean age = 12.7 years) who had an average standard score 2.4SD below the normalised mean on the MT reading test (Cornoldi & Colpo, 1995; Sartori, Job, & Tressoldi, 1995) and ninety-nine relatively good readers (mean age = 12.8 years) matched for chronological age who had a standard score within 1SD of the normalised mean on the same test. The visual stimuli consisted of five-letter, Italian words that were presented in the fovea. Inter-letter spacing was varied between 0.24 and 0.59º. A 1IFC procedure was employed in which participants had to read the words as quickly as possible and reaction time was measured. Results showed that increasing inter-letter spacing had a facilitatory effect up to about 0.32º in readers with dyslexia but not relatively good readers. Although these findings are consistent with the modified receptive field hypothesis it is unclear if the abnormal crowding effects reported by Spinelli et al. (2002, Experiment 1, Experiment 2) may have arisen because a 2IFC procedure was used that necessitated comparisons across sequentially present stimuli.

Several studies have shown that readers with dyslexia cannot incorporate prior knowledge about stimulus statistics to reduce perceptual memory load on tasks

in which comparisons have to be made across sequentially presented stimuli (see section 1. 3. 3.). That is, some of the abnormal crowding effects reported in developmental dyslexia might have arisen due to the use of 2IFC paradigms. To explore this possibility Shovman and Ahissar (2006) administered an object identification task to twenty readers with developmental dyslexia (mean age = 23.6 years) and twenty-four relatively good readers (mean age = 24.2 years) matched for non-verbal IQ. Although participants in the dyslexia group were recruited on the basis of a documented history of reading difficulties they performed significantly worse than relatively good readers on a measure of phonological decoding ability (Deutsch & Bentin, 1996). The visual stimuli consisted of symbols that were either presented in isolation or were flanked by two other symbols. A 1IFC procedure was used in which participants had to identify the isolated or flanked symbols and thresholds were measured to determine the minimum stimulus duration needed for reliable task performance. Results showed that duration thresholds were similar across readers with dyslexia and relatively good readers regardless of whether the symbols appeared in isolation or were flanked by two other symbols. These findings suggest that differences between readers with dyslexia and relatively good readers in Spinelli et al. (2001, Experiment 1, Experiment 2) might reflect the fact that a 2IFC paradigm was used to assess visual crowding. They highlight the need for further research using 1IFC paradigms to investigate visual crowding in developmental dyslexia as this would rule out alternative explanations based on an inability to form a perceptual anchor. It is also unclear if differences in visual crowding are found between readers with developmental dyslexia and relatively good readers when contrast sensitivity is

measured instead of percent correct, reaction time, or duration thresholds (Bouma & Legein, 1977; Shovman & Ahissar, 2007; Spinelli et al., 2001).

To determine if the effects of visual crowding are larger in readers with dyslexia than relatively good readers when contrast sensitivity is measured Martelli et al. (2009, Experiment 1) administered a letter identification task to five children (mean age not specified) with developmental dyslexia who had a standard score at least 2SD below the normalised mean on the MT Reading test (Cornoldi & Colpo, 1995; Sartori, Job, & Tressoldi, 1995) and five relatively good readers (mean age not specified). The stimuli either consisted of single letters or ten-letter, Italian words that were presented in the fovea for 200ms. A 1IFC procedure was used to measure contrast sensitivity in which participants had to identify the single letter or the central letter of the ten-letter word. Results showed that readers with dyslexia had significantly lower contrast sensitivity than relatively good readers when the visual stimuli comprised ten-letter words but not single letters. Although these findings support the modified receptive field hypothesis and previous research showing that the effects of visual crowding are larger for letter and word stimuli in readers with dyslexia than relatively good readers (Bouma & Legein, 1977; Spinelli et al. 2002, Experiment 1, Experiment 3) such a small sample size makes these findings very insecure. It is also unclear if the reader groups were well matched for chronological age. Further research is needed to explore the developmental trajectory of crowding (Whitney & Levi, 2011) but several studies in the general population have shown that it limits visual perception to a greater extent in children under the age of eight (Atkinson et al., 1988; Farzin et al., 2010; Jeon et al., 2010). This raises the possibility that the results of Martelli et

al. (2009) may reflect age differences across the participant groups rather than larger effects of visual crowding in developmental dyslexia *per se*.

The modified receptive field hypothesis predicts that visual crowding should be impaired in readers with dyslexia for stimuli comprising letters or words regardless of stimulus duration. To investigate if visual crowding in readers with dyslexia is influenced by stimulus duration Martelli et al. (2009, Experiment 1) measured contrast sensitivity when the duration of the single letters and ten-letter words was 200 or 2000ms. The same five children with developmental dyslexia (mean age not specified) and five relatively good readers (mean age not specified) took part in the experiment. Results showed that readers with dyslexia had significantly lower contrast sensitivity for ten-letter words but not single letters when stimulus duration was 200ms, consistent with previous research (Bouma & Legein, 1977, Spinelli et al., 2002). However, a different pattern emerged when the stimuli were presented for 2000ms. Contrast sensitivity was similar across readers with dyslexia and relatively good readers when the visual stimuli comprised single and ten-letter words. These findings suggest that visual crowding in readers with dyslexia is modulated by stimulus duration. It is possible to reconcile these results with the modified receptive field hypothesis but only if it is assumed that readers with dyslexia are able to select an optimally sized letter detector when stimulus duration is relatively long (2000ms). Thus, reading acquisition might impact upon the development of putative mechanisms underlying scale selection rather than decreasing receptive field size *per se*.

The modified receptive field hypothesis predicts that the effects of visual crowding should be significantly higher in readers with dyslexia than relatively good readers but such a deficit could manifest in several different ways. Bouma's (1970) law states that the distance between objects needed to prevent visual crowding (i.e. critical spacing) scales as a function of eccentricity with a proportionality constant of ~0.50 (Martelli et al., 2005; Pelli et al., 2004; Strasburger et al., 1991; Toet & Levi, 1992). Thus, it is unclear if larger effects of visual crowding in developmental dyslexia manifest as increased critical spacing at all eccentricities or a greater proportionality of scaling with eccentricity. An alternative possibility is that both phenomena co-occur in readers with dyslexia. To disentangle these possibilities Martelli et al. (2009, Experiment 2) conducted an additional experiment in which a letter identification task was administered to twenty-nine readers with developmental dyslexia (mean age = 11.7 years) who scored at least 2SD below the normalised mean on the MT Reading test (Cornoldi & Colpo, 1995; Sartori, Job, & Tressoldi, 1995) and thirty-two relatively good readers (11.2 years). The visual stimuli comprised single letters that were flanked by two other letters. A 1IFC procedure was used in which participants had to identify the flanked letter and critical spacing was varied across a range of eccentricities to determine the minimum distance needed to achieve reliable task performance. Results showed that critical spacing was significantly larger in readers with dyslexia across all eccentricities tested. Fitting a linear function to the data for each participant revealed that critical spacing scaled with a greater proportionality constant in readers with dyslexia than relatively good readers (Figure 10). The mean slope of the line fitted to the data was 0.95 and 0.62 in

readers with dyslexia and relatively good readers, respectively. These findings support the modified receptive field hypothesis as they show that visual perception in developmental dyslexia is limited by a combination of increased critical spacing at all eccentricities and a greater proportionality of scaling with eccentricity.

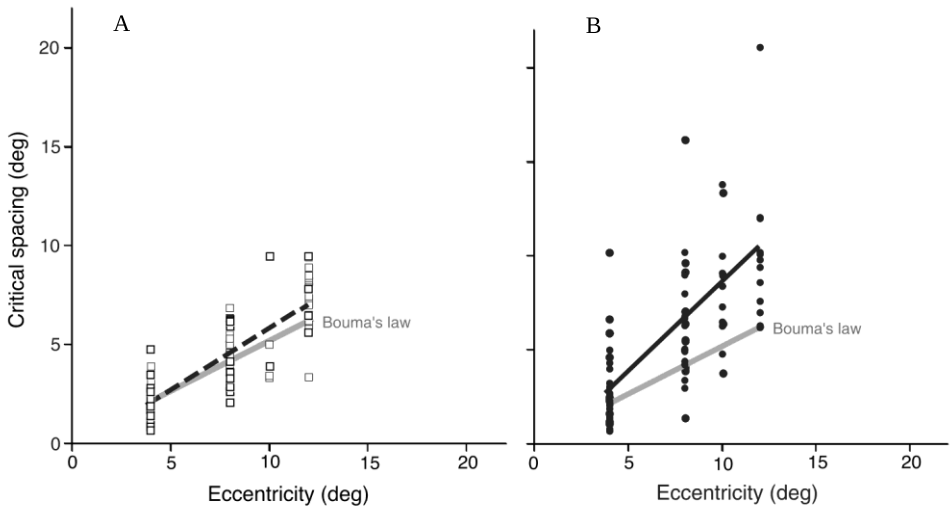


Figure 10. Graphs showing critical spacing as a function of eccentricity for readers with developmental dyslexia (right) and relatively good readers (left). The black lines (solid = readers with dyslexia; dashed = relatively good readers) represent the mean linear fit that was used to determine the proportionality constant for each participant in the entire sample. The grey lines represent the predictions of Bouma's law. Adapted from Martelli et al. (2009).

The modified receptive field hypothesis makes testable predictions about visual crowding, in which objects surrounded by neighboring stimuli merely become unrecognizable, but not ordinary masking, in which objects completely disappear and cannot be detected (Pelli, 2004). Thus, it is important to distinguish between these two phenomena. Several studies in the general population have shown that critical spacing is not influenced by stimulus size, whereas visual masking is highly dependent upon stimulus size (Levi et al., 2002; Pelli et al., 2004; Tripathy & Cavanagh, 2002). To confirm that visual crowding is impaired in readers with dyslexia rather than ordinary masking Martelli et al. (2009, Experiment 2) measured critical spacing at an eccentricity of 8º when the flanked letters subtended either 1 or 3º of visual angle. The same twenty-nine readers with developmental dyslexia (mean age = 11.7 years) and thirty-two relatively good readers took part in this experiment (mean age = 11.2 years). Results showed that visual crowding was independent of stimulus size in both reader groups, consistent with previous research that has explored visual crowding in the general population (Pelli et al., 2004). Critical spacing was significantly larger in readers with dyslexia than relatively good readers when the size of the stimuli was 1 or 3º. These findings confirm that visual crowding as opposed to ordinary masking is impaired in readers with dyslexia, consistent with the modified receptive field hypothesis.

Larger critical spacing may impact upon the speed at which readers with dyslexia are able to encode text. Research in the general population has shown that reading rate increases as print size increases but only up to a point called the 'critical print size' after which it become asymptotic and no longer

improves (Chung, Mansfield, & Legge, 1998; Legge, Mansfield, & Chung, 2001). Increasing print size impacts upon the centre-to-centre distance between letters in words so readers with dyslexia should have a larger critical print size than relatively good readers for the modified receptive field hypothesis to be supported. To investigate critical print size Martelli et al. (2009, Experiment 3) conducted another experiment in which reading rate was measured in thirteen children with developmental dyslexia (mean age not specified) who scored at least 2SD below the normalised mean on the MT Reading test (Cornoldi & Colpo, 1995; Sartori, Job, & Tressoldi, 1995) and sixteen relatively good readers (mean age not specified). The stimuli comprised Italian words that were presented in the fovea. Reading rate was measured using a 1IFC, rapid serial visual presentation (RSVP) task in which the number of words read correctly was measured. To determine the critical print size, a two-limbed function was fitted to each participant's data (Figure 11). Results showed that reading rate was significantly slower in readers with dyslexia than relatively good readers. In addition, the critical print size (i.e. the presentation rate at which performance became asymptotic) was larger in readers with dyslexia than relatively good readers. These findings are consistent with the modified receptive field hypothesis and support previous research showing that the effects of visual crowding for letter and word stimuli are larger in readers with dyslexia than relatively good readers (Bouma & Legein, 1977; Martelli et al., 2009, Experiment 1, Experiment 2; Spinelli et al., 2002, Experiment 1, Experiment 3).

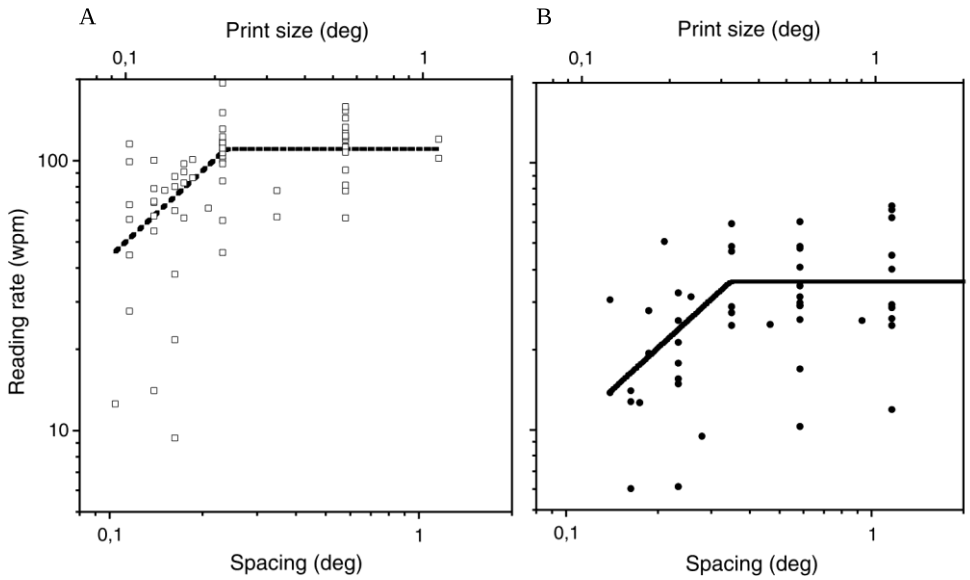


Figure 11. Graphs showing print size as a function of reading rate in readers with developmental dyslexia (right graph) and relatively good readers (left graph). The black lines represent the mean fit of a two-limbed function that was used to determine the critical print size (i.e. the point at which reading rate is no longer limited by print size) for each participant in the entire sample. Adapted from Martelli et al. (2009, Experiment 3).

As previously mentioned, the modified receptive field hypothesis predicts that visual crowding in developmental dyslexia should only be impaired for letter and word stimuli but not other types of visual stimuli such as objects or symbols. To explore visual crowding in readers with dyslexia Doron et al. (2015) administered a Vernier discrimination task to nineteen Hebrew-speaking readers with developmental dyslexia (mean age = 24.9 years) and twenty-seven relatively good readers (mean age = 25.6 years) who were also native Hebrew speakers. Participants in the dyslexia group were recruited on the basis of a documented history of reading difficulties but they performed significantly worse than relatively good readers on a measure of phonological decoding ability (Deutsch & Bentin, 1996). Both reader groups were matched for non-verbal IQ. The visual stimuli comprised two vertical lines that were presented for 150ms. One of the lines was offset to the left or the right on each trial. A 1IFC procedure was used in which participants had to judge the direction of this offset and Vernier thresholds were measured to determine the minimum spacing between the two lines that was needed for reliable task performance. Results showed that Vernier thresholds were similar across readers with dyslexia and relatively good readers when the stimuli were presented in isolation and when they were flanked by additional lines. These findings support the modified receptive field hypothesis as it predicts that visual crowding in readers with dyslexia should only be impaired for letter and word stimuli.

1. 3. 5. The dorsal stream vulnerability hypothesis

Vulnerability of the dorsal stream during development has been suggested as a primary origin of impairment in individuals with developmental dyslexia and a range of other neurodevelopmental disorders (e.g. Williams syndrome, autism spectrum disorder, developmental dyspraxia and children born preterm) (Atkinson & Braddick, 2013; Braddick et al., 2003; Braddick & Atkinson, 2011). In order to understand this hypothesis, it is important know a little about the cortical dorsal and ventral processing streams.

1. 3. 5. 1. The dorsal and ventral streams

The dorsal stream vulnerability hypothesis assumes that two anatomically distinct and functionally independent processing streams can be discerned in the primate cortex, each specialised for encoding different types of visual information (Goodale & Milner, 1992; Milner & Goodale, 1995; Ungerleider & Mishkin, 1982; but see Mather, Pavan, Marotti, Campana, & Casco, 2013; Schenk & McIntosh, 2010). It is not uncommon for the subcortical magnocellular and parvocellular pathways (see section 1. 3. 1. 1.) to be conflated with the cortical dorsal and ventral processing streams (Skottun, 2014, 2015ab). For many years the magnocellular and parvocellular pathways were thought to provide major feedforward input to the dorsal and ventral processing streams, respectively (Livingstone & Hubel, 1988; Merigan & Maunsell, 1993; Zeki & Shipp, 1988). However, more recent research in non-human primates has shown that this is almost certainly an oversimplification (Nassi & Callaway, 2009; Sincich & Horton, 2005; Vidyasagar et al., 2002). The dorsal stream projects from V1 to the parietal lobes and is often referred to

as the ‘where’ pathway because it is involved in tasks such as determining the global motion of objects, spatial cognition and visual motor planning (Braddick et al., 2000; Milner & Goodale, 2006, 2008; Norman, 2002). In contrast, the ventral stream projects from V1 to the temporal lobes and has been termed the ‘what’ pathway because it is involved in tasks such as global shape perception, visual memory and recognition of familiar objects/faces (Braddick et al., 2000; Milner & Goodale, 2006, 2008; Norman, 2002). Dorsal stream vulnerability is claimed to manifest as a selective deficit in the processing of global motion (Figure 12A & 12B), relative to global form (Figure 12C & 12D) but the selectivity of this deficit is equivocal (Grinter, Mayberry, & Badcock, 2010; Johnston et al., 2017).

1. 3. 5. 2. Random-dot kinematograms

A large body of research has used random-dot kinematograms (RDKs) to investigate the dorsal stream vulnerability hypothesis in readers with developmental dyslexia (Grinter et al., 2010; Johnston et al., 2017). These stimuli comprise a series of discrete images, each containing a pattern of local dots, that when presented in succession, create the perception of apparent motion (Figure 12A & Figure 12B). In one type of widely used RDK (e.g. Newsome & Paré, 1988), some of the dots are constrained to move in the same direction on each image update (*signal* dots), whilst others move randomly (*noise* dots). By changing the relative proportion of signal and noise dots the coherence of the stimulus can be varied. Motion coherence thresholds are defined as the minimum percentage of signal dots needed to detect or identify

reliably the global direction of motion (Britten, Shadlen, Newsome, & Movshon, 1992; Salzman, Murasugi, Britten, & Newsome, 1992; Newsome & Paré, 1988).

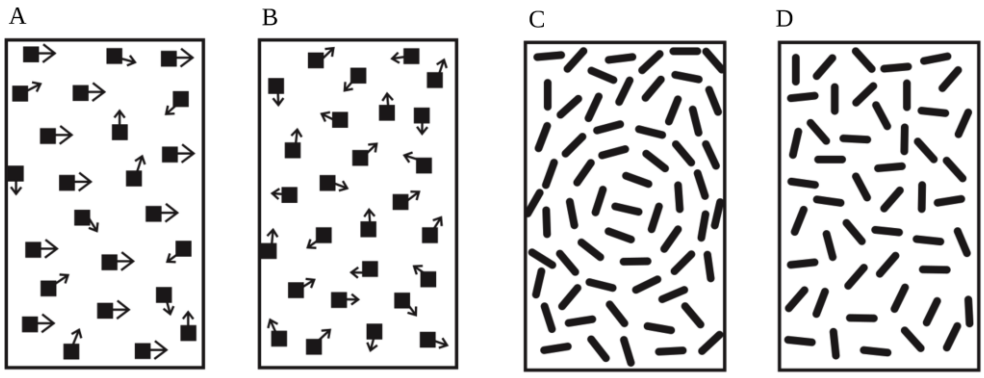


Figure 12. A schematic illustration of visual stimuli that have been widely used to study the processing of global motion and global form in the general population and neurodevelopmental disorders such as developmental dyslexia. In this particular type of global motion task (A & B) participants were shown random-dot kinematograms that contained a proportion of *signal* dots moving in the same direction (in this case rightwards), whilst other *noise* dots moved randomly (A). They had to discriminate these patterns from stimuli that only contained randomly moving *noise* dots (B). In this particular type of static global form task (C & D) participants were shown stimuli that contained a proportion of *signal* lines that were orientated coherently to form a concentric pattern, whilst other *noise* lines were orientated randomly (C). They had to discriminate these patterns from stimuli that only contained randomly orientated *noise* lines (D). Adapted from Hansen, Stein, Orde, Winter and Talcott (2001).

1. 3. 5. 3. Studies using global motion tasks

To investigate the dorsal stream vulnerability hypothesis Cornelissen et al. (1995, Experiment 1) administered a global motion task to fourteen children with developmental dyslexia (mean age = 9.73 years) who had a reading age at least 2SD below that predicted by their chronological age and full-scale IQ on the BAS Reading Test (Elliott, Murray, & Pearson, 1979). The performance of this group of readers with dyslexia was compared to that of fourteen relatively good readers (mean age = 9.89 years) matched for full-scale IQ who had a reading age greater than that predicted by their chronological age on the same test. The visual stimuli consisted of two random-dot patterns that were presented simultaneously either to the left or the right of a central fixation cross. One of the patterns was spatially divided into horizontal segments by constraining dots in adjacent segments to move in opposing directions (leftwards or rightwards). A 1IFC procedure was used to measure coherence thresholds in which participants had to discriminate the spatially divided stimulus from a pattern containing uniform motion that reversed direction periodically every 240ms. The coherence of the two random-dot patterns was varied in the conventional manner, between 0 and 100%, by changing the relative proportion of signal to noise dots. Results showed that children with dyslexia had significantly higher coherence thresholds than relatively good readers on the global motion task, consistent with the dorsal stream vulnerability hypothesis. However, it is currently unclear if a similar pattern of impairment is found in adults with developmental dyslexia.

It is possible that the development of global motion perception might simply be delayed in developmental dyslexia. To address this issue Cornelissen et al. (1995, Experiment 2) conducted a second experiment in which a global motion task was administered to twenty-nine adults with developmental dyslexia (mean age = 29 years) who had a documented history of reading difficulties and twenty-nine relatively good readers (mean age = 28.10 years) matched for sex. The task and visual stimuli were identical to those used in their previous experiment (Cornelissen et al. 1995, Experiment 1). Results showed that readers with dyslexia had significantly higher coherence thresholds than relatively good readers on the global motion task. These findings show that deficits in the processing of global motion extend to adults with dyslexia but Cornelissen et al. (1995, Experiment 2) did not control for factors that are known to be associated with performance on global motion tasks such as non-verbal IQ. Several studies in the general population have shown that individuals with a lower non-verbal IQ have significantly higher coherence thresholds than individuals with a higher IQ on tasks requiring the processing of global motion (Arranz-Paraíso & Serrano-Pedrazza, 2016; Cook, Hammett, & Larsson, 2016; Melnick, Harrison, Park, Benetto, & Tadin, 2013; Tadin, 2015). A further criticism of the study by Cornelissen et al. (1995) is that the type of RDK stimuli used were spatially complex and potentially not a straightforward test of sensitivity to global motion (Table 2). That is, one of the patterns presented on each trial was spatially divided into horizontal segments, on the basis of the signal dot's directions, and thus comprised "second-order" image cues in the form of motion-defined boundaries (Cavanagh & Mather, 1989). Consequently, the global motion task used by Cornelissen et al. (1995)

necessitated a degree of segmentation, as well as integration, of local visual cues and these may be mediated by distinct mechanisms in human vision (Albright & Stoner, 1995; Braddick, 1993; Johnston et al., 2017; Nakayama, 1985; Tadin, 2015). This raises the possibility that motion-based segmentation might be impaired in children and adults with developmental dyslexia rather than global motion perception *per se*. Whether or not this class of RDK can be relied upon to clearly dissociate activity in brain regions that have been implicated in the processing of global motion is also debatable. Human neuroimaging studies (Larsson, Heeger, & Landy, 2010; Tyler, Likova, Kontsevich, & Wade, 2006; Zeki, Perry, & Bartels, 2003) and neurophysiological work in non-human primates (Mysore et al., 2006, 2008; Chen et al., 2016; Sary et al., 1995) has shown that motion-defined boundaries are encoded in several different brain regions. Some of these areas have been implicated in global form (shape) perception so impaired performance on the motion task used by Cornelissen et al. (1995) may not be indicative of a deficit specific to the processing of global motion.

To explore the dorsal stream vulnerability hypothesis Raymond and Sorensen (1998, Experiment 1) devised a more conventional global motion task than that used by Cornelissen et al. (1995). It was administered to ten children with developmental dyslexia (mean age = 9.9 years) who had a reading age at least 1.5SD below that predicted by their chronological age on a range of tests including the (WRMT) (Woodcock, 1987). The performance of this group of readers with dyslexia was compared to that of ten relatively good readers (mean age = 9.9 years) matched for sex, chronological age and non-verbal IQ

who had at reading age equal to or greater than that predicted by their chronological age on the same tests. The visual stimuli consisted of conventional RDKs, in which the signal and noise dots were dispersed throughout the display in a homogenous manner. A 1IFC procedure was used to measure coherence thresholds in which participants had to judge the overall direction of the stimulus (leftwards vs. rightwards). Results showed that children with dyslexia had significantly higher coherence thresholds than relatively good readers on the global motion task. Deviance analyses were then performed to determine the proportion of readers with dyslexia who exhibited impaired task performance. Six out of the ten readers with dyslexia had coherence thresholds greater than 2SD above the mean of the control group. These findings offer some support for the dorsal stream vulnerability hypothesis but it is not compelling evidence because no global form task was administered. They highlight the fact that not all readers with dyslexia exhibit impaired performance on tasks requiring the processing of global motion. Inter-subject variability is a characteristic feature of studies that have explored global motion perception in readers with dyslexia. It questions the explanatory power of the dorsal stream vulnerability hypothesis and suggests that factors other than reading ability might influence performance on tasks requiring the processing of global motion (Johnston et al., 2017).

Research has shown that performance on global motion tasks improves when the number of images in the motion sequence is increased (McKee & Welch, 1985; Snowden & Braddick, 1989ab). This 'temporal recruitment' effect has been attributed to lateral interactions between directionally selective neurons

with receptive fields at discrete locations along the motion trajectory (Watamuniak, McKee & Grzywacz, 1995). To investigate if the underlying nature of the visual deficit in readers with dyslexia reflects impaired temporal recruitment, rather than dorsal stream vulnerability Raymond and Sorensen (1998, Experiment 2) conducted a second experiment in which a global motion task was administered to twelve readers with developmental dyslexia (mean age = 11.6 years) who had a reading age at least 1.5SD below that predicted by their chronological age on a range of tests including the WRMT (Woodcock, 1987). The performance of this group of readers with dyslexia was compared to that of twelve relatively good readers (mean age = 9.3 years) who had a reading age equal to or above that predicted by their chronological age on the same tests. The visual stimuli and task were identical to those used in their previous experiment (Raymond & Sorensen, 1998, Experiment 1) except the number of images in the global motion sequence and image duration was varied systematically across several experimental conditions. Results showed that coherence thresholds were similar across readers with dyslexia and relatively good readers when the RDKs consisted of two relatively brief frames (12ms) and two relatively long frames (32 ms). However, a different pattern emerged when the RDKs consisted of seven relatively brief frames (each 12ms) as readers with dyslexia had significantly higher coherence thresholds than relatively good readers. These findings support the view that temporal recruitment is impaired in developmental dyslexia but they are difficult to reconcile with the dorsal stream vulnerability hypothesis as it predicts that readers with dyslexia should exhibit impaired performance on global motion tasks regardless of the number of images in the motion sequence.

An additional factor that is known to influence performance on global motion tasks in the general population is stimulus duration. Evidence suggests that global motion perception improves when stimulus duration is increased (Nakayama & Silverman, 1984). To explore if this is also the case in readers with dyslexia Talcott et al. (2000, Experiment 1) administered a global motion task to ten adults with developmental dyslexia (mean age = 25.2 years) who had a reading age at least 1.3SD below that predicted by their full-scale IQ on the WRAT (Jastak & Wilkinson, 1984). The performance of this group of readers with dyslexia was compared to that of ten relatively good readers (mean age = 22.2 years) matched for full-scale IQ who had a reading age equal to or above that predicted by their full-scale IQ on the same test. The visual stimuli comprised conventional RDKs that were presented at each of a range of durations between 200 and 1804ms. A 1IFC procedure was used to measure coherence thresholds in which participants had to judge the overall direction of the stimulus. Results showed that readers with dyslexia had higher overall coherence thresholds than relatively good readers on the global motion task, consistent with previous research (Cornelissen et al., 1995, Raymond & Sorensen, 1998). Coherence thresholds in both reader groups decreased as stimulus duration increased but no significant reader group by duration interaction was found. These results suggest that readers with dyslexia have higher coherence thresholds than relatively good readers on global motion tasks regardless of stimulus duration but task performance in readers with dyslexia could be influenced by other stimulus factors such as the dot density.

To explore whether or not this is the case Talcott et al. (2001, Experiment 2) conducted a second experiment in which a global motion task was administered to the same ten adults with developmental dyslexia (mean age = 25.2 years) and ten relatively good readers (mean age = 22.2 years) matched for full-scale IQ. The task and visual stimuli were identical to those used in their previous experiment (Talcott et al., 2001, Experiment 1) except that dot density ranged from 1.5 to 12.2 dots/deg^2. Results showed that readers with dyslexia had significantly higher coherence thresholds than relatively good readers on the global motion task. There was some evidence to suggest that the performance of readers with dyslexia and relatively good readers was similar at the highest dot density tested. The authors speculated that directionally-selective neurons in readers with dyslexia might have a lower response gain, which could explain why increasing the dot density (thereby increasing the total contrast motion energy present in the stimulus) had a facilitatory effect on task performance. However, no significant reader group by dot density interaction was found so firm conclusions concerning the nature of the visual deficit in dyslexia could not be drawn.

1. 3. 5. 4. Studies using global motion and form tasks

Dorsal stream vulnerability is thought to manifest as a selective deficit in the processing of global motion (Braddick et al., 2003; Grinter et al., 2010) and most of the studies cited so far point to a deficit in the processing of global motion in some readers with dyslexia (Cornelissen et al., 1995; Eden et al., 1996; Talcott et al., 2003; Hill & Raymond, 2002; Raymond & Sorenson, 1998;

Slaghuis & Ryan, 1999; Talcott et al., 2001). However, the issue of whether global form perception, which is widely assumed to be mediated by the ventral stream (Braddick et al., 2000; Milner & Goodale, 2006, 2008; Norman, 2002), is also impaired in developmental dyslexia is unknown. To address this issue Hansen et al. (2001) administered a global motion task and a global form task to fifteen adults with developmental dyslexia (mean age = 28.9 years) who had an average standard score below the normalised mean on the WRAT (Jastak & Wilkinson, 1984). The performance of this group of readers with dyslexia was compared to that of sixteen relatively good readers (mean age = 24 years) matched for non-verbal IQ who had an average standard score greater than the normalised mean on the same test. The stimuli in the global motion task were conventional RDKs (Figure 12A & 12B). In contrast, the global form stimuli (Figure 12C & 12D) contained an array of static line segments that were orientated to form a concentric pattern (Atkinson et al., 1997; Braddick et al., 2000; Spencer et al., 2000). A 2IFC procedure was used to measure coherence thresholds. Participants had to discriminate RDKs (Figure 12A) from stimuli containing randomly moving noise dots (Figure 12B) in the global motion task, whereas in the global form task they had discriminate concentric structure (Figure 12C) from stimuli containing randomly orientated elements (Figure 12D). Results showed that readers with dyslexia had significantly higher coherence thresholds than relatively good readers on the global motion task, consistent with previous research (Table 2). However, a different pattern was found on the global form task. No significant difference was found between the two readers groups regardless of whether the position of the concentric pattern was fixed on each trial or randomised. These findings support the dorsal stream

vulnerability hypothesis but they also speak directly to the external noise exclusion hypothesis (see section 1. 3. 2.). This theory predicts that readers with dyslexia should have exhibited impaired performance on the global motion task and the global form task as both contained high levels of external visual noise. That readers with dyslexia had higher coherence thresholds than relatively good readers on the global motion task but not the global form task casts further doubt on the external noise exclusion hypothesis. The results of Hansen et al. (2001) also challenge the anchoring deficit hypothesis (see section 1. 3. 3.). If readers with dyslexia have difficulty incorporating prior knowledge about stimulus statistics into their judgements they should have exhibited impaired performance on the global motion task and the global form task as both required comparisons to be made across sequentially presented stimuli.

