# The Relationship Between High-Level Vision and Reading Ability

A Thesis Submitted for the Degree of Doctor of Philosophy
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# Thesis Abstract

Reading is a skill that is required for formal education, human communication, and cognitive development. Approximately 5-12% of the population display difficulties with reading because they are affected by developmental dyslexia (DD), a reading disorder that has a neurobiological origin. The most popular and well-developed theory of DD is the phonological deficit theory which postulates that problems with reading are as a result of failing to learn the relationship between spelling and sounds. However, the phonological account does not explain why many dyslexic readers have measurable visual deficits. Specifically, there is increasing evidence to suggest that impaired function in the magnocellular pathway, which is sensitive to low contrast, low spatial and high temporal frequency stimuli, is associated with reading difficulties. The purpose of the current set of experiments is to test if performance in high-level visual tasks, e.g., object recognition, is associated with reading ability, and to include conditions designed to bias the magnocellular pathway, as previous work has focused on lower-level tasks, e.g., contrast detection, and/or has not specifically included a magnocellular condition. In conditions where the magnocellular pathway was stimulated, slow readers typically performed significantly worse over a range of high-level visual tasks: object recognition, visual search, scene gist classification, emotional face perception and optical illusions. In contrast, differences were not observed between groups in chromatic conditions which suggests that the parvocellular pathway, associated with high spatial acuity and colour vision, is intact. It is suggested that the deficits seen here are as a result of dysfunctional magnocellular input to various high-level regions interfering with top-down facilitation, attentional mechanisms, and global processing. Intervention programmes for DD often focus on improving phonological processing. The data presented across this thesis highlights the potential of visual training programmes to specifically target and strengthen the magnocellular pathway to improve visual-based tasks. Specifically, the use of games and illusions provide an engaging, practical method for potentially identifying those at risk in the pre-reading phase. Targeting those at risk during this critical period can prevent a spiral of negative effects that can occur in individuals with dyslexia. Overall, the findings provide new insight into the link between reading ability and high-level visual processing.

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# Covid Statement

Due to the COVID-19 pandemic, the initial set of in-person lab-based experiments were converted to online versions where possible, or abandoned with new online, suitable, and relevant experiments taking their place. Hence, all of the experimental chapters are based on online-collected behavioural data (chapters 2, 3, 4, 5 and 6). Also, recruitment of participants was originally set to take place through the Brunel dyslexia service, but due to suspended services during the pandemic participants were recruited from the Testable Minds participant pool. They were subsequently categorised based on reading speed, rather than a formal diagnosis of dyslexia. Reading groups were formed based on speed on lexical decision making; a slow-reading group (some of which were likely to be dyslexic), and a fast-reading group, which were considered as neurotypical. This was motivated by research which presents very slow and effortful reading in dyslexic readers, while their accuracy is largely preserved (Tressoldi, Stella, & Faggella, 2001; Zoccolotti et al., 1999). Additionally, English language is an inconsistent orthography categorised by reading speed (Harm, McCandliss & Seidenberg, 2003) and since only monosyllabic stimuli were used to assess reading, accuracy was high across participants (see chapter 2 for further details).

# Chapter 1: General Introduction and Literature Review

## 1.0. Chapter Overview

This chapter will give a brief introduction to the theories surrounding reading and developmental dyslexia (DD). The main challenges facing research will be outlined and how problems with vision in dyslexic readers, such as the proposed magnocellular deficit theory, may address some of the gaps in literature. It should be noted that there are different theories of dyslexia and consequently the current most accepted version of each theory will be described. The chapter will conclude with the main aims of the thesis. To present the aims of this thesis, it is important to provide a background on how the eye transmits signals to the brain once visual input hits the retina. An overview of the structure of the eye and brain will be provided and its role in reading acquisition. The two major visual pathways (the magnocellular and parvocellular pathways) and their projection to sub-cortical structures will be discussed, including how their segregation and sensitivity can be measured using psychophysical tests which can provide insight into higher order visual areas.

## 1.1. Learning to Read

It has been well established in education and psychology that reading disorders are unlikely to occur in one form only as the nature of reading requires a complex range of processes (Castles, Rastle & Nation, 2018). Learning to read is a key outcome of early education, unlike language acquisition which evolves from childhood. Children that do not acquire the skills to read often enter a downward spiral of negative consequences, such as low educational attainment, poor employment opportunities, and low-self-esteem that make them more susceptible to other conditions such as depression (Bazen et al., 2023). The high cognitive complexity of reading requires an integration of visual, orthographic, phonological, semantic information and linguistic processes; hence models of reading have been developed to attempt to explain this complex process (Rayner & Reichle, 2010). The two models that have received the greatest amount of recognition include the dual-route cascaded model (see below for further details, Coltheart et al., 2001) or connectionist models, otherwise known as the “triangle” model of reading which accentuates a single interconnected system rather than two separate routes i.e., connections between units as opposed to letter-sound mapping rules (Harm & Seidenberg, 1999; Plaut et al., 1996; Seidenberg & McClelland, 1989).

The foundational skills to reading include print concept (the ability to distinguish features of print such as the layout of text and moving from left to right on a page), phonological awareness (the awareness of sounds in a word), phonics (the mapping of speech sounds (phonemes) to letter(s) that represent them (graphemes)) and fluency (the accurate and automatic decoding of words in a text) (Chard & Osborn, 1999). Reading is essentially a process that entails recognising the visual form of printed words and their associated sounds which leads to decoding of written information and word identification, i.e., to understand the meaning of written text (Denton & Otaiba, 2011).

It has been established that learning to read involves a complex process which has led to a history of attempts to classify subtypes of reading disorders (Olsen et al., 1985; Coltheart et al., 1993; Plaut et al., 1996). Prior to the invention of explicit theoretical models for reading, researchers tended to use descriptive methods to categorise reading (Waern, 1980). While this was useful for characterising a particular population, it did not specify the reasons why children were reading a certain way or allow predictions to be made about reading profiles. Models of the reading system allows us to make predictions about expected patterns in developmental reading disorders and about other types of reading profile that might be identifiable (Schmalhofer et al., 2002; Coltheart et al., 2001; Zorzi, Houghton, & Butterworth, 1998). The dual-route theory of reading was described in the early 1970’s and was the first model to suggest two cognitive routes involved in reading leading to the same outcomes, the pronunciation of a written stimulus (Ellis & Young, 1988; Coltheart et al., 1993, 2001; Zorzi, 2010).

According to the dual-route model (figure 1.1), skilled reading is thought to occur through two separate paths: the lexical route and the non-lexical route (Coltheart, 1978; Morton & Patterson, 1980; Coltheart et al., 1993, 2001). The lexical route is the process whereby a reader accesses a lexicon (memory store) of previous written words. The non-lexical route allows the decoding of letters (graphemes) into their corresponding sounds (phonemes). While activation of both routes is triggered by written input, they differ in the type of input for accurate reading, for example, the lexical route will process all familiar words (regardless of if they have regular or irregular letter-sound relationships), but will fail to recognise unfamiliar words or non-words as they do not have lexical representations (e.g., filt) (Castles, 2006). On the other hand, the non-lexical (or sub-lexical) route allows the correct reading of non-words and regular words that follow the correct grapheme-phoneme correspondence irrespective of their familiarity level (e.g., farmer) but will not process irregular words that do not correspond to typical correspondence rules (e.g., yacht). Therefore, testing irregular word reading would measure lexical route function as these words can only be read via this route, while non-lexical route function would be assessed by non-word reading since these items can be successfully read by non-lexical rules (Castles, 2006). According to this model individuals with surface dyslexia are predicted to show greater deficits in the lexical route (which first activates orthographic and then phonological representations) whereas phonological dyslexics show greater deficits in the non-lexical route (Wang et al., 2014).

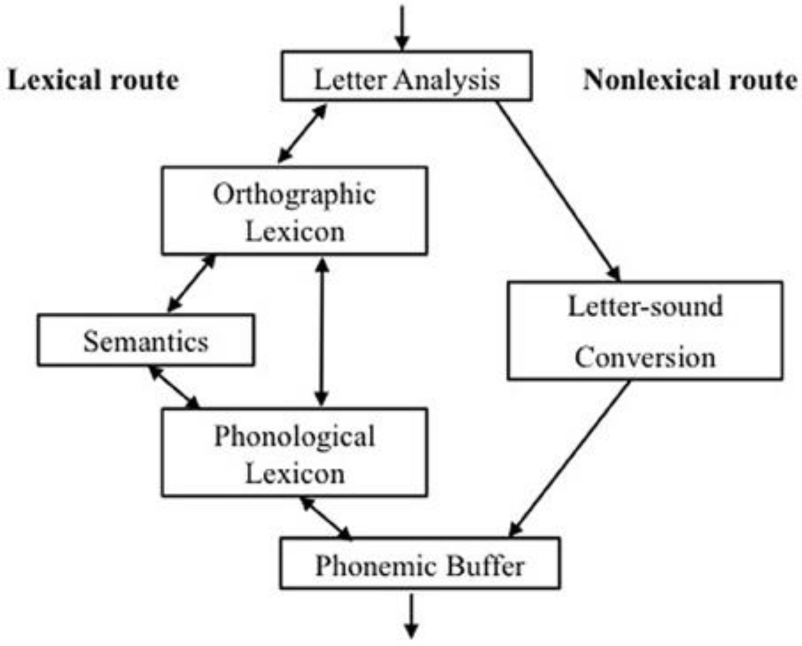

***Figure 1.1.*** *The dual-route model of reading (Coltheart, 2006).*

In terms of word recognition, the connectionist multiple-trace memory model considers the differences in global vs local reading procedures (Ans, Carbonnel, & Valdois, 1998). The global procedure involves scanning the entire letter string whereas the local procedure has a perceptual window that is restricted to segments (syllables) across a word. The dual-route model of reading (Colheart et al., 1993, 2001) also considers parallel whole word processing (lexical route) and the smallest units of words successively merged into one word (sublexical route). The multi-trace model proposes that difficulties in extending the perceptual window prevents the reading process suggested by the dual route model (a global-parallel) mode, affecting lexical processing. This theory was tested by Franceschini et al., (2021) who used global and local Navon tasks to induce transient perceptual priming before testing reading. They found that local (as opposed to global) perceptual priming lead to slower phonological processing of irregular words, implying that local interference can impair fast processing of letter strings required for lexical reading.

## 1.2. Identifying the Causes of DD

In contrast to acquired dyslexia which forms as a result of insults to a fully developed system, such as stroke or head trauma, DD is a lifelong learning difficulty that affects the developing reading system, leading to less efficient and automised reading (Yan, 2022). Despite adequate instruction, intelligence and intact sensory abilities, children with dyslexia have difficulties with fluent word recognition and spelling (Snowling, 2000). Approximately one in 10 people worldwide are classified as dyslexic, of which 4% have severe symptoms (Watson, 2023). DD is more predominant in males with a ratio of 1.5-3 per one female and has comorbidity with other developmental disorders such as attention-deficit hyperactivity disorder (ADHD), anxiety, autism, dyscalculia, specific language impairment (SLI) and more (see Peterson & Pennington, 2012).