Some investigators have failed to uncover deficits in the processing of global motion, relative to global form, in children with dyslexia. For example, White et al. (2006) administered a global motion task and a global form task to twenty-three children with developmental dyslexia (mean age = 10.5 years) who had an average score approximately 1SD below the normalised mean on the WRAT (Jastak & Wilkinson, 1984). The performance of this group of readers with dyslexia was compared to that of twenty-two relatively good readers (mean age = 10.32 years) matched for non-verbal IQ who had an average score approximately 1SD above the normalised mean on the same test. The task and visual stimuli were identical to those used by Hansen et al. (2001) (Figure 12). Results showed that coherence thresholds on the global motion

task and the global form task were similar across readers with dyslexia and relatively good readers. These findings are difficult to reconcile with other research showing global motion processing deficits in children with dyslexia (Raymond & Sorensen, 1998) but there was a marked imbalance between the ratio of males to females in the participant groups. The group of children with dyslexia comprised fourteen males and nine females, whereas the group of relatively good readers comprised nine males and thirteen females (Table 2). There is some evidence to suggest that females may have significantly higher coherence thresholds than male adults on tasks requiring the processing of global motion (Billino et al., 2008; Hutchinson et al., 2012; Snowden & Kavanagh, 2006). Sex differences on global motion tasks have not been found in children aged between five and twelve years (Braddick et al., 2016ab) but the RDKs used in these studies created the perception of circular (rotational) as opposed to translational motion. Evidence suggest that this particular type of global motion is processed upstream of hMT in the medial superior temporal (MST) region (Duffy & Wurtz, 1991ab; Strong, Silson, Gouws, Morland, & McKeefry, 2017ab; Tanaka et al., 1986; Tanaka & Saito, 1989) so it remains a possibility that a significant difference between children with dyslexia and relatively good readers on the global motion task could have been masked by sex differences in the study by White et al. (2006).

A criticism of the global motion and global form tasks described thus far is that they are not always strictly comparable in terms of stimulus complexity and task demands (Table 2). To overcome this problem Tsermentseli, O'Brien and Spencer (2008) administered two directly analogous global motion and global

form tasks to twenty adults with developmental dyslexia (mean age = 23.4 years) who had a documented history of reading difficulties and twenty relatively good readers (mean age = 28.4 years) matched for full scale IQ. The stimuli in the global form task comprised an array of dot triplets that were oriented to form a concentric structure. Identical stimuli were used in the global motion task except the dots were displaced from the first position in the triplet to the last position, which created the perception of circular motion. A 1IFC task was used to measure coherence thresholds. In the global motion task, participants had to discriminate circular motion from stimuli containing randomly moving noise dots, whereas in the global form task they had to discriminate concentric structure from patterns containing randomly oriented dot triplets. Results showed that coherence thresholds on the global motion task and the global form task were similar across readers with dyslexia and relatively good readers. However, it is important to note that previous research has shown that readers with dyslexia only have marked difficulty on global motion tasks when local motion cues have to be integrated across extended trajectories (Raymond & Sorenson, 1998). The global motion sequences in Tsermentseli et al. (2008) comprised three discrete frames (two successive displacements), which may not have been sufficient to reveal differences between readers with dyslexia and relatively good readers.

1. 3. 5. 5. Sublexical vs. lexical processing

There is some evidence to suggest that contrast sensitivity for stimuli changing rapidly over time is only impaired in generally poor readers who have a deficit

with both phonological decoding and whole-word lexical processing (Borsting et al., 1996; Slaghuis & Ryan, 1999). However, it is currently unknown if global motion perception is more strongly related to some components underlying reading skill than others. To investigate this issue Slaghuis and Ryan (1999) used the Adult Dyslexia Test to identify five individuals for whom whole-word lexical processing skills were specifically impaired, three individuals for whom phonological decoding skills were specifically impaired, and seven individuals for whom both whole-word lexical processing skills and poor phonological decoding skills were impaired. A global motion task was also administered comprising conventional RDKs and a 1IFC procedure was used to measure coherence thresholds. On each trial, participants had to judge the overall direction of the stimulus (upwards, downwards, leftwards, rightwards). Results showed that dyslexic readers with a combination of poor whole-word lexical processing skills and poor phonological decoding skills had higher coherence thresholds than relatively good readers on the global motion task. These findings suggest that the performance of generally poor readers and individuals with poor phonological decoding skills, consistent with the dyslexic profile, differs on low-level visual perception tasks. However, the study design was very unbalanced and the number of participants in each group was very small. As previously mentioned, this important issue will be systematically addressed in Chapter 3.

1. 3. 5. 6. Orthographic regularity

A related issue concerns whether dyslexic readers of more regular orthographies such of German, which are characterised by more consistent grapheme to phoneme mappings than English, might exhibit a different pattern of performance on contrast sensitivity tasks. This is currently unclear because most of the studies cited so far investigated the dorsal stream vulnerability hypothesis in native English speakers (Table 2). To address this issue Kronbichler, Hutzler and Wimmer (2002) administered a global motion task to twenty-two German-speaking readers with developmental dyslexia (mean age = 13.71 years) who had a standard score at least 1.25SD below the normalised mean on a German oral reading test (Huttenlocher & Cohen-Levine, 1990). The performance of this group of readers with dyslexia was compared to that of twenty relatively good readers (mean age = 13.3 years) who were also native German speakers. Both reader groups were matched for non-verbal IQ. The stimuli in the global motion task were conventional RDKs. A 2IFC procedure was used to measure coherence thresholds. On each trial, participants had to discriminate RDKs (Figure 12A) from stimuli containing randomly moving noise dots (Figure 12B). Results showed that coherence thresholds on the global motion task did not differ significantly across readers with dyslexia and relatively good readers. These findings suggest that performance on global motion tasks is only impaired in dyslexic readers of more irregular orthographies such as English but Talcott et al. (2003) failed to replicate this results. They administered a global motion task to nineteen dyslexic readers of Norwegian, which has a regular orthography, and twenty-two relatively good readers who were also native Norwegian speakers. Participants in the dyslexia group had a reading age at least 1.5SD below that predicted by their

chronological age on a Norwegian reading test (Høien & Lundberg, 1991). It was not reported whether the reader groups were matched for chronological age and sex. The stimuli in the global motion task were conventional RDKs. As in the study by Kronbichler et al. (2002) a 2IFC procedure was used to measure coherence thresholds in which participants had to discriminate RDKs (Figure 12A) from stimuli containing randomly moving noise dots (Figure 12B). Results showed that readers with dyslexia had significantly higher coherence thresholds than relatively good readers on the global motion task. These findings do not corroborate those of Kronbichler et al. (2001) but dot speed was twice as fast in the study by Talcott et al. (2003) and it remains to be seen if this difference could account, in part, for the discrepancy between the results of the two studies. This is particularly important because a growing body of research has shown that these two factors play a critical role in the development of global motion perception during infancy and early childhood (Hadad, Schwartz, Maurer, & Lewis, 2015; Kiorpes & Movshon, 2004; Narasimhan & Giaschi, 2012; Meier & Giaschi, 2014, 2017).

The majority of studies cited so far that investigated the dorsal stream vulnerability hypothesis point to a deficit in the processing of global motion in some readers with dyslexia (Cornelissen et al., 1995; Raymond & Sorenson, 1998; Talcott et al, 2001) but the neural correlates of this impairment are still a matter of debate. It is possible that readers with dyslexia who exhibit elevated coherence thresholds on global motion tasks have atypical neural activity in brain regions that have been implicated in the processing of global motion such as hMT (Amano, Wandell, & Dumoulin, 2009; Braddick et al., 2000; Rees,

Friston, Koch, 2000; Tootell et al., 1995; Zeki et al., 1991). To address this issue Eden et al. (1996) asked six readers with developmental dyslexia (mean age = 26.8 years) who had a reading age at least 2SD below that predicted by their verbal IQ on the GORT (Gray, 1967) and eight relatively good readers (mean age = 25.5 years) matched for chronological age to passively view random-dot kinematograms inside an MRI scanner. Despite the small sample size, results showed that in relatively good readers, RDKs evoked a strong bi-lateral BOLD response in hMT, consistent with previous research (Amano et al., 2009; Braddick et al., 2000; Rees et al., 2000; Tootell et al., 1995). In readers with dyslexia, no significant bi-lateral BOLD response was found in hMT. These results support previous research showing that readers with dyslexia have lower bi-lateral activity in hMT than relatively good readers in response to drifting gratings (Demb et al., 1998b). They tell us something about the neural locus of the visual deficit in readers with dyslexia, but the computational underpinnings of this impairment are still unclear. Neuroimaging is not yet at the stage where it can inform us about computations that are being performed across populations of neurons in the human brain so the neural correlates of the global motion processing deficit in readers with dyslexia is still relatively unclear (Logothetis, 2008; Olman, 2015; Todd, Nystrom, & Cohen, 2013).

1. 3. 5. 7. Genotypic variation

Evidence suggests that contrast sensitivity for rapidly changing visual stimuli is impaired to a greater extent in dyslexic readers who have a deletion on the

DCDC2 candidate susceptibility gene (Cichinni et al. 2015; Morrone et al., 2011). It is possible that performance on global motion tasks might only be impaired in this subgroup of readers with dyslexia, which could provide an alternative explanation for why some studies have failed to uncover deficits in the processing of global motion in readers with dyslexia. To address this issue Cichinni et al. (2015) administered a global motion task to seven readers with developmental dyslexia who scored at least 2SD below the normalised mean on the MT Reading Test (Cornoldi & Colpo, 1995; Sartori, Job, & Tressoldi, 1995). Genotyping revealed that these individuals had the genetic deletion on *DCDC2*. The performance of this group of readers with dyslexia was compared to that of eight relatively good readers who did not have the genetic deletion. A 1IFC procedure was used to measure coherence thresholds in which participants had to judge the overall direction on the stimulus (upwards vs. downwards). Results showed that dyslexic readers with the genetic deletion had higher coherence thresholds than relatively good readers. However, it is unknown if dyslexic readers with the genetic deletion would also have had significantly higher coherence thresholds than dyslexic readers without the genetic deletion because Cicchini et al. (2015) did not investigate this issue. The sex composition of the group of dyslexic readers with the genetic deletion is also unknown and sample size is notably small (Table 2). An interesting question for future research is whether a deletion on the *DCDC2* gene mediates the relationship between the sex of an individual and coherence thresholds on global motion tasks.

1. 3. 5. 8. The causality question

A series of eye movements and fixations are made during reading, which means the position of words on the retinae is constantly changing over time (Rayner, 1998). The dorsal visual processing stream has been implicated in the processing of time-varying stimuli (Goodale & Milner, 1992; Milner & Goodale, 1995; Ungerleider & Mishkin, 1982) but a controversial issue is whether a putative deficit in this pathway is the primary cause or merely a consequence of developmental dyslexia (Boets et al., 2011; Gori, Seitz, Ronconi, Franceschini & Facoetti, 2016; Goswami, 2015; Olulade, Napoliello, & Eden, 2013). One way to address the causality question is to explore if global motion coherence thresholds measured before the commencement of formal reading training predict reading ability after formal reading training has begun. For example, Kevan and Pammer (2009) administered a global motion task and a global form task to nineteen children (mean age = 5.66 years) identified as being at high-risk of developmental dyslexia and thirty-nine children who were selected from the general population (mean age = 5.66 years). The visual stimuli and task were identical to those used by Hansen et al. (2001) and White et al. (2006). Results showed that coherence thresholds measured during kindergarten (before formal reading training had begun) did not predict scores on the Word Identification or Word Attack subtests of the WJ-III (Woodcock-Johnson et al., 2001) at Grade 1 (after formal reading training had begun). Importantly, scores on both WJ-III subtests measured at Grade 1 were significantly associated with coherence thresholds on the global motion task but not global form task also measured at Grade 1. These findings

suggest that a selective deficit in the dorsal stream is a consequence rather than the proximal cause of developmental dyslexia.

To further investigate this issue Gori et al. (2016, Experiment 1) administered a global motion task to seventy children during preschool (before the commencement of formal reading training). The visual stimuli were conventional RDKs. A 1IFC procedure was used in which participants had to judge the overall direction of the stimulus (upwards, downwards, leftwards, or rightwards). The number of correct responses was measured across four different coherence levels (10, 20, 30 and 40%). At Grade 1 (after formal reading training had begun) the MT Reading Test was administered (Cornoldi & Colpo, 1995; Sartori, Job, & Tressoldi, 1995). Participants were classified as having developmental dyslexia is they scored less than 1.5SD below the mean of the entire sample. Results showed that children who met this criterion for diagnosing dyslexia at Grade 1 performed significantly worse on the global motion task during preschool than children who were not classified as having dyslexia at Grade 1. These findings do not support the results of Kevan and Pammer (2009) but the 1IFC task used by Gori et al. (2016) necessitated a judgement about the overall direction of the stimulus. In the study by Kevan and Pammer (2009) participants performed an arguably less demanding detection task in which they had to discriminate RDKs from stimuli containing randomly moving noise dots (Table 2). Further research using directly comparable global motion tasks is needed to explore if a deficit in the dorsal visual processing stream is the proximal cause of dyslexia or reflects a lack of

reading experience during early childhood (Dehaene et al., 2010; Dehaene et al., 2015; Szwed et al., 2011; Szwed et al., 2012).

Neuroimaging studies also have a direct bearing on the direction of causality between reading ability and elevated coherence thresholds on global motion tasks. If a deficit in the dorsal stream is the proximal cause of dyslexia bi-lateral neural activity in hMT should be significantly lower in readers with dyslexia than relatively good readers matched for chronological age and reading age. If, on the other hand, a deficit in the dorsal stream is merely a consequence of dyslexia and reflects a lack of reading experience during infancy bi-lateral neural activity in hMT should be lower in readers with dyslexia than relatively good readers matched for chronological age but not reading age. To disentangle these possibilities Olulade et al. (2013) asked fourteen children with developmental dyslexia (mean age = 9.9 years) and fourteen relatively good readers matched for chronological age (mean age = 9.1 years) to view RDKs inside an MRI scanner. Twelve children with developmental dyslexia (mean age = 10.4 years) and twelve relatively good readers matched for reading age (mean age = 7.5 years) on the Word Identification subtest of the WJ-III (Woodcock-Johnson et al., 2001) also took part in the experiment. Results showed that readers with dyslexia had significantly lower bi-lateral activity in hMT than relatively good readers matched for chronological age but not reading age. These findings support the view that a selective deficit in the dorsal visual processing stream is more likely to be a consequence rather the proximal cause of developmental dyslexia but the bi-lateral BOLD signal in hMT was calculated by contrasting the neural

response to RDKs and static dots dispersed throughout the display in a homogenous manner. It is unclear if this localisation procedure is able to clearly differentiate activity in hMT because the motion and form stimuli were not directly analogous.

Intervention studies have also been carried out to investigate the causality question (Goswami, 2015). If a deficit in the dorsal visual processing stream reflects a lack of reading experience during infancy, an intervention specifically targeting the reading process should increase bi-lateral neural activity in hMT. To explore this hypothesis Olulade et al. (2013) conducted an additional experiment in which twenty-two children with developmental dyslexia (mean age range = 7.4 to 12 years) who had an average score below the normalised mean on the Word Identification and Word Attack subtests of the WJ-III Reading Test (Woodcock et al., 2001) viewed RDKs inside an MRI scanner. Data acquisition took place before and after an eight-week phonological-based intervention or a control intervention in which participants underwent mathematical training. Results showed that neural activity in right but not left hMT was significantly larger following the phonological-based intervention but not the math-based intervention. These findings suggest that reading experience has a strong influence on neural activity in hMT but it is unclear why the effect was more prominent in the right hemisphere than the left hemisphere. As previously mentioned, females typically have higher coherence thresholds than males on global motion tasks (Billino et al., 2008; Hutchinson et al., 2012; Snowden & Kavanagh, 2006). The neural correlates of this effect are yet to be determined but evidence suggests that hMT in the right

hemisphere of the male has a significantly larger volume and surface area than the corresponding region in the female cortex (Amunts et al., 2007; de Lacoste, Horvath, & Woodward, 1991; Kovalev, Kruggel, & von Cramon, 2003). The group of readers with developmental dyslexia who took part in the intervention study comprised thirteen males and nine females (Table 2). Thus, it is possible increased neural activity in right hMT following the phonological-based training in readers with dyslexia might reflect sex differences rather than reading experience *per se*.

Evidence suggests that readers with dyslexia have significantly lower bi-lateral neural activity in hMT than relatively good readers matched for chronological, but not reading age (Eden et al. 1996; Olulade et al., 2013). However, it is important to ascertain whether or not behavioural measures corroborate these fRMI results because human neuroimaging studies (Huk & Heeger, 2002; Villeneuve, Kupers, Gjedde, Ptito, & Casanova, 2005) and neurophysiological research in non-human primates (Horwitz & Newsome, 1999; Li et al., 2013; Schmid et al., 2014) has shown that several sub-cortical and cortical regions are involved in the processing of global motion (Gilaie-Doton, 2016). To further explore the causality question Gori et al. (2016, Experiment 2) conducted an additional experiment in which a global motion task was administered to fifteen children with developmental dyslexia (mean age = 11.13 years). The performance of this group of readers with dyslexia was compared to that of twenty-three relatively good readers matched for chronological age (mean age = 10.78 years) and thirteen relatively good readers matched for reading age (mean age = 8.46 years) on the MT Reading

Test (Cornoldi & Colpo, 1995; Sartori, Job, & Tressoldi, 1995). The task and visual stimuli were identical to those used in their previous experiment (Gori et al., 2016, Experiment 1). Results showed that readers with dyslexia performed significantly worse than relatively good readers matched for chronological age and reading age at all coherence levels tested. Although these findings support the dorsal stream vulnerability hypothesis they are difficult to reconcile with previous research showing that deficits in the processing of global motion are a consequence rather than the proximal cause of developmental dyslexia. (Kevan & Pammer, 2009; Olulade et al., 2013). Hence, the direction of causality between reading ability and elevated coherence thresholds on global motion tasks is still indeterminate.

Study	Matching criteria	Orthography	Age (years)		Sex ratio (m: f)		Motion task	Form task	Procedure	Motion deficit	Form deficit
			Dyslexia	Good	Dyslexia	Good					
Cicchini et al. (2015)	--	Italian	--	--	--	16:13	RDKs	--	1IFC	Yes	--
Cornelissen et al. (1995, Exp. 1)	FSIQ	English	9.73	9.89	23:6	13:6	Spatial segmentation	--	1IFC	Yes	--
Cornelissen et al. (1995, Exp. 2)	FSIQ	English	29	28.10	16:13	16:13	Spatial segmentation	--	1IFC	Yes	--
Gori et al. (2016)	--	Italian	11.13	8.46-10.78	--	--	RDKs	--	1IFC	Yes	--
Hansen et al. (2001)	NVIQ	English	28.9	24	--	--	RDKs	Static lines	2IFC	Yes	No

Kevan & Pammer (2009)	--	English	5.66	5.66	--	--	RDKs	Static lines	2IFC	Yes	No
Kronbichler et al. (2002)	NVIQ	German	13.71	13.3	--	--	RDKs	Static lines	2IFC	No	--
Raymond & Sorenson (1998, Exp. 1)	NVIQ	English	9.9	9.9	5:5	5:5	RDKs	--	1IFC	Yes	--
Raymond & Sorenson (1998, Exp. 2)	NVIQ	English	11.6	9.3	--	--	RDKs	--	1IFC	Yes	--
Talcott et al. (2001, Exp. 1)	FSIQ	English	25.2	22.2	--	--	RDKs	--	1IFC	Yes	--
Talcott et al. (2001, Exp. 2)	FSIQ	English	25.2	22.2	--	--	RDKs	--	1IFC	Yes	--
Talcott et al. (2003)	--	Norwegian	--	--	--	--	RDKs	Static lines	2IFC	Yes	--
Tsermentseli et al. (2008)	FSIQ	English	23.4	28.4	--	--	RDKs	Dot triplets	1IFC	No	No

White et al. (2006)	NVIQ	English	10.5	10.32	14:9	9:13	RDKs	Static lines	2IFC	No	No

Table 2. A summary of research that has explored the dorsal stream vulnerability hypothesis. FSIQ = full-scale IQ; NVIQ = non-verbal IQ; 1IFC = single-interval, forced-choice; 2IFC = two-interval, forced-choice.

1. 4. Summary

Although developmental dyslexia is primarily associated with poor phonological decoding skills (see section 1. 2.) evidence suggests that readers with dyslexia also have a visual deficit that could either be the proximal cause or merely a consequence of their difficulties with reading (Gori et al., 2016; Goswami, 2015; Kevan & Pammer, 2009; Olulade et al., 2013). Although five major theories have been proposed to explain the underlying nature of the visual deficit in developmental dyslexia (e.g. the magnocellular deficit hypothesis, the external noise exclusion hypothesis, the anchoring deficit hypothesis, the modified receptive field hypothesis and the dorsal stream vulnerability hypothesis) they have only received some support as described in the sections above. The aim of this thesis is to explore the origin of visual impairment in readers with dyslexia by addressing several key issues that remain unclear.

1. It is unknown if the global motion perception deficit in readers with dyslexia reflects a difficulty processing motion, temporal information or integrating local visual cues across multiple (>2) dimensions. To address this issue four diagnostic, global motion and form tasks were administered to large sample of adult readers in Chapter 3.

2. There are controversies regarding how developmental dyslexia should been defined (see section 1. 2.). For example, it has been suggested that dyslexia represents a distinct type of reading difficulty associated with

poor phonological decoding skills, whilst others have argued that it reflects the lower end of a normal distribution of reading ability (Fletcher, 2009; Siegel, 2006). To address this issue, two sets of analyses were conducted in Chapter 3. First, to investigate if general reading skills are associated with performance on each of the four visual tasks, a series of whole-sample analyses were conducted using a composite measure of reading ability. Second, to explore if performance on each of the four visual tasks differs across readers for whom phonological decoding skills are specifically impaired, consistent with the dyslexic profile, and relatively good readers, a series of between-group analyses were conducted.

3. Previous research has failed to control for factors that may be associated with performance on global motion tasks such as the sex of an individual and non-verbal IQ (Arranz-Paraíso & Serrano-Pedrazza, 2016; Billino et al., 2008; Cook et al., 2016; Hutchinson et al., 2012; Melnick et al., 2013; Snowden & Kavanagh, 2006; Tadin, 2015). These factors were directly investigated and systematically controlled for in all of the experiments outlined in this thesis.

4. To successfully parse the visual scene into meaningful entities, such as text into words, or words into letters, the visual system must also segment local features arising from different objects (Braddick, 1993). There is some evidence that the visual deficit in dyslexia extends to spatial segmentation, but previous research exploring this issue

confounded integration with segmentation and relied on measuring sensitivity at a single segment size (Cornelissen et al., 1995). These issues were directly addressed in Chapter 4 by administering a motion-based spatial segmentation task and an analogous form task to thirty-eight adults whose reading abilities ranged along a continuum.

5. The position of words on the retinae is constantly being updated during reading as a discrete series of eye movements and fixations are made (Rayner, 1998). Effective decoding of text, therefore, requires local visual information to be segmented over time, as well as across space. There is some evidence to suggest that the underlying nature of the visual deficit in dyslexia extends to temporal segmentation but previous research relied on a single measurement of sensitivity and failed to delineate temporal segmentation of motion and form information (Talcott et al., 1998). These issues were addressed in Chapter 6 by administering temporal versions of the spatial segmentation tasks to thirty-eight adults with a wide range of reading abilities.

6. The anchoring deficit hypothesis (see section 1. 3. 3.) proposes that individuals with dyslexia cannot utilise stimulus repetitions to form a perceptual anchor. However, it has not yet been studied using global motion and form tasks. This issue was addressed in Chapter 7 by administering a 2IFC global motion detection task and an analogous form detection task to forty-four adults with a wide range of reading skills. By varying the degree of uncertainty associated with the axis of

global motion or orientation, the ability to form a perceptual anchor was manipulated across different blocks of trials.

Chapter 2

General methods

2. 1. Participants

Participants were recruited either via an undergraduate research participation scheme or Student Support Services at the University of Nottingham. The latter was necessary to obtain a sufficient proportion of participants with reading difficulties. An advantage of recruiting adult University students is that factors known to be associated with reading skill such as non-verbal IQ are similar, so the results of this thesis are likely to reflect genuine differences in visual processing in relation to reading ability and developmental dyslexia. A disadvantage is that one cannot be sure if these differences also occur in children but this could be explored in future research. There is some evidence to suggest that visual processing in readers with dyslexia may be influenced by orthographic regularity (see section 1. 3. 1. 5.) so participants were required to have English as their first language. They were excluded from taking part if they had a neurodevelopmental disorder other than developmental dyslexia (e.g. ADHD, developmental dyspraxia, autism spectrum disorder, amblyopia) or a history of ocular ill health. Participants born less than thirty-two weeks gestation were also excluded because research has shown that individuals born preterm often exhibit atypical performance on global motion perception tasks (Taylor, Jakobson, Maurer, & Lewis, 2009). All participants had normal or

corrected-to-normal visual acuity and gave informed consent to take part. The ethics committee at the School of Psychology, University of Nottingham, granted ethical approval for all the experiments outlined in this thesis.

2. 2. Psychometric tests

Each participant completed conventional tests of reading ability and non-verbal IQ. Three measures of reading ability were included to assess different components underlying reading skill. First, the National Adult Reading Test (NART) was administered followed by the Test of Word Reading Efficiency (TOWRE) Sight Word Efficiency subtest and the TOWRE Phonemic Decoding Efficiency subtest. Finally, Raven's Standard Progressive Matrices (SPM) was administered to assess non-verbal IQ. Research has shown that non-verbal IQ but not verbal IQ is associated with performance on global motion tasks (Arranz-Paraíso & Serrano-Pedrazza, 2016). Thus, it was critical to determine if reading ability explained any additional variance in task performance after controlling for the effects of non-verbal IQ. Specific details relating to each of the three reading tests and Raven's SPM are provided in the sections below.

2. 2. 1. The National Adult Reading Test

To assess whole-word lexical processing skills the NART was administered (Nelson, 1991). It comprised fifty irregular words of increasing difficulty that

could not be pronounced using conventional phonetic rules (e.g. chord, placebo, beatify, sidereal). The test was non-timed. Participants were asked to read slowly down the list of words and the number of words read correctly was measured.

2. 2. 2. The Test of Word Reading Efficiency

To provide a measure of speeded reading the TOWRE was administered (Torgesen, Wagner, & Rashotte, 1999). This standardised measure of reading ability consists of two subtests: the TOWRE Sight Word Efficiency subtest and the TOWRE Phonemic Decoding Efficiency subtest. Specific details relating to each subtest are given below.

2. 2. 2. 1. Sight Word Efficiency subtest

The TOWRE Sight Word Efficiency subtest consists of 104 regular words of increasing difficulty (e.g. spell, describe, alienate, transient). Participants were given forty-five seconds to read as many words as possible and the number of words read correctly was measured.

2. 2. 2. 2. Phonemic Decoding Efficiency subtest

The TOWRE Phonemic Decoding Efficiency subtest consists of 63 non-words of increasing difficulty (e.g. ip, chur, dreker, pelnador). As in the TOWRE Sight Word Efficiency subtest, participants were given forty-five seconds to

read as many words as possible and the number of words read correctly was measured.

2. 2. 3. Raven's Standard Progressive Matrices

To assess non-verbal IQ Raven's SPM was given (Raven, Raven, & Court, 1988). This psychometric test comprises twelve sets of five problems. In each problem, participants were shown a matrix of geometric figures with one missing figure. An example of a problem similar to one in Raven's SPM is shown in Figure 13. The participant's task was to recognise similarities within the matrix and implement a rule to correctly identify the missing figure from a panel of six to eight different alternatives. The number of figures correctly identified was measured. Raven's SPM is not timed but it takes approximately forty-five minutes to complete.

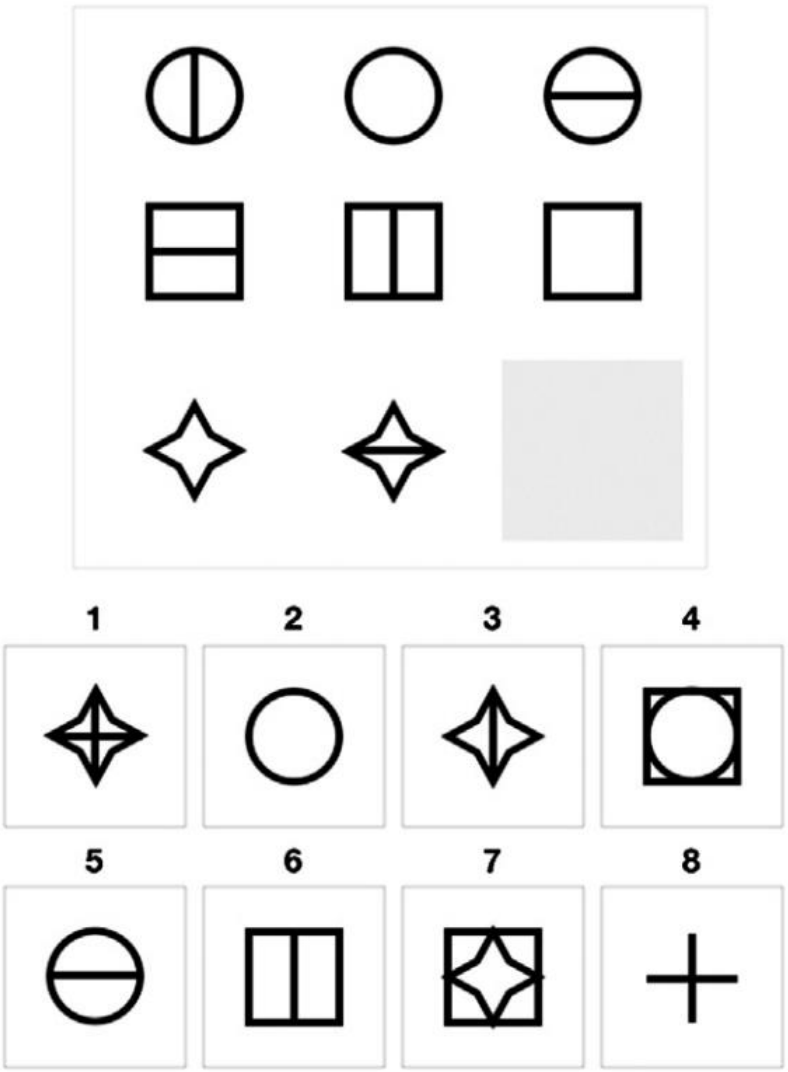


Figure 13. An example of a problem similar to one in Raven's SPM (Raven et al., 1988). The participant's task was to select the figure from the bottom panel that matches both the rows and columns of the matrix. Adapted from Kunda, McGreggor and Goel (2013).

2. 3. Statistical analyses

It is currently unclear if performance on low-level visual perception tasks can differentiate individuals with poor phonological decoding skills, consistent with the dyslexic profile, from generally poor readers because sample size was very small in previous studies that addressed this issue (Borsting et al., 1996; Slaghuis & Ryan 1999). To overcome this limitation, two types of analyses were conducted in Chapter 3. First, to investigate if general reading skills are associated with visual task performance, a series of whole-sample analyses were conducted using a composite measure of reading ability. Within these analyses the influence of the sex of an individual and non-verbal IQ on visual task performance were also investigated. Second, to explore if performance on the visual tasks differs across readers with dyslexia who had poor phonemic decoding skills (standard score $\leq$ 85 on TOWRE Phonemic Decoding Efficiency subtest) and good readers, a series of between-group analyses were conducted. These groups were matched for non-verbal IQ. This enabled performance on the visual tasks to be determined across individuals with developmental dyslexia compared to generally poor readers.

2. 4. Composite reading score

To explore how general reading ability relates to performance on the visual tasks a composite measure of reading skill was needed. First, raw scores for each of the three reading tests (the NART, TOWRE Sight Word Efficiency subtest, TOWRE Phonemic Decoding Efficiency subtest) were z-transformed, to allow direct comparisons to be made between sets of scores that may have very different means and/or standard deviations. Bivariate correlations (Pearson's product-moment correlation coefficient) were then performed to investigate the relationships between the individual measures of reading ability. Correlations between the three reading tests ranged from weak to strong in all the experiments conducted in this thesis. For this reason, principal component analysis (PCA) was used to calculate the composite measure of reading skill as it's utility is not dependent upon correlation strength unlike taking a simple average z-score of each reading test. Raw scores on the three individual measures of reading ability were entered into the PCA, which was performed on the correlation matrix.

2. 5. Apparatus and visual stimuli

Visual stimuli were generated using either an *Apple Macintosh G5* or an *Apple Mac mini* computer and custom software written in either the "C" programming language or MATLAB using elements of Psychtoolbox (Brainard, 1997). They were displayed on an *Intergraph Interview 24hd96* cathode ray tube (CRT) monitor (frame refresh rate of 100Hz unless otherwise stated), which was carefully gamma-corrected using a photometer and look-up-tables. As an additional precaution, commonly used psychophysical methods were used to check the adequacy of the gamma-correction (Ledgeway & Smith, 1994; Nishida, Ledgeway, & Edwards, 1997). The maximum luminance available with this apparatus was 68cd/m^2.

Grey-scale stimuli with (nominal) eight-bit luminance resolution were used for the visual perception tasks. They were each composed of a spatial array of local elements, either static or dynamic, on a homogenous background presented within the confines of a window located at the centre of the display. Some of the visual tasks reported in this thesis investigated the ability of participants to integrate these elements, to determine their global motion or global form. Other tasks used required the participants to segment the display into adjacent regions, based upon differences in the properties of the local elements comprising the stimulus. In all cases objective, forced-choice, psychophysical methods were employed to measure a coherence threshold for each participant on each visual task. Precise details of the visual stimuli used in

each of the experiments, will be described in the subsequent experimental chapters.