The next sub-sections provide an overview of the main causal theories associated with DD. It has become apparent that dyslexia is linked to biological, neurological, perceptual and cognitive factors that can impair these individuals’ ability to read (Siegel, 2006). Although there is considerable evidence for the different origins (Ramus, 2003), the phonological theory remains the most persuasive and well-established (Peterson & Pennington, 2012; Vellutino, 1979). The theory postulates that children fail to acquire the skill to segment letter strings appropriately into phonemes and blend them into words. This is often referred to as ‘phonemic awareness’, which can appropriately be assessed by getting children to read pseudowords, however this cannot explain all accounts of dyslexia (Brady & Shankweiler, 1991; Snowling, 1981; Snowling, 2000). Competing theories suggest a predominantly neurological basis for dyslexia that can lead to problems with visual and rapid auditory processing (Tallal, 1980; Tallal et al., 1993; Lovegrove et al., 1980; Stein & Walsh, 1997; Stein, 2018, 2021). Although current theories share a neurological element, their emphasis on perception and cognition differ.

### 1.2.1. The Phonological Deficit Theory

A general language deficit is the dominant account for the most unifying hypothesis for DD, otherwise known as the phonological deficit theory (Ramus, 2003; Snowling, 2000; Wagner & Torgeson, 1987). This theory postulates that dyslexic individuals have a specific impairment in the representation, storage and retrieval of speech sounds in words (Ramus, 2003; Snowling 2001). The theory proposes reading impairments can be traced to the level of grapheme-phoneme correspondence, i.e., the correspondence between letters and constituent speech sounds, but also considers larger units such as rhymes and syllables. The learning of the alphabet system can be affected if these sounds are poorly represented, stored and/or retrieved (Bradley & Bryant, 1978; Vellutino, 1979; Brady & Shankweiler, 1991).

Grapheme-to-phoneme correspondence requires the translation of visual symbols to units of sound at a letter level, and acquiring this skill allows flexibility when reading new or complex words (McMurray & Thompson, 2016). For example, a reader that is familiar with the visual word forms “sat” and “pit” will have knowledge of their phonemes /s/ /a/ /t/ /p/ /i/ /t/ which will allow them to recombine the related graphemes to recognise words with related phoneme combinations, e.g., “sit” and “pat”. The recognition of phonemes associated with individual graphemes can vary depending on the adjacent grapheme in the word, for example the vowel /i/ in the word ‘pit’ is sharper compared to ‘pin’. A reader must therefore have an accumulation of highly developed phonological representations to match the appropriate phoneme to the grapheme (Share, 1995). A dyslexic reader, on the other hand, will struggle to relate phonology to larger units such as words or syllables (Snowling, 2000). While dyslexics may rely on visual word form recognition (Werth, 2021) to read familiar words, the absence of grapheme-to-phoneme awareness means that they lack the ability to decode complex novel words, demonstrated by their profound inability to decode non-words compared to neurotypical readers (Snowling, 2002; Snowling, 1981; Snowling, Goulandris & Defty, 1996).

There have been numerous reports of deficits in phonological awareness, confirming the association between this language skill and non-lexical reading ability (Hulme & Snowling, 1992), however the mechanism by which phonological awareness (the conscious awareness of sounds that make up words) affects reading acquisition has been heavily debated (Castles & Coltheart, 2004; Nicolson & Fawcett, 1990; Fawcett, Nicolson, & Dean, 1996; Tallal, 1980). Since words represent individual phonemes (speech sounds) which is further represented by a grapheme (a letter or group of letters), awareness of phonemic segments in spoken words is required to be able to learn their correspondence with letters (Milankov et al., 2021). Phonological awareness is a prerequisite for development of non-lexical reading skills; however, this may not be the only factor accounting for phonological dyslexia. Lines of evidence have proposed that DD can be characterised by many phenotypic manifestations of a phonological deficit, i.e., phonological short-term memory (the ability to maintain verbal information in the working memory), and phonological re/decoding (i.e., rapid automatized naming (RAN)) (Çaylak, 2010; Kuerten, Mota & Segaert, 2020). The combination of phonological awareness and RAN (the speed of processing language) constitutes the double deficit theory (Wolf & bowers, 1999; Wolf et al., 2000, 2002) and reflects a general impairment in low-level subprocesses required for reading. Although there are many theories on the nature of phonological deficits, the causal role of phonology in dyslexia is often agreed upon (Tallal, 1980; Nicolson et al., 2001; Stein, 2001).

From a neurobiological point of view, the phonological-deficit theory presumes that dyslexia is a congenital disorder of the left-hemisphere perisylvian section of the brain underlying phonological representations or conjoining phonological and orthographic representations (Geschwind & Galaburda, 1985). fMRI evidence has shown dysfunction of the left perisylvian region, the area of the brain responsible for language, as a basis for the phonological deficit (Paulesu et al., 1996). Damage to this area results in impaired phonological processing required for sublexical spelling. Other evidence to support the phonological theory comes from tasks that require phonological awareness, i.e., conscious segmentation and manipulation of speech sounds (Snowling, 2000). Dyslexics usually perform poorly in these tasks compared to normal readers. Challengers of this theory have suggested that the disorder has deeper roots in sensory, motor or learning processes, and that the phonological deficit is just one characteristic or outcome of a more generalised disorder. Despite this, the theory proposes a causal link between cognitive impairment (phonological processing) and the behavioural outcome (reading difficulties).

### 1.2.2. The Rapid Auditory Processing Theory

One way to challenge the phonological theory is with the hypothesis that DD results from an underlying auditory deficit. This theory postulates that problems with reading arise from the impaired ability to recognise auditory stimuli that are short in duration and occur in rapid succession (Tallal, 1980; Tallal et al., 1993). This deficit can ultimately compromise temporal analysis of speech at the level of phonemes and therefore, the construction of accurate phoneme representations. Evidence for this theory arises from problems in distinguishing between rapidly presented non-speech auditory stimuli and reproducing their order (such as that presented in discrimination and repetition tasks) (McAnally & Stein, 1996; Tallal, 1980). Tasks usually involve distinguishing between or reproducing the order of complex tones of varying frequency. Further to this, abnormal neurophysiological responses to several auditory stimuli (e.g., 70 millisecond complex tones varying in frequency and therefore perceived pitch) have been established (McAnally & Stein, 1996; Nagarajan et al., 1999). Failure to accurately correspond to short sounds and fast transitions would lead to further difficulties, such as impaired reading, especially because acoustic events (transmission and reception of sound) are the cues to phonemic contrasts. For example, when exposed to the sounds /ba/ versus /da/, normal readers will have a cut-off point for when the sound is heard, whereas a dyslexic readers perception of the phonemes would have a shallow function (Adlard & Hazan, 1998; Sernicles et al., 2001). Furthermore, research has shown that dyslexics have problems in the categorical perception of contrasts i.e., the minimal difference of voicing between (k) and (j) in leak and league (Mody et al., 1997; Adlard & Hazan, 1998). This interpretation, therefore, sees an auditory deficit as a direct cause of phonological problems which ultimately leads to the reading difficulties experienced by individuals with DD. However, many studies are limited by processing of unnatural sounds modulated in amplitude and are unlikely to observe direct responses from higher-level linguistic information.

### 1.2.3. Visual Factors

Although the most common and established theory of DD is the phonological deficit hypothesis, studies have suggested that visual and language processing deficits are concurrent in dyslexic individuals (Slaghuis, Lovegrove & Davidson, 1994; Slaghuis, Twell & Kingston, 1996). The study of visual deficits in dyslexic children trace back to the late 19th and early 20th century where multiple cases of 'word-blindness', otherwise known as strephosymbolia (reversed symbols, phrases, words and letters), were recorded (Morgan, 1896; Orton, 1925). Indeed, half of dyslexic children complain of problems related to vision (Wilkins, 1995). Many authors later attributed these visual deficits to dysfunction in the magnocellular pathway (Stein, 1997, 2001), which will be outlined in section 1.2.5, although other explanations have also been proposed (Hogben, 1997; Iles, Walsh, & Richardson, 2000). Visual deficit theories propose that dyslexic individuals have problems with the processing of printed letters and words on a page (Lovegrove et al., 1980; Stein & Walsh, 1997). This may take place in the form of unstable binocular fixations, poor vergence or increased visual crowding (Cornelissen et al., 1993; Stein & Fowler, 1993; Spinelli et al*.,* 2002). These theories consider the possibility of a phonological deficit but accentuate the role of vision in reading difficulties.

Many individuals with reading difficulties are affected by scotopic sensitivity syndrome (otherwise known as 'Meares-Irlen syndrome' or 'visual stress'), a type of perceptual dysfunction that causes visual disturbance and discomfort (Evans, 1997). Visual stress has a sensorial origin and describes the inability to see comfortably and without distortion. This can lead to excessive luminosity amplification (photophobia), visual fatigue and several other symptoms of perceptual distortion such as blurring, flickering, and fading of the visual stimulus. Irlen (1997), found that the condition affects 12-14% of the general population, but this number increased to 46% in the dyslexic population, although the exact relationship between dyslexia and visual stress is not well characterised. Individuals may experience words and letters moving across the page or exchanging, halos can also appear around words and text may flow down the page. The brains attempt to ‘’fix’’ these issues can lead to eye strain and headaches which makes reading tiring and unpleasant for the individual. An aetiological link between the magnocellular pathway and visual stress in dyslexia was speculated after the beneficial effects of colour were seen in dyslexics, i.e., the use of coloured overlays alleviated symptoms of visual stress (Chase et al., 2003; Edwards et al., 1996; Irlen, 1997). Scott et al. (2002) demonstrated that while impaired readers show signs of visual stress after ten minutes of reading black text on white paper, these affects are removed when coloured overlays are used over text in the same conditions. However, currently, many researchers believe the theories of dyslexia and visual stress are unrelated and distinctive, with not enough supportive evidence (Kriss & Evans, 2005; Kruk et al., 2008). There are limited and contradictory evidence on visual stress, yet there are reports of its high incidence across university students with dyslexia (Singleton & Trotter, 2005). Additionally, visual stress can cause perceptual distortions that can impair sensory function which could, in theory, be a causal factor in binocular instability (Evans, 1997).

Deficits in the magnocellular pathway have also has been linked to abnormal binocular control and visuospatial attention (via the posterior parietal cortex) (see chapter 3) (Stein & Walsh, 1997; Hari et al*.,* 2001). Supportive evidence for a deficit in the magnocellular pathway of dyslexic individuals comes from anatomical studies which have shown malfunctions in the magnocellular layers of the lateral geniculate nucleus (LGN) and psychophysical studies that have shown sensitivity in magnocellular range, i.e., low contrast, low spatial frequencies and high temporal frequencies (Lovegrove et al*.,* 1980; Cornelissen et al*.,* 1995; Eden et al*.,* 1996). For example, sensitivity to dynamic visual stimuli (Cornelissen et al.,1995; Livingstone et al.,1991; Mason et al., 1993), perception of opposite-direction motion in random dot kinematograms (Pammer & Wheatley, 2001), and perception of apparent global movement in the Ternus visual illusion (Cestnick & Coltheart, 1999; Slaghuis, Twell, & Kingston, 1996). The magnocellular deficit theory of dyslexia will be reviewed in detail in section 1.2.5, and its link to high-level vision will be discussed throughout the experimental chapters.