2. 6. Psychophysical procedure

Performance on the visual tasks was measured using a 3-down, 1-up adaptive staircase procedure tracking the 79% correct performance level (Cornsweet, 1962; Levitt, 1971; Wetherill & Levitt, 1965). The graph in Figure 14 shows an example of how the staircase converged upon a coherence threshold for a single participant in four separate blocks of trials. A reversal occurred when the coherence of the stimulus increased, when it had last decreased, or vice versa. Unless otherwise stated, the staircase terminated when a minimum number of twelve reversals had been reached and the arithmetic mean of the last six reversals was calculated as the threshold for that particular staircase. The initial step size was equal to the total number of elements in the display and it halved after every reversal. Participants completed at least four blocks of trials on each visual task administered. The arithmetic mean threshold and the standard error of the mean (SEM) were then calculated as measures of task performance.

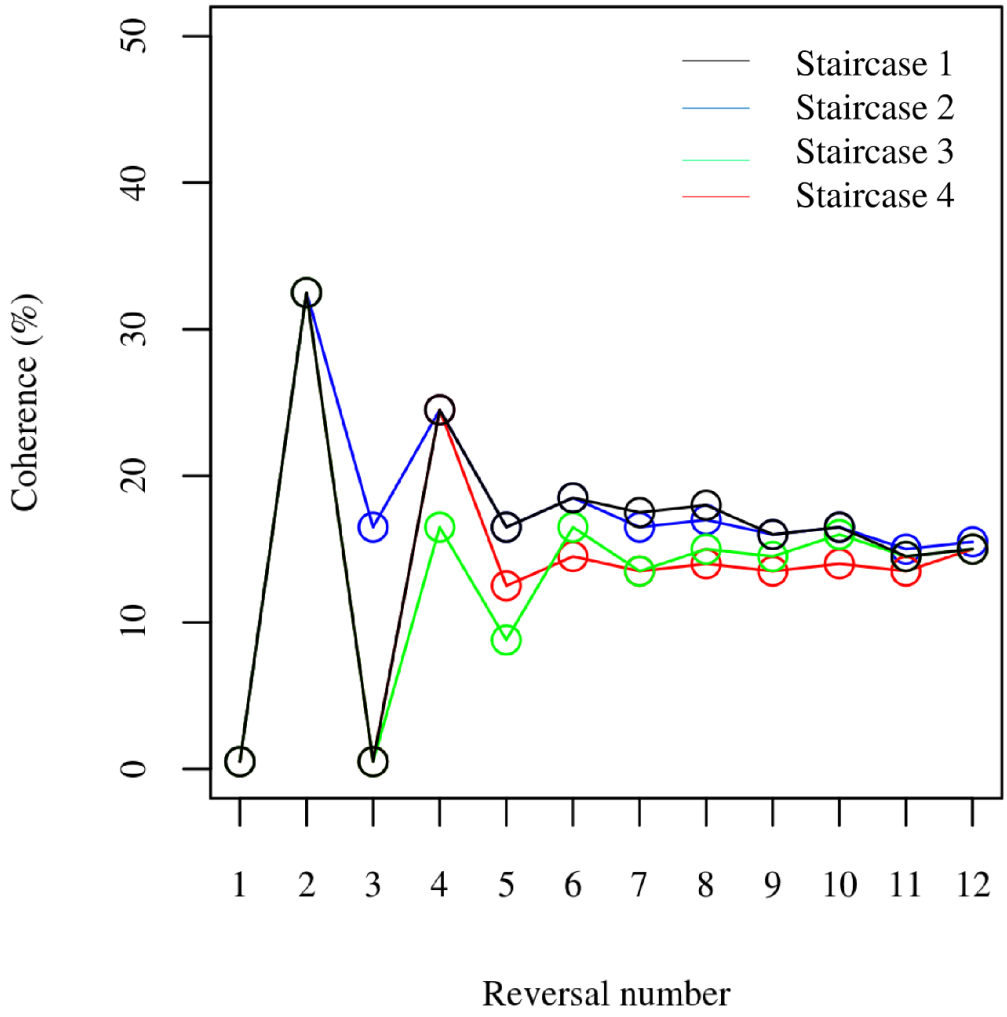


Figure 14. An example graph showing how the adaptive staircase procedure converged upon a coherence threshold for a single participant in four separate blocks of trials. A reversal occurred then the coherence of the stimulus decreased, when it had last increased, and vice versa.

Chapter 3

Why is the processing of global motion impaired in adults with developmental dyslexia?[1]

3. 1. Introduction

Vulnerability of the dorsal visual processing stream has been suggested as a primary origin of impairment in readers with developmental dyslexia and a range of neurodevelopmental disorders (Atkinson & Braddick, 2013; Braddick et al., 2003; Braddick & Atkinson, 2011). Dorsal stream vulnerability is claimed to manifest as a selective deficit in the processing of global motion, relative to global form (see section 1. 3. 5.). Several studies have shown that both children and adults with dyslexia have significantly higher coherence thresholds than relatively good readers on global motion tasks (Cornelissen et al., 1995, Cicchini et al., 2015, Gori et al., 2015b, Hansen et al., 2001; Kevan & Pammer, 2009; Raymond & Sorenson, 1998; Slaghuis & Ryan, 1999; Talcott et al., 2001) but such a deficit may reflect a difficulty processing motion, temporal information or integrating local visual cues across multiple (>2) dimensions. Previous research has also failed to investigate factors that

[1] The results outlined in this chapter have been published in *Brain and Cognition*. Citation: Johnston, R., Pitchford, N. J., Roach, N. W., Ledgeway, T. (2016). Why is the processing of global motion impaired in adults with developmental dyslexia? *Brain and Cognition, 108*, 20-31.

are known to be associated with performance on global motion tasks such as the sex of an individual and non-verbal IQ (Arranz-Paraíso & Serrano-Pedrazza, 2016; Billino et al., 2008; Cook et al., 2016; Hutchinson et al., 2012; Melnick et al., 2013; Snowden & Kavanagh, 2006; Tadin, 2015). To resolve these issues in the present study four global motion and global form tasks were administered to a large sample of adult readers (N = 106) to characterise their perceptual abilities. These were: a random-dot global motion task, a spatially 1-D global motion task, a static global form task and a temporally-defined global form task (Figure 15).

There are controversies regarding how developmental dyslexia should been defined. Some have argued that dyslexia represents a distinct type of reading difficulty associated with poor phonological decoding skills, whilst others have argued that it reflects the lower end of a normal distribution of reading ability (Fletcher, 2009; Siegel, 2006). Thus, two sets of analyses were conducted in the present study. First, to investigate if general reading skills are associated with performance on each of the four visual tasks, a series of whole-sample analyses were conducted using a composite measure of reading ability. Within these analyses the effects of sex and non-verbal IQ on visual task performance were also investigated. Second, to explore if performance on each of the four visual tasks differs across readers for whom phonological decoding skills are specifically impaired, consistent with the dyslexic profile, and relatively good readers, a series of between-group analyses were conducted. The two reader groups were matched for non-verbal IQ, which enabled performance on the

visual tasks to be delineated across individuals with dyslexia compared to generally poor readers.

The four visual tasks administered were specifically designed to reveal the underlying nature of the perceptual deficit in readers with dyslexia. Specific predictions relating to the pattern of impairment expected on these tasks are given in Table 3. If, as previously claimed, readers with dyslexia have a specific difficulty processing motion, they would be expected to have significantly higher coherence thresholds on both the random-dot global motion task and the spatially 1-D global motion task. If, on the other hand, the perceptual deficit in readers with dyslexia reflects a difficulty with temporal processing, they would be expected to have significantly higher coherence thresholds on the tasks requiring precise transmission of time-varying information, namely the random-dot global motion task, spatially 1-D global motion task and temporally-defined global form task. Finally, if readers with dyslexia have a difficulty confined to the most computationally-demanding tasks, requiring spatiotemporal integration of local information across multiple (>2) dimensions, they would be expected to have significantly higher coherence thresholds on the random-dot global motion and temporally-defined global form tasks. Similar predictions could be made for individuals who are generally poor readers (using the composite measure of reading skill across the three reading tasks) if reading ability is shown to relate to performance on the visual tasks.

Source of difficulty	Impaired	Typical
Motion processing	Random-dot global motion Spatially 1-D global motion	Static global form Temporally-defined global form
Temporal processing	Random-dot global motion Spatially 1-D global motion Temporally-defined global form	Static global form
Multi-dimensional integration (>2 dimensions)	Random-dot global motion Temporally-defined global form	Spatially 1-D global motion Static global form

Table 3. Predicting performance on the four global motion and global form tasks. Impaired = generally poor readers and individuals with dyslexia expected to have significantly higher coherence thresholds than relatively good readers; Typical = no significant difference expected between generally poor readers/individuals with dyslexia and relatively good readers.

3. 2. Materials and methods

3. 2. 1. Participants

A large sample of adults (*N* = 106; 64 female and 42 male) with a wide range of reading abilities was recruited to participate in the study. The mean age of the participants was 22.02 years (*SD* = 62.47 months). Additional information on how the sample was recruited and exclusion criteria is provided in Chapter 2 (see section 2. 1.).

3. 2. 2. Psychometric tests

Each participant completed tests of non-verbal IQ and reading ability (see section 2. 2.).

3. 2. 3. Visual stimuli

Stimuli were viewed binocularly at a distance of 114cm and were presented within the confines of a square display window in the centre of the monitor, subtending 12ºx12º. Each stimulus was composed of an ensemble of "black" elements (0.01cd/m^2), either dots (diameter 0.12º) or elongated bars (0.12ºx12º), presented against a uniform "grey" (34cd/m^2) background. These elements were either static or could be made to move or flicker depending on the nature of the visual task employed. More precise details relating to stimulus generation in each of the four visual tasks are given below.

3. 2. 3. 1. Random-dot global motion task

Stimuli in the random-dot global motion task (Figure 15A) were conventional RDKs. They consisted of eight images, each containing 200 dots that were presented consecutively at a rate of 18.75Hz to create the perception of apparent motion. Each individual dot was displaced by 0.12º on each update, resulting in a drift speed of 2.26º/s. The "strength" or coherence of the stimulus could be varied between 0 and 100% by constraining some of the dots to move in a common direction (*signal* dots) and the remainder to move randomly (*noise* dots). Whether an individual dot was assigned to be signal or noise was randomised on every displacement, so the direction in which that dot moved was limited in time. The subjects' task was to judge the global (overall) direction of the RDK, which was chosen to be upwards or downwards on each trial with equal probability. This task required the integration of local information across two spatial dimensions and over time (*x*, *y*, & *t*).

3. 2. 3. 2. Spatially one-dimensional (1-D) global motion task

Stimuli in the spatially 1-D global motion task (Figure 15B) were directly analogous to the random-dot global motion patterns previously described, except they comprised 50 horizontal bars, rather than dots. The coherence of the stimulus could be varied between 0 and 100% by constraining some the bars to move in a common direction (*signal* bars) and others to move randomly (*noise* bars). As in the random-dot global motion task, the speed of the bars was identical (2.26º/s), regardless of whether they were assigned to be signal or

noise. Again, the subject's task was the judge the global direction of the stimulus, which was chosen to be upwards or downwards on each trial with equal probability. This task required the integration of local information across one dimension of space and over time (*y* & *t*).

3. 2. 3. 3. Static global form task

Stimuli for the static global form task (Figure 15C) were generated using a full 8-frame random-dot global motion sequence. The individual frames were then spatially superimposed to create a static image (Simmers et al. 2005). Some of the dots in the stimulus (*signal* dots) formed localised streaks, orientated along a common axis, whilst others (*noise* dots) formed random groupings. By changing the relative proportions of signal to noise dots in the image the coherence of the stimulus could be varied between 0 and 100%. The subjects' task was to judge the overall orientation of the stimulus, which was chosen to be vertical or horizontal on each trial with equal probability. This required local information to be integrated across two dimensions of space (*x* & *y*).

3. 2. 3. 4. Temporally-defined global form task

Stimuli in the temporally-defined global form task (Figure 15D) consisted of 200 dots that were randomly replotted asynchronously at a rate of 18.75Hz. Half the dots (population 1) were spatially jittered, whilst the other half (population 2) remained the static. The converse then occurred, and so on throughout the presentation. An orientated boundary was created by

constraining more of population 1 to fall in one half of the display and population 2 in the opposing part. The coherence of the temporal information, giving rise to the perceptual boundary, could be varied between 0 and 100%. The subjects' task was to judge the overall orientation of the perceptual boundary, which was chosen to be vertical or horizontal on each trial with equal probability. This task required local information to be integrated or compared across two spatial dimensions and over time (*x*, *y*, & *t*).

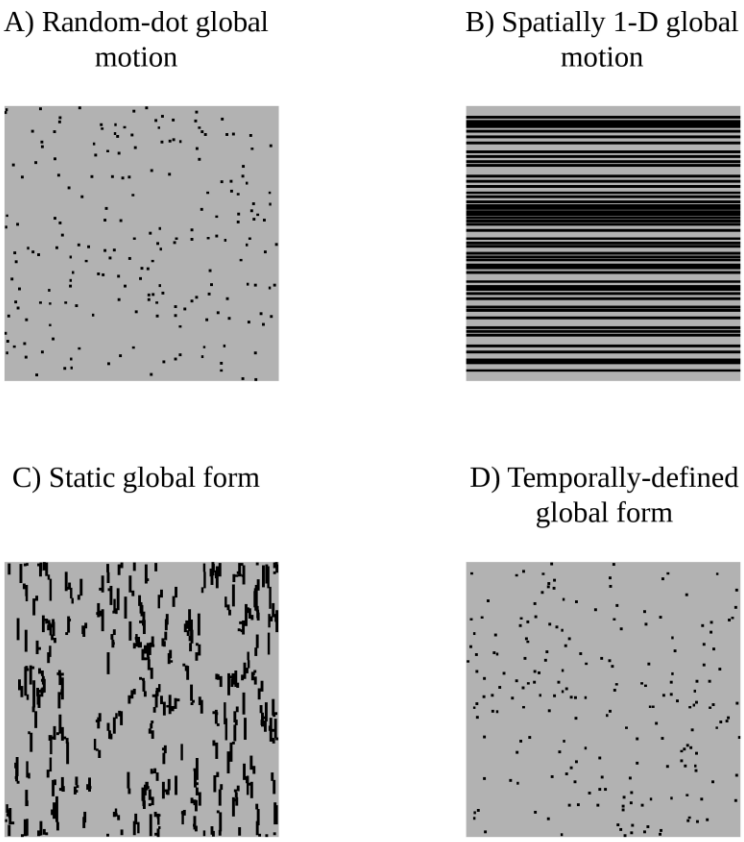


Figure 15. Schematic illustration of the visual stimuli used in A) the random-dot global motion task, B) the spatially 1-D global motion task, C) the static global form task and D) the temporally-defined global form task. Note that the temporally-defined global form task cannot be adequately depicted in this figure, as its apparent spatial structure arises from the asynchronous jittering of individual dots over time.

3. 2. 4. Procedure

Coherence thresholds were obtained for each of the visual tasks using a single-interval, forced-choice procedure and a 3-down, 1-up adaptive staircase. The initial step size was equal to the total number of elements in the display and this decreased by half after each reversal. Additional information on how the staircase converged on a coherence threshold for each participant is given in Chapter 2 (see section 2. 6.).

3. 2. 5. Statistical analyses

The whole-sample and between-group regression analyses are outlined below.

3. 2. 5. 1. Whole-sample analyses: hierarchical regression

These analyses were conducted to explore how general reading ability relates to performance on each of the four visual tasks so a composite measure of reading skill was needed. Information on how the composite score was generated can be found in Chapter 2 (see section 2. 4.). The aim of this study was to explore if general reading ability is associated with performance on each of the four visual tasks, so a regression model was built for each task with coherence threshold as the dependent variable and reading ability as the independent variable. However, the overall pattern of results did not change when reading ability was the dependent variable and coherence threshold was the independent variable. As previous research has found that the sex of an

individual and non-verbal IQ are associated with performance on tasks requiring motion processing (Arranz-Paraíso & Serrano-Pedrazza, 2016; Billino et al., 2008; Cook et al., 2016; Hutchinson et al., 2012; Melnick et al., 2013; Snowden & Kavanagh, 2006; Tadin, 2015), these were entered as control variables at step 1. Scores on the composite measure of reading skill were introduced at step 2. The R^2 change at step 2 was evaluated to determine if reading ability explained any additional variance after controlling for the effects of the sex of an individual and non-verbal IQ. A variation of Cohen's f^2 was used to calculate local effect size with 0.02 considered a small, 0.15 a medium and 0.35 a large effect, respectively (Cohen, 1988; Selya, Rose, Dierker, Hedeker, & Mermelstein, 2012).

3. 2. 5. 2. Between-group analyses: hierarchical regression

To investigate if the performance of individuals that have poor phonemic decoding skills, consistent with the dyslexic profile, differs from that of good readers across the four visual tasks, a series of between-group regression analyses were conducted. Evaluation of the individual measures of reading ability revealed forty-three participants (40.6% of the entire sample) had standard scores less than or equal to 85 (at or below the 15th percentile) on the TOWRE Phonemic Decoding Efficiency subtest, which falls into the conventional range for identifying individuals with developmental dyslexia (Heath, Bishop, Hogben, & Roach, 2006; Pugh et al. 2014). Performance of this group of readers with dyslexia was compared to that of relatively good readers who did not exhibit a phonological deficit. To identify the group of

good readers standard scores on the TOWRE Phonemic Decoding Efficiency subtest were ranked and the top forty-three individuals were selected (range of standard scores = 93-120). This ensured a balanced design in which all of the good readers' scores were either within, or better, than the normal range (±1*SD*) on the TOWRE Phonemic Decoding Efficiency subtest. The group of readers with dyslexia (identified by poor phonemic decoding skills) also had significantly lower scores than the group of good readers on the NART and TOWRE Sight Word Efficiency subtest, as reported in Table 4. Importantly, there was no significant group difference on the SPM measure of non-verbal IQ, hence any differences in the performance of the dyslexia group compared to the good readers on the four visual tasks cannot be attributed to differences in non-verbal intelligence. A series of regression analyses were then conducted to compare the performance of readers with dyslexia and relatively good readers across the four visual tasks. For each task, a model was built with coherence threshold as the dependent variable. As above, the sex of an individual and non-verbal IQ were entered at step 1 as control variables then Reading Group (Good = 0; Dyslexia = 1) was introduced at step 2. The R^2 change was evaluated to determine if Reading Group explained any additional variance after controlling for the effects of sex and non-verbal IQ. As above, Cohen's f^2 was used to calculate local effect size (Cohen, 1988; Selya et al., 2012).

	Dyslexia ($N = 43$)				Good ($N = 43$)				t_{84}
	M	*Median*	*SD*	*Range*	*M*	*Median*	*SD*	*Range*	
NART raw score (max 50)	23.72	24.00	6.03	7.00-33.00	29.63	29.00	4.32	21.00-44.00	5.22***
TOWRE Sight Word Efficiency	78.16	77.00	6.24	66.00-96.00	92.53	90.00	12.06	71.00-113.00	6.94***
TOWRE Phonemic Decoding Efficiency	80.72	83.00	4.91	62.00-85.00	104.33	103.00	9.61	93.00-120.00	14.34***
SPM raw score (max 60)	50.02	51.00	5.63	39.00-58.00	50.79	51.00	3.91	42.00-57.00	0.73

Table 4. Group psychometric statistics. Standard scores ($M = 100$, $SD = 15$) are shown unless otherwise stated. NART = National Adult Reading Test; TOWRE = Test of Word Reading Efficiency; SPM = Raven's Standard Progressive Matrices. * $p < .05$; ** $p < .01$; *** $p < .001$.

3. 2. 5. 3. Independence of visual tasks: bivariate correlations

Finally, we wanted to investigate the proposed independence of the dorsal and ventral processing streams, as measured by tasks of global motion and global form perception (Atkinson & Braddick, 2013; Braddick et al., 2003; Braddick & Atkinson, 2011). To explore relationships between the four psychophysical tasks across the entire sample (N = 106) raw coherence thresholds were z-transformed for each task, and then bivariate correlations (Pearson's product-moment correlation coefficient) were calculated.

3. 3. Results

3. 3. 1. Composite reading score: PCA

The correlations between the three individual measures of reading ability ranged from weak to strong (r = 0.27 to 0.61, see Figure 16) so PCA was conducted to calculate the composite measure of reading skill (see Chapter 2, section 2.5 Composite reading score). Raw scores for the three reading tests were entered in the analysis, which was performed on the correlation matrix. Results showed a single principal component that accounted for 64% of the total variance amongst the three measures of reading ability (*Eigenvalue 1* = 1.93; *Eigenvalue 2* = 0.74; *Eigenvalue 3* = 0.33). Loadings for the NART and the TOWRE Sight Word Efficiency subtest were within the same range (0.71 and 0.79, respectively) but the TOWRE Phonemic Decoding Efficiency subtest contributed slightly more to the construct (loading = 0.90). Principal component scores were thus extracted for each participant in the entire sample and entered into the whole-sample regression analyses.

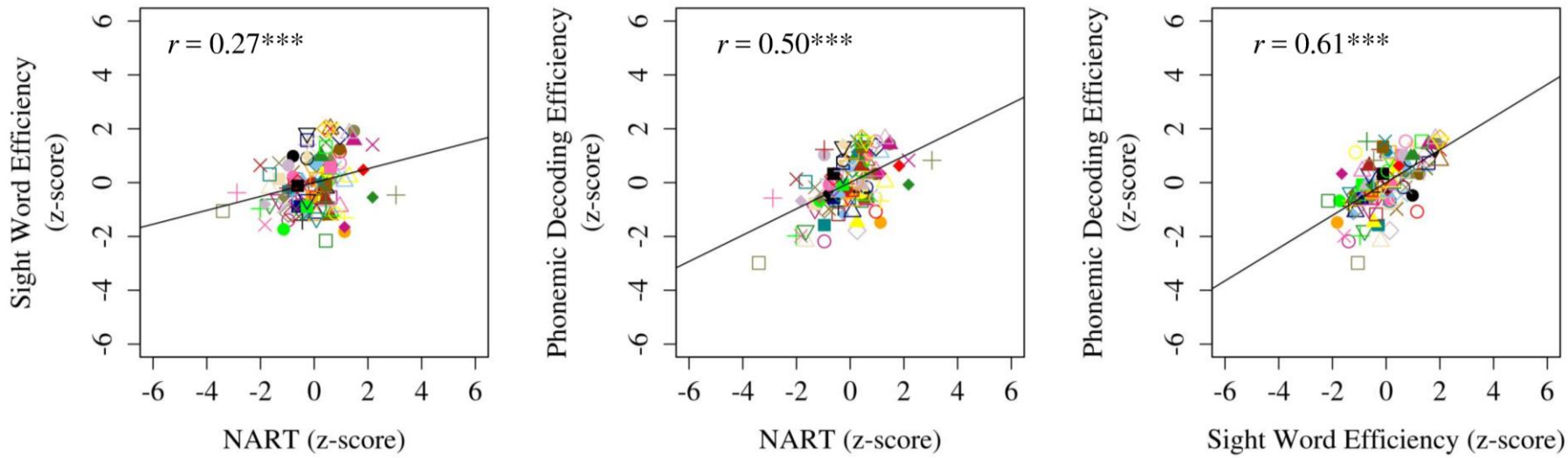


Figure 16. Bivariate scatter plots showing relationships between scores on the three individual measures of reading ability in the entire sample (*N* = 106). Positive and negative z-scores indicate scores better than and worse than the mean of the sample, respectively. Note that z-scores were used for illustrative purposes only and did not influence the correlations. NART = National Adult Reading Test; TOWRE = Test of Word Reading Efficiency. * = $p < .05$; ** = $p < .01$; *** = $p < .001$.

3. 3. 2. Whole-sample analyses: hierarchical regression

Results for the whole-sample analyses are described in the sections below. Table 5 reports the raw coherence thresholds for the four visual tasks across the entire sample. Regression analysis results for each of the four visual tasks are reported in Table 6.

3. 3. 2. 1. Random-dot global motion task

In the regression model for the random-dot global motion task, the control variables explained 16% of the variance, $F_{2, 103} = 9.79$, $p < 0.001$. The sex of an individual was associated with performance on the task. Females' coherence thresholds were significantly higher than those of males. In addition, non-verbal IQ was a significant predictor of performance. Individuals with a lower IQ had higher coherence thresholds on the random-dot global motion task. At step two, the R^2 change was significant, $F_{1, 102} = 7.80$, $p < 0.01$. General reading skill was negatively associated with performance on the task. It explained an additional 6% of the variance after controlling for the effects of sex and non-verbal IQ. Coherence thresholds were elevated in those who were generally poor at reading i.e. had lower scores on the composite measure of reading skill.

3. 3. 2. 2. Spatially 1-D global motion task

The control variables explained 8% of the variance in the model for the spatially 1-D global motion task, $F_{2, 103} = 4.33$, $p = 0.02$. There was no effect of sex but non-verbal IQ was a significant predictor of performance. Individuals with lower IQ had higher coherence thresholds on the spatially 1-D global motion task. The R^2 change at step two was significant, $F_{1, 102} = 5.15$, $p = 0.03$. General reading skill was negatively associated with performance on the task. It explained an additional 4% of the variance after controlling for the effects of sex and non-verbal IQ. Coherence thresholds were higher in those who had lower composite scores for reading.

3. 3. 2. 3. Static global form task

In the model for the static global form task, the control variables did not explain a significant proportion of the variance, $F_{2, 103} = 0.28$, $p = 0.76$. Furthermore, the R^2 change at step two did not reach statistical significance, $F_{1, 102} = 0.20$, $p = 0.65$. Reading skill was not associated with performance on the static global form task.

3. 3. 2. 4. Temporally-defined global form task

The sex of an individual and non-verbal IQ did not explain a significant amount of variance in the model for the temporally-defined global form task, $F_{2, 103} = 1.60$, $p = 0.21$. However, the R^2 change at step two was significant, $F_{1, 102} = 11.16$, $p < 0.01$. General reading skill was negatively associated with performance on the task. It explained an additional 10% of the variance after

controlling for the effects of sex and non-verbal IQ. Coherence thresholds were elevated in those who were generally poor at reading compared to those with higher reading scores.

	Male (N = 42)			Female (N = 64)		
	M	*Median*	*SD*	*M*	*Median*	*SD*
Random-dot global motion	16.80	15.64	6.68	21.89	18.47	10.78
Spatially 1-D global motion	18.74	13.97	11.32	18.15	15.53	11.67
Static global form	14.87	14.04	4.31	14.90	14.54	3.81
Temporally-defined global form	91.47	91.88	6.10	91.96	92.92	5.45

Table 5. Coherence threshold (%) statistics for the entire sample of readers (N = 106).

Visual task	*N*	Step	R^2	ΔR^2	*B*	*SE B*	β	f^2
Random-dot global motion	106	Step 1	**0.16*****					
		Sex			**4.48**	**1.79**	**0.23***	**0.06**
		SPM			**-0.63**	**0.19**	**-0.31****	**0.11**
		Step 2	**0.22*****	**0.06****				
		Sex			**4.79**	**1.73**	**0.24****	
		SPM			**-0.56**	**0.18**	**-0.27****	
		Reading skill			**-2.39**	**0.85**	**-0.25****	**0.08**
Spatially 1-D global motion	106	Step 1	**0.08***					
		Sex			-1.25	2.22	-0.05	
		SPM			**-0.68**	**0.23**	**-0.28****	**0.09**
		Step 2	**0.12****	**0.04***				
		Sex			-0.94	2.18	-0.04	
		SPM			**-0.61**	**0.23**	**-0.25****	
		Reading skill			**-2.44**	**1.08**	**-0.21***	**0.05**
Static global Form	106	Step 1	0.01					
		Sex			-0.03	0.80	-0.00	
		SPM			-0.06	0.08	-0.07	
		Step 2	0.01	0.00				
		Sex			-0.01	0.81	-0.00	
		SPM			-0.06	0.09	-0.07	
		Reading skill			-0.18	0.40	-0.04	
Temporally-defined global form	106	Step 1	0.03					
		Sex			0.29	1.13	0.03	
		SPM			-0.21	0.12	-0.17	
		Step 2	**0.13****	**0.10****				
		Sex			0.52	1.08	0.04	
		SPM			-0.15	0.11	-0.13	
		Reading skill			**-1.78**	**0.53**	**-0.31****	**0.11**

Table 6. Whole-sample analyses. A model was run for each visual task with threshold as the dependent variable. The control variables (i.e. the sex of an individual and non-verbal IQ) were entered into the models at step one. Scores on the composite measure of reading skill (derived from the PCA) were introduced at step two. The performance of the entire sample was considered (N = 106). SPM = Raven's Standard Progressive

Matrices. * $p < .05$; ** $p < .01$; *** $p < .001$.

3. 3. 3. Between-group analyses: hierarchical regression

Results from the between-group analyses are described in the sections below. Raw coherence thresholds for the group of readers who met conventional criteria for diagnosing dyslexia and relatively good readers are reported in Table 7. For each task, results from the between-group regression analyses are reported in Table 8 and described in the sections below.

3. 3. 3. 1. Random-dot global motion task

In the regression model for the random-dot global motion task, the control variables explained 19% of the variance, $F_{2, 83} = 9.89$, $p < 0.001$. The sex of an individual was associated with performance on the task. Females' coherence thresholds were significantly higher than those of males. In addition, non-verbal IQ was a significant predictor of performance. Individuals with a lower IQ had higher coherence thresholds on the random-dot global motion task. At step two, the R^2 change was significant, $F_{1, 82} = 8.25$, $p < 0.01$. Reading group was associated with performance on the task. It explained an additional 8% of the variance after controlling for the effects of sex and non-verbal IQ. Coherence thresholds were significantly higher in readers with dyslexia who had poor phonemic decoding skills.

3. 3. 3. 2. Spatially 1-D global motion task

The control variables explained 6% of the variance in the model for the spatially 1-D global motion task, $F_{2, 83} = 2.55$, $p = 0.08$. There was no significant effect of sex but non-verbal IQ was negatively associated with performance. Individuals with a lower IQ had higher coherence thresholds on the spatially 1-D global motion task. The R^2 change at step two approached but did not reach statistical significance, $F_{1, 82} = 3.20$, $p = 0.08$. Coherence thresholds did not differ between the two reader groups. However, there was a non-significant trend.

3. 3. 3. 3. Static global form task

The sex of an individual and non-verbal IQ did not explain a significant amount of variance in the model for static global form task, $F_{2, 83} = 0.11$, $p = 0.90$. Moreover, the R^2 change at step two failed to reach statistical significance, $F_{1, 82} = 0.10$, $p = 0.75$. Reading group was not associated with performance on the static global form task. Coherence thresholds did not differ significantly between the two groups.

3. 3. 3. 4. Temporally-defined global form task

The control variables did not explain a significant amount of variance in the model for the temporally-defined global form task, $F_{2, 83} = 1.49$, $p = 0.23$. However, the R^2 change at step two was significant, $F_{1, 82} = 6.02$, $p = 0.02$. Reading group was associated with performance on the task. It explained an additional 7% of the variance after controlling for the effects of sex and non-

verbal IQ. Coherence thresholds were significantly higher in the group of readers with dyslexia who had poor phonemic decoding skills.

	Male ($N = 33$)						Female ($N = 53$)					
	Dyslexia ($N = 17$)			Good ($N = 16$)			Dyslexia ($N = 26$)			Good ($N = 27$)		
	M	*Median*	*SD*	*M*	*Median*	*SD*	*M*	*Median*	*SD*	*M*	*Median*	*SD*
Random-dot global motion	16.61	16.35	5.91	15.61	15.26	5.27	27.77	25.38	12.76	18.84	17.12	7.68
Spatially 1-D global motion	21.72	15.20	12.98	14.60	12.33	8.94	21.00	16.93	14.68	17.41	15.27	9.59
Static global form	14.37	14.93	3.57	15.49	13.81	5.70	15.06	15.15	3.30	14.78	13.15	4.58
Temporally-defined global form	93.49	93.39	4.09	88.33	89.77	7.89	92.75	93.92	5.05	90.76	92.67	5.89

Table 7. Group coherence threshold (%) statistics.

Visual task	*N*	Step	R^2	ΔR^2	*B*	SE B	β	f^2
Random-dot global motion	86	Step 1	**0.19*** **					
		Sex			**6.63**	**2.04**	**0.32****	**0.12**
		SPM			**-0.57**	**0.21**	**-0.27****	**0.09**
		Step 2	**0.27*** **	**0.08****				
		Sex			**6.80**	**1.96**	**0.33*** **	
		SPM			**-0.52**	**0.20**	**-0.25***	
		Group			**5.47**	**1.91**	**0.27****	**0.11**
Spatially 1-D global motion	86	Step 1	0.06					
		Sex			0.42	2.63	0.02	
		SPM			**-0.59**	**0.27**	**-0.24***	**0.06**
		Step 2	**0.09***	0.03				
		Sex			0.56	2.59	0.02	
		SPM			**-0.55**	**0.26**	**-0.22***	
		Group			4.51	2.52	0.19	
Static global form	86	Step 1	0.00					
		Sex			-0.03	0.95	-0.00	
		SPM			-0.04	0.10	-0.05	
		Step 2	0.00	0.00				
		Sex			-0.04	0.96	-0.00	
		SPM			-0.05	0.10	-0.05	
		Group			-0.29	0.93	-0.03	
Temporally-defined global form	86	Step 1	0.03					
		Sex			0.57	1.32	0.05	
		SPM			-0.22	0.13	-0.18	
		Step 2	**0.10***	**0.07***				
		Sex			0.67	1.28	0.05	
		SPM			-0.19	0.13	-0.16	
		Group			**3.06**	**1.25**	**0.26***	**0.07**

Table 8. Between-group analyses. A model was run for each visual task with threshold as the dependent variable. The control variables (i.e. the sex of an individual and non-verbal IQ) were entered into the models at step one. Group (Good = 0; Dyslexia = 1) was introduced at step two. SPM = Raven's Standard Progressive Matrices. * $p < .05$; ** $p < .01$; *** $p < .001$.

3. 3. 4. Independence of visual tasks: bivariate correlations

Scatterplots illustrating performance of the entire sample across the four visual tasks are shown in Figure 17. As expected, a strong and significant correlation was found between thresholds across the two global motion tasks and the two global form tasks (random-dot global motion task and spatially 1-D global motion task, $r_{106} = 0.58$, $p < 0.001$; static global form task and temporally-defined global form task, $r_{106} = 0.23$, $p = 0.02$). However, significant and positive correlations were also found across tasks measuring the processing of global motion and global form (random-dot global motion task and static global form task, $r_{106} = 0.28$, $p < 0.01$; spatially 1-D global motion task and static global form task, $r_{106} = 0.29$, $p < 0.01$). In contrast, no significant correlation was found between the spatially 1-D global motion task and the temporally-defined global form task, $r_{106} = 0.16$, $p = 0.10$ or the random-dot global motion task and the temporally-defined global form task, $r_{106} = 0.17$, $p = 0.09$.

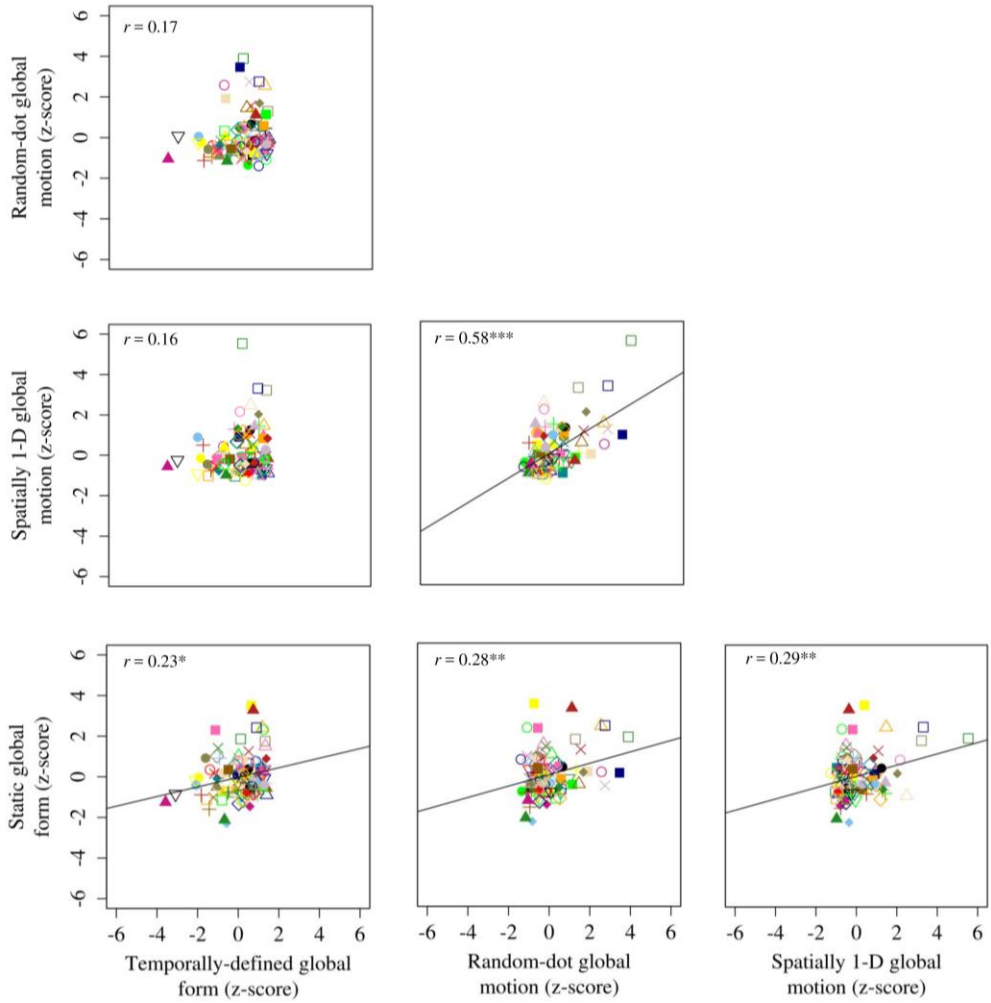


Figure 17. Independence of the visual tasks. Scatterplots showing the relationships between coherence thresholds for the visual tasks in the entire sample of readers (N = 106). Positive and negative z-scores indicate performance that is worse and better than the mean of the sample, respectively. Note that z-scores were used for illustrative purposes only and did not influence the correlations. NART = National Adult Reading Test; TOWRE = Test of Word Reading Efficiency. * = $p < .05$; ** = $p < .01$; *** = $p < .001$.

3. 4. Discussion

Several studies have shown that the processing of global motion is impaired in both children and adult with dyslexia (Cornelissen et al., 1995, Cicchini et al., 2015, Gori et al., 2015b, Hansen et al., 2001; Hill & Raymond, 2002, Kevan & Pammer, 2009; Raymond & Sorenson, 1998; Slaghuis & Ryan, 1999; Talcott et al., 2001). However, the underlying nature of the visual deficit in developmental dyslexia is currently unknown as previous studies used visual tasks that were not always comparable in terms of stimulus complexity or task demands. In addition, they did not always control for factors that are known to be associated with performance on global motion tasks such as the sex of an individual and non-verbal IQ (Arranz-Paraíso & Serrano-Pedrazza, 2016; Billino et al., 2008; Cook et al., 2016; Hutchinson et al., 2012; Melnick et al., 2013; Snowden & Kavanagh, 2006; Tadin, 2015). To address these issues in the present study a large undifferentiated sample of readers were tested using a novel stimulus paradigm. The four visual tasks administered were specifically designed to disentangle whether readers with dyslexia have a difficulty processing motion, temporal information, or integrating local visual cues across multiple (>2) dimensions (Table 3).

A similar pattern of results was found across the whole-sample analyses, involving the entire sample of readers, and the between-group analyses, comparing performance of readers with dyslexia who had poor phonemic decoding skills and relatively good readers. Consistent with previous studies, readers with dyslexia had significantly higher coherence thresholds than relatively good readers on the random-dot global motion task but not the static

global form task (Hansen et al. 2001). The same pattern was found for generally poor readers. In addition, with the novel task of spatially 1-D global motion, both generally poor readers and individuals with dyslexia showed elevated coherence thresholds compared to relatively good readers although this difference did not reach significance in the between-group analyses (p = 0.08). However, the amount of variance explained after controlling for the effects of sex and non-verbal IQ was similar across analyses (whole-sample analyses = 4% of total variance; between-group analyses = 3% of total variance), consistent with a modest deficit in the processing of 1-D global motion. We also found in both analyses that reading ability/group was significantly associated with coherence thresholds on the temporally-defined global form task, as both readers with dyslexia and generally poor readers showed elevated thresholds on this task compared to relatively good readers. These unique findings suggest that the underlying nature of the visual deficit in both groups of poor readers reflects a difficulty integrating temporal information rather than motion *per se*.

The consistent pattern of results found across the four visual tasks for readers with dyslexia, who had poor phonemic decoding skills, and generally poor readers suggests that performance on low-level visual tasks cannot differentiate these two groups of poor readers. This is important to demonstrate because definitions of developmental dyslexia are highly controversial. Some that have argued that dyslexia best represents the lower end of a normal distribution of reading ability, whilst others have suggested that it is a distinct type of reading difficulty associated with poor phonological decoding skills (Fletcher, 2009;

Siegel, 2006). One cannot rule out the possibility that readers with dyslexia differ from generally poor readers on other tasks, but it is clear that on tasks of global motion and global form processing they perform similarly to generally poor readers.

The results of the present study are difficult to reconcile with the dorsal stream vulnerability hypothesis as it predicts that readers with dyslexia should exhibit a selective deficit in the processing of global motion, relative to global form (see section 1. 3. 5.). They also cast further doubt on the external noise exclusion hypothesis (see section 1. 3. 2.). This theory predicts that readers with dyslexia should have exhibited impaired performance on all four visual tasks as they contained relatively high levels of perceptual noise but this was not the case. Taken together, these results suggest that external noise exclusion is not the proximal cause of the perceptual deficit shown in generally poor readers and individuals with dyslexia.

It is interesting to note that after controlling for the effects of sex and non-verbal IQ, scores on the composite measure of reading skill explained more of the variance (10%) in performance on the temporally-defined global form task than any of the other visual tasks. Unlike the other three visual tasks the temporally-defined form task requires some degree of segmentation, as well as integration, of local cues. That is, to identify the global orientation of the perceptual boundary visual information provided by temporally asynchronous jitter cues must be integrated within each half of the display but also segmented from those in the opposing half of the image. That reading ability was the

strongest predictor of performance on this particular task is consistent with previous studies that have investigated motion-based spatial segmentation in developmental dyslexia (Cornelissen et al., 1995).

Our results also showed that non-verbal IQ was negatively associated with coherence thresholds on the spatially 1-D global motion task and the random-dot global motion task in both the whole-sample and between-group analyses. Previous research has reported a link between intelligence and motion processing (Arranz-Paraíso & Serrano-Pedrazza, 2016; Billino et al., 2008; Cook et al., 2016; Hutchinson et al., 2012; Melnick et al., 2013; Snowden & Kavanagh, 2006; Tadin, 2015). The differential performance of individuals with relatively low and high IQs might reflect differences in spatial suppression; an inhibitory process that reduces the response of some neurons in area MT/V5 to large background-like stimuli (Tadin et al. 2003). It has been suggested that individuals with a high IQ have an enhanced ability to suppress ecologically less relevant information in the visual field (Melnick et al., 2013; Tadin, 2015). In contrast, intelligence was not associated with thresholds on the static global form task nor the temporally-defined global form task. Further research needs to establish why non-verbal IQ appears to be associated with performance on global motion tasks but not those involving analogous global form.

The sex of an individual was also a significant predictor of thresholds on the random-dot global motion task. Females' coherence thresholds were significantly higher (1.3 times) than those of males, consistent with some

previous research (Billino et al. 2008; Snowden & Kavanagh, 2006). The fact that sex was not significantly associated with performance on the temporally-defined global form task suggests that some females have a specific difficulty on random-dot global motion tasks, which is distinct from the temporal processing impairment exhibited by generally poor readers and individuals with dyslexia. Although speculative, this effect might reflect differences in inter-hemispheric asymmetry. For example, extrastriate motion area MT/V5 in the right hemisphere of the male is reported to have a significantly larger volume than the corresponding region in the female cortex (Amunts et al. 2007; de Lacoste et al. 1991; Kovalev et al. 2003). It has been suggested that this provides additional neural resources or "space" for the processing of computationally-demanding visual stimuli. To some extent, the results of the current study are consistent with this hypothesis, given that the sex of an individual was not associated with coherence thresholds for the simpler spatially 1-D global motion task. Further research is needed to determine why sex does not significantly predict coherence thresholds for global form tasks. A highly tentative possibility is that the parts of the brain involved in the processing of global form are not characterized by the same left-right asymmetry that is observed in area MT/V5 of the male. Regardless of the underlying mechanism of the effect, that females have typically higher thresholds than males for random-dot global motion, could explain why some studies have failed to find differences between reading groups on this task (Amitay et al. 2002; White et at. 2006). For example, very marked sex differences between participant groups (i.e. more females than males in the control group and vice versa for the group of readers with dyslexia) could

potentially mask differences in performance driven by reading ability. Thus future studies need to control for the sex of an individual when performing between-group analysis.

On a related note, the results of the between-group analyses showed that there was considerable inter-subject variability in coherence thresholds amongst the group of readers with dyslexia even after controlling for the effects of sex and non-verbal IQ. This is consistent with previous studies exploring sensory theories of developmental dyslexia (Amitay et al. 2002; Ramus et al. 2003; Roach et al. 2004). It was especially marked for the two global motion tasks, as indicated by the relatively large standard deviations in Table 7. A potential explanation for this is that visual deficits only occur in a sub-group of readers with dyslexia. Some have argued that this might reflect genotypic variation (Gori et al., 2015a; Cichinni et al. 2015; Morrone et al., 2011) but results are mixed meaning that further research is needed to establish if this is the case. Interestingly, the intra-subject variability (i.e. variability in each individual's thresholds measured across different staircases) was only slightly (and not significantly) higher in readers with dyslexia (average SD = 9.08%) than in good readers (average SD = 7.41%), suggesting that an individual's reading ability does not greatly affect the reliability of their performance across trials on the visual tasks.

Finally, our results also have a direct bearing on the proposed independence of the dorsal and ventral processing streams and the types of information that each pathway encodes. Consistent with the two-streams hypothesis, across the

entire sample we found a significant, positive correlation between coherence thresholds for the two global motion tasks and also for the two global form tasks. However, the results that are difficult to reconcile with the dorsal-ventral dichotomy are the significant correlations between thresholds for the static global form task and the two global motion tasks. This latter result is important because it is indicative of some degree of cross-talk between the dorsal and ventral streams, or the existence of a later common processing stage that serves to provide a unified representation of an object's global properties. There is mounting evidence from other psychophysical studies that the processing of global motion and global form is not strictly independent (Mather et al. 2013). For example, Ross et al. (2000) showed that a series of temporally uncorrelated Glass patterns, containing global oriented structure created by pairs of dots related by a rotational shift, induced precepts of global rotational motion consistent with the spatial information. Clearly, this has implications for future studies and for the interpretation of previous findings.

3. 5. Summary

In summary, the results of this study demonstrate that the visual deficit in both generally poor readers and individuals with dyslexia is better characterised as a difficulty integrating temporal information rather than motion *per se*. The almost identical pattern of results found across the four visual tasks in readers with dyslexia, who had poor phonological decoding skills, and generally poor readers suggests that visual difficulties do not differentiate these two groups of poor readers. Interestingly, the sex of an individual and non-verbal IQ were significantly associated with coherence thresholds on the random-dot global motion task. This is important to show as many studies exploring the dorsal stream vulnerability hypothesis did not control for these factors, which could explain why some investigators failed to uncover a global motion processing deficit in children and adults with developmental dyslexia (Johnston et al., 2017). Finally, the results of the present study suggest that the processing of global motion and global form are not strictly independent in the human visual system as significant, positive correlations between thresholds were found for the static global form task and the two global motion tasks. Thus, the use of global motion and global form tasks in vision experiments cannot be guaranteed to readily dissociate activity in the dorsal and ventral processing streams, respectively.

Chapter 4[1]

Spatial segmentation of motion and form information in adult poor readers

4. 1. Introduction

The results of Chapter 3 showed that the origin of visual impairment in generally poor readers and individuals with dyslexia reflects a difficulty integrating temporal information rather than motion *per se*. However, to successfully parse the visual scene into meaningful entities, such as text into words, or words into letters, the visual system must also segment local features arising from different objects in the world (Braddick, 1993). There is some evidence to suggest that the underlying nature of the visual deficit in dyslexia extends to spatial segmentation. For example, Cornelissen et al. (1995) showed that both children and adults with dyslexia had significantly higher coherence thresholds than relatively good readers on a motion-based segmentation task in which participants had to discriminate a spatially segmented stimulus from a pattern containing uniform motion that reversed direction periodically (see section 1. 3. 5. 3.). A criticism of this study is that due to the nature of the task it is unclear if poor readers' difficulties were directly indicative of a spatial

[1] The results outlined in this chapter have been published in *Scientific Reports*. Citation: Johnston, R., Pitchford, N. J., Roach, N. W., & Ledgeway, T. (2017). Visual perception in dyslexia is limited by sub-optimal scale selection. *Scientific Reports, 7,* 6593.

segmentation impairment or simply a deficit in global motion perception. That is, if participants had based their decision on each trial by identifying the uniform pattern containing the dots moving in a common direction, then the poorer performance of the readers with dyslexia could reflect the known difficulty in processing global motion (i.e. integration) rather than spatial segmentation. Thus, the interpretation of the pattern of results found by Cornelissen et al. (1995) is somewhat equivocal.

Evidence suggests that performance on spatial segmentation tasks is dependent on several stimulus parameters such as segment size (Nakayama & Tyler 1981; van Doorn & Koenderink, 1982a; Watson & Eckert, 1994). For example, Burr et al. (2006) devised a two-interval, temporal forced-choice procedure to investigate the mechanisms underlying motion-based segmentation. Observers viewed random-dot stimuli that were spatially divided into horizontal segments. Local dots in adjacent segments were constrained to move in opposing directions at a speed of 4°/s. The task required participants to discriminate this stimulus from one containing identical motion cues that were spatially intermingled. First, spatial resolution (acuity) limits were measured to determine the smallest segment size needed to reliably perform the motion task. This was achieved using an adaptive staircase that varied segment size, whilst the coherence of the stimulus was held constant at 100%. Coherence thresholds were then measured separately for each of a range of segment sizes. They found that thresholds initially decreased as segment size increased, but then exhibited a plateau (i.e. performance became asymptotic) at the largest segment sizes tested. These findings demonstrate that a single measurement of

sensitivity at a fixed segment size cannot fully characterise performance on tasks requiring spatial segmentation.

In summary, the results of Chapter 3 demonstrate that generally poor readers and individuals with dyslexia have difficulty on visual tasks requiring integration of temporal information. However, it is unclear if the visual deficit in developmental dyslexia extends to spatial segmentation, a fundamental process that has been implicated in orthographic processing (Dehaene et al., 2005; Grainger & van Heuven, 2003; Whitney, 2001). Previous research exploring this question has confounded integration with segmentation and relied on a single measurement of sensitivity at a fixed segment size (Cornelissen et al., 1995). In the present study, these issues were directly addressed by administering a motion task and an analogous form task to thirty-eight adults whose reading abilities ranged along a continuum. The psychophysical stimuli were designed to provide a sensitive measure of spatial segmentation at each of a range of segment sizes. Moreover, a curve was fitted to each participant's data, which allowed the shape of the threshold versus segment size function to be characterised and different components of the processes underpinning task performance to be systematically investigated.

4. 2. Materials and methods

4. 2. 1. Participants

Thirty-eight adults (Male = 15, Female = 23) with a wide range of reading abilities were recruited to take part in the study (see section 2. 1.). The mean age was 23.6 years (*SD* = 36 months).

4. 2. 2. Psychometric tests

Each participant completed standardised tests of reading ability and non-verbal IQ (see section 2. 2.). Summary statistics characterizing the reading abilities of the entire sample are shown in Table 9. It is important to note that 16 participants (42% of the sample) had standard scores ≤ 85 (at or below the 15th percentile) on the TOWRE Phonemic Decoding Efficiency subtest, which falls into the conventional range for diagnosing developmental dyslexia (Heath et al., 2006; Pugh et al. 2014).

	M	*Median*	*SD*	*Range*
NART raw score (max 50)	26.97	29.00	6.57	7.00-39.00
TOWRE Sight Word Efficiency	85.63	82.00	12.58	69.00-113.00
TOWRE Phonemic Decoding	92.63	88.00	15.45	62.00-120.00
SPM raw score (max 60)	51.18	51.00	5.48	39.00-59.00

Table 9. Psychometric summary statistics for the entire sample of readers (N = 38). Standard scores (M = 100, SD = 15) are shown unless otherwise stated. NART = National Adult Reading Test; TOWRE = Test of Word Reading Efficiency; SPM = Raven's Standard Progressive Matrices.

4. 2. 3. Visual stimuli

The visual stimuli were viewed binocularly at a distance of 60cm. They were presented within the confines of a square display window in the centre of the monitor (frame refresh rate = 100Hz), which subtended 7x7º. Each stimulus was composed of an ensemble of "black" (0.01cd/m^2) dots (diameter 0.035º) presented against a uniform "grey" (34cd/m^2) background. More precise details relating to stimulus generation in the motion and form tasks are given below.

4. 2. 3. 1. Motion task

The stimuli in the motion task (Figure 18) consisted of forty-three images, each containing 256 dots that were presented consecutively at a rate of 100Hz to create the perception of apparent motion. Individual dots were displaced by 0.035º on each positional update, which resulted in a speed of 3.5º/s. Two patterns were presented in succession on each trial, in a random order, with equal probability. They were separated by an ISI of 0.52s. The test stimulus was spatially divided into horizontal segments by constraining local dots in adjacent segments to move in opposing directions (leftwards or rightwards). On each trial, the vertical spatial position of the segment boundaries was jittered randomly to make them unpredictable. The participants' task was to discriminate the test stimulus from a comparison stimulus containing identical motion cues that were spatially intermingled. Each dot had a limited lifetime of 0.22s (22 frames). At the beginning of the motion sequence it was assigned a random 'age' in frames between 1 and 22. On each image update, the 'age'

parameter was incremented by 1. The dot was replotted at a random location within the same segment when the limit of 22 frames was exceeded. Coherence could be varied between 0 and 100% by constraining some of the dots (*signal* dots) to move in the same direction on each image update and others to move randomly (*noise* dots). The "strength" or coherence of the test and comparison stimuli was identical on a given trial. Thus, the only difference between the patterns was the spatial distribution of the dots.

4. 2. 3. 2. Form task

The stimuli in the form task (Figure 18) were generated by computing a 4-frame, random-dot motion sequence. The individual frames were then spatially superimposed to create a static image (Simmers et al. 2005). Some of the dots in the stimuli (*signal* dots) formed localised streaks, orientated (vertically or horizontally) along a common axis, whilst others (*noise* dots) formed random clusters. The length of each dot streak was 0.14º. Two patterns were randomly presented in succession on each trial with equal probability. They were separated by an ISI of 0.52s. The test stimulus was spatially divided into horizontal segments by constraining the differently oriented dot streaks to fall in adjacent segments. As in the motion task, the vertical spatial position of the segment boundaries was jittered randomly on each trial. The participants' task was to discriminate the test stimulus from a comparison stimulus containing exactly the same form cues but these were spatially intermingled. The coherence of the test and comparison stimuli was identical on a given trial.

Coherence could be varied between 0 and 100% by changing the relative proportion of signal to noise dot streaks.

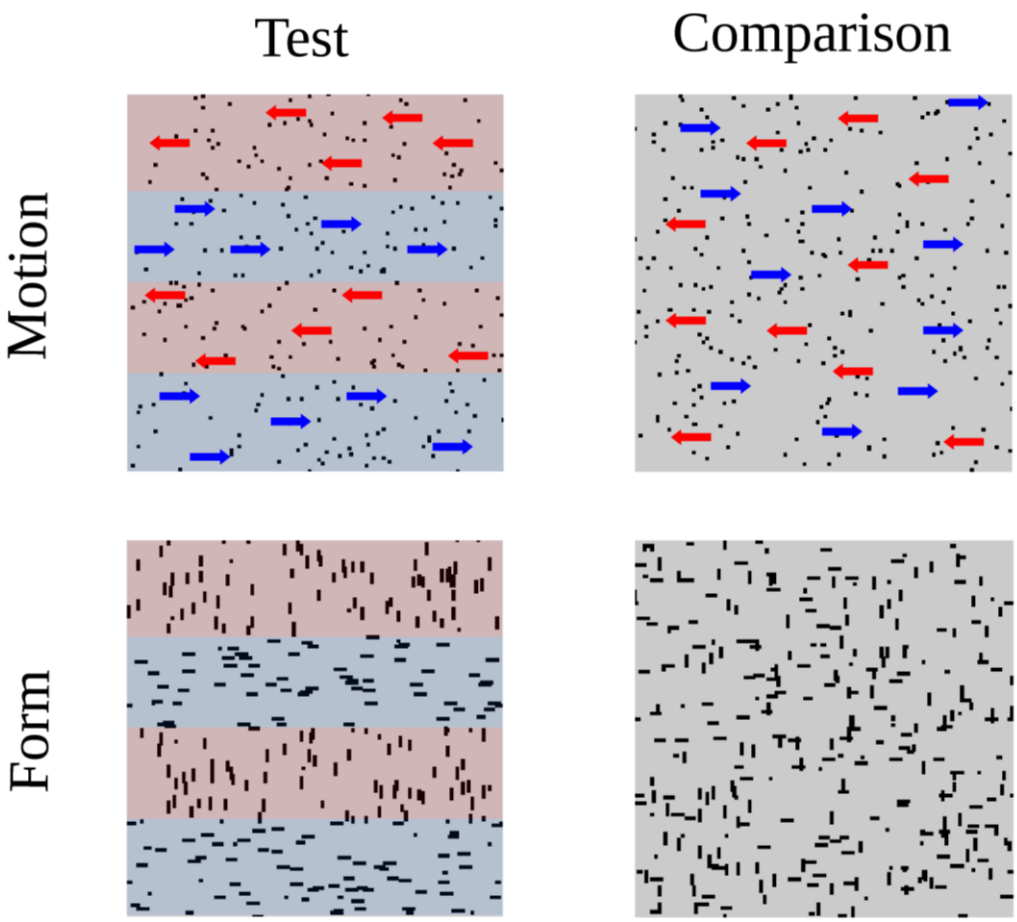


Figure 18. A schematic of the stimuli in the motion and form tasks. Coloured overlays and arrows have been added for illustrative purposes only and depict how the test stimuli were spatially segmented.

4. 2. 4. Procedure

4. 2. 4. 1. Spatial resolution limits

To determine the smallest segment size needed for an observer to perceive reliably a spatially segmented pattern, the spatial resolution (acuity) limits were measured. The coherence of the stimuli was held constant at 100% in each trial block. Segment size was varied on each trial using a two-interval, temporal forced-choice procedure and a 3-down, 1-up adaptive staircase (see section 2. 6.). The initial step size of the staircase was 3.5º and this decreased by half after each reversal. The participants' task was to identify the spatially segmented test stimulus.

4. 2. 4. 2. Coherence thresholds

Coherence thresholds were obtained in a similar manner to acuity limits. However, segment size was held constant in each trial block. It ranged from 0.438 to 3.5º in equal logarithmic steps. Stimulus coherence was varied on each trial using a 3-down, 1-up adaptive staircase (see section 2. 6.). The initial step size of the staircase was equal to the total number of elements in the display and this decreased by half after each reversal. The participants' task was to identify the spatially segmented test stimulus.

4. 2. 5. Curve-fitting

To quantify the relationship between segment size and perceptual performance a two-limbed curve was fitted to each participant's data using a conventional least-squares fitting procedure (Levenberg–Marquardt algorithm). This was done separately for each observer in the entire sample. In all cases, the data were well described (Mean R^2 for the motion task = 0.95, *SD* = 0.05, Range = 0.74 to 0.99; Mean R^2 for the form task = 0.94, *SD* = 0.04, Range = 0.83 to 0.99) by a function that has previously been used to characterise and quantify performance on motion perception tasks (Allen, Hutchinson, Ledgeway, & Gayle, 2010; Hutchinson & Ledgeway, 2010; Hutchinson, Ledgeway, Allen, Long, & Arena, 2013):

$$y = \left[\frac{(\mathrm{sgn}(k-x)+1)\left(\frac{x}{k}\right)^{s} + \mathrm{sgn}(x-k)+1}{2} \right] t, \qquad (1)$$

where x is segment size, and k, t, and s are constants. Parameter k is the knee-point of the function and represents the segment size above which performance no longer improves. Parameter t is the coherence threshold at asymptote, whilst parameter s is the slope of the descending limb of the curve. Sgn(), the signum function, is equal to either -1, 0 or +1 depending on whether the argument in parentheses is < 0, 0 or > 0, respectively. In four cases, the knee-point estimate (parameter *k)* for the motion segmentation task was greater than the largest segment size condition (3.5°). For these four cases, a conservative approach was taken to deal with this issue and the curves were re-fitted with the knee-point parameter held constant at 3.5°. Data for a single participant on the motion task and the form task are shown in Figure 19A and 19B, respectively.

The empirically measured acuity limit together with the three best-fitting parameters derived from the curve-fit procedure (knee-point, coherence threshold at asymptote, and slope) are depicted in Figure 19C.

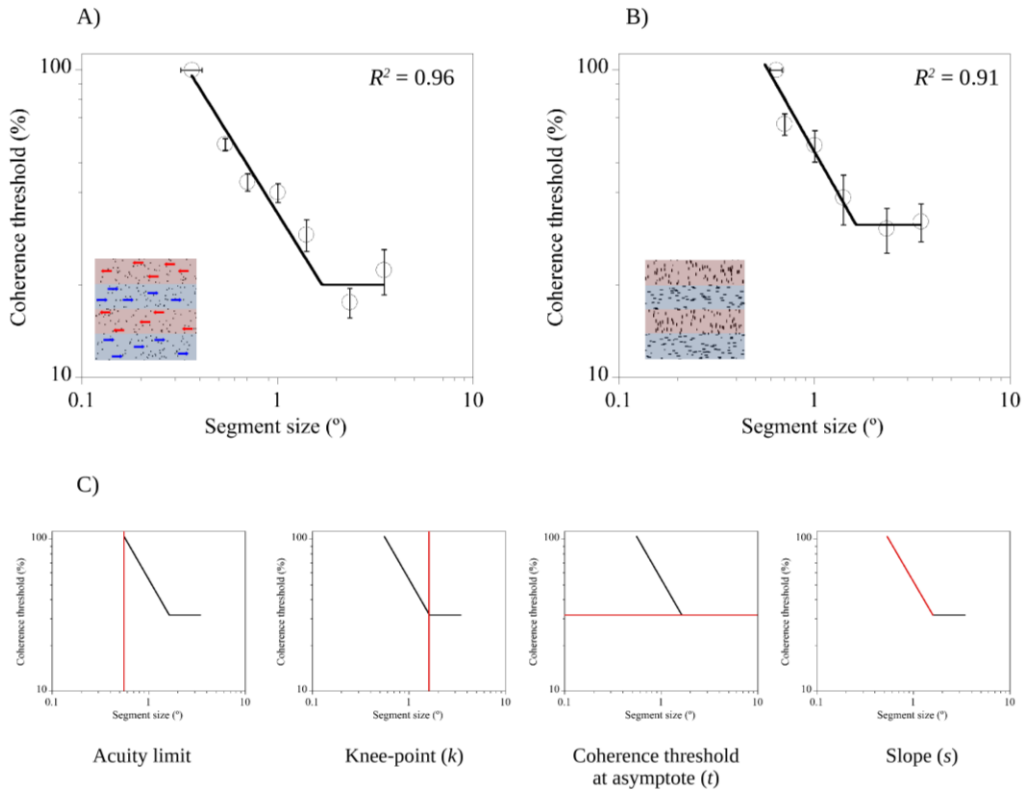


Figure 19. Data for a single participant on A) the motion task and B) the form task. The dashed red line in C) represents the spatial acuity limit and the three best-fitting parameters (*k, t, & s)* from Equation 1. Error bars, ±1 sem.

4. 2. 6. Statistical analyses

The results of Chapter 3 showed that performance on low-level visual perception tasks, requiring the processing of motion and form, cannot differentiate generally poor readers from individuals with poor phonological decoding skills consistent with the dyslexic profile. Preliminary analyses demonstrated that this was also the case in the present study, so a series of whole-sample analyses were conducted using a composite measure of reading skill (see section 2. 4.). The results of Chapter 3 also confirmed previous reports that the sex of an individual and non-verbal IQ are associated with performance on global motion tasks (Arranz-Paraíso & Serrano-Pedrazza, 2016; Billino et al., 2008; Cook et al., 2016; Hutchinson et al., 2012; Melnick et al., 2013; Snowden & Kavanagh, 2006; Tadin, 2015). Therefore, semi-partial correlations were used to investigate if reading ability explained any additional variance in performance on the motion and form task after controlling for the effects of these variables. Acuity limits and curve-fit values for the motion and form task violated the assumption of normality, so correlations were assessed using Spearman's rank-order correlation coefficient. However, conducting parametric tests did not change the overall pattern of results. Cohen's *d* was calculated as a measure of effect size with 0.2 considered a small, 0.5 a medium, and 0.8 a large effect (Cohen, 1988).

4. 3. Results

4. 3. 1. Composite reading score: PCA

Correlations between scores for the three individual measures of reading ability were moderate to strong (r = 0.45 to 0.75, $p < .01$, Figure 20) so PCA was used to calculate the composite measure of reading skill. Raw scores for the individual measures of reading ability were entered into the analysis, which was based on the correlation matrix. A single principal component accounted for 75% of the total variance amongst the three individual measures of reading ability (*Eigenvalue 1* = 2.26; *Eigenvalue 2* = 0.55; *Eigenvalue 3* = 0.19). Loadings for the NART and the TOWRE Sight Word Efficiency subtest were within the same range (0.81 and 0.85, respectively) but the TOWRE Phonemic Decoding subtest contributed slightly more to the single dimension of common variation (loading = 0.94). PCA scores for each individual were entered into the whole-sample analyses to investigate how general reading ability relates to performance on the motion and form tasks.