Unstable binocular fixation during reading have been reported in approximately 63% of children with dyslexia, as opposed to 1% of typical readers (Stein & Fowler, 1981, 1993) and has been correlated to their visual perceptual instability (Stein & Fowler, 1993; Eden et al., 1994). As mentioned, researchers have linked this to magnocellular deficits (Stein & Walsh, 1997; Stein & Talcott, 1999), leading to problems in processing orthographic information and poor reading comprehension, but other causes have also been reported such as the cerebellar hypothesis (Fawcett & Nicolson, 1996). Poor binocular coordination can also cause a range of other eye symptoms, such as blurred text, eye strain and fatigue, and line skipping (Kristjánsson & Sigurdardottir, 2023). Thus, if such visual abnormalities usher reading difficulties, abnormal oculomotor ability should present in non-reading task. This is the case when dyslexic readers view paintings, where they have been shown to exhibit large differences in the amplitude of saccadic movements of both eyes, suggesting problems with binocular coordination (Kapoula et al., 2009). Compared to aged-matched controls, children with dyslexia had more involuntary saccadic eye movements when asked to fixate on a circle (Tiadi et al., 2016). Additionally, when prompted to sequentially fixate on digits from left to right or vice versa, dyslexic children were more likely to look back in both directions compared to normal readers (Pavlidis, 1981). Hawelka et al. (2010) recognised that abnormally high fixation numbers and strong word length effect in dyslexics was due to poor orthographic whole-word recognition and a tendency to over rely on serial sublexical processing. Since eye movements are highly correlated to the shift of attention, high fixation numbers may result from a reduced attention window (Kristjánsson, 2011; Craighero & Rizzolatti, 2005; Rayner, 1998).

The high-level visual dysfunction hypothesis has been well supported by behavioural and neuroscientific studies (Sigurdardottir et al., 2021). High-level vision involves the response of neurons in anterior or high-level regions such as the ventral visual pathway to complex shapes, whole objects and words and other complex features in words (Tanaka et al., 1991; Desimone, 1991; McClelland & Rumelhart, 1981). High-level vision is also responsible for changes in font or resizing and repositioning, whilst also preserving the object structure or identity (Logothetis & Sheinberg, 1996; Pegado et al., 2011; Zhou, Vilis, & Strother, 2019). Whilst the visual recognition of words mostly does not share the same high-level features as other objects, they may rely on common neural mechanisms (Sigurdardottir, Ólafsdóttir & Devillez, 2021). Fine shape discrimination, such as discriminating between various kinds of birds, butterflies, flowers, abstract figures, etc., has been shown to be impaired in dyslexic readers (Collins et al., 2017; Gabay et al., 2017; Huestegge et al., 2014; Sigurdardottir et al., 2015, 2018, 2019). Poor readers may therefore have difficulties with distinguishing between visually similar objects. Previous research has frequently shown a hypoactive left fusiform gyrus, a region of the ventral visual stream (Cohen et al., 2000; Cohen et al., 2002). This area is involved in the perception of words, faces, and other homogeneous or complex objects. Sigurdardottir et al. (2015) found that dyslexic individuals relied on high level ventral stream regions in a variety of different tests. Dyslexic participants on average reported poorer performance on facial recognition, however, they did not show atypical holistic processing of faces (one of the hallmarks of face processing). This is consistent with their left fusiform hypoactivation as the right hemisphere is generally more involved in holistic processing (See chapter 4 for more details). Furthermore, dyslexic participants that took part in non-face object recognition showed significant impairment compared to normal readers.

It has not been clearly established how differences in visual processing in dyslexic readers relate to other abnormalities, such as attentional deficits, crowding and atypical eye movements. For example, reading in Chinese is usually marked with a left-side bias due to its dependence on featural information. However, Tso et al. (2020) found that dyslexic readers showed stronger holistic processing and a weaker left-side bias as a result of difficulties with part-based processing leading to worse reading performance since featural processing is required for reading in Chinese. However, specific associations between featural/part-based processing do not seem to be related to attentional issues (Sigurdardottir et al., 2021).The magnocellular theory was the predominant visual based theory for dyslexia in the 1990s, however early lack of supporting evidence for poor performance in simple low-level tasks led to revised concepts (Quercia et al., 2013) that consider spatio-temporal attention networks, i.e., visual deficits in people with dyslexia are associated to difficulties with the spatio-temporal allocation of attention linked to weakened magnocellular input to the dorsal stream (see chapter 3) (Vidyasagar & Pammer, 1999; Stein, 2014). This concept considers that high-level dysfunction seen in dyslexics may be the manifestation of underlying low-level deficits. Conversely, Wright, Conlon, and Dyck (2012) implied that attentional deficits and magnocellular dysfunction are independent of one another, this is consistent with suggestions by other researchers (Iles, Walsh, & Richardson, 2000; Roach & Hogben, 2004; Steinman, Steinman, & Garzia, 1996). Moreover, visual attentional deficits seen in less competent readers have been investigated in visual search tasks, where participants are asked to find a stimulus amongst a variety of different visual stimuli (Vidyasagar & Pammer, 1999; Vialatte et al., 2023). Overall, the decoding of words involves a tight control of attentional shift, and according to Vidyasagar (2010), this is linked to the magnocellular-dorsal stream which plays a role in the serial scanning of letters. The orderly processing of word requires attention as it serves as a sequential gating mechanism for the conversion of graphemes and their encoding into phonemes, hence disrupting this process can lead to phonological symptoms.

Evidence for the attentional deficit theory in dyslexics has also been provided from measuring the activation of the frontoparietal attentional system and surrounding areas (Eden & Zeffiro, 1998). Although the left frontoparietal system has been linked to auditory processing of word form, the right side plays an important role in automatic attentional shifting and is hence linked to reading acquisition (Corbetta & Shulman, 2011). Dysfunction in this area has been observed in dyslexics and treatment with high-frequency repetitive transcranial magnetic stimulation (rTMS) have been shown to improve both left and right inferior parietal regions and accuracy in non-word reading (Costanzo et al., 2013). The ability to shift attention has led to improvements in several visual tasks such as visual search (Vialatte et al., 2023), contrast sensitivity (Boyer & Ro, 2007), crowding (Yeshurun & Rashal, 2010) and texture segmentation (Yeshurun, Montagna & Carrasco, 2008) (see, Facoetti, 2001; Facoetti & Molteni, 2000; Montani, Facoetti, & Zorzi, 2014; Reynolds & Heeger, 2009, for more reviews). In line with the “sluggish attentional shifting” (SAS) hypothesis proposed by Hari and Renvall (2001) and the “perceptual noise exclusion deficit“ (i.e., deficits in speech are present in noise over silence) (Sperling et al., 2015), attention cannot be easily disengaged once engaged as in neurotypical readers, leading to atypical temporal masking in dyslexic readers (Ruffino et al., 2010, 2014).

The effect of crowding is another visual deficit highlighted in children with reading difficulties and has been attributed to imprecise spatial focusing of attention (Stasburger, 2005). Crowding is a perceptual phenomenon in which a target (e.g., a letter or shape) is rendered more difficult to identify when flanked by other ‘distractor’ elements (other letters or shapes). The crowding effect is largely dependent on the retinal eccentricity of the target letter and density (the number of times a letter appears), number and proximity of the surrounding distractor elements (Stuart & Burian, 1962). Visual span, which has been shown to affect reading speed in tasks, describes the range of letters in text, which can be recognised without eye movement. Legge et al. (2007) found three factors which contribute to this; crowding, decreased resolution of peripheral vision and letter misallocation. To investigate this, Legge and colleagues created trigrams and asked participants to report the letters from left to right over a wide range of contrasts. They found a strong statistically significant correlation between reading speed and visual span size. In another experiment, reading speed and visual-span profiles were measured at different character sizes (Legge et al., 2007). Shrinkage of the visual span was shown for larger characters and reading speed was highly correlated to visual span size. These results provide strong support for the visual-span hypothesis. Findings from Pelli et al. (2007) were supportive of Bouma’s law which claims that letters can be recognised independently, but issues with word identification occur due to crowding, except if they are separated by critical spacing. Equally, reducing the crowding effect by increasing letter-spacing (Perea et al., 2012) or blurring letters (Spinelli et al., 2002; Williams & LeCluyse, 1990) can help alleviate the negative effects of crowding experienced by dyslexic individuals, for example, by increasing the accuracy of letter position coding (such as “form” and “from”). Blurring letters may also help reduce part-based processing while keeping holistic processing intact (Goffaux & Rossion, 2006; Hughes et al., 1990).

The association between visual processing strategies and reading models requires more investigation. The connectionist multiple-trace memory model for polysyllabic word reading (Ans, Carbonel, & Valdois, 1998) puts forward two procedures that considers the analysis of irregular and pseudoword reading: a global procedure which uses knowledge about the whole world and an analytical procedure which activates word syllabic segments. Based on the visual attention window (VAW) an analytical processing style requires narrowing of the VAW and the phonological output corresponds to each attentional sequence, while the global processing styles extends attention span through the whole letter sequence and the phonological output occurs at once (Ans, Carbonel, & Valdois, 1998). In general, words stored in the mental lexicon that individuals are familiar with are computed through a global VAW, while pseudo-words are recorded analytically when global processing fails. A reduction in the VAW size, therefore, halts global processing leading to impaired irregular word reading (Ans et al., 1998).

In summary, dyslexics consistently show abnormalities in visual processing which have been linked to high-level regions i.e., problems with object and face recognition and focusing attention. Although many researchers have implied that this is due to a generalised problem with high-level visual processing, others have specifically linked these deficits to problems with low-level vision, i.e., the magnocellular deficit theory of dyslexia (see section 1.2.5) (Vidyasagar & Pammer, 1999; Stein, 2014). Early detection of visual deficits before a child reaches reading age provides an opportunity for early interventions before the negative effects of reading are felt, especially since children have a higher degree of brain plasticity, which means they may have stronger benefits from cognitive and perceptual training compared to adults.