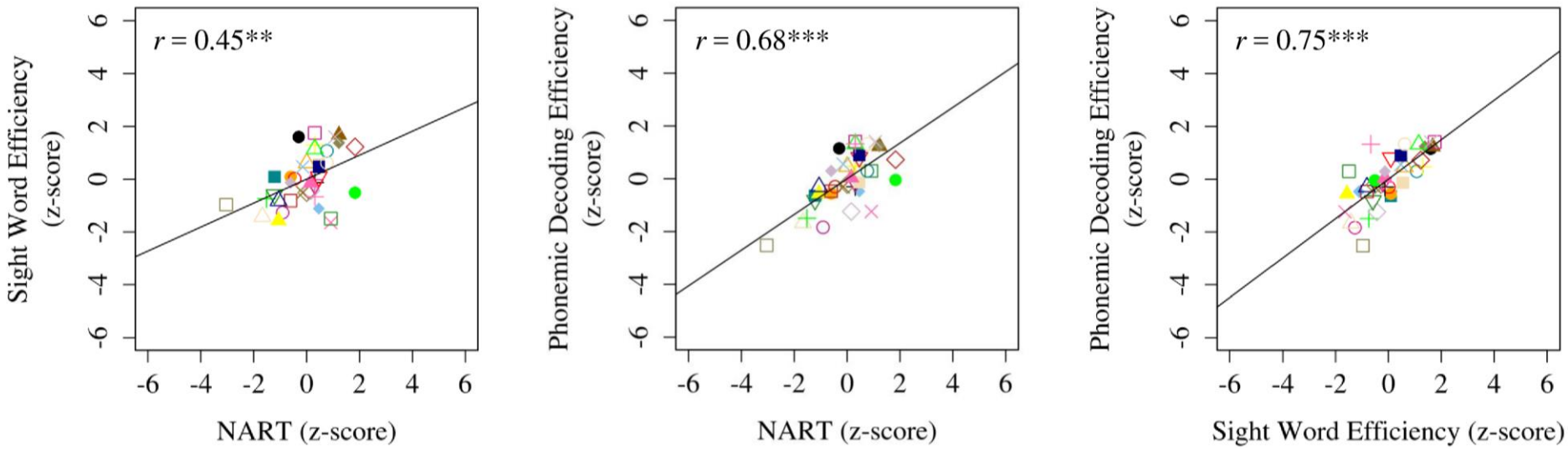


Figure 20. Scatter plots showing the relationships between scores on the three individual measures of reading ability in the entire sample (N = 38). Positive and negative z-scores indicate scores better than and worse than the mean of the sample, respectively. Note that z-scores were used for illustrative purposes only and did not influence the correlations. NART = National Adult Reading Test; TOWRE = Test of Word Reading Efficiency. * = $p < .05$; ** = $p < .01$; *** = $p < .001$.

4. 3. 2. Whole-sample analyses: semi-partial correlations

The results of the whole-sample analyses are described in the sections below. Scatterplots showing the relationships between reading ability and various components underpinning performance on the motion and form task are shown in Figure 21 and Figure 22, respectively.

4. 3. 2. 1. Motion task

The correlation between general reading skill and acuity limits on the motion task was not statistically significant, r_s = 0.09, p = 0.60, Cohen's d = 0.18. However, there was a significant, negative correlation between reading ability and the knee-point of the curves, r_s = -0.43, p < 0.01, Cohen's d = 0.95. The segment size at which performance became asymptotic was larger in generally poor readers (i.e. those with lower composite scores for reading) than relatively good readers (i.e. those with higher composite scores for reading). No significant correlation was found between reading skill and coherence thresholds at that asymptote, r_s = -0.02, p < 0.89, Cohen's d = 0.04, but there was a significant, negative correlation between general reading ability and the slope of the descending limb of the curves, r_s = -0.46, p < 0.01, Cohen's d = 1.04. The rate of improvement as segment size increased was shallower in generally poor readers than relatively good readers. The sex of an individual and non-verbal IQ were not significantly associated with acuity limits nor any of the curve-fit values.

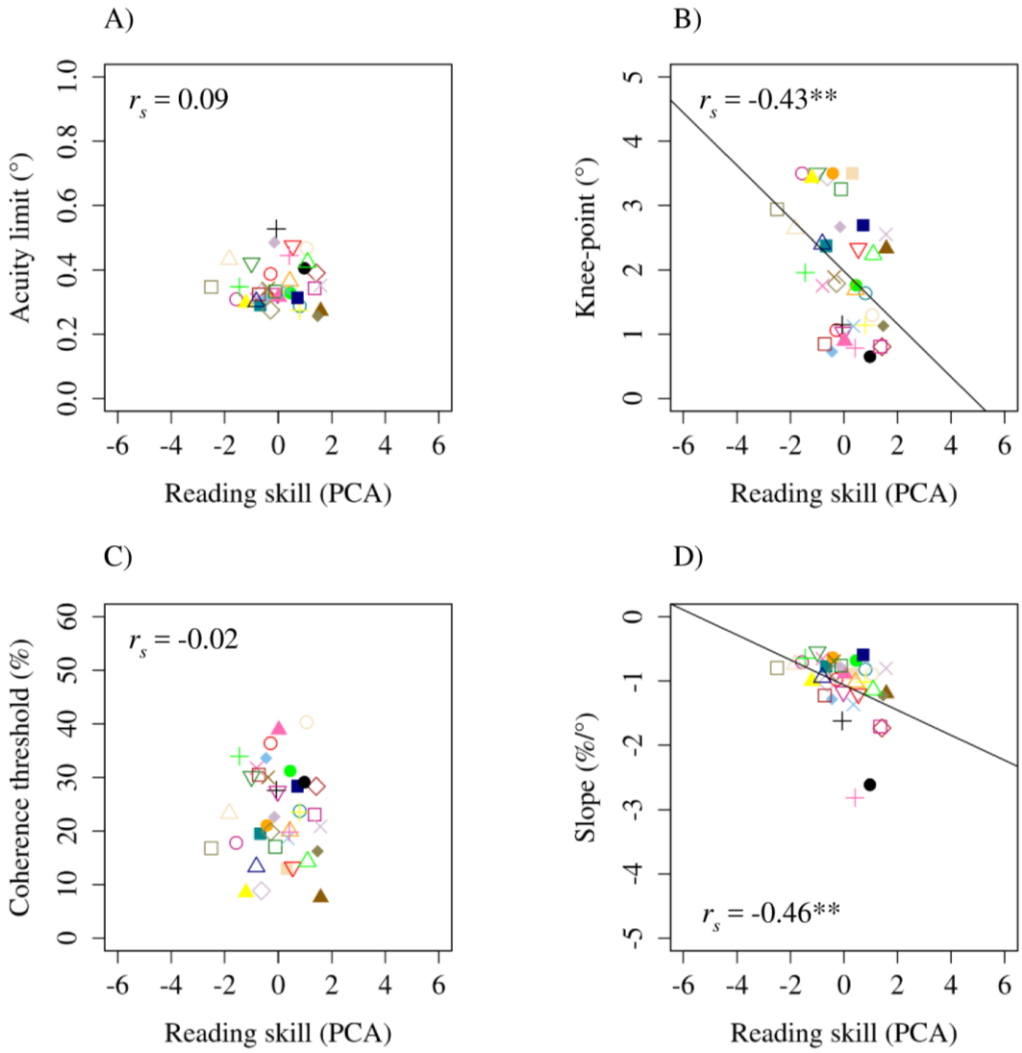


Figure 21. Scatter plots for the motion task in the entire sample of readers (N = 38) showing the relationships between reading ability and acuity limits A), the knee-point of the curves B), coherence thresholds at asymptote C) and the slope of the descending limb D). Note that the correlations were calculated after controlling for the effects of sex and non-verbal IQ. In B) we only see the multiple regression solution in the plane of the knee-point and reading ability data set. Each coloured symbol represents an individual participant. * $p < .05$; ** $p < .01$; *** $p < .001$.

4. 3. 2. 2. Form task

The correlation between the composite measure of reading skill and acuity limits on the form task was not statistically significant, r_s = -0.05, p = 0.76, Cohen's d = 0.10. Furthermore, no significant correlation was found between reading ability and the knee-point of the curves, r_s = -0.13, p = 0.44, Cohen's d = 0.26. Reading ability was not significantly correlated with coherence thresholds at asymptote, r_s = -0.02, p = 0.92, Cohen's d = .04, nor the slope of the descending limb of the curves, r_s = -0.08, p = 0.64, Cohen's d = 0.16. The sex of an individual and non-verbal IQ were not significantly associated with acuity limits nor any of the curve-fit values for the form task.

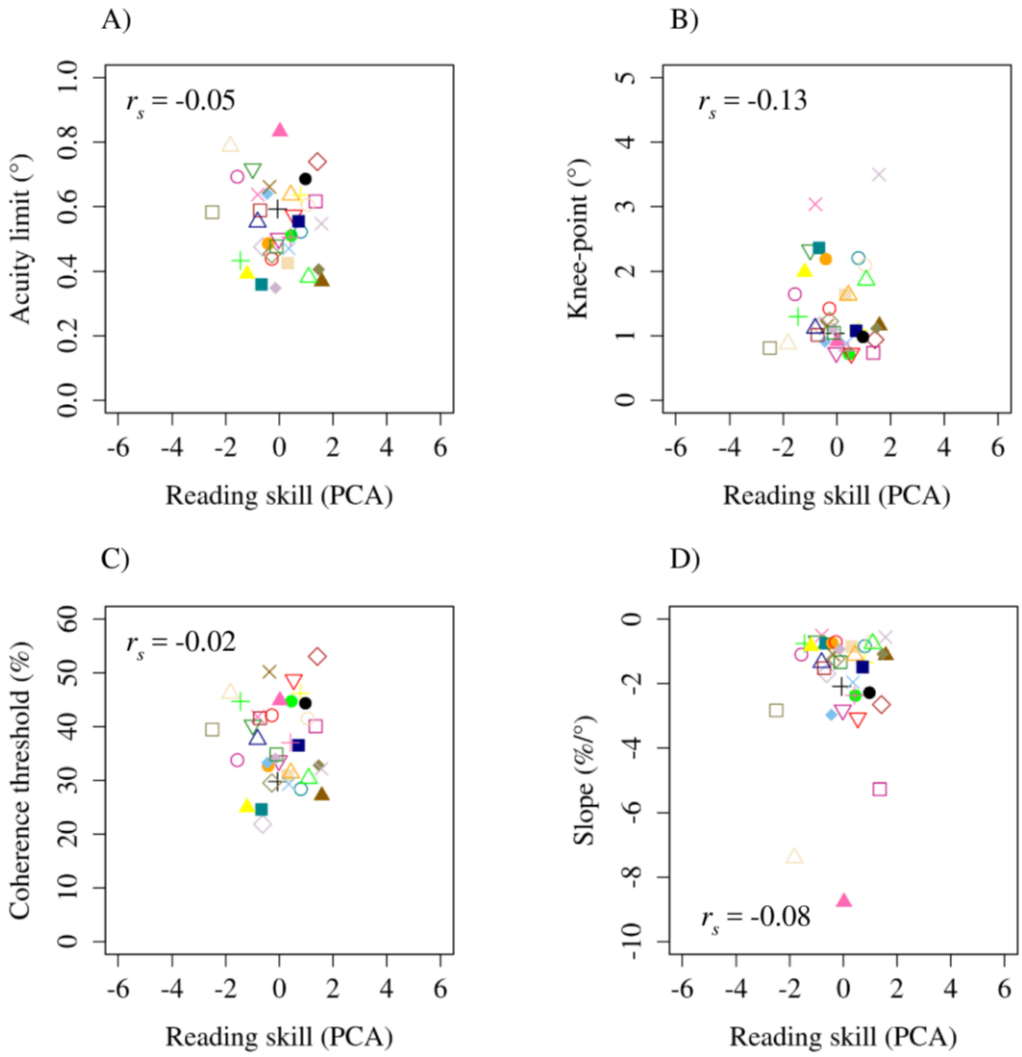


Figure 22. Scatter plots for the form-based spatial segmentation task in the entire sample of readers (N = 38) showing the relationships between reading ability and acuity limits A), the knee-point of the curves B), coherence thresholds at asymptote C) and the slope of the descending limb D). Each coloured symbol represents an individual participant. * p < .05; ** p < .01; *** p < .001.

4. 4. Discussion

The results of Chapter 3 showed that the origin of visual impairment in generally poor readers and individuals with dyslexia reflects a difficulty integrating temporal information rather than motion *per* se. However, it is unclear if the underlying nature of the visual deficit in developmental dyslexia extends to object segmentation. In the present study, this issue was systematically addressed by investigating different components of the processes underpinning performance on directly comparable motion and form tasks. Results showed that acuity limits were independent of reading ability, indicating that the minimum segment size needed to perform the motion and form tasks was normal in less-skilled readers. Reading ability was significantly associated with performance but crucially only for the motion task, such that the segment size at which performance became asymptotic (i.e. the knee-point) was larger in the poorest readers and resulted in a flattening of the descending limb of the curves. Importantly, these results demonstrate that the underlying nature of the perceptual deficit in developmental dyslexia extends to spatial segmentation, but only on tasks containing motion (i.e. time-varying) information.

The results of the present study suggest that overall sensitivity on the spatial segmentation tasks was normal in adult poor readers, as coherence thresholds at asymptote were not significantly associated with reading ability. This might seem at odds with the results of Cornelissen et al. (1995) as they reported that readers with dyslexia had significantly higher coherence thresholds on a

similar motion task (see section 1. 3. 5. 3.). However, segment size was fixed at 0.48° in their study and represents a single point along the descending limb of the function (Figure 19A). The poorest readers in our sample had higher coherence thresholds than good readers at this point too, highlighting the importance of not relying on a single measurement of sensitivity to characterise performance.

The results of Chapter 3 challenged the dorsal stream vulnerability hypothesis (see section 1. 3. 5.) as an explanation for visual deficits in developmental dyslexia and the putative independence of the dorsal and ventral streams as coherence thresholds on RDK tasks and static global form tasks were significantly and positively correlated. In addition, it is unclear if the dorsal pathway is actually involved in the spatial segmentation of motion cues, as cells in the ventral stream (e.g. area V4) of primates respond to kinetic boundary stimuli similar to those used in the present study (Mysore et al., 2006, 2008; Chen et al., 2014; Sary et al., 1995). The external noise exclusion hypothesis (see section 1. 3. 2.), the anchoring-deficit hypothesis (see section 1. 3. 3.) and the modified receptive field hypothesis (see section 1. 3. 4.) are also not supported by the current study. All these theories predict that readers with dyslexia should show impaired performance on the form task as well as the motion task, but this was not found to be the case.

Most research has conducted between-group analyses to compare visual and neurocognitive function in adults with and without dyslexia, whereas in the present study a series of whole-sample analyses were performed using a

composite measure of reading skill. Between-group analyses are more likely to suffer from low statistical power than whole-sample analyses because sample size is effectively halved in the former, relative to the latter. This has been identified as a contributing factor to the lack of reproducibility in the neurosciences (Button et al., 2013; Duas-Mallet et al., 2005; Loannidis, 2005). In addition, reading difficulties are notoriously difficult to define (see Section 1. 2.). Hence, a wide range of criteria has been used to identify individuals with dyslexia, which might also have contributed to inconsistencies across studies. The finding that visual difficulties cannot differentiate generally poor readers from individuals with dyslexia justifies the use of whole-sample analyses in future research. Adopting these types of experimental design will improve the reliability of scientific research as they enhance statistical power and do not require decisions to be made regarding controversial definitional criteria and arbitrary cut-offs.

In the present study, semi-partial correlations were conducted to investigate if composite reading scores predicted task performance after controlling for the effects of sex and non-verbal IQ, which are known to be associated with motion perception (Arranz-Paraíso and Serrano-Pedrazza, 2016; Cook et al., 2011; Melnick et al., 2013). Results showed that performance on the motion and form tasks was not significantly associated with non-verbal IQ. These findings are in stark contrast to those in Chapter 3 as non-verbal IQ was a significant predictor of performance on the random-dot global motion and the spatially 1-D global motion tasks, both of which required integration of local motion cues. They cast a shadow of doubt on the notion that differential

performance of individuals with relatively low and high IQs on global motion perception tasks reflects differences in spatial suppression as neurons exhibiting this characteristic type of behaviour are thought to play a key role in spatial segmentation (Allman, Miezin, & McGuinness, 1985; Pack, Hunter, & Born, 2005; Tadin, 2015).

The results of Chapter 3 also showed that performance on the random-dot global motion task but not the other three visual tasks was significantly associated with the sex of an individual. Females had significantly higher coherence thresholds than males, consistent with some previous research (Billino et al. 2008; Hutchinson et al., 2012; Snowden & Kavanagh, 2006). No significant association was found between the sex of an individual and performance on the motion and form tasks in the present study. Thus, it appears that the sex of individual predicts performance on random-dot global motion tasks necessitating the integration but not spatial segmentation of local visual cues.

4. 5. Summary

In summary, the results of this chapter show that the underlying nature of the visual deficit in developmental dyslexia extends to spatial segmentation but only on tasks containing motion information. The rate of improvement on the motion task was shallower in adult poor readers than relatively good readers and the segment size at which coherence thresholds reached asymptote was larger. Interestingly, the sex of an individual and non-verbal IQ were not significantly associated with performance on the motion or form task. This is important to show as it suggests that these control variables are associated with performance on tasks requiring integration but not spatial segmentation of local motion cues.

Chapter 5[1]

Is visual perception in adult poor readers limited by sub-optimal scale selection?

5. 1. Introduction

The results of Chapter 4 showed that the underlying nature of the visual deficit in developmental dyslexia extends to spatial segmentation but only on tasks containing motion information. The rate of improvement on the motion task was significantly shallower in adult poor readers than relatively good readers and the segment size at which coherence thresholds reached asymptote was significantly larger (see Figure 21). However, it is unclear why such a deficit on tasks requiring spatial segmentation of motion information should arise in developmental dyslexia. To address this issue a biologically-motivated computational model was devised. It is outlined in the sections below.

[1] The results outlined in this chapter have been published in *Scientific Reports*. Citation: Johnston, R., Pitchford, N. J., Roach, N. W., & Ledgeway, T. (2017). Visual perception in dyslexia is limited by sub-optimal scale selection. *Scientific Reports, 7,* 6593.

5. 2. Computational model of motion-based spatial segmentation

Computational modeling was performed on an Apple Macintosh computer using bespoke software written in the "C" programming language. The test and comparison stimuli used in these analyses were identical to those in the motion task (see section 4. 2. 3. 1.) except the motion-sequences comprised two frames for computational efficiency. At each location (i, j) in the image the net opponent motion (rightwards minus leftwards) was calculated as the sum of the horizontal direction components of all the dots (T) contained within a circular integration field of variable diameter (Figure 23) centred at that location:

$$R_{ij} = \sum_{d=0}^{T} cos\theta_d \qquad (2)$$

where R_{ij} is the net opponent motion and θ_d is the direction of each dot. This type of analysis is biologically plausible as electrophysiology, human brain imaging, and psychophysics support the existence of motion opponency in visual cortex (Heeger, Boynton, Demb, Seidemann, & Newcome, 1999; Zemany, Stromeyer, Chaparro, & Kroneauer, 1998). Furthermore, motion-sensitive neurons operate over a range of spatial scales and there is considerable scatter in the size of receptive fields available at each location in the visual field (Gattas & Gross, 1981; Felleman & Kaas, 1984).

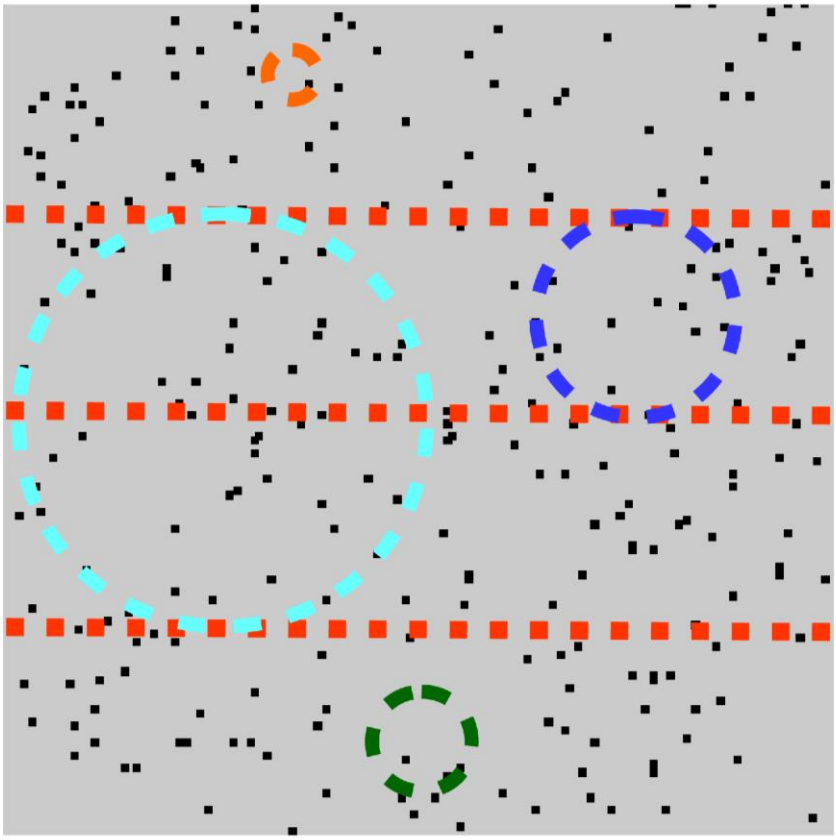


Figure 23. A schematic illustration of the computational analyses performed at a range of spatial scales. Circular integration fields of various sizes are shown superimposed upon a single frame of the spatially-segmented test stimulus, in which the dots underwent motion.

The directional variance across space was then computed for each motion sequence as:

$$\sigma^2 = \frac{1}{n}\sum\left(R_{mean} - R_{ij}\right)^2 \quad (3)$$

where R_{mean} is the mean net opponent motion, averaged across all spatial locations (n) in the image.

Acuity limits and coherence thresholds were obtained using a 3-down, 1-up adaptive staircase procedure (see section 2. 6.). A decision was made on each trial, regarding the identity of the test stimulus, based on the motion sequence with the largest directional variance. If σ^2 for the test stimulus exceeded σ^2 for the comparison, the decision was correct. In the rare circumstance that the two variances were identical, the response was randomly assigned either correct or incorrect with equal probability.

First, integration field size was varied between 0.438 and 3.5° (Figure 24A). Acuity limits increased as integration field size increased. This resulted in a rightward shift of the curves and suggests that acuity limits represent the minimum integration field size that can be used. Secondly, coherence thresholds decreased as segment size increased, regardless of integration field size. There is evidence of asymptotic behaviour when the integration field size matched the segment size. For example, coherence thresholds became asymptotic at ~0.88° when the integration field size was 0.88°.

Next, integration field size was varied in proportion to segment size (Figure 24B). Coherence thresholds were lowest when integration field size matched the segment size but performance worsened when it decreased by 25 or 50%. There was a dramatic increase in coherence thresholds when the integration field size was larger (e.g. 200%) than the segment size. These findings suggest that performance on the motion task is optimal when the size of the integration field closely matches the segment size. Overall sensitivity is greatly reduced when larger integration fields are employed to perform the task.

Nominal upper (1.24°) and lower (0.62°) bounds were then introduced to constrain the analyses. The upper bound corresponds to the maximum integration field size that can be used to perform the motion task, whilst the lower bound determines the acuity limit. When segment size increases beyond the upper bound coherence thresholds become asymptotic because a smaller, sub-optimal integration field has to be employed. Figure 24C shows that coherence thresholds decreased as segment size increased. The slope of the descending limb of the curve was much shallower when integration field size was chosen at random on each trial so that it did not always match the segment size and the. The knee-point at which coherence thresholds became asymptotic was also larger. These results are qualitatively similar to those observed in readers with dyslexia and imply sub-optimal integration fields might be used to perform the motion task. However, the change in slope and knee-point of the curves in the computational analyses was only driven by two data points (Figure 24C) so further empirical research is needed to systematically explore this novel scale selection hypothesis.

To explore if increased levels of internal noise could provide an alternative explanation for our results Gaussian noise was added to the model's encoded direction of each dot (Figure 24D). Integration field size was set to match the segment size (100%), whilst the *SD* of the Gaussian noise distribution was varied between 0 and 90°. Adding a relatively small amount of internal noise (*SD* 30-60°) did not change the overall pattern of results, but the acuity limit and coherence threshold at asymptote increased dramatically when the standard deviation of the Gaussian noise was 90°. Crucially, there was no change in the slope of the descending limb or the knee-point of the curve. These findings are the opposite of those observed in the poorest readers and demonstrate that elevated levels of internal noise cannot readily explain their performance on the motion-based segmentation task.

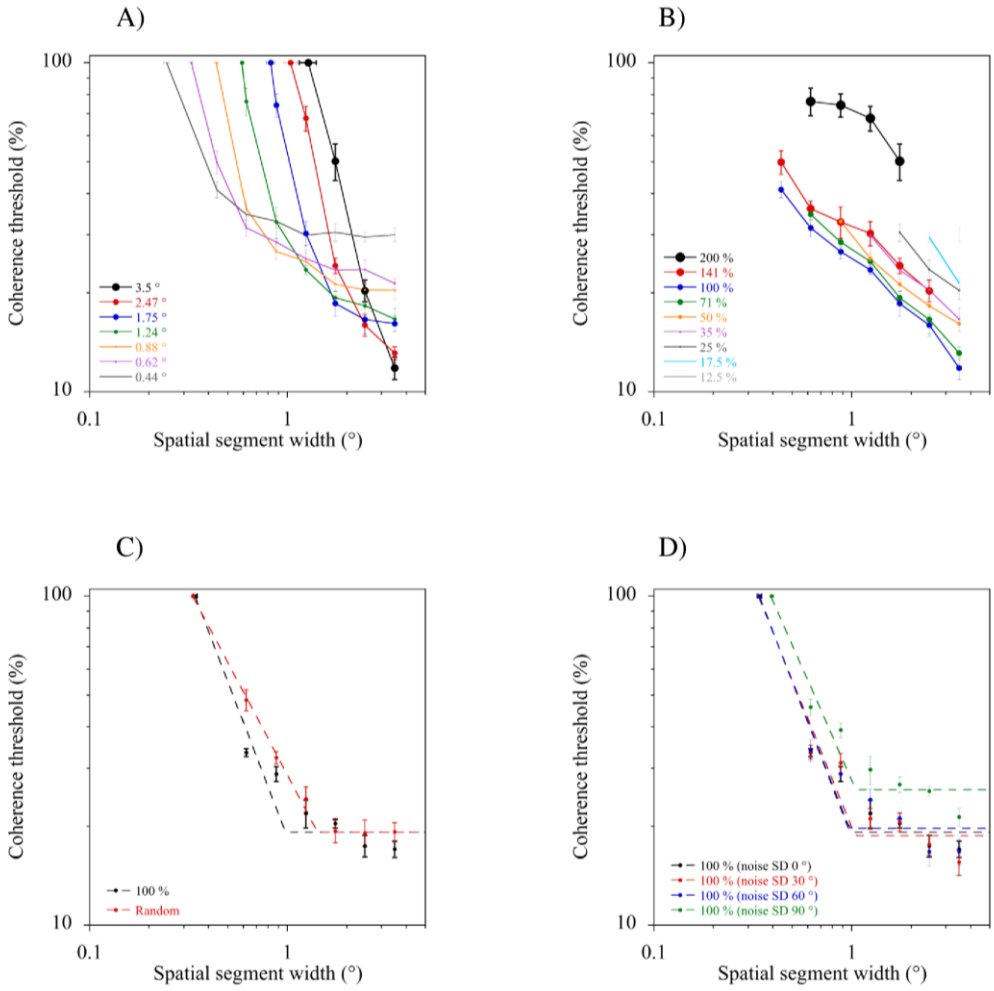


Figure 24. Results of the computational analyses. The graphs display acuity limits and coherence thresholds as a function of segment size when integration area is either fixed A) or varied in proportion to segment size B). Upper and lower bounds on field size were introduced to constrain the analyses and produced a qualitatively similar pattern of performance to that associated with poor reading when integration field size was randomised (sub-optimal) on each trial C), but not when internal noise levels were elevated D).

The results of the computational analyses suggest that poor readers' difficulties on the motion task in Chapter 4 reflect a deficit with scale selection but further research is needed to determine if this is the case because the change in slope and knee-point of the curves was only driven by two data points (Figure 24C). A direct prediction of the scale selection hypothesis is that relatively good readers should exhibit a qualitatively similar pattern of performance to readers with dyslexia when scale uncertainty is introduced into the motion task. The segment size at which performance becomes asymptotic should be significantly larger and the slope of the descending limb of the curve significantly shallower when segment size is varied on each trial, in comparison to when it is made predictable. In the present study, this prediction was tested by administering the same motion task (see Figure 18) to a group of twelve relatively good readers who did not meet conventional criteria for diagnosing dyslexia (standard scores ≤ 85 on the TOWRE Phonemic Decoding Efficiency subtest). Coherence thresholds were measured when the segment size was either made predictable on successive trials or when it was unpredictable to determine if the performance of relatively good readers mimics that of readers with dyslexia when information about segment size is uncertain.

5. 3. Materials and methods

5. 3. 1. Participants

Twelve participants (10 females and 2 males) were recruited to take part in the study. The mean age was 19.92 years (*SD* = 0.12 months).

5. 3. 2. Psychometric tests

Each participant completed standardised tests of reading ability and non-verbal IQ (see section 2. 2.). Summary statistics characterising the reading abilities of the participant sample are shown in Table 10. It is important to note that none of the participants met conventional criteria for diagnosing dyslexia i.e. standard scores ≤ 85 (at or below the 15th percentile) on the TOWRE Phonemic Decoding Efficiency subtest (Health et al., 2006, Pugh et al., 2014).

	M	*Median*	*SD*	*Range*
NART raw score (max 50)	26.25	26.00	3.91	17.00-32.00
TOWRE Sight Word Efficiency	100.17	99.00	11.20	82.00-113.00
TOWRE Phonemic Decoding	102.42	100.00	11.94	87.00-120.00
SPM raw score (max 60)	49.83	50.00	3.81	44.00-59.00

Table 10. Psychometric summary statistics for the entire sample of readers ($N = 12$). Standard scores ($M = 100$, $SD = 15$) are shown unless otherwise stated. NART = National Adult Reading Test; TOWRE = Test of Word Reading Efficiency; SPM = Raven's Standard Progressive Matrices.

5. 3. 3. Visual stimuli

The visual stimuli were identical to those in Chapter 4 (see section 4. 2. 3.).

5. 3. 3. 1. Motion task

The motion task was identical to that administered in Chapter 4 (see section 4. 2. 3. 1.).

5. 3. 4. Procedure

5. 3. 4. 1. Spatial resolution limits

Spatial resolution limits (i.e. the smallest segment size needed for reliable task performance) were measured in the same manner as those in Chapter 4 using a 3-down, 1-up adaptive staircase (see section 2. 6.). The staircase procedure terminated when eight reversals had been reached.

5. 3. 4. 2. Coherence thresholds

Coherence thresholds were measured across two experimental conditions. In the blocked condition, the segment size was predictable, and identical on, successive trials. It ranged from 0.438 to 3.5º in equal logarithmic steps. In the random condition, the segment size was made unpredictable on each trial and chosen randomly from a set of three values spanning a two octave (four-fold)

range of sizes. Coherence thresholds in the blocked and the random conditions were measured in the same manner as those in Chapter 4 using a 3-down, 1-up adaptive staircase (see section 2. 6.). The staircase terminated when eight reversals had been reached.

5. 3. 5. Curve-fitting

To quantify the relationship between segment size and performance on the motion task a two-limbed function was fitted to each participant's data (see section 4. 2. 5.). The data for both the blocked and random conditions were well described by this function (Mean R^2 for the blocked condition = 0.93, *SD* = 0.05, Range = 0.82 to 0.99; Mean R^2 for the random condition = 0.94, *SD* = 0.05, Range = 0.85 to 0.99) as shown in the graphs of Figure 25.

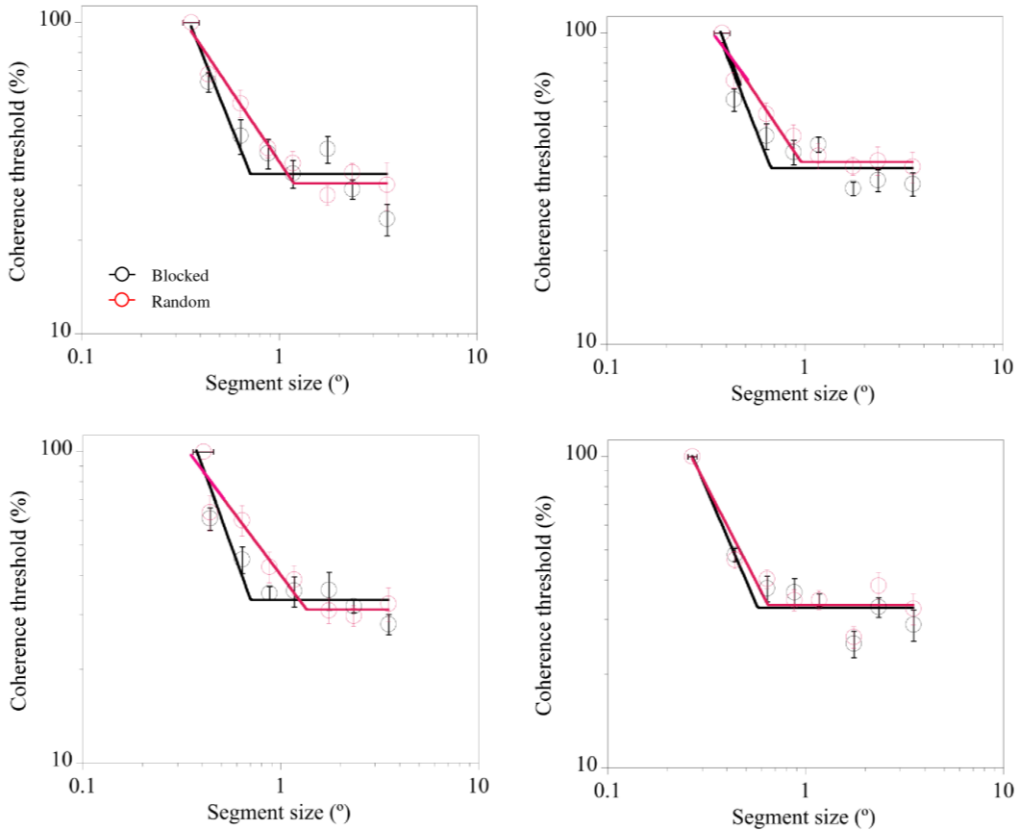


Figure 25. The data of four typical participants on the motion task when the segment size was made either predictable (blocked condition) or unpredictable (random condition) on each trial. Error bars, ±1sem.

5. 3. 6. Statistical analyses

To investigate if the three curve-fit parameters differed across the blocked and random conditions in the twelve relatively good readers a series of dependent-samples t-tests were conducted. Cohen's *d* was calculated as a measure of effect size with 0.2 considered a small, 0.5 a medium and 0.8 a large effect (Cohen, 1988). The results of Chapter 4 showed that control variables such as the sex of an individual and non-verbal IQ are not associated with performance on tasks requiring the spatial segmentation of local visual cues so it was not necessary to control for these factors in present analyses.

5. 4. Results

Descriptive statistics for the three curve-fit parameters in the twelve relatively good readers are displayed in Figure 26. Results for the dependent samples t-tests are given below.

5. 4. 1. Dependent samples t-tests

The mean knee-point of the curves was significantly larger in the random condition than the blocked condition, $t_{11} = 5.15$, $p < .001$, Cohen's $d = 1.49$. It increased from 0.85º when the segment size was made predictable on successive trials to 1.20º when the segment size was randomised on each trial. Importantly, coherence thresholds at asymptote were not significantly different in the blocked and random conditions, $t_{11} = 1.66$, $p = 0.13$ Cohen's $d = 0.48$. The mean slope of the descending limb of the curves was significantly shallower when the segment size was made predictable on successive trials in comparison to when it was unpredictable, $t_{11} = 4.29$, $p < 0.01$, Cohen's $d = 1.24$. The mean slope of the descending limb of curve was -1.60%/º in the blocked condition, whereas in the random condition it was -1.05%/º.

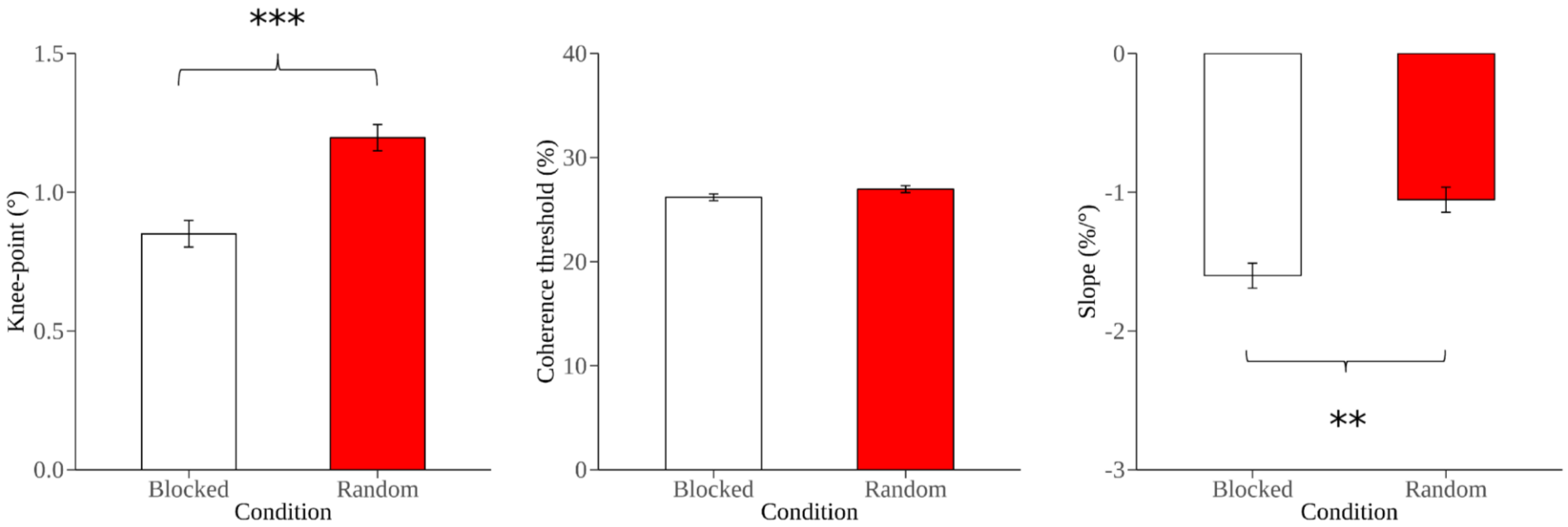


Figure 26. Graphs showing the three curve-fit parameters in the twelve relatively good readers when the segment size was made either predictable (blocked condition) or unpredictable (random condition) on each trial. * $p < .05$; ** $p < .01$; *** $p < .001$.

5. 5. Discussion

The results of Chapter 4 showed that the underlying nature of the visual deficit in readers with dyslexia extends to spatial segmentation but only on tasks containing motion information. The rate of improvement on the motion task was significantly shallower in adult poor readers than relatively good readers and the segment size at which coherence thresholds reached asymptote was significantly larger (see Figure 21). To explore why such a pattern of impairment might arise in developmental dyslexia a biologically-motivated computational model was devised. Although results showed that poor readers' difficulties on the motion task might reflect a deficit with scale selection further research is needed to qualify this because the change in slope and knee-point of the curves in the computational analyses was only driven by two data points (Figure 24C).

A direct prediction of the scale selection hypothesis was that relatively good readers should exhibit a qualitatively similar pattern of performance to readers with dyslexia when scale uncertainty is introduced into the motion task. To address this issue the same motion task (see Figure 18) was administered to a group of relatively good readers who did not meet conventional criteria for diagnosing dyslexia. Coherence thresholds were measured when the segment size was either made predictable on successive trials or when it was unpredictable. Results showed that the knee-point of the curves was significantly larger and the slope of the descending limb of the curves was

significantly shallower when the segment size was unpredictable on successive trials (random condition) in comparison to when it was predictable (blocked condition). Importantly, coherence thresholds at asymptote were not significantly different in the twelve relatively good readers across the blocked and random conditions. These results support the scale selection hypothesis as they show that the performance of relatively good readers mimics that of readers with dyslexia when information about segment size (scale) is uncertain.

An important issue concerns why readers with dyslexia had difficulty selecting optimally sized integration fields on the motion task but not the form task in Chapter 4. During reading characteristic saccadic eye movements and fixations are made (Rayner, 1998), changing the position of words on the retinae over time. The motion task also contained time-varying information, whereas the visual cues in the form task remained relatively static throughout the stimulus presentation because participants were required to maintain steady fixation in the centre of the display. Thus, readers with dyslexia might have a deficit with scale selection on visual tasks that require segmentation of a temporally-changing input.

A key issue for future research is whether or not a deficit with scale selection can explain why performance on conventional RDKs is impaired in developmental dyslexia (see section 1. 3. 5.). RDKs require spatio-temporal integration and for typically developing adults thresholds have been shown to improve when stimulus size increases, presumably because more visual information becomes available (Barlow & Tripathy, 1997; Watamaniuk &

Sekuler, 1992). If readers with dyslexia select (say) smaller integration fields than skilled readers, it may explain why they also have elevated coherence thresholds on RDKs (Benassi et al., 2010).

5. 6. Summary

In summary, the results of the computational modeling show that poor readers' difficulties on the motion task in Chapter 4 may have arisen because of a deficit with scale selection. A direct prediction of this novel hypothesis is that relatively good readers should exhibit a qualitatively similar pattern of performance to readers with dyslexia when scale uncertainty is introduced into the motion task. Indeed, the results of the present study are consistent with this prediction. Further research is needed to explore if a deficit with scale selection can readily explain why performance on conventional RDKs is impaired in developmental dyslexia (see section 1. 3. 5.)

Chapter 6[1]

Temporal segmentation of motion and form information in adult poor readers

6. 1. Introduction

The results of Chapter 5 suggest that poor readers' difficulties on tasks requiring the spatial segmentation of motion information reflect a deficit with scale selection. However, the position of words on the retinae is constantly being updated during reading as a discrete series of eye movements and fixations are made (Rayner, 1998). Effective decoding of text, therefore, requires local visual information to be segmented over time, as well as across space. There is some evidence to suggest that temporal segmentation of the auditory speech stream is impaired in readers with developmental dyslexia (Goswami, 2011; Lehongre, Ramus, Villiermet, Schwartz, & Giraud, 2011; Lehongre, Morillon, Giraud, & Ramus, 2013). This raises the possibility that difficulties with temporal segmentation might represent a generic deficit in developmental dyslexia and thus should arise in other sensory modalities, such as vision.

[1] The results outlined in this chapter have been published in *Journal of Vision*. Citation: Johnston, R., Pitchford, N. J., Roach, N. W., Ledgeway, T. (2017). Encoding of rapid time-varying information is impaired in adult poor readers. *Journal of Vision, 17(5)*, 1-13.

Critical flicker fusion (CFF) thresholds can be measured to determine the maximum temporal frequency needed to segment temporally-changing visual input. To explore the relationship between CFF thresholds and reading ability Talcott, Hansen, Willis-Owen, McKinnnell, Richardson and Stein (1998) asked thirty-eight adult readers to discriminate flickering equiluminant stimuli from patterns that did not appear to flicker. Results showed that CFF thresholds were significantly correlated with scores on a standardised measure of reading ability. The temporal frequency needed to detect the flickering stimuli was lower in relatively poor readers than relatively good readers. However, Edwards et al. (2004) failed to replicate these findings using the method of adjustment to measure CFF thresholds. As previously mentioned, a disadvantage of using the method of adjustment is that it is subjective and thus it is impossible to determine the response criterion participants use to perform the task (see section 1. 3. 1. 2.). Furthermore, as is the case for spatial segmentation tasks, relying on a single measurement of sensitivity is insufficient to characterise performance on temporal segmentation tasks. For example, van Doorn and Koenderink (1982b) found that coherence thresholds for detecting a temporally segmented random-dot display depend upon temporal frequency.

In summary, the results of Chapter 5 showed that readers with dyslexia have a deficit with scale selection, which manifests as a difficulty on visual tasks requiring the spatial segmentation of motion information. However, it is currently unclear if temporal segmentation is also generally impaired in developmental dyslexia as previous research relied on a single measurement of

sensitivity and no studies have compared temporal segmentation of motion and form information (Talcott et al., 1998). In the current study, these issues were addressed by administering temporal versions of the spatial segmentation tasks used in Chapter 4 to thirty-eight adults with a wide range of reading abilities. Coherence thresholds were measured at each of a range of oscillation rates (segment durations). In addition, a curve was fitted to each participant's data, which allowed the shape of the threshold versus segment duration function to be systematically investigated.

6. 2. Materials and methods

6. 2. 1. Participants

Thirty-eight adults (Male = 6; Female = 32) with a wide range of reading abilities were recruited to take part in the study (see section 2. 1.). The mean age was 20.35 years (*SD* = 2.82 months).

6. 2. 2. Psychometric tests

Each participant completed standardised tests of reading ability and non-verbal IQ (see section 2. 2.). Summary statistics characterising the reading abilities of the participant sample are shown in Table 11. It is important to note that three participants had standard scores ≤ 85 (at or below the 15th percentile) on the TOWRE Phonemic Decoding Efficiency subtest, which falls into the conventional range for diagnosing dyslexia (Heath et al., 2006; Pugh et al. 2014)

	Mean	*Median*	*SD*	*Range*
NART raw score (max 50)	25.87	26.00	5.16	16.00-40.00
TOWRE Sight Word Efficiency	97.34	98.00	11.10	71.00-113.00
TOWRE Phonemic Decoding	99.05	97.00	11.46	73.00-120.00
SPM raw score (max 60)	49.63	50.00	5.33	38.00-59.00

Table 11. Psychometric summary statistics for the entire sample. Standard scores (M = 100, SD = 15) are shown unless otherwise stated. NART = National Adult Reading Test; TOWRE = Test of Word Reading Efficiency; SPM = Raven's Standard Progressive Matrices.

6. 2. 3. Visual stimuli

The visual stimuli were directly analogous to those in Chapter 4 (see section 4. 2. 3.).

6. 2. 3. 1. Motion task

The stimuli in the motion task (Figure 27) consisted of forty-three images, each containing 256 dots that were presented consecutively at a rate of 100Hz to create the perception of apparent motion. Individual dots were displaced by 0.035º on each positional update (speed = 3.5º/s). The "strength" or coherence of the stimuli could be varied between 0 and 100% by constraining some of the dots to move in the same direction on each image update (*signal* dots) and others to move randomly (*noise* dots). Two patterns were randomly presented in succession on each trial with equal probability. They were separated by an ISI of 0.52s. The signal dots in the test stimulus oscillated back and forth (leftwards and rightwards) at each of a range of rates. Observers discriminated this temporally segmented stimulus from a comparison stimulus containing identical motion cues that were temporally intermingled. Each signal dot had a limited lifetime of 0.22s (22 frames). At the beginning of the motion sequence it was assigned a random 'age' in frames between 1 and 22. On each image update the 'age' parameter was incremented by 1. The dot was replotted at a random location when the limit of 22 frames was exceeded.

6. 2. 3. 2. Form task

Stimuli in the form task (Figure 27) were generated by computing a 4-frame, random-dot motion sequence in which the signal dots were constrained to move either vertically or horizontally. The individual frames were then spatially superimposed to create a single static image (Simmers et al., 2005; Johnston et al., 2016a, 2016b) in which the signal dots formed localised streaks, orientated (vertically or horizontally) along a common axis, whilst the noise dots formed random clusters. The length of each dot streak was 0.18º. The coherence of the stimuli could be varied between 0 and 100% by changing the relative proportion of signal to noise dot streaks. As in the motion task, two patterns were randomly presented in succession on each trial with equal probability. They were separated by an ISI of 0.52s. The dot streaks in the test stimulus oscillated back and forth (vertical and horizontal) at each of range of rates. Participants discriminated this temporally segmented stimulus from a comparison stimulus containing identical form cues that were temporally intermingled.

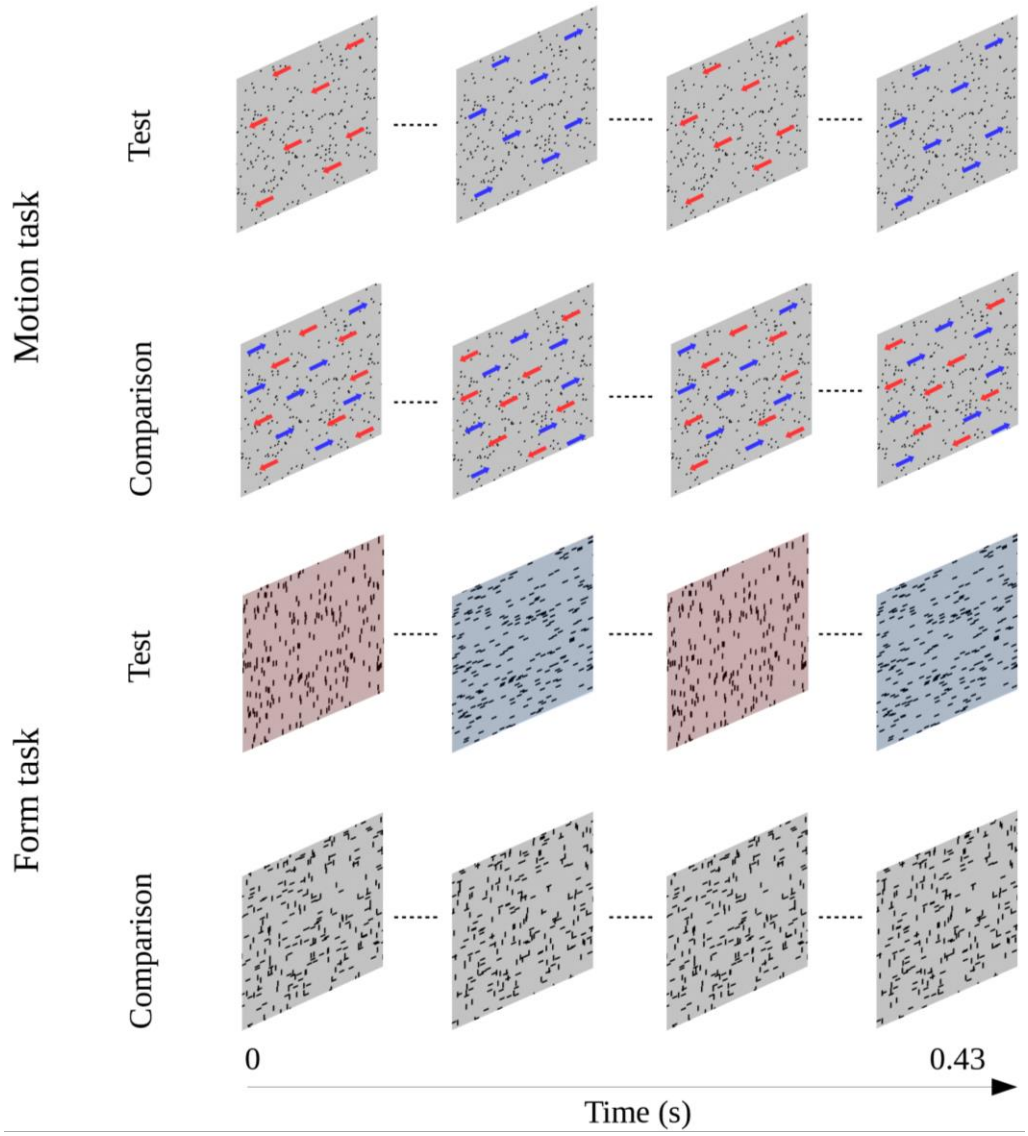


Figure 27. Schematic of the stimuli in the motion and form tasks. Coloured overlays and arrows have been added for illustrative purposes only and depict how the test stimuli were temporally segmented.

6. 2. 4. Procedure

6. 2. 4. 1. Temporal resolution limits

To determine the shortest segment duration (i.e. maximum oscillation rate) needed to reliably perform the motion and form task temporal resolution (acuity) limits were measured. The coherence of the stimuli was held constant at 100% in each trial block. Segment duration was varied on each trial using a two-interval, temporal forced-choice procedure and a 3-down, 1-up adaptive staircase (see section 2. 6.). The initial step size was 0.215s and this decreased by half after each reversal. The participants' task was to identify the temporally segmented test stimulus.

6. 2. 4. 2. Coherence thresholds

Coherence thresholds were obtained in a similar manner to acuity limits. However, segment duration was held constant in each trial block. It ranged from 0.03 to 0.215s in equal logarithmic steps. Stimulus coherence was varied on each trial using a 3-down, 1-up adaptive staircase (see section 2. 6.). The initial step size of the staircase was equal to the total number of elements in the display and this decreased by half after each reversal. The participants' task was to identify the temporally segmented test stimulus.

6. 2. 5. Curve-fitting

To quantify the relationship between segment duration and perceptual performance a two-limbed curve was fitted to each participant's data (see section 4. 2. 5.). In all cases, the data were well described by the function (Mean R^2 for the motion task = 0.94, *SD* = 0.05, Range = 0.79 to 0.99; Mean R^2 for the form task = 0.95, *SD* = 0.04, Range = 0.82 to 0.99). Representative data for a single participant on the motion task and the form task is shown in Figure 28A and 28B, respectively. The empirically measured acuity limit together with the three best-fitting parameters derived from the curve-fit procedure (knee-point, coherence threshold at asymptote, and slope) are depicted in Figure 28C.

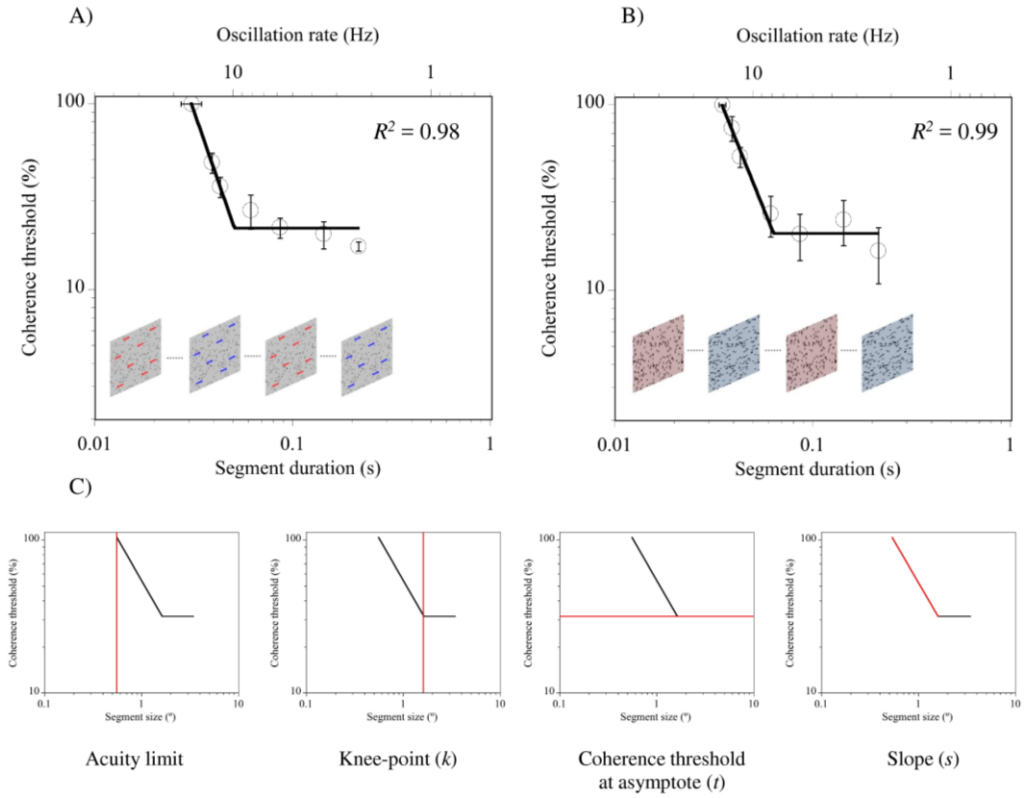


Figure 28. Illustrative data for a single participant on A) the motion task and B) the form task. The dashed red line in C) represents the temporal acuity limit and best-fitting parameters (*k, t, & s)* from Equation 1. Error bars, ±1 sem.

6. 2. 6. Statistical analyses

There is now strong evidence to suggest that performance on low-level visual perception tasks, requiring the processing of motion and form, cannot differentiate generally poor readers from individuals who meet conventional criteria for diagnosing dyslexia (see Chapter 3). Thus, a series of whole-sample analyses were conducted using a composite measure of reading skill (see section 2. 4.). Control variables such as the sex of an individual and non-verbal IQ are often associated with performance on tasks necessitating integration, but not spatial segmentation, of local visual motion cues. However, it is currently unclear if these control variables are associated with temporal segmentation so semi-partial correlations were used to investigate if reading ability explained any additional variance in task performance after controlling for the sex of an individual and non-verbal IQ. This is especially important in the current study, as considerably more females than males participated.

Several of the best-fitting parameters for the motion task (acuity limits, the knee-point of the curves, and the slope of the descending limb of the curves) and the form task (the knee-point of the curves, and the slope of the descending limb of the curves) violated the assumption of normality (Shapiro-Wilk test: $p < 0.03$). Thus, a series of non-parametric, semi-partial correlations were performed on these variables using Spearman's rank-order correlation coefficient (r_s). Acuity limits for the motion task and coherence thresholds at asymptote for both tasks did not violate the assumption of normality (Shapiro-Wilk test: $p > 0.08$) so a series of parametric, semi-partial correlations were

performed on these variables using Pearson's product-moment correlation coefficient (*r*). Cohen's *d* was calculated as a measure of effect size with 0.2 considered a small, 0.5 a medium, and 0.8 a large effect (Cohen, 1988).

6. 3. Results

6. 3. 1. Composite reading score: PCA

Scatters plots showing the relationships between scores on the three individual measures of reading ability are shown in Figure 29. The correlations between the individual measures of reading ability ranged from moderate to strong (r = 0.55 – 0.78, $p < 0.001$) so PCA was conducted to calculate the composite measure of reading skill. Raw scores for the three reading tests were entered into the analysis, which was performed on the correlation matrix. A single principal component accounted for 77% of the total variance amongst the individual measures of reading ability (*Eigenvalue 1* = 2.30; *Eigenvalue 2* = 0.49; *Eigenvalue 3* = 0.22). Loadings for the TOWRE Sight Word Efficiency subtest and the TOWRE Phonemic Decoding Efficiency subtest were within the same range (0.92 and 0.90, respectively) but the NART contributed slightly less (loading = 0.81). PCA scores for each individual were entered into the whole-sample analyses to investigate how general reading ability relates to performance on the motion and form tasks.

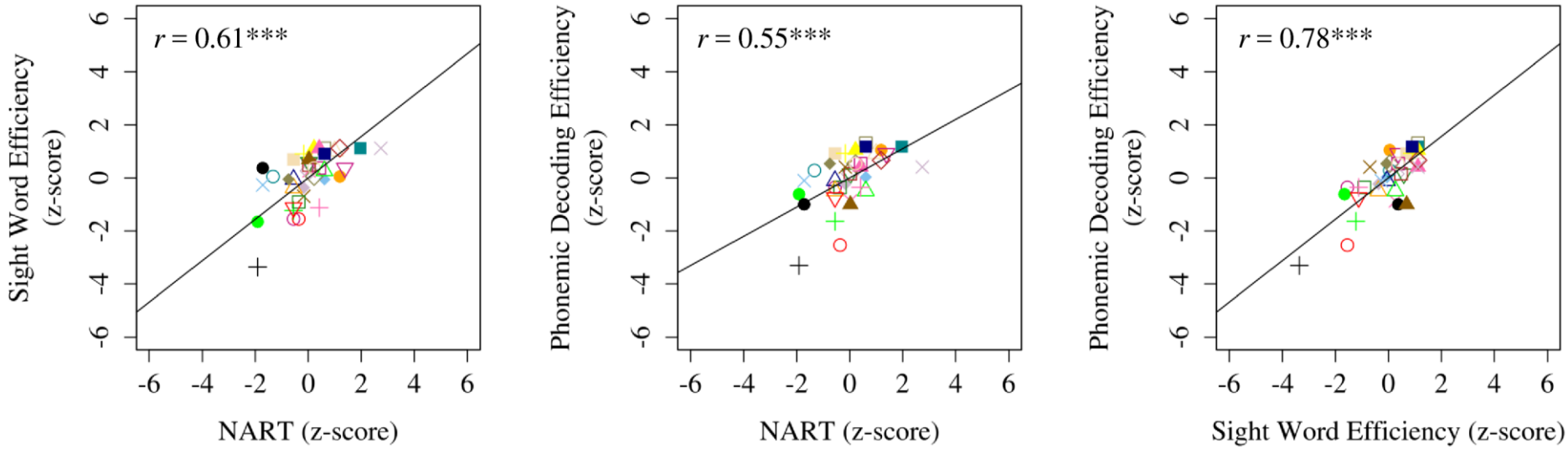


Figure 29. Scatter plots showing the relationships between scores on the three individual measures of reading ability in the entire sample ($N = 38$). Positive and negative z-scores indicate scores better than and worse than the mean of the sample, respectively. Note that z-scores were used for illustrative purposes only and did not influence the correlations. NART = National Adult Reading Test; TOWRE = Test of Word Reading Efficiency. * = $p < .05$; ** = $p < .01$; *** = $p < .001$.

6. 3. 2. Whole-sample analyses: semi-partial correlations

The results of the whole-sample analyses are described in the sections below. Scatterplots showing the relationships between reading ability and various components underlying performance on the motion and form task are shown in Figure 30 and Figure 31, respectively.

6. 3. 2. 1. Motion task

Scores on the composite measure of reading skill were significantly and negatively correlated with temporal acuity limits on the motion task, r_s = -0.46, $p < 0.01$, Cohen's d = 1.04. The minimum segment duration needed to detect the test stimulus was longer in relatively poor readers (i.e. those with lower composite scores for reading) than relatively good readers (i.e. those with higher composite scores for reading). General reading ability was not significantly correlated with the knee-point of the curves, r_s = 0.07, p = 0.68, Cohen's d = 0.14. A non-significant trend was found between composite reading scores and coherence thresholds at asymptote, r = -0.33, p = 0.051, Cohen's d = 0.70. However, coherence thresholds at asymptote were significantly correlated with non-verbal IQ, r = -0.46, $p < 0.01$, Cohen's d = 1.04. Individuals with a lower IQ had higher coherence thresholds at asymptote than individuals with a higher IQ. The point on the y-axis at which performance became asymptotic was lower in relatively poor readers than relatively good readers. Reading ability was not significantly correlated with

the slope of the descending limb of the curves, $r_s = 0.26$, $p = 0.12$, Cohen's $d = 0.54$.

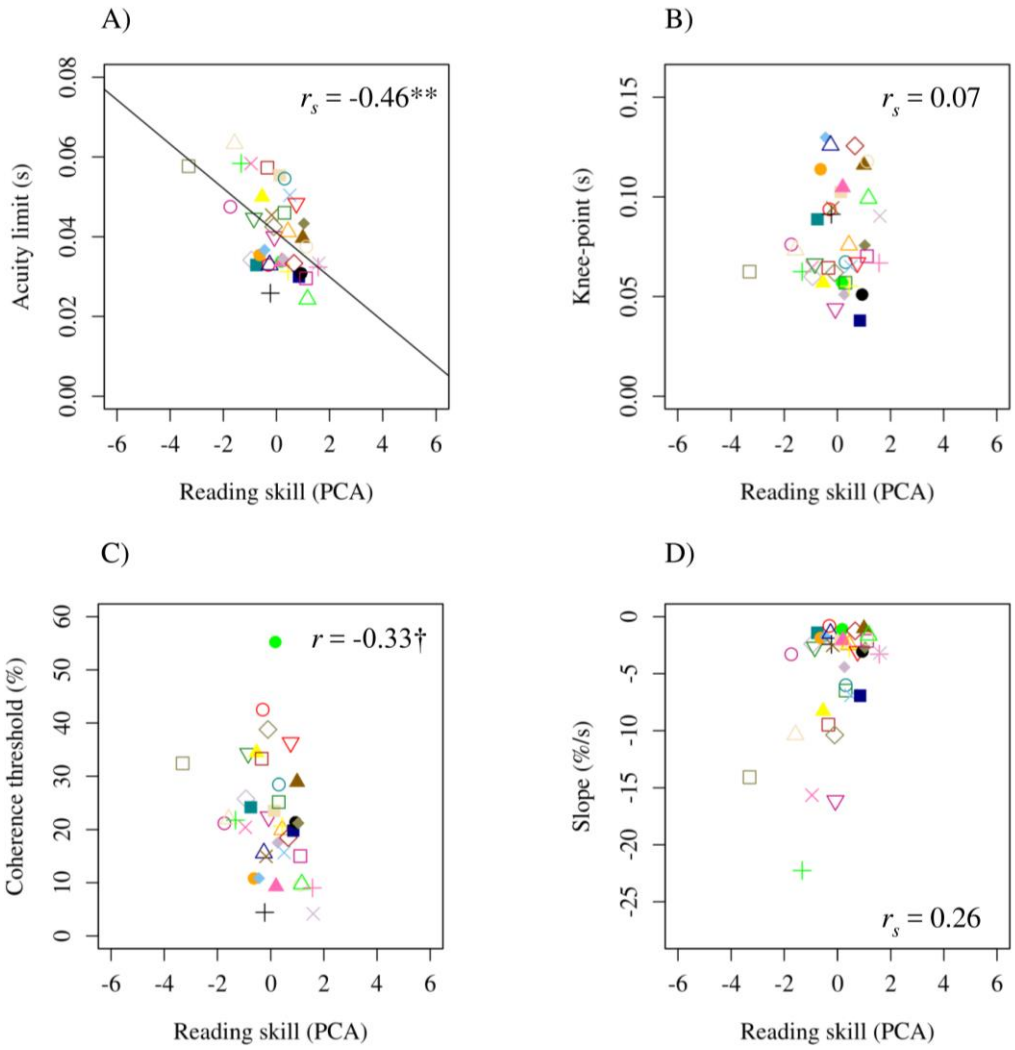


Figure 30. Scatter plots for the motion task showing the relationships between reading ability and temporal acuity limits A), the knee-point of the curves B), coherence thresholds at asymptote C) and the slope of the descending limb D). Each coloured symbol represents an individual participant. Positive and negative scores on the composite measure of reading skill indicate performance that is better or worse than the mean of the sample, respectively. † Non-significant trend; * $p < .05$; ** $p < .01$; *** $p < .001$.