### 1.2.4. The Cerebellar Deficit Theory

A logical explanation for developmental dyslexia would be a sensory deficit in the auditory and visual domain since reading requires the incorporation of visual and sound information. However, an alternative hypothesis is that deficits in motor skills can impact reading ability (Nicolson & Fawcett 1990, 2005, 2007). The cerebellar deficit theory is the biological claim that the cerebellum of dyslexic individuals is mildly dysfunctional which leads to cognitive impairments (Nicolson & Fawcett, 1990). The cerebellum plays a major role in motor control, speech articulation and in the automatisation of repeated tasks such as reading. A weak ability to automise can impact the learning of grapheme-phoneme correspondences (Fawcett et al., 1996). Support for this theory comes from impaired performance of dyslexic readers in a battery test of motor balance, in dual tasks demonstrating impaired automatisation of balance, and in time estimation (a non-motor cerebellar task) (Fawcett et al., 1996; Nicolson & Fawcett, 1990; Nicolson et al., 1995). Follow-up studies have compared the cognitive profiles of dyslexic children using tests that were both linked and had no relation to literacy, consistently finding deficits in processing speed of information, motor skills, memory and balance (Nicolson & Fawcett, 1994). The theory reconceptualises the cause of dyslexia to a neurological level (the cerebellum), and in doing so it acknowledges that phonological symptoms that present in dyslexic readers are a secondary cause to the primary neurological deficit.

Approximately half of the neurons in the brain reside in the cerebellum, which are implicated in many motor tasks (Ito, 1984; Stein & Glickstein, 1992). The main principle of the cerebellar deficit hypothesis is that when skills become automatised, the cerebellum becomes less active. The inability to perform skills automatically can affect the different processing stages of literacy (figure 1.2). A delay in speech resulting from cerebellar abnormality can affect how fast these skills are learnt, leading to lack of fluency when processing familiar words. Impaired formation of speech sounds can have direct implications on onset, time sensitivity and the development of phonological awareness. Phonological working memory is also compromised, indirectly, since a cerebellar deficit can lead to limited allocation of attentional resources to articulatory tasks (Baddeley et al., 1975). As well as impairing reading and spelling, a cerebellar deficit can lead to loss of dexterity in writing since the cerebellum is responsible for fine motor movement and the ability to determine limb position (Nicolson, Fawcett & Dean, 2001).

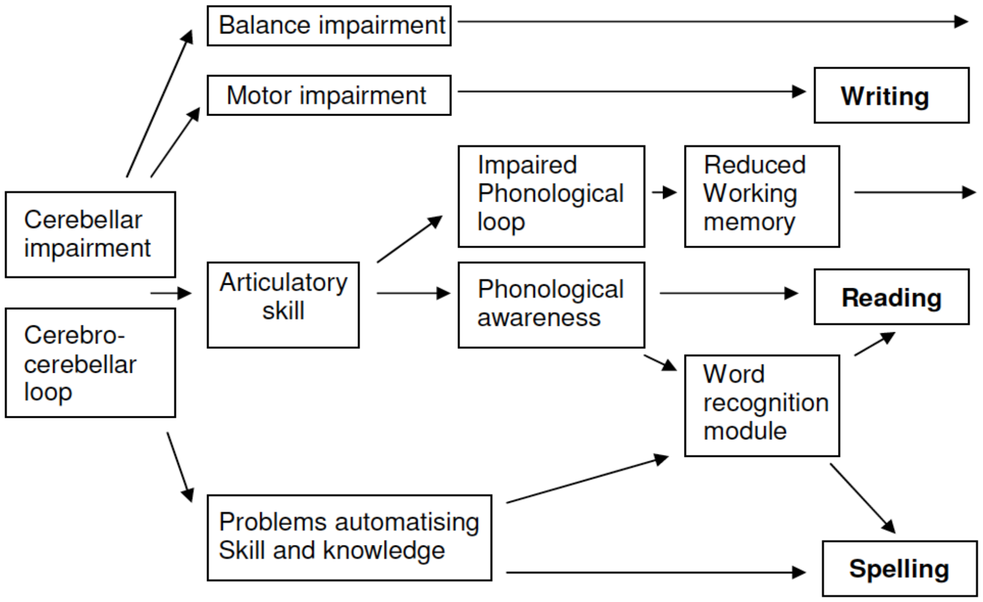

***Figure 1.2.*** *A theoretical causal chain of the cerebellar deficit hypothesis (Nicolson, Fawcett & Dean, 2001).*

Evidence for a cerebellar deficit in dyslexia comes from comparing the symptoms of dyslexic readers to patients with acute cerebellar damage (Ivry & Keele 1989; Stoodley & Stein, 2013). Patients with cerebellar damage have shown temporal processing deficits, similar to dyslexic readers. For example, Ivry and Keele (1989) found that adults with cerebellar damage had difficulties in time estimation judgments but performed similar to controls when estimating the volume of a stimulus. The experiment was later replicated by Nicolson et al. (1995) in dyslexic readers who also showed similar effects. However, Stoodley and Stein (2013) made the claim that impaired cerebellar function may not be a cause of dyslexia, but rather a symptom of a more central neurodevelopmental malfunction that impairs the reading network.

Brain imaging studies have also displayed anatomical, metabolic and activation variation in the cerebellum of dyslexics (Rae et al., 1998; Nicolson et al., 1999). For example, a functional imaging study by Jenkins et al. (1994) showed significantly less cerebellar activation in the right hemisphere compared to controls when learning a sequence of eight button presses. Rae et al. (2002) also found the level of cerebellar symmetry was associated with the severity of dyslexic readers phonological decoding deficit using MRI.

In response to Nicolson, Fawcett and Dean (2001) who proposed that cerebellar deficits are the cause of reading and writing impairments in dyslexia, Zeffiro and Eden (2001) proposed that the cerebellum might not be directly involved in DD and that cerebellar symptoms may reflect damage to the neocortical perisylvian which indirectly effects cerebellar function. This was proposed since dyslexic readers lacked the gross manifestations of a cerebellar deficit and cerebellar patients retained the ability to read fluently. Regions of the cerebellum are linked to thalamic nuclei, pontine, and inferior olivary nuclei so deficits in these regions may affect cerebellar function and mimic a primary cerebellar deficit (Zeffiro & Eden, 2001). The authors suggest that other abnormalities presented by dyslexic readers and cerebellar patients such as problems with smooth pursuit movements (slow tracking movement where eyes remain fixated on a moving object) may be caused by deficits in the visual input channel influenced by the extrastriate cortex which effects sensorimotor integration.

### 1.2.5. The Magnocellular Deficit Theory

The magnocellular deficit theory suggests that dyslexia is as a result of an abnormality in the magnocellular part of the visual system (Lovegrove, 1996; Lovegrove et al., 1980; Stein, 2014, 2019). The magnocellular-dorsal pathway begins from retinal ganglion cells, and projects through the inner two layers of the LGN, terminating in the occipital and parietal cortices (Maunsell & Newsome, 1987). So far, the auditory, visual and motor accounts of dyslexia have been described, however Stein and Walsh’s (1997) unifying proposal of a magnocellular deficit as the root cause of DD considers evidence across different modalities. The magnocellular theory is a generalisation of the visual deficit theory which suggests that magnocellular dysfunction is not restricted to the visual pathway (Stein & Walsh, 1997). Moreover, as the cerebellum receives major input from the magnocellular system, it is also expected to be affected by a general magnocellular failing (Stein, 2001). As a single biological cause, the theory merges all identified manifestations of dyslexia, i.e., visual, auditory, tactile, motor and phonological issues (Facoetti et al., 2003a; Hari & Renvall, 2001). The magnocellular pathway is blind to colours and supports visual sensitivity at low spatial frequency (slow changes over space) and high temporal frequency (fast changes over time) (Merigan & Maunsell 1993) and has been shown to extend to cortical regions that are involved in motion perception and attention. In neurotypical readers, magnocellular function has been recognised as fully developed before a child typically starts to read (Atkinson, 1992). Training using action video games (AVGs) have lately been of great interest for alternative motivational and engaging interventions for DD (Peters et al., 2021). Participants that had greater improvements in low-contrast magnocellular processing following AVG training showed improvements in reading accuracy, linking this pathway to the attentional network.

Besides indirect links, evidence specific to the magnocellular theory comes from post-mortem analysis of dyslexic's brains which have shown disordered auditory magnocellular neurons in magnocellular regions of the thalamus (Galaburda, Menard & Rosen, 1994; Livingstone et al., 1991). Trussell (1997) determined that auditory magnocellular cells are involved in frequency tracking and acoustic change responses to amplitude modulation. The involvement of magnocellular neurons on vibrotactile sensitivity (interpreting sound vibrations through the sense of touch) were suggested by Stoodley et al. (2000). Stein, Talcott and Witton (2001) later argued that magnocellular cells were responsible for motor and automatisation deficits in the cerebellum. This claim was rejected by Nicolson, Fawcett and Dean (2001) who claimed that a magnocellular deficit is not broad enough to cover the range of symptoms that occur with dyslexia, such as problems with time estimation and weaker core muscles. Overall visual and auditory issues in dyslexia provide strong links to magnocellular dysfunction (Stein, 2001, 2019).

Tasks employing stimuli that preferentially bias the magnocellular or parvocellular pathways has allowed for the direct study of magnocellular deficits using behavioural/psychophysical methods (Cushing et al., 2019; Stein, 2019). Since the parvocellular pathway responds to fine detail, i.e., high spatial frequencies, colour and high contrasts this allows psychophysical and physiological comparisons to be made between the two components of visual processing in normal versus dyslexic readers (Farrag, Khedr & Abel-Naser, 2002; Ahmadi et al, 2015). Many psychophysical tasks have used a uniform field sinusoidal grating, where the luminance of the image varies gradually across space determined by a sine wave function (Merrigan & Maunsell, 1993; Ahmadi et al., 2015). Gratings can differ in their spatial frequency, orientation, phase, contrast, and mean intensity. They can also be counterphase modulated at high temporal frequency (>15 Hz) (Merrigan & Maunsell, 1993). Early perceptual stages implicated in dyslexia rely on spatial frequency measurements.

### 1.2.5.1. Psychophysical Evidence

Contrast sensitivity refers to the ability to perceive sharp and clear outlines/edges of objects which facilitates their segmentation from the background (Kaur & Gurnani, 2022). Contrast detection becomes more difficult at low spatial and high temporal frequencies (Skottun, 2000). Differences in contrast sensitivity (contrast sensitivity as a function of spatial frequency) for poor readers was first reported by Lovegrove et al. (1980) - dyslexics demonstrated much lower contrast sensitivity with low spatial frequencies, i.e., they needed greater contrast at low spatial frequencies in order to reliably detect the contrast. Conversely, contrast sensitivity was higher than controls at high spatial frequencies, which bias the parvocellular pathway. The effect was worsened when the gratings were flickered (corresponding to impaired temporal resolution); low contrast sensitivity was displayed at both high and low frequencies. Also, greater contrasts were required to detect the gratings irrespective of size. The authors concluded that dyslexics do not have a general visual impairment and instead that mild impairments in the magnocellular system existed (originally referred to as “the transient” system). Following from this study, the “mild” impairments that were originally demonstrated by Lovegrove et al. (1980) had substantially greater effects with a reduction in contrast sensitivity of up 10 times in subsequent studies, especially in short stimulus durations, low spatial frequencies, high temporal frequencies, and low luminance levels (see also, Lovegrove et al., 1982; Martin & Lovegrove, 1984; Cornelissen et al., 1995; Evans et. al., 1994). Approximately 75% of dyslexics may be affected with poor contrast sensitivity, particularly if a phonological deficit is evident (Habib, 2000).