6. 3. 3. 2. Form task

Scores on the composite measure of skill were significantly and negatively correlated with temporal acuity limits on the form task, r = -0.40, p = 0.02, Cohen's d = 0.87. The minimum segment duration needed to detect the test stimulus was longer in relatively poor readers than relatively good readers. No significant correlation was found between reading ability and the knee-point of the curves, r_s = -0.04, p = 0.83, Cohen's d = 0.08. The correlation between reading ability and coherence thresholds at asymptote also did not reach statistical significance, r = -0.23, p = 0.18, Cohen's d = 0.47. However, a significant correlation was found between non-verbal IQ and coherence thresholds at asymptote, r = -0.48, $p < 0.01$, Cohen's d = 1.09. Individuals with a lower IQ had higher coherence thresholds at asymptote than individuals with a higher IQ. The slope of the descending limb of the curves was not significantly correlated with reading ability, r_s = 0.27, p = 0.11, Cohen's d = 0.56.

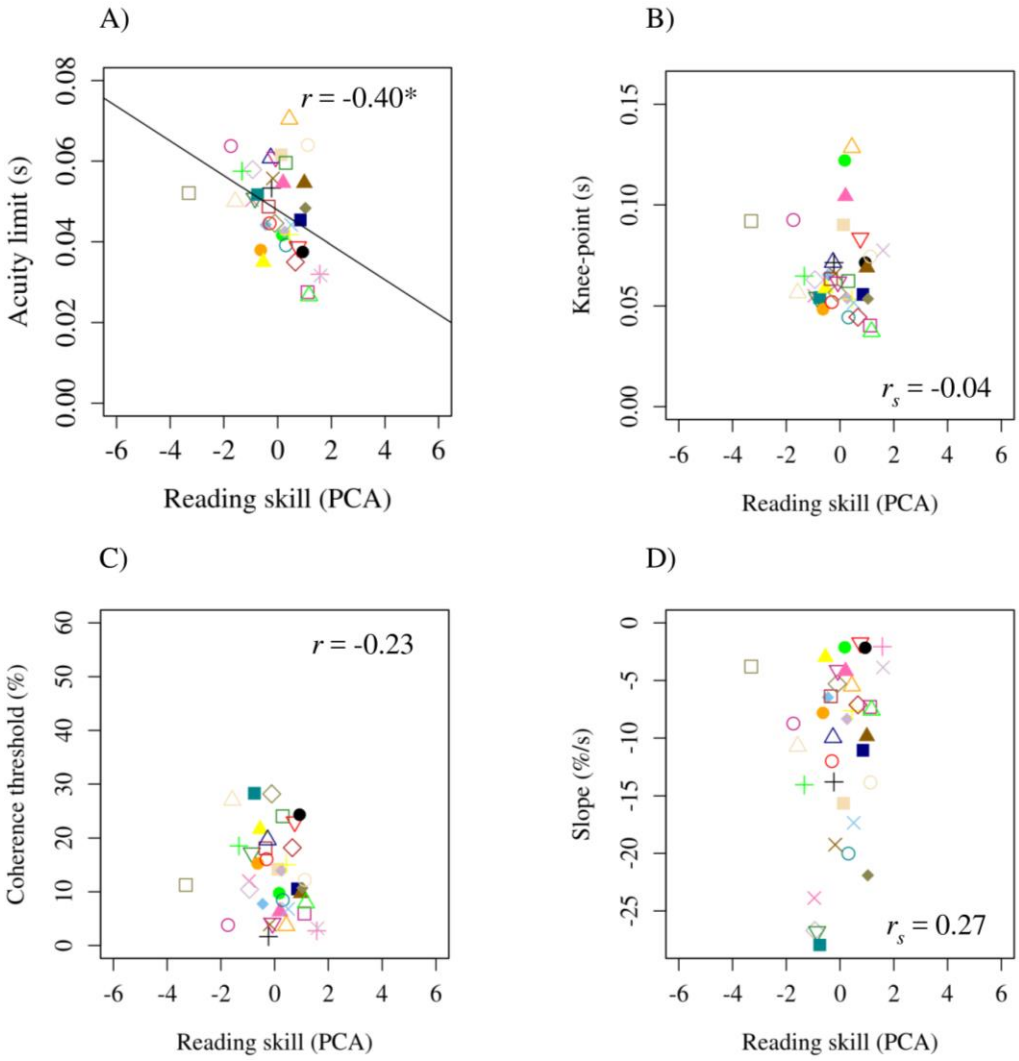


Figure 31. Scatter plots for the form task showing the relationships between reading ability and temporal acuity limits A), the knee-point of the curves B), coherence thresholds at asymptote C) and the slope of the descending limb D). Each coloured symbol represents an individual participant. Positive and negative scores on the composite measure of reading skill indicate performance that is better or worse than the mean of the sample, respectively. * $p < .05$; ** $p < .01$; *** $p < .001$.

6. 4. Discussion

The results of Chapter 5 suggest that poor readers' difficulties on tasks requiring the spatial segmentation of motion information reflect a deficit with scale selection. However, the effects of reading ability on temporal segmentation are currently unclear as previous work has relied on a single measurement of sensitivity and has failed to delineate temporal segmentation of motion and form information (Talcott et al., 1998). In the present study, these limitations were systematically addressed by administering a new set of motion and form tasks, that were temporal versions of the spatial segmentation tasks used in Chapter 4. Results showed that temporal acuity limits for both the motion and form tasks were significantly and negatively correlated with scores on the composite measure of reading skill, consistent with previous research that has explored the effects of reading ability on CFF thresholds (Holloway, Náñez, & Seitz, 2013; Talcott et al., 1998). The minimum segment duration needed to detect the test stimulus was longer in relatively poor readers than relatively good readers. However, our results extend previous findings in two key ways. First, our results suggest that relatively poor readers have a generic difficulty with temporal segmentation that transcends domains as a similar pattern of results (both strength and significance of correlation) was found for both the motion and form tasks. Second, our results reveal that the difficulties with temporal segmentation of motion and form information shown by relatively poor readers are pronounced at short segment durations.

The results of the current study cast further doubt on the notion that adult poor readers have a selective impairment in the dorsal visual processing stream (see section 1. 3. 5.) as temporal acuity limits for the motion and form task were significantly correlated with general reading ability. Braddick et al. (2016) have suggested that visual deficits found in generally poor readers are qualitatively distinct to those observed in developmental dyslexia. However, other studies have shown that visual difficulties cannot differentiate generally poor readers from individuals with impaired phonological decoding skills consistent with the dyslexic profile (Hulslander et al., 2004; Talcott et al., 1998). In the current study, three participants met the conventional criterion for developmental dyslexia (i.e. ≤ 85 on the TOWRE Phonemic Decoding Efficiency subtest) but they were indistinguishable from generally poor readers on the basis of their visual performance, with the exception of one reader with dyslexia who had the shallowest slope parameter on the motion task. Further research is needed to address the reliability of this finding but at present there is strong evidence to suggest that performance on low-level visual perception tasks, requiring the processing of motion and form, cannot typically differentiate adult poor readers from individuals with developmental dyslexia.

The findings of the current study are consistent with the notion that adult poor readers have difficulty on visual tasks requiring rapid encoding of temporal information in the brain. In the present study, the stimuli in the motion task consisted of individual dots that were displaced on each frame to create the perception of apparent motion, whereas the stimuli in the form task comprised directly analogous dot streaks (Simmers et al., 2005). Although both tasks

necessitated segmentation of local visual cues over time, the motion task required a finer, additional scale of temporal processing than the form task because the positions of local dots was constantly being updated. The correlation between temporal acuity limits and scores on the composite measure of reading skill was slightly stronger for the motion task than the form task. As adult poor readers also exhibit impaired performance on auditory tasks containing acoustic signals that are constantly changing over time, this implies a generic deficit with the parsing of time-varying information that extends to other sensory modalities (Giraud & Poeppel, 2012; Goswami, 2011; Lehongre et al., 2011; Lehongre et al., 2013; Pammer, 2014).

The results of Chapter 5 suggest that readers with dyslexia have a deficit with scale selection. To reliably perform the motion and form tasks in the present study local visual cues had to be integrated over a certain period of time. Our results are not indicative of a deficit with temporal scale selection, as the knee-point and slope of the descending limb of the curves for the motion and form tasks were not significantly associated with general reading skill. Thus, the underlying nature of the visual deficit in adult poor readers appears to have at least two distinct components, one spatial and one temporal. That is, a difficulty in selecting the spatial scale optimal for performance and an insensitivity to visual stimuli that change over time, particularly when that temporal change is rapid.

A deficit in temporal acuity could also explain why reading ability is significantly correlated with coherence thresholds on conventional RDK tasks

but not global form tasks, as relatively poor readers could sample individual frames of the motion sequence at a lower rate. However, under certain conditions, reduced temporal sampling can have a facilitatory effect. Research has shown that RDK tasks cannot be reliably performed when a delay greater than ~100ms is introduced between consecutive frames (Baker & Braddick, 1985). Mather and Tunley (1995) found that larger inter-frame-intervals could be tolerated when low-pass temporal filtering was applied to the motion-sequence in order to reduce sampling rate. Hence, it should be possible to simulate conditions under which relatively poor readers outperform relatively good readers on RDKs tasks i.e. when a relatively long temporal delay is introduced between consecutive frames.

In the present study, we conducted semi-partial correlations to investigate if composite reading scores predicted task performance after controlling for the sex of an individual and non-verbal IQ, which are known to be associated with motion perception (Arranz-Paraíso and Serrano-Pedrazza, 2016; Cook et al., 2016; Melnick et al., 2013). The very limited number of male participants in the current study (6/38) precludes a meaningful investigation of how the sex of an individual relates to visual performance. However, additional analyses across the whole sample revealed that non-verbal IQ was significantly and negatively correlated with coherence thresholds at asymptote on both the motion task (r = -0.46, $p < 0.01$) and the form task (r = -0.48, $p < 0.01$), after partialling out reading ability and the sex of an individual. Individuals with a lower IQ had reduced sensitivity at asymptote than individuals with a higher IQ. These results extend previous findings by showing that non-verbal IQ is

also associated with tasks in which either motion or form cues need to be segmented over time. Why non-verbal IQ is significantly associated with performance on some psychophysical tasks but not others is currently unclear. Nonetheless, our results highlight the critical importance of controlling for non-verbal IQ when exploring visual performance in dyslexia and other neurodevelopmental disorders.

One factor that may limit the conclusions drawn in this experiment is the relatively small variation in reading ability, as indicated by the standard deviations in Table 11. Hence, the effect sizes reported in this experiment are likely to have been conservative and may be larger in the general population (see Section 8. 5. 4.). Another limiting factor is the sex composition of the participants. As previously mentioned, the number of male participants was relatively small. This raises the possibility that a generic deficit with the temporal segmentation of motion and form information at relatively short segment durations might only arise in female poor readers. Further research is needed to explore if such a deficit extends to male poor readers.

6. 5. Summary

In summary, the results of the present study demonstrate that adult poor readers have difficulty segmenting temporally-changing motion and form cues, particularly at short segment durations. They are not indicative of a deficit with temporal scale selection, as the knee-point and slope of the descending limb of the curves for the motion and form tasks were not significantly associated with scores on the composite measure of reading skill. Thus, the underlying nature of the visual deficit in adult poor readers appears to have at least two distinct components, one spatial and one temporal. Interestingly, individuals with a lower IQ had reduced sensitivity at asymptote than individuals with a higher IQ. These results extend previous findings by showing that non-verbal IQ is also associated with visual tasks in which either motion or form cues need to be segmented over time.

Chapter 7

Effects of perceptual uncertainty on global motion and form detection in developmental dyslexia

7. 1. Introduction

Taken together, the results of Chapters 3 to 6 suggest that the visual deficit in generally poor readers and individuals with dyslexia has at least two distinct components, one spatial and one temporal. That is, a difficulty in selecting the spatial scale optimal for task performance and an insensitivity to visual stimuli that are changing rapidly over time. An alternative theory of the origin of visual impairment in developmental dyslexia is the anchoring deficit hypothesis (see section 1. 3. 3.). This framework proposes that individuals with dyslexia cannot utilise stimulus repetitions to form a perceptual anchor. Such a deficit is thought to manifest as a difficulty on 2IFC tasks that necessitate comparisons across sequentially presented stimuli (Ahissar et al., 2006; Ahissar, 2007; Jaffe-Dax et al., 2015, 2016). The anchoring deficit hypothesis cannot readily explain the results of Chapters 4 and 6 in which the effects of reading ability on spatial and temporal segmentation were systematically investigated. However, it has not yet been studied using more conventional

global motion and form stimuli that necessitate integration, as opposed to segmentation, of local visual cues. To address this issue in the present study a 2IFC global motion detection task and an analogous form detection task were administered to forty-four adults with a wide range of reading skills. By varying the degree of uncertainty associated with the axis of global motion or orientation the ability to form a perceptual anchor was manipulated across different blocks of trials. The anchoring deficit hypothesis predicts that reading ability should be significantly associated with performance when the axis of global motion or orientation is identical i.e. when it is chosen randomly on each trial from a uniform distribution spanning 0°. When the axis of global motion or orientation is chosen randomly on each trial from a uniform distribution spanning ±45 or ±90° reading ability should not be significantly associated with performance as the lack of stimulus repetitions means that no perceptual anchor can be formed.

7. 2. Materials and methods

7. 2. 1. Participants

Forty-four adults (32 female, 12 male) with a wide range of reading abilities were recruited to take part in the study (see section 2. 1.). The mean age of the participants was 22.58 (*SD* = 0.38 months).

7. 2. 2. Psychometric tests

Each participant completed tests of non-verbal IQ and reading ability (see section 2. 2.). Summary statistics characterising the reading abilities of the participant sample are shown in Table 12. It is important to note that eleven participants had standard scores ≤ 85 (at or below the 15th percentile) on the TOWRE Phonemic Decoding Efficiency subtest, which falls into the convention range for diagnosing dyslexia (Heath et al., 2006; Pugh et al., 2014).

	Mean	*Median*	*SD*	*Range*
NART (raw score/50)	28.05	28.00	5.19	15.00-40.00
TOWRE Sight Word Efficiency	91.39	92.00	13.02	66.00-113.00
TOWRE Phonemic Decoding	95.61	95.00	14.98	67.00-120.00
SPM (raw score/60)	50.70	51.00	4.59	38.00-60.00

Table 12. Psychometric summary statistics for the entire sample. Standard scores (M = 100, SD = 15) are shown unless otherwise stated. NART = National Adult Reading Test; TOWRE = Test of Word Reading Efficiency; SPM = Raven's Standard Progressive Matrices.

7. 2. 3. Visual stimuli

Stimuli were viewed binocularly at a distance of 114cm and were presented within the confines of a circular display window (diameter = 12°) in the centre of the monitor. Each stimulus was composed of an ensemble of "black" (0.01cd/m^2) dots (diameter = 0.12°) presented against a uniform "grey" (34cd/m^2) background. More precise details relating to stimulus generation in the global motion and form task are given below.

7. 2. 3. 1. Global motion task

Stimuli in the global motion task were conventional RDKs (Figure 32). They consisted of eight images, each containing 200 dots that were presented consecutively at a rate of 18.75 Hz. Individual dots were displaced by 0.12° on each image update, which resulted in a drift speed of 2.26°/s. Two patterns were presented in succession on each trial, in a random order, with equal probability. They were separated by an ISI of 0.52s. The test stimulus contained a proportion of dots that were constrained to move in a common direction (*signal* dots), whilst others (*noise* dots) moved randomly. The "strength" or coherence of the test stimulus could be varied between 0 and 100% by changing the relative proportion of signal to noise dots. Whether an individual dot was assigned to be signal or noise was randomised on every

displacement so the direction in which that dot moved was limited in time. In contrast, the comparison stimulus only contained randomly moving noise dots. Participants had to judge whether the test stimulus appeared in the first or second temporal interval.

7. 2. 3. 2. Global form task

Stimuli in the global form task (Figure 32) were generated using a full 8-frame random-dot global motion sequence. The individual frames were then spatially superimposed to create a static image (Simmers et al., 2005). As in the global motion task, two patterns were presented in succession on each trial, in a random order, with equal probability. They were separated by an ISI of 0.52s. The test stimulus contained a proportion of dots (*signal* dots) that formed localised streaks, with a common orientation, whilst others (*noise* dots) formed random groupings. The coherence of the test stimulus could be varied between 0 and 100% by changing the relative proportions of signal to noise dots in the image. In contrast, the comparison stimulus only contained random groupings of noise dots. Participants had to judge whether the test stimulus appeared in the first or second temporal interval.

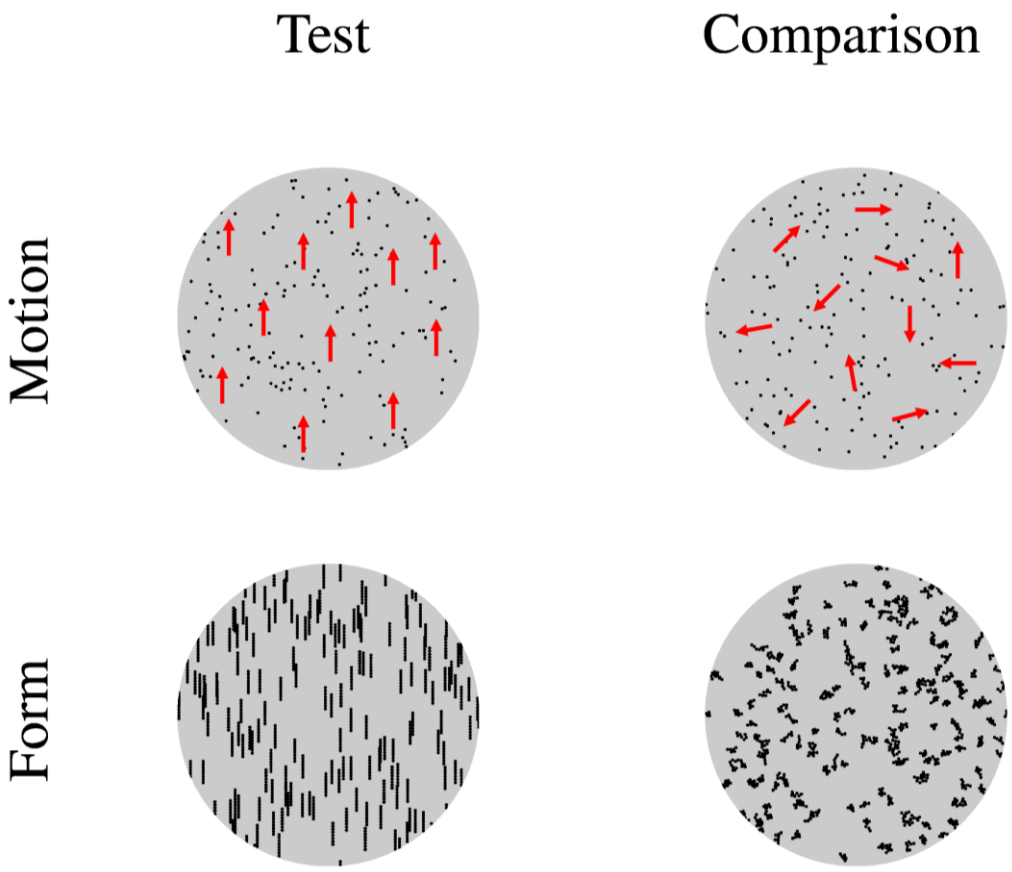


Figure 32. Schematic illustration of the test and comparison stimuli used in the global motion and form tasks. In this particular example, the coherence of the test stimulus was 100%. The axis of global motion or orientation was chosen from a uniform distribution, centred on vertical, spanning 0°.

7. 2. 4. Procedure

Coherence thresholds for the global motion and form tasks were measured using a 3-down, 1-up adaptive staircase (see section 2. 6.). The initial step size of the staircase was equal to the total number of elements in the display and this decreased by half after each reversal.

7. 2. 5. Perceptual uncertainty

By changing the degree of uncertainty associated with the axis of global motion or orientation across different trial blocks the ability to form a perceptual anchor was manipulated. The axis of global motion or orientation was chosen randomly on each trial from a uniform distribution, centred on vertical, spanning either 0, ±45 or ±90°. Note that the global direction of motion was always upwards when the degree of uncertainty associated with the axis of global motion was 0° (Figure 32). Allowing the test stimulus to move in any direction along its axis of global motion (e.g. upwards or downwards) would have introduced additional uncertainty, which may have confounded the results.

7. 2. 6. Statistical analyses

To explore if reading ability is associated with performance on the global motion and form tasks when the ability to form a perceptual anchor is manipulated a series of whole-sample analyses were conducted using a composite measure of reading skill (see section 2. 4.). A regression model was

run for each task and perceptual uncertainty condition with coherence threshold as the dependent variable. As the results of Chapter 3 showed that the sex of an individual and non-verbal IQ are associated with performance on tasks requiring the integration of motion information these were entered as control variables at step 1. Scores on the composite measure of reading skill were entered at step 2. The R^2 change at step 2 was evaluated to determine if reading ability explained any additional variance after controlling for the effects of sex and non-verbal IQ. A variation of Cohen's f^2 was used to calculate local effect size with 0.02 considered a small, 0.15 a medium and 0.35 a large effect, respective (Cohen, 1988; Selya et al., 2012).

7. 3. Results

7. 3. 1. Composite reading score: PCA

The correlations between the three individual measures of reading ability ranged from weak to strong (r = 0.35 to 0.75 $p < 0.02$, Figure 33) so PCA was conducted to calculate the composite measure of reading skill. Raw scores for the three reading tests were entered into the analysis, which was performed on the correlation matrix. Results showed a single principal component that accounted for 73% of the total variance amongst the three measures of reading ability (*Eigenvalue 1* = 2.20, *Eigenvalue 2* = 0.52, *Eigenvalue 3* = 0.29). Loadings for the TOWRE Sight Word Efficiency subtest and the TOWRE Phonemic Decoding Efficiency subtest were within the same range (0.80 and 0.86, respectively) but the NART contributed slightly more to the construct (0.90). Principal component scores were extracted for each participant and entered into the whole-sample regression analyses.

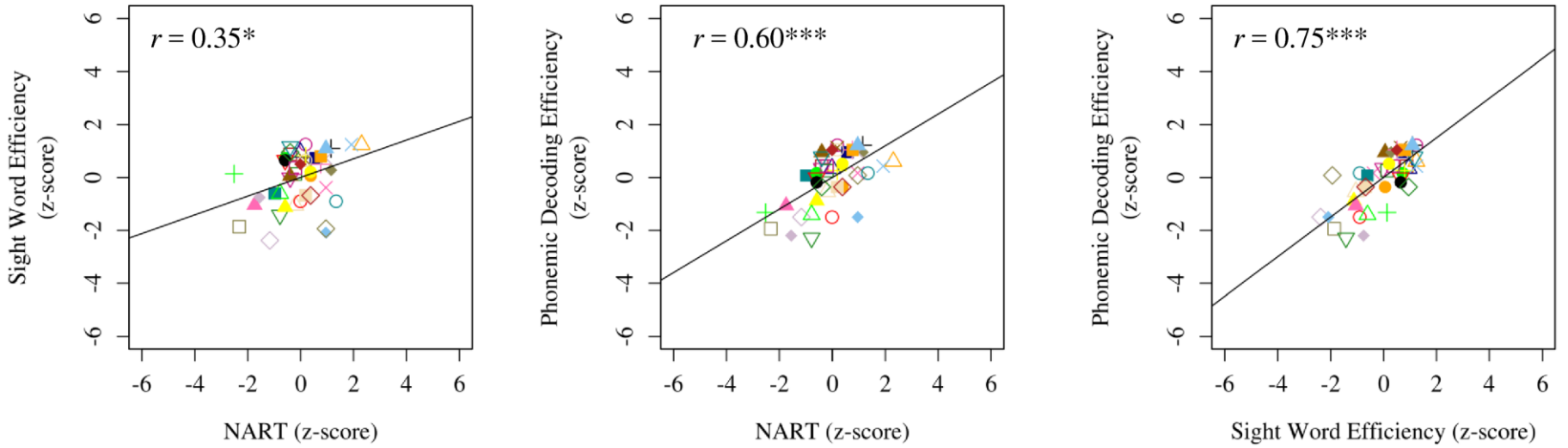


Figure 33. Scatter plots showing the relationships between scores on the three individual measures of reading ability in the entire sample (N = 44). Positive and negative z-scores indicate performance that is better than and worse than the mean of the sample, respectively. Note that z-scores were used for illustrative purposes only and did not influence the correlations. NART = National Adult Reading Test; TOWRE = Test of Word Reading Efficiency. * = $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

7. 3. 2. Whole-sample analyses: Hierarchical regression

Results for the whole-sample analyses are described in the sections below. Table 13 reports raw coherence thresholds on the global motion and form tasks across each perceptual uncertainty condition. Regression analysis results for the global motion and form tasks are reported in Table 14 and 15, respectively.

Task	Perceptual uncertainty (°)	Male (N = 12)			Female (N = 32)		
		M	*Median*	*SD*	*M*	*Median*	*SD*
Motion	0	13.13	13.02	4.34	20.18	19.47	7.69
	45	15.86	14.35	6.34	23.41	22.58	6.90
	90	17.56	17.05	5.50	24.09	21.98	6.87
Form	0	16.71	17.71	3.92	16.76	16.06	3.44
	45	18.73	18.34	3.77	19.56	18.31	4.55
	90	20.81	21.25	6.74	17.32	15.97	4.90

Table 13. Coherence threshold (%) statistics for the entire sample on the global motion and form tasks across each perceptual uncertainty condition.

7. 3. 2. 1. Global motion task

7. 3. 2. 1. 1. Perceptual uncertainty: 0°

The control variables explained 18% of the variance in performance on the global motion task when the axis of global motion was fixed at 0° (i.e. when it was upwards on each trial), $F_{2, 41} = 4.55$, $p = 0.02$. There was no significant effect of non-verbal IQ but the sex of an individual was a significant predictor of performance. Females had higher coherence thresholds than males. The R^2 change at step two did not reach statistical significance, $F_{1, 40} = 0.52$, $p = 0.47$. Reading skill was not significantly associated with performance on the global motion task when the axis of global motion was identical on each trial.

7. 3. 2. 1. 2. Perceptual uncertainty: ±45°

When the axis of global motion was chosen randomly on each trial from a uniform distribution spanning ±45° the control variables explained 25% of the variance in task performance, $F_{2, 41} = 6.82$, $p < 0.01$. There was no significant effect of non-verbal IQ. However, the sex of an individual was a significant predictor of performance as females had higher coherence thresholds than males. At step two, the R^2 change was not statistically significant, $F_{1, 40} = 0.17$, $p = 0.68$. Reading skill was not significantly associated with task performance when the axis of global motion was chosen randomly on each trial from a uniform distribution spanning ±45°.

7. 3. 2. 1. 3. Perceptual uncertainty: ±90°

The control variables explained 18% of the variance in task performance when the axis of global motion was chosen randomly on each trial from a uniform distribution spanning ±90°, $F_{2, 41} = 4.65$, $p = 0.02$. There was no significant effect of non-verbal IQ but the sex of an individual was a significant predictor of task performance. Females had higher coherence thresholds than males. The R^2 change at step two did not reach statistical significance, $F_{1, 40} = 0.12$, $p = 0.73$. Reading skill was not significantly associated with task performance when the axis of global motion was chosen randomly on each trial from a uniform distribution spanning ±90°.

Perceptual uncertainty (°)	*N*	Step	R^2	ΔR^2	*B*	*SE B*	*β*	f^2
0	44	Step 1	**0.18***					
		Sex			**-6.67**	**2.48**	**-0.39***	**0.17**
		SPM			-0.21	0.24	-0.13	0.01
		Step 2	**0.19***	0.01				
		Sex			**-6.56**	**2.50**	**-0.38***	
		SPM			-0.23	0.25	-0.13	
		Reading skill			0.80	1.11	0.10	0.01
±45	44	Step 1	**0.25****					
		Sex			**-6.93**	**2.29**	**-0.42****	**0.23**
		SPM			-0.35	0.22	-0.21	0.05
		Step 2	**0.25****	0.00				
		Sex			**-6.99**	**2.31**	**-0.42****	
		SPM			-0.34	0.23	-0.21	
		Reading skill			-0.42	1.03	-0.06	0.00
±90	44	Step 1	**0.18***					
		Sex			**-6.21**	**2.26**	**-0.39****	**0.18**
		SPM			-0.18	0.22	-0.12	0.01
		Step 2	**0.19***	0.01				
		Sex			**-6.26**	**2.29**	**-0.40****	
		SPM			-0.17	0.22	-0.11	
		Reading skill			-0.35	1.02	-0.05	0.01

Table 14. Whole-sample analyses for the motion task. A model was run for each perceptual uncertainty condition with coherence threshold as the dependent variable. The sex of an individual and non-verbal IQ were entered into the models at step one. Composite reading scores were introduced at step two. Statistically significant results are shown in bold font. SPM =

Raven's Standard Progressive Matrices. * $p < .05$; ** $p < .01$; *** $p < .001$.

7. 3. 2. 2. Global form task

7. 3. 2. 2. 1. Perceptual uncertainty: ±0°

When the axis of global orientation was fixed at 0° (i.e. when it vertical on each trial) the control variables explained 19% of the variance in performance on the global form task, $F_{2, 41} = 4.93$, $p = 0.01$. The sex of an individual was not significantly associated with task performance. However, non-verbal IQ was a significant predictor of performance as individuals with a lower IQ had higher coherence thresholds than those with a higher IQ. At step two, the R^2 change did not reach statistical significance, $F_{1, 40} = 1.49$, $p = 0.23$. Reading skill was not significantly associated with task performance when the axis of global orientation was identical on each trial.

7. 3. 2. 2. 2. Perceptual uncertainty: ±45°

The control variables did not explain a significant amount of the variance in task performance when the axis of global orientation was chosen randomly on each trial from a uniform distribution spanning ±45°, $F_{2, 41} = 0.84$, $p = 0.44$. In addition, the sex of an individual and non-verbal IQ were not significant predictors of performance. The R^2 change at step two did not reach statistical significance, $F_{1, 40} = 0.26$, $p = 0.61$. Reading skill was not significantly associated with task performance when the axis of global orientation was chosen randomly on each trial from a uniform distribution spanning ±45°.

7. 3. 2. 2. 3. Perceptual uncertainty: ±90°

When the axis of global orientation was chosen randomly on each trial from a uniform distribution spanning ±90° the control variables did not explain a significant amount of the variance in task performance, $F_{2, 41} = 2.12$, $p = 0.13$. In addition, the sex of an individual and non-verbal IQ were not significantly associated with task performance. At step two, the R^2 change did not reach statistical significance, $F_{1, 40} = 0.55$, $p = 0.46$. Reading skill was not significantly associated with task performance when the axis of global orientation was chosen randomly on each trial from a uniform distribution spanning ±90°.

Perceptual uncertainty (°)	*N*	Step	R^2	ΔR^2	*B*	*SE B*	*β*	f^2
0	44	Step 1	**0.19***					
		Sex			0.57	1.12	0.07	0.00
		SPM			**-0.34**	**0.11**	**-0.45****	**0.23**
		Step 2	**0.22***	0.03				
		Sex			0.48	1.11	0.06	
		SPM			**-0.33**	**0.11**	**-0.43****	
		Reading skill			-0.60	0.49	-0.17	0.04
±45	44	Step 1	0.04					
		Sex			-1.13	1.49	-0.12	0.01
		SPM			0.17	0.15	0.18	0.04
		Step 2	0.05	0.01				
		Sex			-1.18	1.51	-0.12	
		SPM			0.18	0.15	0.19	
		Reading skill			-0.34	0.67	-0.08	0.01
±90	44	Step 1	0.09					
		Sex			3.76	1.88	0.30	0.09
		SPM			-0.15	0.18	-0.13	0.01
		Step 2	0.11	0.02				
		Sex			3.66	1.89	0.29	
		SPM			-0.14	0.19	-0.12	
		Reading skill			-0.62	0.84	-0.11	0.02

Table 15. Whole-sample analyses for the form task. A model was run for each perceptual uncertainty condition with coherence threshold as the dependent variable. The sex of an individual and non-Verbal IQ were entered into the models at step one. Composite reading scores were introduced at step two. Statistically significant results are shown in bold font. SPM = Raven's

Standard Progressive Matrices. * $p < .05$; ** $p < .01$; *** $p < .001$.

7. 4. Discussion

The results outlined in this thesis have demonstrated that the visual impairment in generally poor readers and individuals with dyslexia has at least two distinct components, one spatial and one temporal. That is: 1) a difficulty in selecting the spatial scale optimal for task performance; and 2) an insensitivity to visual stimuli that are changing rapidly over time. An alternative theory that has been proposed to explain the underlying nature of the visual deficit in developmental dyslexia is the anchoring deficit hypothesis (see section 1. 3. 3.). This framework is challenged by the results of Chapters 4 and 6 but it has not yet been investigated using more conventional global motion and form stimuli that require integration, as opposed to segmentation, of local visual cues. To address this issue in the present study a global motion detection task and an analogous form detection task were administered to forty-four adults with a wide range of reading skills. By varying the degree of uncertainty associated with the axis of global motion or orientation the ability to form a perceptual anchor was manipulated across different blocks of trials.