Temporal processing deficits in dyslexia has received a considerable amount of attention (Farmer & Klein, 1995; Slaghuis et al., 1993; Benassi et al., 2010; Demb et al., 1998). Poor temporal processing has been linked to compromised visual and auditory processing. It appears that dyslexics do not have difficulty in the detection and identification of a single stimulus, and when stimuli are presented simultaneously or if they are presented slowly sequentially (Farmer & Klein, 1995). However, difficulties arise when dyslexics have to process temporally ordered stimuli rapidly, as the temporal intervals are brief. Stein (2019) argued that poor temporal processing (leading to impaired visual and auditory sequencing) is caused by the magnocellular system. Tests that measure temporal processing, such as coherent motion detection, visible persistence and flicker sensitivity have been used to directly test magnocellular function since the magnocellular system is well isolated by temporal frequency. Slaghuis et al. (1993) first reported visual persistence (ability to retain an image) differs between dyslexic and typical readers, as a function of spatial frequency. Persistence was found to be much longer at lower spatial frequencies compared to high spatial frequencies compared to typical readers. This suggests that reading difficulties arise from processing rapid sequences of stimuli managed by the magnocellular system.

Studies investigating neuronal networks in monkeys have shown that the most effective way of measuring the magnocellular dorsal pathway is by studying the motion area of the posterior parietal cortex (Sheth & Young, 2016). One of the most popular methods used to investigate motion detection or sensitivity is using a random dot kinematogram (RDK) where the percentage of dots that move together in the same direction are varied while the remainder of dots move in random directions across trials. The minimum number of dots required to detect global motion is known as motion coherence threshold (Britten et al., 1992). Difficulties in motion processing have been extensively reported and offers a measure of magnocellular sensitivity (Benassi et al., 2010). The ratio of dyslexic readers with a deficit in motion coherence sensitivity rages from roughly 21% (Cornelissen et al., 1995) to 70% (Raymond & Sorenson, 1998) and is present in all dyslexia subtypes (Ridder et al., 2001) with a study claiming that it may even be a better indicator of dyslexia than contrast sensitivity (Demb et al., 1998). When dyslexic participants are asked to detect or discriminate motion carried by coherently moving dots in a random field of moving dots, they tend to be significantly less sensitive to coherent motion and have higher coherent threshold than typical readers (3-4% higher), i.e., they need more dots to move coherently in the same direction to have a similar level of accuracy to typical readers (Benassi et al., 2010). Cornelissen et al. (1998)

grouped 24 ‘good’ (low detection threshold) and 24 ‘poor’ (high detection threshold) coherent motion detectors from an unselected sample of young adults and found that those classified as ‘poor’ coherent motion detectors were less accurate in determining letter position encoding (worse in the phonological lexical decision task).

Performance on flicker fusion threshold tasks modulated at low (5%) and high (75%) temporal contrast was compared in dyslexic and neurotypical readers, and as expected the dyslexic group had a lower ability to detect flicker at high temporal frequencies (Peters et al., 2020). Flicker fusion threshold performance had a 79.3% accuracy rate in distinguishing between dyslexics with a magnocellular deficit and the neurotypical group. In aim to investigate whether these low-level impairments affect reading acquisition, McClean et al. (2011) used a chromatic flicker perception task to investigate temporal aspects of magnocellular function and found significant deficits in dyslexics for magnocellular temporal resolution compared with controls. The two groups, however, had similar performance in parvocellular temporal resolution. Gori et al. (2014a) also measured the magnocellular and parvocellular pathways in dyslexics with age-matched controls by measuring temporal frequency (using the frequency doubling illusion) and static stimuli sensitivity. They found a specific deficit in magnocellular-dorsal oscillation specific to poor phonological decoders (75% of nonword readers were minimum 1 SD below the mean of typical readers), i.e., a magnocellular deficit may specifically impair sub-lexical processing. Other longitudinal studies have used magnocellular deficits in pre-readers to predict future reading acquisition (for example, Boets et al., 2008; Kevan & Pammer, 2009). Improvements in visual attention deficits by training the magnocellular pathway with perceptual learning also provides evidence for deficits in the magnocellular-dorsal stream since reading abilities can also improve with this specific training (Gori & Facoetti, 2014).

Researchers have interestingly found that deficits in the magnocellular-dorsal pathway linked to children with DD may be associated with a genetic susceptibility (Mascheretti et al., 2015). The authors found, for the first time, a deletion in intron 2 of the DCDC2 in children with DD resulted in them needing a significant increase in contrast to process illusory motion (processing by the magno-dorsal stream), as opposed to those without the deletion and aged-matched controls. In contrast, children with DD performed relative to controls in the parvocellular task (irrespective of genetic variant). This was an important step in establishing that a magnocellular deficit is a neurobiological risk factor for DD rather than a cause of phonological deficits.

Other tasks that require much simpler temporal resolution tasks and less complex judgments include stimulus individuation, temporal order judgments and discrimination of sequences (Farmer & Klein, 1995; Davis & Rorden, 2009). For stimulus individuation, participants are tasked to detect a gap between two vertical lines in the same location presented sequentially (Farmer & Klein, 1995). Dyslexic participants needed longer interstimulus interval (ISI) compared to controls to be able to detect the gap and reach a 75% accuracy rate. For temporal order judgments, dyslexic participants who were 4 years behind in reading fluency were much worse in judging the order of red and yellow flashing lights in comparison to children that were only 2 years behind in reading (Farmer & Klein, 1995). For sequence discrimination, dyslexics are less able to replicate the correct location and identity of letters when presented rapidly in a sequence, but when letters were presented simultaneously, they showed similar performance to controls i.e., problems are only presented in sequential presentation (Farmer & Klein, 1995).

Although some studies failed to find significant differences in magnocellular-biased stimuli perception between DD and controls (e.g., Johannes et al., 1996; Williams et al., 2003), approximately 90% of studies that have tested subcortical magnocellular deficits in dyslexic readers have confirmed magnocellular impairments in these groups using stimuli to preferentially stimulate the magnocellular pathway (i.e., low contrast, low spatial and high temporal frequency) (see Stein, 2012 for a full literature review).

#### 1.2.5.2. Electrophysiological Evidence

Electrophysiological evidence in support of a magnocellular deficit in dyslexics followed after a decade of psychophysical research. Dyslexic participants have been shown to have diminished visually evoked potentials (VEP) to rapid, low-contrast stimuli but had comparable performance to typical readers in response to slow or high contrast stimuli, which is consistent with a deficit in the magnocellular pathway (Livingstone et al., 1991). Shandiz et al. (2017) found that when comparing pattern visual evoked potential (PVEP) components in dyslexic versus normal readers there were no differences in high contrast PVEP components, or at 100% contrast (parvocellular system remained intact), whereas significant differences were shown in PVEP between groups at a 25% contrast (magnocellular system which carries low-contrast information is compromised). This was also seen in a previous study by Kobayashi et al. (2014) who found lower peak PVEP amplitude in reversed patterns of white and black sinusoidal gratings recorded at low spatial frequency, low contrast and high reversal frequency (7.5 Hz) which stimulated the magnocellular pathway. Jednoróg et al. (2011) compared N2 responses (an event-related potential component in the right tempo-parietal area) in typical vs dyslexic readers. They found higher N2 amplitude for coherent compared to random motion in the right hemisphere for typical readers but not for dyslexics. This was reflective of longer reaction times to random motion in dyslexic compared to typically reading children and supports abnormalities in the magnocellular-dorsal pathway in dyslexic readers.

#### 1.2.5.3. Functional Magnetic Resonance Imaging

Other studies have measured the brain activity of dyslexics using functional magnetic resonance imaging (fMRI) in conditions designed to preferentially stimulate the magnocellular pathway. Dyslexic readers showed diminished brain activity in the primary visual cortex (V1) and in extrastriate areas compared to controls (Demb, Boynton & Heeger, 1998). This included area MT and adjacent motion-sensitive areas (MT+) that primarily received magnocellular input. Speed discrimination thresholds were also measured which was highly correlated to brain activity and reading speed. Participants that had higher V1 and MT+ responses were faster at reading (lower perceptual thresholds). These results support the relationship between the magnocellular pathway, visual motion perception and reading ability. In normal readers, fMRI images have revealed activation of both V1 and higher visual cortices (V2, V3, V4 and V5) in response to black-and-white sinusoidal gratings, however, the overall activity in these areas was shown to be reduced in dyslexic participants (Yamamoto et al., 2013), confirming that by using low spatial and high reversal frequency stimuli to stimulate the primary visual cortex through magnocellular activation, impairments in the visual magnocellular system can be seen.

#### 1.2.5.4. Anatomical Evidence

The most direct evidence for impairments in the magnocellular system was provided by Livingstone et al. (1991) where they found neurones in the LGN of dyslexics were more disorganised, some 30% smaller than in control brains. In comparison, parvocellular layer showed no difference compared to normal readers. They concluded that smaller cell bodies are likely to have thinner axons and thus slower conduction velocity (i.e., they send slower signals). This is consistent with the functional outcomes seen in physiological and psychophysical findings and provide a persuasive neurobiological explanation for the impairments seen by dyslexic readers. In more recent years, Chica, Hegarty, and Schneider (2015) provided further support by measuring the anatomical boundaries of the LGN in 13 dyslexic readers versus 13 controls. They showed significantly smaller volume of the left LGN in dyslexic readers and also differences in shape. No differences were observed between subjects for the right LGN, consistent with a magnocellular deficit. A detailed discussion of the distinct functional properties of the magnocellular pathway in comparison to the parvocellular pathway will be provided in section 1.5.

## 1.3. Can the Phonological Account Explain Reading Difficulties?

Though it is the subject of decades of debates and research, the underlying mechanism of DD has not been fully clarified (Ramus, 2003). Research has established a complex and dynamic interaction between the various processes involved in reading, but a single unique deficit responsible for dyslexia is still in development (Kuerten, Mota & Segaert, 2020). The most popular account for DD, the phonological deficit hypothesis, has been heavily scrutinised (Goswami, 2015; Peterson & Pennington, 2015; Snowling, 1981; Szenkovits et al., 2016; Share, 2021). The deficit manifests as problems with extracting phonemes with speech, remembering verbal material, finding words and repeating pseudowords (Peterson & Pennington, 2015; Share, 2021). A phonological processing deficit can disrupt the mapping of phonemic and phonological representation of speech sound to written language (Torgesen, 2005). Deficits in phonological awareness cannot fully explain the many observed forms of DD and the additional competing explanations, such as a rapid auditory processing deficit (Tallal & Piercy, 1973; Tallal, 1980), a cerebellar deficit (Nicolson, Fawcett, & Dean, 2001) and a magnocellular deficit (Stein & Walsh, 1997), which have all attempted to explain some of the non-language differences seen in the dyslexic population. Poor phonological skills are one of the most important identifiers of dyslexia and up to 75% of people with DD show symptoms of phonological processing. However, the high correlation between phonological deficits and dyslexia does not mean this is a causation. In fact, Professor Margaret Moustafa at California State University in Los Angeles has emphasised that there is no evidence for phonemic awareness training (Moustafa, 2001) to help improve reading difficulties. This was supported by Krashen (1999a) who after a review of ten studies found no significant difference in phonemic awareness after specific training. Later, he reviewed another 15 studies and concluded that phonemic awareness training effects performance in tests of phonemic awareness rather than real-world reading and comprehension (1999b).

According to Castles and Coltheart (2004), it is difficult to distinguish whether phonological deficits cause impairments in non-lexical reading or whether they arise as a result of these impairments. Competent learners usually develop their linguistic repertoire by combining two different neurolinguistic processes, orthographic and phonological mastery. Orthographic mastery requires visual form processing of words concerning their shapes, and order of letters in words (Çaylak, 2010). This allows words to be processed as a whole unit rather than their constituent sounds to capture the meaning. Phonological mastery required the translation of letters into sounds (i.e., phonemes) for unfamiliar words (Çaylak, 2010). Since all words are unfamiliar to children, problems in the representation and use of phonological information are more apparent during this stage of reading acquisition (Goswami, 2000). There is growing evidence that a child mainly uses orthographic knowledge to carry out a phonological task, for example, performance may be affected by the visualisation of the spoken words and non-words rather than the sounds (Castles et al., 2001). Therefore, it could be that availability of orthography during word learning can impact performance in phonological awareness tasks, not oral language skills itself, and hence, issues with phonological processing can be seen as a symptom, rather than a cause of dyslexia.

Supporting this, a study by Hart (2004) found that 55 individuals were described as having a severe case of phonological dyslexia based on the dual-route model, but performance on phonological awareness tests remained normal. A case study of a 13-year-old girl was analysed, she had an average IQ, but performed lower than average for non-word reading for her age group. After a series of tests, she was found to perform above average for syllable deletion, syllable manipulation, non-word repetition, auditory phoneme discrimination, phoneme deletion, and phoneme manipulation compared to her age group (Jackson & Coltheart, 2001). Jackson and Coltheart (2001) suggested that this means phonological dyslexia, on a dual route account, occurs within the reading system at a grapheme-phoneme conversion level only and is not a generalised language processing deficit. On this account alone, phonological awareness did not cause a non-lexical deficit and therefore may not account for all cases of phonological dyslexia.

Intriguingly, it may be that a phonological awareness deficit is the outcome of another underlying condition, such as specific language impairment (SLI), which can co-occur with DD. Children with SLI present with difficulties in word reading as well as oral language (Brizzolara et al., 2006; Chilosi et al., 2009). Most studies do not consider the high comorbidity of SLI with DD, even though both are separate developmental conditions, limiting phonological awareness deficits as the causal role specific to DD. Employing well-controlled, longitudinal studies may prove useful in finding the cause, however controlling for a history SLI raises the risk of excluding many individuals with DD (Gori & Facoetti, 2015).

Notably, this does not invalidate the significance of phonological processing deficits, with a substantial amount of evidence suggesting a causal link between phonological awareness and reading ability (Castles & Coltheart, 2004). Bradley and Bryant (1978) found that a child’s ability to categorise sounds can predict future reading success. Supporting these results, Schatschneider et al. (2004) found that children who scored poorly on phonological awareness, naming speed of letters and letter-to-sound knowledge had a greater chance of developing reading problems.

Furthermore, brain event-related potential (ERP) responses to speech sounds in dyslexic children have been shown to differ from normal reading children (Guttorm et al., 2005). Hämäläinen et al. 2017 also used ERP to investigate speech processing mechanism in the native language of children from Finland and the United States for common and uncommon sound contrasts (/ba/-/da/-/ga/ and /ata/-/at:a/). ERPs showed that the children could differentiate between speech sound contrasts despite their native language with phoneme length contrast highly correlating to poor reading skills. However, the pattern of results was not as clear for children from the US suggesting that differences in phonological processing occur based on native language.

The most challenging issue for the phonological deficit theory of dyslexia is that it does not have great surface validity, i.e., the extent to which it claims to measure reading difficulties. It should be viewed with caution when classifying reading as primarily a phonological activity since it requires turning visually presented information into meaning rather than phonological representations. Although there is a clear role of phonological representations in reading, other non-phonological related deficits are present for many dyslexic individuals. Giofrè et al. (2019) tested 300 dyslexic children using the Wechsler intelligence scale for children (WISC-IV) and found two clusters of dyslexic children, one cluster presented with greater phonological issues, however both clusters showed visual processing deficits indicating that DD cannot be explained as an isolated phonological problem. O'Brien and Yeatman (2021) found that over 30% of dyslexic individuals are misdiagnosed with a phonological processing deficit. They also analysed visual processing and standardised measures of phonological processing and found that deficits in perceptual decision-making, visual motion processing and phonological processing are independent of each other, challenging dyslexia as a unifying deficit. Deficits have been found in dyslexics in range of phonological and non-phonological tasks including visual processing, implicit learning, attention, and executive functions (Menghini et al. 2010). When controlling for age, IQ and phonological skills, Menghini and colleagues noted individual differences independent of phonological ability (23.3% for word, 19.3% in non-word reading). They suggested deficits may not be limited to linguistic areas and suggest a multifocal cortical system.

Despite the evidence between phonological processing and reading ability, Castles and Colheart (2004) have argued there are a lack of studies demonstrating a sufficient control to conclude that phonology alone influences reading, rather than an unnamed third variable. Here, the authors claimed that phonology is a proximal cause or symptom of a visual deficit. Similarly, other studies claim that phonological impairment may reflect problems with underlying motor, auditory and other non-linguistics skills (Nicolson, & Fawcett, 1990; Fawcett, Nicolson, & Dean, 1996; Tallal, 1980). While it is apparent that dyslexia is characterised by an impairment in phonological representations, the claim that it is the direct and only cause of reading difficulties is reasonably disputable.

Stein (2018) stated that the phonological deficit theory does not explain the root cause of dyslexia. He explained that the theory simply restates the issue that children fail to read because they are unable to acquire the skills needed to read and challenges its use in diagnosing dyslexia. Although he acknowledges that phonology is essential for learning to read, every poor reader will display phonological deficits regardless of if they have underlying dyslexia, making it difficult to distinguish dyslexic readers from other causes of reading failure (Stein 2018, 2020). However, in response Share (2021) sates that this view does not address the complexity of phonological processing as separating speech into phonemes is only one of the characteristics of phonological processing. Overall, it has been agreed that problems with phonological processing do present in DD, but this is unlikely to be the sole determining factor behind reading difficulties and several mechanisms come to play in this highly complex disorder.

The complex and multifactorial nature of DD poses challenges for researchers, the main one being finding one hypothesis to cover the variability in symptoms and aetiology. There have been recent multifactorial accounts of dyslexia which have gained recognition (Catts & Petscher, 2022; Haft et al., 2016; Pennington et al., 2012; van Bergen et al., 2014; Vandermosten et al., 2016; McGrath et al., 2020). A risk-resilience model was introduced by Catts and Petscher (2002) who proposed that dyslexia occurs from the cumulative effects of risk and resilience factors. This view considered that various components effect important human attributes, for example a combination of genetic, socioemotional and cognitive resilience and other exogenous factors can influence reading fluency – thus a single factor cannot account for individual variability. Children who have both visual and phonological deficits are at a greater risk of DD than those that only have one risk factor (Catts et al., 2017; McGrath, Peterson & Pennington, 2020). An abundant amount of research has been conducted on the genetic, biological, cognitive and behavioural roots of dyslexia (Tallal et al., 1993; Stein & Walsh, 1997; Nicolson et al., 2001; Schumacher et al., 2007). Despite this, it would appear that scientists are a long way from agreeing on a unified, coherent account for the cause of reading difficulties. It remains a widely disputed topic with much research focusing on isolated features of reading deficits. There is widespread disagreement on the cause of dyslexia, or whether there is more than one cause, and whether it is language specific. A large body of evidence suggests that impairments in the magnocellular pathway is responsible for the visual and auditory issues that dyslexics experience, which cannot be explained by the phonological deficit theory alone. This may address some of the remaining gaps in dyslexia research (Stein, 2018).

### 1.4. The Structure and Function of the Eye

Visual processing occurs when cells in the retina of the human eye detect the photons of light reflected from different objects in the visual field. The crossing of light rays diverging from varied points on an object causes images of the object in the visual field to be inverted. As the image is inverted by the eye’s lens, the superior half of the visual field is projected onto the inferior half of the retina (Tsuchitani, 2020). When the lens produces a reverse image, the temporal half of the retina (receives contralateral visual input) is projected to the nasal half of each eye’s retina (receives ipsilateral visual input) (Kuffler, 1953). Processing of this visual information occurs before signals reach the brain.

#### 1.4.1 From Photoreceptors to Ganglion Cells

The stage in which cells receive light (via photoreceptors) to the stage where cells transmit visual information from the eye to the brain (via retinal ganglion cells) requires a process called lateral inhibition, where excited neurons reduce the activity of neighbouring neurons to enhance image contrast and improve the perception of edges (creating a sharper image) (Johnston & Lagnado, 2015). Before reaching the brain, photoreceptors and retinal ganglion cells are of utmost importance in the processing of a visual signal. Photoreceptors are specialised neurons found in the eye's retina responsible for converting light into electrical signals that stimulate physiological processes (Molday & Moritz, 2015). They are the first cells in the retina to receive a visual signal that enters the eye. This early stage of receiving visual input is where the process of visual perception begins. There are two types of photoreceptors within the retina: cones (responsible for day vision) and rods (responsible for night vision). Cones are involved in detecting colour and operate optimally in high luminance conditions, whereas rods are colour-blind and are specialised for perceiving stimuli in low luminance conditions (Molday & Moritz, 2015). The fovea, located in the centre of the macula region of the retina is involved in central vision and contains densely packed cones while the peripheral retina, the area of the retina outside the macula is involved in peripheral vision and contains a larger number of rods (Rehman et al., 2022).