Results showed that scores on the composite measure of reading skill were not significantly associated with performance on the global motion task when the axis of global motion was identical on each trial or when it was randomly chosen from a uniform distribution spanning either ±45 or ±90°. A similar pattern of results was found on the global form task. General reading ability was not significantly associated with performance when the axis of global orientation was identical on each trial or when it was randomly chosen from a

uniform distribution spanning either ±45 or ±90°. These findings are difficulty to reconcile with the anchoring deficit hypothesis. It predicts that reading ability should be significantly associated with performance when the axis of global motion or orientation is the same on each trial but this was not the case.

Previous research has shown that individuals with dyslexia have significantly higher coherence thresholds than relatively good readers on global motion but not global form detection tasks (Hansen et al., 2001; but see White et al., 2006). The results of the present study challenge these findings as reading ability was not significantly associated with performance on either task. A possible explanation for this discrepancy is that previous research did not always control for factors that are now known to be associated with performance on visual motion perception tasks such as the sex of an individual and non-verbal IQ (Arranz-Paraíso & Serrano-Pedrazza, 2016; Cook et al., 2016; Hutchinson et al., 2012; Melnick et al., 2013; Snowden & Kavanagh, 2006; Tadin, 2015). In the present study, these factors were entered into the regression analyses to determine if reading ability explained any additional variance in task performance after controlling for the effects of sex and non-verbal IQ.

The results of the present study demonstrate that reading ability is not significantly associated with performance on global motion or form detection tasks. These tasks differ from those administered in Chapter 3 because participants simply had to detect movement or spatial structure irrespective of

its direction or orientation. In Chapter 3, participants had to judge the overall direction (upwards vs. downwards) or orientation (vertical vs. horizontal) of the stimuli in the global motion and form tasks, respectively. That generally poor readers and individuals with dyslexia exhibited impaired performance on the two global motion tasks and the temporally-defined global form task in Chapter 3 suggests that the temporal component of the visual deficit in developmental dyslexia reflects a difficulty judging the global direction or orientation of stimuli changing rapidly over time. It is currently unclear why such a deficit should arise in developmental dyslexia. To determine the global direction or orientation of a stimulus, the brain must perform a computation to integrate (e.g. pool, combine or compare) early visual signals into a coherent percept (Pouget, Dayan, & Zemel, 2000). The type of computation employed by the visual system is currently unclear but some possibilities have been proposed including a vector average (i.e. the average of the preferred direction/orientation of individual neurons weighted in proportion to the magnitude of their responses), winner-take-all (i.e. the preferred direction/orientation of the most active neuron) or maximum likelihood (i.e. the direction/orientation that is most likely given the population response). Evidence suggests that cortical pooling algorithms are somewhat dependent upon stimulus complexity and task demands (Nichols & Newsome, 2002; Salzman & Newsome, 1994; Webb, Ledgeway, & McGraw, 2007, 2010; Webb, Ledgeway, & Rocci, 2011). A highly speculative explanation for why generally poor readers and individuals with dyslexia exhibit impaired performance on tasks requiring a judgement about the global direction or orientation of stimuli changing rapidly over time is that they cannot employ the

cortical pooling algorithm that is needed for optimal task performance. This issue could be addressed in the future using a combination of behavioural psychophysics and computational modeling.

The results of the present study also showed that the sex of an individual was a significant predictor of performance on the global motion task regardless of whether the axis of global motion was identical on each trial or chosen randomly from a uniform distribution spanning either ±45 or ±90°. Females had higher coherence thresholds than males, consistent with some previous findings (Billino et al., 2008; Snowden & Kavanagh, 2006). No significant association was found between reading ability and performance on the global form task. The results of Chapter 3 showed that females had higher coherence thresholds than males on the random-dot global motion task but not the spatially 1-D global motion task, the static global form task, or the temporally-defined global form task. Taken together, these findings demonstrate that the sex of an individual is associated with performance on random-dot global motion tasks irrespective of whether participants are asked to detect movement or judge the overall direction of motion. Further research is needed to explore the neurobiological basis of this effect (see section 1. 3. 5. .8).

It is interesting to note that non-verbal IQ was not a significant predictor of performance on the global motion task regardless of whether the axis of global motion was identical on each trial or chosen randomly. That individuals with a lower non-verbal IQ performed worse than individuals with a higher non-

verbal IQ on the two global motion tasks but not the two global form tasks in Chapter 3 suggests that non-verbal IQ is associated with performance on global motion discrimination tasks but not global motion detection tasks. It is currently unclear why non-verbal IQ was a significant predictor of performance on the global form task in the present study when the orientation was the same on each trial but not when it was chosen at random from a uniform distribution spanning ±45 or ±90°. Individuals with a lower non-verbal IQ performed worse than those with a higher non-verbal IQ. This finding is important because non-verbal IQ is typically only associated with performance on visual perception tasks containing motion or time-varying information (Arranz-Paraíso & Serrano-Pedrazza, 2016; Cook et al., 2016; Melnick et al., 2013; Tadin, 2015). It suggests that the relationship between non-verbal IQ and task performance may be more complex than originally thought.

7. 5. Summary

In summary, the results of the present study are difficult to reconcile with the anchoring deficit hypothesis, as it predicts that reading ability should be significantly associated with performance on the global motion and form tasks when the direction or orientation was the same on each trial but this was not found to be the case. The fact that reading ability was not a significant predictor of performance on the global motion and form tasks suggests that the temporal component of the visual deficit in developmental dyslexia reflects a difficulty judging the global direction or orientation of stimuli changing rapidly over time. The results of the present study also extend those of Chapter 3 as they show that females have higher coherence thresholds than males on global motion detection and discrimination tasks. Non-verbal IQ was not significantly associated with performance on the global motion task in the present study but it did predict performance on the global form task when the orientation was identical on each trial. This finding suggests that the relationship between non-verbal IQ and performance on tasks requiring integration of local visual cues may be more complex than once thought.

Chapter 8

General discussion

8. 1. Summary of the present research findings

8. 1. 1. Why is the processing of global motion impaired in adults with developmental dyslexia?

Several studies have shown that readers with developmental dyslexia have significantly higher coherence thresholds than relatively good readers on global motion tasks (Benassi et al., 2010) but such a deficit could reflect either: 1) a difficulty processing motion; 2) a difficulty processing temporal information; or 3) a difficulty integrating local visual cues across multiple (>2) dimensions. Previous research has also failed to investigate factors that are known to be associated with performance on global motion tasks such as the sex of an individual and non-verbal IQ (Arranz-Paraíso & Serrano-Pedrazza, 2016; Billino et al., 2008; Cook et al., 2016; Hutchinson et al., 2012; Melnick et al., 2013; Snowden & Kavanagh, 2006; Tadin, 2015). To address these issues four global motion and global form tasks were administered to a large sample of adults in Chapter 3. Results were similar across a series of whole-sample analyses, conducted to investigate if general reading skills were associated with coherence thresholds on the four visual tasks, and a series of between-group analyses, conducted to explore if performance differed between readers with

poor phonological decoding skills, consistent with dyslexic profile, and relatively good readers. Generally poor readers and individuals who met conventional criteria for diagnosing developmental dyslexia had significantly higher coherence thresholds than relatively good readers on the random-dot global motion task and the spatially 1-D global motion task (Table 16). Both groups of poor readers also exhibited impaired performance on the temporally-defined global form task but not the static global form task. These findings are difficult to reconcile with the magnocellular deficit hypothesis, the external noise exclusion hypothesis, the anchoring deficit hypothesis and the dorsal stream vulnerability hypothesis (Table 17). They demonstrate that the underlying nature of the visual deficit in generally poor readers and individuals with developmental dyslexia is a difficulty integrating information that changes over time rather than a motion-specific impairment. The almost identical pattern of results found in the whole-sample and between-group analyses suggests that visual difficulties do not differentiate these two groups of poor readers.

Independent variable	Chapter 3 – Why is the processing of global motion impaired in adults with developmental dyslexia?	Chapter 4 – Spatial segmentation of motion and form information in adult poor readers	Chapter 5 – Is visual perception in adult poor readers limited by sub-optimal scale selection?	Chapter 6 – Temporal segmentation of motion and form information in adult poor readers	Chapter 7 – Effects of perceptual uncertainty on global motion and form detection in developmental dyslexia
Reading ability	Poor readers had higher thresholds than good readers on the two global motion tasks and the temporally-defined global form task	Poor readers had a larger knee-point and shallower slope than good readers but only on the motion task	N/A	Minimum segment duration longer in poor readers than good readers	Reading ability not associated with task performance
Sex	Females had higher thresholds than males on the random-dot global motion task	Sex not associated with task performance	N/A	Limited number of males precluded meaningful analysis	Females had higher thresholds than males but only on the motion task
NVIQ	Individuals with a lower NVIQ had higher thresholds than those with a higher NVIQ on the two global motion tasks	NVIQ not associated with task performance	N/A	Individuals with a lower NVIQ had higher thresholds at asymptote than those with a higher NVIQ	Individuals with a lower NVIQ had higher thresholds than those with a higher NVIQ on the form task when the degree of uncertainty was 0°

Table 16. Comparing findings across each of the experimental chapters. NVIQ = non-verbal IQ; N/A = the effects of reading ability, sex and NVIQ were not systematically explored.

8. 1. 2. Spatial segmentation of motion and form information in adult poor readers

The results of Chapter 3 showed that the origin of visual impairment in generally poor readers and individuals with dyslexia reflects a difficulty integrating temporal information. However, to successfully parse the visual scene into meaningful entities, such as text into words, or words into letters, the visual system must also segment local features arising from different objects (Braddick, 1993). There is some evidence that the visual deficit in dyslexia extends to spatial segmentation, but previous research exploring this issue devised a task that confounded integration with segmentation and relied on measuring sensitivity at a single segment size (Cornelissen et al., 1995). These issues were directly addressed in Chapter 4 by administering a motion-based spatial segmentation task and an analogous form task to thirty-eight adults whose reading abilities ranged along a continuum. Thresholds were measured for each of a wide range of segment sizes and a curve was fitted to each participant's data to characterise comprehensively their ability to perform the two segmentation tasks. Results showed that acuity limits were independent of reading ability, indicating that the smallest segment size needed to perform the motion and form tasks was normal in less-skilled readers. Reading ability was significantly associated with performance but crucially only for the motion task, such that the segment size at which performance became asymptotic (i.e. the knee-point) was larger in the poorest readers and resulted in a flattening of the descending limb of the curves (Table 16). Thus, the visual deficit in generally poor readers and individuals with dyslexia does extend to spatial

segmentation, but only on tasks containing motion or temporal information. These findings challenge all current theories of visual processing in developmental dyslexia (Table 17).

8. 1. 3. Is visual perception in adult poor readers limited by sub-optimal scale selection?

The results of Chapter 4 showed that when spatial segmentation is based on differences in motion direction between neighbouring regions of a visual scene, relatively poor readers exhibit a different pattern of performance than skilled readers. The rate of improvement on the motion task was significantly shallower in generally poor readers than relatively good readers and the segment size at which coherence thresholds reached asymptote was significantly larger. To explore how such a deficit could arise a biologically-motivated computational model was devised in Chapter 5. The results of the computational analyses suggest that poor readers' difficulties on the motion-based spatial segmentation task in Chapter 4 are indicative of an inability to select a mechanism to perform the task that is well matched to the spatial scale of the motion boundaries in the image. Even though segment size was fixed and predictable within a single block of trials relatively poor readers could not exploit this knowledge about the stimulus set to select the integration field size needed for optimal task performance.

A direct prediction of the scale selection hypothesis is that relatively good readers should exhibit a qualitatively similar pattern of performance to

generally poor readers when scale uncertainty is introduced into the motion-based segmentation task. The segment size at which performance becomes asymptotic should be significantly larger and the slope of the descending limb of the curve significantly shallower when segment size is randomised (and thus made unpredictable) on each trial compared to when it is predictable. This prediction was tested by administering the same motion task to a group of twelve relatively good readers who did not meet conventional criteria for diagnosing dyslexia. Results showed that the knee-point of the curves was significantly larger and the slope of the descending limb of the curves was significantly shallower when the segment size was randomised on successive trials in comparison to when it was predictable. Importantly, coherence thresholds at asymptote were not significantly different between the blocked and random conditions. These results support the scale selection hypothesis as they show that the performance of relatively good readers mimics that of readers with dyslexia when information about segment size is made uncertain.

8. 1. 4. Temporal segmentation of motion and form information in adult poor readers

The results of Chapter 5 suggest that poor readers' difficulties on tasks requiring the spatial segmentation of motion information reflect sub-optimal scale selection. However, the position of words on the retinae is constantly being updated during reading as a discrete series of eye movements and fixations are made (Rayner, 1998). Effective decoding of text, therefore, requires this continuous stream of visual information to be segmented over

time, as well as across space. There is some evidence to suggest that the underlying nature of the visual deficit in dyslexia extends to temporal segmentation but previous research relied on a single measurement of sensitivity and failed to delineate temporal segmentation of motion and form information (Talcott et al., 1998). These issues were addressed in Chapter 6 by administering temporal versions of the spatial segmentation tasks to thirty-eight adults with a wide range of reading abilities. Coherence thresholds were measured at each of a range of oscillation rates (segment durations) and a curve was fitted to each participant's data, to quantify the shape of this function. Results showed that temporal acuity limits for both the motion and form tasks were significantly and negatively correlated with scores on the composite measure of reading skill (Table 16), consistent with previous research that has explored the effects of reading ability on CFF thresholds (Holloway et al., 2013; Talcott et al., 1998). The minimum segment duration needed to detect the test stimulus was longer in relatively poor readers than relatively good readers. These results are difficult to reconcile with the magnocellular deficit hypothesis, the external noise exclusion hypothesis, the anchoring deficit hypothesis and the dorsal stream vulnerability hypothesis (Table 17). They extend previous findings in two key ways. First, they suggest that generally poor readers have a generic difficulty with temporal segmentation that transcends domains as a similar pattern of results was found for both the motion and the form tasks. Second, our results reveal that the difficulties with temporal segmentation of motion and form information shown by generally poor readers are pronounced at short segment durations.

8. 1. 5. Effects of perceptual uncertainty on global motion and form detection in developmental dyslexia

Taken together, the results of Chapters 3 to 6 show that the visual deficit in generally poor readers and individuals with dyslexia has at least two distinct components, one spatial and one temporal. That is: 1) a difficulty in selecting the spatial scale optimal for task performance; and 2) an insensitivity to visual stimuli that are changing rapidly over time. An alternative theory of the origin of visual impairment in developmental dyslexia is the anchoring deficit hypothesis (see section 1. 3. 3.). This framework proposes that individuals with dyslexia cannot utilise stimulus repetitions to form a perceptual anchor. Such a deficit is thought to manifest as a difficulty on 2IFC tasks in which comparisons must be made across sequentially presented stimuli (Ahissar et al., 2006; Ahissar, 2007; Jaffe-Dax et al., 2015, 2016). The anchoring deficit hypothesis cannot readily explain the results of Chapters 4 and 6 in which the effects of reading ability on spatial and temporal segmentation were systematically investigated. However, it has not yet been studied using global motion and form stimuli that necessitate integration, as opposed to segmentation, of local visual cues. This issue was addressed in Chapter 7 by administering a 2IFC global motion detection task and an analogous form detection task to forty-four adults with a wide range of reading skills. By varying the degree of uncertainty associated with the axis of global motion or orientation, the ability to form a perceptual anchor was manipulated across different blocks of trials. Results showed that scores on the composite measure of reading skill were not significantly associated with performance on the

global motion task when the axis of global motion was identical on each trial or when it was randomly chosen from a uniform distribution spanning either ±45 or ±90° (Table 16). A similar pattern of results was found on the global form task. These findings are difficult to reconcile with the anchoring deficit hypothesis as it predicts that reading ability should be significantly associated with performance when the axis of global motion or orientation is the same on successive trials within a block but this was not the case (Table 17). That generally poor readers and individuals with dyslexia exhibited impaired performance on the two global motion tasks and the temporally-defined global form task in Chapter 3 suggests that the temporal component of the visual deficit in developmental dyslexia reflects a difficulty judging the global direction or orientation of stimuli changing rapidly over time.

Theories of vision in developmental dyslexia	Chapter 3 – Why is the processing of global motion impaired in adults with developmental dyslexia?		Chapter 4 – Spatial segmentation of motion and form information in adult poor readers		Chapter 5- Is visual perception in adult poor readers limited by sub-optimal scale selection?		Chapter 6 – Temporal segmentation of motion and form information in adult poor readers		Chapter 7 – Effects of perceptual uncertainty on global motion and form detection in developmental dyslexia	
	Challenge or support?	Why?	Challenge or support?	Why?	Challenge or support?	Why?	Challenge or support?	Why?	Challenge or support?	Why?
The magnocellular deficit hypothesis	Challenge	Reading ability associated with performance on temporally-defined global form task	Challenge	Reading ability not associated with thresholds at asymptote on the motion task	N/A	N/A	Challenge	Reading ability associated with acuity limits on the form task	Challenge	Reading ability not associated with performance on motion task
The external noise exclusion hypothesis	Challenge	All tasks contained high levels of noise	Challenge	Both tasks contained high levels of noise	N/A	N/A	Challenge	Reading ability not associated with thresholds at asymptote	Challenge	Both tasks contained high levels of noise
The anchoring deficit hypothesis	Challenge	1IFC procedure used so little or no perceptual memory load	Challenge	Reading ability only associated with performance on the motion task	N/A	N/A	Challenge	Reading ability not associated with thresholds at asymptote	Challenge	Both tasks contained an invariant reference stimulus

The modified receptive field hypothesis	N/A	N/A	N/A	N/A	Challenge	Thresholds at asymptote increase when a larger integration field is employed	N/A	N/A	N/A	N/A
The dorsal stream vulnerability hypothesis	Challenge	Reading ability associated with performance on temporally-defined global form task	Challenge	Reading ability not associated with thresholds at asymptote on the motion task	N/A	N/A	Challenge	Reading ability associated with acuity limits on the form task	Challenge	Reading ability not associated with performance on motion task

Table 17. Implications of the results from each of the experimental chapters for current theories of vision in developmental dyslexia. N/A = results do not have a direct bearing on the theory.

8. 2. Definitional questions

As previously mentioned, the definition of developmental dyslexia is highly controversial (see section 1. 2.). The results of Chapter 3 are theoretically important because they speak directly to the debate as to whether dyslexia best represents the lower end of a normal distribution of reading ability or a distinct type of reading difficulty associated with poor phonological decoding skills (Fletcher, 2009; Siegel, 2006). The similar pattern of results observed in generally poor readers and individuals with developmental dyslexia implies that performance on low-level visual motion and form tasks cannot differentiate these two groups of poor readers. This supports the view that dyslexia is best-defined as the lower end of a normal distribution of reading ability rather than a distinct type of reading difficulty associated with poor phonological decoding skills. It is highly likely that some of the discrepancies in the literature might reflect the fact that a wide range of diagnostic criteria that have been used across studies. Performing whole-sample rather than between-group analyses means that decisions regarding controversial definitional criteria and categorical assignment of participants do not have to be made. Adopting this type of experimental design might also enhance statistical power and increase the positive predictive value i.e. the likelihood that a positive research finding actually represents a genuine effect. Low sample size has been put forward as a major contributing factor to the lack of reproducibility that currently abides in the neurosciences (Button et al., 2013; Duas-Mallet et al., 2005; Loannidis, 2005) and is prevalent in previous

research that has sought to elucidate the origin of visual impairment in developmental dyslexia.

8. 3. Sex

That the sex of an individual can influence performance on low-level visual perception tasks has been highlighted throughout this thesis. Although some previous evidence suggested that females typically have higher coherence thresholds than males on global motion tasks, those studies were focussed primarily on the ageing visual system (Billino et al., 2008; see Hutchinson et al., 2012; Snowden and Kavanagh, 2006). Sex was a strong predictor of performance on the random-dot global motion task in Chapter 3. Results showed that for participants in early adulthood (mean age = 22.02 ±5.21years) females overall had significantly higher coherence thresholds than males. However, no significant association was found between sex and performance on the static global form task, the spatially 1-D global motion task, or the temporally-defined global form task. These results extend those of previous studies as they show that sex differences on random-dot global motion tasks are not simply a consequence of differential visual decline in ageing.

It is interesting to note that the sex of an individual was not a significant predictor of performance on the motion-based and form-based spatial segmentation tasks reported in Chapter 4. However, a different pattern of results was found in Chapter 6. Females had higher coherence thresholds than males on the global motion detection task but not the global form detection task. Taken together, these findings suggest that: 1) the sex of an individual is significantly associated with performance on random-dot global motion tasks requiring integration but not spatial segmentation of local visual cues; and 2)

Females typically have higher coherence thresholds than males regardless of whether discrimination or detection paradigms are used to measure task performance. The neurobiological substrate of this effect is currently unclear but it might reflect left-right asymmetries in hemispheric specialisation. Amunts et al. (2007) showed that hMT was significantly smaller in the right hemisphere of females than males, consistent with some previous findings (de Lacoste et al., 1991; Kovalev et al., 2003). It was suggested that this left-right asymmetry might provide males with additional neural resources or 'space' for the processing of computationally demanding visual stimuli. A direct prediction of this hypothesis is that females should exhibit better performance on random-dot global motion tasks when the stimuli are presented in the right visual field (left hemisphere) than the left visual field (right hemisphere). This interesting hypothesis is currently untested but it could be explored in future research.

Regardless of the neural substrate, that females have significantly higher coherence thresholds than males on random-dot global motion tasks has important implications for research exploring visual processing in clinical populations (Johnston et al., 2017). It could explain discrepancies between studies and in particular why some research has failed to uncover deficits in the processing of global motion, relative to global form, in developmental dyslexia, as many studies have neglected to take sex into account (Table 2). It has already been suggested that a significant group difference between children with dyslexia and relatively good readers in the study by Milne et al. (2006) may have been masked by a marked imbalance between males and females in

the participant groups. However, the opposite could also be true. Effect size is likely to have been exaggerated if the ratio of males to females is markedly higher in the control group than dyslexic group.

8. 4. Non-verbal IQ

Non-verbal IQ is also known to influence performance on global motion tasks (Arranz-Paraíso & Serrano-Pedrazza, 2016; Cook et al., 2016; Melnick et al., 2013; Tadin, 2015). The results of Chapter 3 corroborate previous findings because the strongest predictor of coherence thresholds on the random-dot global motion task and the spatially 1-D global motion task was non-verbal IQ. Individuals with a lower IQ performed worse than those with a higher IQ. Why non-verbal IQ was not significantly associated with coherence thresholds on the two global form tasks is currently unclear. It could be argued that global motion tasks are more likely to activate neurons in V5/MT than global form tasks. A large proportion of these cells exhibit centre-surround antagonism (i.e. reduced activation when a large, high-contrast stimulus extends beyond the classical receptive field) and it has been suggested that individuals with a higher IQ have an enhanced ability to suppress ecologically less relevant information (Melnick et al., 2013). However, centre-surround interactions also occur in brain regions that have been implicated in the processing of global form (Cheng et al., 1994; Desimone and Schein, 1987). Thus, individuals with a higher IQ should have performed better than individuals with a lower IQ on all four visual tasks in Johnston et al. (2016) if they are better able to suppress less-meaningful visual cues.

It is interesting to note that non-verbal IQ was not significantly associated with performance on the motion and form-based spatial segmentation tasks in Chapter 4. These findings are in stark contrast to those in Chapter 3 and cast

further doubt on the notion that differential performance of individuals with relatively low and high IQs on global motion perception tasks reflects differences in spatial suppression, as neurons exhibiting this characteristic type of behaviour are thought to play a key role in spatial segmentation (Allman et al.,1985; Pack et al., 2005; Tadin, 2015).

Non-verbal IQ was also not significantly associated with performance on the global motion detection task in Chapter 7 irrespective of whether the axis of global motion was identical on each trial or chosen randomly from a uniform distribution spanning either ±45 or ±90°. Thus, although non-verbal IQ appears to be associated with performance on global motion discrimination tasks (see Chapter 3), interestingly it is not significantly correlated with the potentially less demanding task of global motion detection. It is currently unclear why non-verbal IQ was a significant predictor of performance on the global form detection task in Chapter 7 when the orientation was the same on each trial but not when it was chosen at random from a uniform distribution spanning ±45 or ±90°. Individuals with a lower non-verbal IQ performed worse than those with a higher non-verbal IQ. This result is important because non-verbal IQ is typically only associated with performance on visual perception tasks that contain motion or time-varying information (see Chapter 5). Further research is needed to address the reliability of this finding, but it suggests that the relationship between non-verbal IQ and performance on low-level visual perception tasks may be more complex than originally thought.

The fact that non-verbal IQ is a significant predictor of coherence thresholds on global motion discrimination tasks and global form detection tasks has further implications for studies investigating visual perception in clinical populations (Johnston et al., 2017). Some argue that it is "misguided and unjustified" to partial out IQ when studying neurocognitive function in developmental disorders (Dennis et al., 2009). It has been suggested that IQ represents a global outcome measure that is directly attributable to, and confounded by, the neurodevelopmental disorder. However, when investigating the processing of global motion and global form, it seems prudent to control for non-verbal IQ because recent research has confirmed that a strong link exists between this variable and performance on global motion and form tasks even in the general population.

8. 5. Future directions

The results of this thesis have shown that the underlying nature of the visual deficit in generally poor readers and individuals with dyslexia reflects a difficulty in selecting the spatial scale optimal for task performance as well as an insensitivity to visual stimuli changing rapidly over time. Although these findings extend previous research exploring the origin of visual impairment in developmental dyslexia further studies are needed to address several outstanding issues.

8. 5. 1. Do generally poor readers and individuals with dyslexia have a difficulty in the processing of temporal order or a more general insensitivity to visual stimuli changing rapidly over time?

An unresolved issue is whether the temporal component of the visual deficit in generally poor readers, and individuals with dyslexia, arises because of a difficulty in processing dynamic stimuli for which the temporal order of the information is critical for solving the task, rather than a more general insensitivity to stimuli changing rapidly over time (see section 1. 3. 1.). The results of this thesis showed that both groups of poor readers exhibited impaired performance on a range of low-level visual integration and segmentation (spatial and temporal) tasks in which the position of individual elements in the display changed sequentially over time. This raises the interesting possibility that the temporal component of the visual deficit in generally poor readers and individuals with dyslexia may reflect a difficulty

encoding the precise order of events in a visual stream of information. This could explain why (say) global direction discrimination of RDKs is impaired, because if the temporal sequence of spatial displacements of the dots is not faithfully preserved at the encoding level, their trajectories cannot be accurately recovered. A direct prediction of this hypothesis is that both groups of poor readers should not exhibit impaired performance in comparison to relatively good readers on a dynamic global form task that requires a judgement to be made about the overall orientation of a stimulus generated by presenting a new array (stochastic sample) of orientated dot streaks on each image update. Although the individual elements in the display are changing sequentially over time, as the dot streaks in each new array are temporally uncorrelated, the temporal structure of the stimulus is irrelevant for performing the task. Thus, it could be used in future research to disambiguate if generally poor readers and individuals with dyslexia have a difficulty in the processing of temporal order, rather than a more general insensitivity to any visual stimulus that is changing rapidly over time.

8. 5. 2. Effects of reading ability on motion-based spatial segmentation when segment size is made uncertain on each trial.

The results of Chapter 5 showed that poor readers' difficulties on the motion-based spatial segmentation task might reflect a deficit with scale selection. The scale selection hypothesis is supported by the fact that the performance of twelve relatively good readers could be made to mimic that of generally poor readers when information about segment size was made uncertain

(randomised) on each trial in comparison to when it was identical. A key question that could be explored in future research is whether or not reading ability is associated with the extent to which the knee-point and slope of the descending limb of the curves changes when the segment size is made uncertain on each trial? The scale selection hypothesis predicts that generally poor readers already have higher intrinsic levels of uncertainty than relatively good readers and thus should exhibit little or no change in the knee-point and slope of the descending limb when additional uncertainty is introduced by randomising spatial segment size. This is an interesting question for future study.

8. 5. 3. Why do poor readers have a difficulty judging the global direction or orientation of stimuli changing over time?

Another unresolved issue is why generally poor readers and individuals with dyslexia have a difficulty judging the global direction or orientation of stimuli changing over time. Several possible reasons why such a deficit might arise are outlined in the sections below.

8. 5. 3. 1. Scale selection

It is currently unclear whether poor readers' difficulties judging the direction and orientation of stimuli containing time-varying information could reflect the known difficulty with scale selection. For typically developing controls performance on tasks requiring spatiotemporal integration improves when

stimulus size increases, presumably because more visual information becomes available (Barlow & Tripathy, 1997; Hutchinson, Ledgeway, & Kondoni, 2015; Watamaniuk & Sekuler, 1992). If poor readers select (say) smaller integration fields than relatively good readers it could explain why they have difficulty judging the global direction or orientation of time-varying stimuli. A related issue concerns whether the visual deficit in generally poor readers and individuals with dyslexia extends to spatial integration. This could be addressed in future research by measuring coherence thresholds on the four, global motion and form tasks administered in Chapter 3 as a function of stimulus area. Coherence thresholds should decrease as stimulus area increases with some evidence of asymptotic behavior when stimulus area is very large. The same two-limbed function used in Chapters 4, 5 and 6 could then be fitted to the data to investigate the relationships between reading ability and different components underpinning task performance.

8. 5. 3. 2. Temporal acuity

An alternative possibility is that relatively poor readers' difficulties judging the global direction or orientation of time-varying stimuli is a consequence of their temporal acuity deficit. The results of Chapter 5 showed that temporal acuity limits for both the motion- and form-based temporal segmentation tasks were significantly and negatively correlated with reading ability. A reduction in temporal acuity could explain why generally poor readers and individuals with dyslexia have a difficulty judging the global direction or orientation of time-varying stimuli as more of the motion energy will fall outside their reduced

"window of visibility" and thus be effectively invisible. For example, under certain conditions, reduced temporal sampling can have a facilitatory effect on performance on random-dot global motion tasks. Research has shown that random-dot global motion tasks cannot be reliably performed when a delay greater than ~100ms is introduced between consecutive frames (Baker & Braddick, 1985). Mather and Tunley (1995) found that larger inter-frame-intervals could be tolerated when low-pass temporal filtering was applied to the motion-sequence in order to reduce sampling rate. Hence, it should be possible to simulate conditions under which relatively poor readers outperform relatively good readers on tasks requiring a judgement about the orientation or direction of time-varying stimuli i.e. when a relatively long temporal delay is introduced between consecutive frames.

8. 5. 3. 3. Cortical pooling algorithms

To determine the global direction or orientation of a stimulus the brain must perform a computation to integrate (e.g. pool, combine or compare) early visual signals into a coherent percept (Pouget, Dayan, & Zemel, 2000). The cortical pooling algorithms used to achieve this goal are relatively unclear but several potential computations have been proposed including a vector average, winner-take-all or maximum likelihood. Evidence suggests that cortical pooling algorithms are somewhat dependent upon stimulus and tasks demands (Webb, Ledgeway, & McGraw, 2007; Webb et al., 2011). A highly speculative explanation for why poor readers exhibit impaired performance on tasks requiring a judgement about the global direction or orientation of stimuli

changing rapidly over time is that they may utilise potentially less optimal, or even different, pooling strategies to those of skilled readers to decode global structure in a temporally changing image.

8. 5. 4. Sublexical vs. lexical processing

The results of Chapter 3 showed that performance on low-level motion and form tasks cannot differentiate generally poor readers from individuals with poor phonological decoding skills, consistent with the dyslexic profile. However, it is currently unclear if individuals who have poor whole-word lexical processing skills exhibit a different pattern of performance in comparison to these two groups of poor readers. This is unlikely to be the case because PCA loadings for the NART, which assessed whole-word lexical processing, were typically within the same range and did not differ dramatically from those for the TOWRE Sight Word Efficiency subtest and the TOWRE Phonemic Decoding Efficiency subtest. A related issue concerns whether a similar pattern of results would be found in the general population. The effect sizes reported in this thesis are likely to be conservative because the sample comprised University students and thus is unlikely to capture the full range of reading skills in the general population. An advantage of this is that other factors known to be associated with reading skill such as non-verbal IQ are similar, so the results of this thesis are likely to reflect genuine differences in visual processing in relation to reading ability and developmental dyslexia.

8. 6. Concluding remarks

A growing body of research points to a visual impairment in readers with dyslexia (Gori & Facoetti, 2014; Gori & Facoetti, 2015; Stein & Kapoula, 2012) that could either be the proximal cause or merely a consequence of their reading difficulties (Goswami, 2015; Kevan & Pammer, 2009; Olulade et al., 2013). Several major theories have been proposed to explain the underlying nature of the visual deficit in developmental dyslexia (e.g. the magnocellular deficit hypothesis, the external noise exclusion hypothesis, the anchoring deficit hypothesis, the modified receptive field hypothesis and the dorsal stream vulnerability hypothesis). All these frameworks have received some support but they have been unable to fully expose the origin of visual impairment in developmental dyslexia as discussed in Chapter 1. The results of this thesis have shown that the visual deficit in generally poor readers and individuals with dyslexia impacts on the ability to both integrate and segment local cues in the image and has at least two distinct components, one spatial and one temporal. That is, 1) a difficulty in selecting the spatial scale optimal for task performance; and 2) a difficulty judging the global direction or orientation of stimuli changing rapidly over time.

Chapter 9

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