The photoreceptors described above transmit to bipolar cells, which then in turn transmit to retinal ganglion cells (the bridging neurons that transmit visual signals to higher processing centres within the central nervous system) (Rehman et al., 2022). These signals are considered excitatory and are often referred to as the 'vertical' pathway. Each photoreceptor sends signals to several bipolar cells which in turn provide several parallel pathways to the brain (Ichinose & Habib, 2022). The synaptic connection between photoreceptors and bipolar cells occurs in the outer plexiform layer. Bipolar cells can be further subdivided into 'ON' cells (excited by an increase in light) and 'OFF' cells (excited by a decrease in light). Bipolar cells then pass their signal in response to light through ganglion cells via connections in the inner plexiform layer (Nelson & Connaughton, 2012). Rod photoreceptors are pooled to generate a large response in bipolar and ganglion cells making them sensitive to low levels of light (Molday & Moritz, 2015). In contrast, cone photoreceptors are much less convergent so each ganglion cell that governs central vision receives input from only one cone bipolar cell which is contacted by a single cone, making them highly sensitive to spatial resolution but less sensitive to low levels of light (Mustafi, Engel, & Palczewski, 2009). Therefore, when a human eye is presented with a high luminance condition the image will have good spatial resolution, whereas only vague outlines will be seen under low luminance conditions. Since the fovea contains the highest density cone receptors, this explains why stimuli presented in this area of the visual field is clearer and more detailed compared to stimuli presented in the parafoveal and peripheral areas of the retina (Hendrickson, 2009). The different functional properties of these two photoreceptors allows the processing of visual input at a very early stage, such as colour, contrast, and luminance detection. The separation of visual input continues to the visual cortex and to higher cortical areas and highlights the importance of the functioning of both cell types to process a visual image since different features of visual input are split between the two cell types (Cheng et al., 2022).

Incoming images formed on the retina are captured by approximately 100 million photoreceptors (95 percent of which are rods), whilst the output is transmitted by approximately one million retinal ganglion cells. Axon terminals of the ON and OFF bipolar cells stratify into the sublaminae in the inner plexiform layer where ganglion cell dendrites also stratify (Kim et al., 2021). As a results, specific bipolar cells can form connection with specific types of ganglion cells which consequently makes them “ON” and “OFF”. The early formation of ON and OFF pathways leads to the subdivision of vision. Retinal ganglion cells generate action potentials once they receive information from photoceptors through bipolar cells which provides the route to transmitting visual information from the eye to the brain (Nelson & Connaughton, 2012). Lateral connections modulate signals from the vertical pathway (photoreceptors to bipolars to ganglion cells) (Grunert & Martin, 2020). These lateral connections are provided by horizontal cells in the outer plexiform layer which network between the photoreceptor and bipolar synapse. The lateral connections provided by amacrine cells in the inner plexiform layer are inhibitory e.g., they directly inhibit ganglion cells, but other amacrine cells can also inhibit amacrine cells which may affect the total inhibition onto ganglion cells (Grunert & Martin, 2020). Ganglion cells transfer cone photoreceptor signals during the day and rod photoreceptor signals during the night through amacrine cells – they are the first neurons to fire action potentials in the visual pathway and generate transfer responses at the level of bipolar to ganglion cell synapse (Nelson & Connaughton, 2012). The receptive fields size of retinal ganglion cells can change between peripheral and central regions of the eye; the fovea has smaller receptive fields of ganglionic cells than the peripheral region of the retina (Kim et al., 2021). As ganglion cells in the peripheral regions of the retina receive input from a larger number of photoreceptors compared to the foveal region, the peripheral regions of the retina are more sensitive to low light levels and stimulus motion whereas the fovea is specific for high spatial frequencies (Kim et al., 2021).

### 1.4.2. The Centre-Surround Receptive Field

The centre-surround receptive field organisation allows ganglion cells to transmit differences in firing rates of cells in the centre and surround; the strongest cellular response to light exposure on the receptive fields come from when either the centre or the surround of cells is stimulated alone (Protti et al., 2014). When both the centre and surround are stimulated, a weak response is generated in response to light due cancelling effects of the opposing membrane polarisations (Bloomfield & Xin, 2000). Ganglion cells have both excitatory and inhibitory centres and surround; half of them have an excitatory centre and inhibitory surround (ON-centre/OFF-surround receptive fields), while the other half have an excitatory surround and inhibitory centre (OFF-centre/ON-surround receptive fields) (Dowling, 1987). Magnocellular (M) retinal ganglion cells have been shown to have an inhibitory response that is maximally responsive to long light waves (Nelson, 2007) and suppression of M neurons can occur in the presence of diffuse red light (Edwards et al., 1996). The centre-surround receptive field is the key functional property of parvocellular (P) and M neurons (Croner & Kaplan, 1995). The receptor field centre of a ganglion cell reflects the organisation of the excitatory vertical pathways through the retina, while the surround reflects the organisation of inhibitory lateral pathways in horizontal and amacrine cells (Dacey et al., 2000). The centre-surround receptive field organisation of ganglion cells enables the retinotopic mapping, i.e., the mapping of visual input from the retina to neurons within the visual stream. The reflection of different amounts of light from objects creates the retinotopic map, allowing them to be distinguished from one another and their background (Henriksson et al., 2012). The image presented to the visual field is a ‘direct’ copy of this map, which is also preserved in sub-cortical brain structures, namely the LGN and superior colliculus (Huberman, Feller & Chapman, 2008). The organisation of retinotopic maps preserving orderly representation suggest that there are distinct neural representations of the foveal and parafoveal areas (Arcaro et al., 2009). The centre-surround receptive field allows sensitivity of edges and small spots of light over large surfaces. This mechanism can be measured by responses to sinusoidal grating patterns of varying spatial frequency. Since the centre is small, it can respond to both coarse (low frequency) and fine (high frequency) information (Demb, et al., 1999). Spatial resolution is increased as there is a decrease in centre size, whereas the surround only responds to coarse patterns since it is larger, leading to inhibition. This explains why generally humans are much less sensitive to coarse patterns compared to fine patterns.

### 1.4.3. Properties of M and P cells

The three main types of retinal ganglionic cells will now be discussed, one of which forms an integral part of this thesis, M cells. P cells are the most abundant type of cells in the retina and are known as “midget” retinal ganglion cells due to the small sizes of their dendritic trees and cell bodies, they constitute approximately 80% of retinal ganglion cells (Kim et al., 2021). About 10% of all retinal ganglion cells are M cells, which are relatively large in size compared to P cells. The outstanding 10% of ganglionic cells are koniocellular (K). While K cells play a role in visual signal transmission, these cells are involved in colour vision (specifically, they are sensitive along the ‘yellow-blue’ chromatic axis), most of the K cell output goes to the LGN (90%), while 10% of their input goes to the superior colliculus. K cells located in the LGN are in regions called koniocellular layers that project to extrastriate visual areas (anterior to area V1) as well as the primary visual cortex. However, this is not vital to the scope of the current research (see review by Xu et al., 2001).

It was established from early on that P cells respond to coloured lights and to white lights of similar intensity (Derrington et al., 1984). For colour vision to occur, it requires the receptive fields of P cells to compare signals of photoreceptors such as long wavelengths (‘L-cones’, often called red photoreceptors) to those of medium wavelengths (‘M-cones’, often called green photoreceptors), therefore they respond best to red-green chromatic modulation (Derrington et al., 1984), this is an approximate 90º rotation in colour space from the yellow-blue axis. In contrast, M cells do not display colour selectivity and respond to lights that modulate M- and L-cones which appear yellow, therefore responding best to luminance modulation (Lennie et al, 1993). The role of short wavelengths (‘S-cones’, often called blue photoreceptors) to the receptive fields of P- and M- cells have been heavily debated, with some researchers claiming that P-cells (and M-cells to a small degree) receive input from S-cones (Klug et al., 2003; Wool et al., 2019; Thoreson & Dacey, 2019).

More central to the current thesis is the distinction between M and P cells, which allow them to be stimulated separately. It is essential to highlight the differences between these two unique cell types and their cortical projections to show how manipulation of these pathways can affect visual processing. Difference in M and P cells are visible from when connections between photoreceptors and bipolar cells occur (Shapley, 1995). The number of photoreceptors converging onto a ganglion cell is a direct reflection of its spatial resolution. P retinal ganglion cells have a small number of photoreceptors mapping onto them which means they have high spatial resolution required for the analysis of fine textures and small objects, and is necessary for reading (Mustafi, Engel & Palczewski, 2009). Spatial resolution will be compromised if a greater number of photoreceptors converge on to a ganglion cell, as shown with M cells that have larger receptive fields (>2x larger than that of P cells) (Kaplan & Shapley, 1986). The dendritic fields of bipolar and ganglion cells in parvocellular and magnocellular pathways both increase in size leading to a greater number of bipolar cells receiving input from photoreceptors and thus a greater number of ganglion cells receiving input. M ganglionic cells have larger dendritic fields and can contact hundreds of bipolar cells whereas P ganglion cells have smaller dendritic fields and contact smaller numbers of bipolar cells. M-ganglion cells require much more cone photoreceptors to sample from (100s) compared to P-ganglion cells (10). This essentially leads to the subdivision of early vision in primate (Dacey and Petersen, 1992; Grunert and Martin, 2020). The characteristic of M cells makes them highly suited for motion detection (Rokszin et al., 2010), and their large receptive field is important for sudden stimulus detection so that spatial attention can be redirected towards that new stimulus (Stein, 2014). This large receptive field means that M cells sample across a larger area meaning their spatial resolution is much lower than that of P cells so only show benefits for the perception of coarse-grain, global visual input (Zou et al., 2023). A major distinguishing factor for M and P cells is their timed response to changes in luminance levels; both have strong initial response, but P cells have been shown to be relatively ‘sustained’ compared to much more ‘transient’ M cells (Solomon, 2021).

Furthermore, it has been established that peripheral regions receive a large number of inputs from photoreceptors by ganglionic cells, mainly by M cells (the most common retinal ganglionic cell in the extrafoveal regions) (Dacey, 1993). In contrast, P cells are most abundant in the foveal area of the retina, although are also found in the parafoveal and peripheral areas but to a much lesser extent (Dacey, 1993). Since the fovea mainly sampled by P cells, it is responsible for high-acuity vision (respond to fine-grain detail and colour stimuli) (Hendrickson, 2009). Compared to P cells, M cells are much less abundant in the retina, so M cells compromise with their low numbers by having much thicker axons (where electrical impulses occur) (Yoonessi & Yoonessi, 2011) and have greater myelination which means they have faster conduction velocity (by approximately 20ms) in comparison to P cells (Lamme & Roelfsema, 2000; Schmolesky et al., 1998). This means that M cells have are much more efficient in detecting high temporal frequencies. Since M cells cannot detect high spatial frequencies, images viewed outside the fovea (at an eccentricity of 50 degrees) are much less defined and colour sensitive (i.e., spatial resolution is lost) (Masri, Grünert & Paul, 2020). These vast difference between P and M cells opens an avenue to explore in reading, especially since words are clearer when they are presented in the fovea occupied by P cells (Rehman et al., 2022).

In summary, P cells are the most common type of ganglionic cells that enrich the foveal region and have high spatial frequency and low temporal frequency. M cells are the most common type of ganglionic cells that resonate in the extra-foveal region and have low spatial frequency and high temporal frequency. They have faster conductance rates and detect motion, global information, depth, and luminance.

### 1.5. From the Eye to the Brain

In the previous section, the distinct properties of M and P cells were outlined including their contribution to stimulus perception in the central and peripheral visual field. These early differences in the visual field reflect their roles to higher areas of the brain.

The axons of around 1.2 million retinal P, M and K ganglionic cells converge at the optic disc to form the optic nerve which carries the signal from the eye to the brain (Laha, Stafford & Huberman, 2017). The optic nerves of both eyes meet at the optic chiasm to form two optic tracts. Each optic tract projects to its corresponding cerebral hemisphere to reach the LGN. The LGN represents the first stage in the visual pathway and plays an integral part in cortical top-down feedback signals which may affect information processing (Prasad & Galetta, 2011). It is the major target of retinal ganglion cell axons in primates with histological analysis revealing layers of densely packed neuronal cell bodies in this region (Hickey & Guillery, 1979). LGN neurons send their axons through the optic radiation to the primary visual cortex (V1). The group of axons that allow this connection to take place is the geniculostriate pathway (the main projection of the optic nerve) (Purves et al., 2001). This mediates a selection of high-level visual functions e.g., object recognition, spatial orientation, form perception, and sensorimotor control (Westwood, 2009).

To a lesser extent, the optic nerve also has projections to the superior colliculus (SC) involved in tracking eye-movements, orienting motor responses, visuospatial attention, and perceptual decision-making (Cooper & McPeek, 2021). Visual input to the SC is thought to be transmitted by M cell axons, and hence, this suggests a role of the magnocellular pathway in directing attention towards appropriate stimuli in the visual field and enabling the production of saccades in eye movements (Rodieck & Watanabe, 1993; White & Munoz, 2011). Coronal section of the anterior-posterior axis of the nucleus shows clear organisation of dorsal and ventral layers; the more dorsal layers having smaller cell bodies (P layers) and the more ventral layers having larger cell bodies (M layers) (Solomon, 2021). The neurons, otherwise known as ‘relay cells’ within these layers receive synaptic input from ganglion cells (10% of the neurons in the LGN are inhibitory interneurons) (Solomon, 2021).

The segregation between the magnocellular and parvocellular pathway in the LGN, along with earlier stages of visual processing has been outlined. The magnocellular visual pathways convey fast coarse information from ganglionic M cells in the retina to the superior colliculus and the LGN. In contrast, the P pathway is mainly responsible for the transmission of high-resolution visual information to the cortex and processing of fine-grained stimulus from central areas of the retina to the LGN.

### 1.5.1. Segregation of Ventral and Dorsal Streams

The previous sections discussed how the properties of M and P cells have led to their segregation throughout the visual cortex. Here, evidence will be provided for the segregation of the magnocellular and parvocellular pathway to the two major higher cortical processing streams; the ventral (parvocellular) and dorsal (magnocellular) streams. The majority of researchers have agreed that processing of a visual stimulus depends on two separate processes that are related, hence, these two pathways have been studied separately (Ramus, 2003; Sheth & Young, 2016). Trevarthern (1968) shed light on the distinction between focal and ambient visual mechanisms for perception. This twofold structure of the visual system suggests that each hemisphere could be separately presented with different stimuli. The focal system involves accessing details (attention) through central vision and is sensitive to decreases in spatial frequency, while ambient systems navigate the space around the body and involves peripheral vision (Trevarthen, 1968). For example, focal mediation is needed whilst reading but spatial orientation is maintained by the ambient system if you are walking while reading with minimal conscious effort. A functional focal system is required for the recognition of objects and ambient system for guiding visual behaviour. This idea was further developed by Ungerleider and Mishkin (1982) who proposed the two-stream hypothesis: the ventral stream (from the occipital to temporal cortex) is heavily involved in object recognition whilst the dorsal stream (occipital to parietal) is involved in visually guiding motor behaviours, otherwise known as the “what” and “where” stream, respectively. This idea was first tested via lesioning studies on monkeys, i.e., when lesions were present in the parietal cortex (dorsal stream), this led to difficulty locating stimuli (“where” the object was), and when lesions were present in the inferior temporal cortex (ventral stream) object recognition was impaired (“what” the object was). Neuroscientific support for the distinction of these visual pathways was provided by Haxby et al (1991) who found separate extrastriate visual pathways for object recognition and spatial localisation in young men using fMRI. For face matching and dot-location matching together, the lateral occipital cortex was activated but face discrimination alone activated an area anterior and inferior to the occipital lobe, whilst the spatial location task alone specifically activated a section of the lateral superior parietal cortex. The results demonstrated functionally dissociable regions in the visual extrastriate cortex.

The evidence presented above led to the development of neurophysiological models for reading comprehension. A functional neuroimaging study by Pugh et al. (2000) suggested that fluent word identification was dependent on the dorsal and ventral left hemisphere posterior systems, which is functionally disrupted in DD. Interestingly they also found that impaired readers had an overreliance on frontal and right hemisphere posterior regions, seemingly to compensate for the weaknesses presented in the left hemisphere. They proposed, on a neurobiological account, that neurotypically developed readers require analytical skills, predominantly in the dorsal processing stream, and it is this that is necessary for the integration of orthographic features with the phonological and lexical-semantic features of written words. Later on, once reading develops, fluent word recognition is thought to develop in the ventral stream. Once words have been acknowledged in lexical memory, the ventral processing stream will allow faster recognition of words as whole units, i.e., they propose that the dorsal stream is the first step involved in reading acquisition.

The neural correlates of lexical and sublexical processes in reading were assessed by Joubert (2004) in aim to show that different brain regions and networks accommodate lexical and sublexical processing. They used three different types of tasks, (1) silent reading of very high frequency regular words which readers are often familiar with (activates lexical processing, ventral stream) (2) silent reading of nonwords (activates sublexical processing, dorsal stream, since they have not been accessed by the lexicon) and, (3) silent reading of very low frequency regular words which are not commonly used, such as “strait” (activates sublexical processing, dorsal stream). The lexical condition activated areas at the border between the left angular and supramarginal gyri. Activation found here suggests that this region is implicated in the mapping orthographic to phonological whole word representations. The sublexical conditions had greater activation in the left inferior prefrontal gyrus involved in grapheme-to-phoneme conversion and verbal working memory processes. Another fMRI study by Borowsky et al. (2006) compared exception words (follows normal spelling rules such as “one”) processed by the ventral stream and pseudohomophones (that have nonword spelling but are pronounced like words, such as “wun’) processed by the dorsal stream. These findings supported Joubert (2004) where they found independent ventral-lexical and dorsal-sublexical streams.

Magnocellular and parvocellular contributions to the dorsal and ventral streams have also been studies. The dorsal stream, or where pathway, receives strong projections from V1 which connects directly to the middle temporal area (MT) and the medial superior temporal area (MST); the primary sources for analysing stimulus motion and directing eye movements (Kravitz et al., 2011). The receptive fields of MT cells are around 10 times larger than those of V1 (Jones et al., 2013). Cells projecting directly from layer 4B of V1 to MT are thought to receive main input from magnocellular-recipient layer 4Cα (Nassi & Callaway, 2006). The termination of the dorsal visual pathway occurs in the posterior parietal cortex which is responsible for the localisation of objects in space and behaviours that depend on spatial perception (Sheth & Young, 2016). Furthermore, MT cells projecting in layer 4B of V1 are mingled with distinct populations of cells in layer 4B of V1 that extend to V3 and V2 (Nassi & Callaway, 2006). Such populations can provide indirect projections to MT but lack of clear categorisation within V1 along with its heterogeneity makes it challenging to predict the exact contributions of M and P pathways to these specialised circuits. The ventral steam passes from V1 through V2 and V4 to areas of the inferior temporal lobe (Zeki, 1973) which respond selectively to visual features important for object recognition such as identification, colour, shape and texture (Ungerleider & Mishkin, 1982).

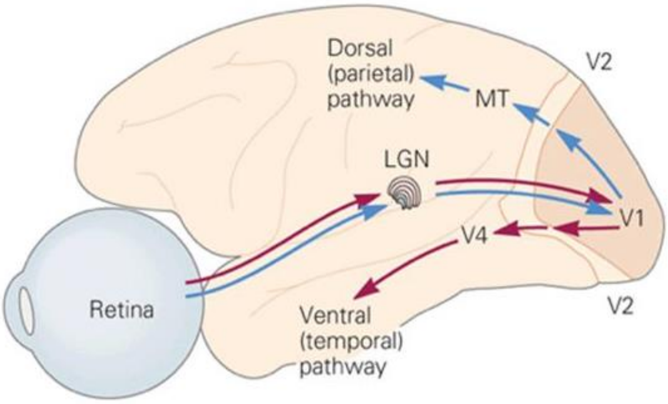

***Figure 1.3.*** *The magnocellular-dorsal and parvocellular-ventral pathways presented as two different streams of information projecting from the LGN to the parietal and temporal lobe, respectively (Kandell et al., 2012)*

Although there is ongoing debate about the association between magnocellular and parvocellular contribution to the dorsal and ventral streams, it was traditionally accepted that there is a strong distinction between the two pathways and their associated streams. This theory was reviewed by Merigan and Maunsell (1993) who established that both pathways can be distinguished anatomically and functionally. Their claim that the dorsal and ventral streams are two largely independent subsystems was seen through their observation of different classes of visual behaviours, e.g., the dorsal pathway is required for spatial relationships and object motion and the ventral pathway for colour, pattern and shape. Neurons of the ventral and dorsal stream also exhibit different response properties. This segregation was thought to be as a result of division between the magnocellular and parvocellular pathways (Desimone & Ungerleider, 1989; Livingstone & Hubel, 1987, 1988; Maunsell & Nealey, 1990). An alternative suggestion was later suggested by Nealey and Maunsell (1994), they argued that the ventral streams depended on both magnocellular and parvocellular input. They tested the hypothesis that parvocellular signals dominate the ventral pathway to the temporal cortex by inactivating M or P subdivisions of the LGN and recording visual responses from superficial layers of V1. Inactivating P layers of the LGN lead to reduced neuronal responses in the superficial layers of V1 while the magnocellular layers had substantial contribution to the superficial layers, hence, this suggests regions in V1 that form the early stages of temporal processing are not specific to parvocellular signals. However, when Maunsell, Nealey and De Priest (1990) carried out a similar procedure, they found that blocking the magnocellular layers of the LGN lead to decreased responses in MT. Blocking the parvocellular layer, however, had little effect on MT cells. This led to the conclusion that the MT area, and hence the dorsal stream and parietal cortex have predominantly magnocellular input (approximately 90%). Many researchers now believe that the dorsal stream is magnocellular dependent, however there is still debate as to the relative contributions of the magnocellular and parvocellular pathways into the ventral stream.

There is limited evidence of parvocellular stream involvement in motion areas of the brain, with red and green coloured stimuli (parvocellular cells have red-green centre-surround) being more difficult to detect in this region (Dobkins & Albright, 1998). Although motion is impaired when detecting red-green stimuli, it can still be perceived to some extent suggesting minimal parvocellular involvement. However, Lee et al. (1998) explained this in terms of the magnocellular pathways ability to distinguish borders defined by red and green contrast, even with impaired colour signalling information. According to Skottun and Skoyles (2007) magnocellular cells also provide 50% input to the ventral occipital pattern and form analysing system, which is another pathway leading to the inferotemporal cortex. Magnocellular input in the ventral pathway is thought to be involved in drawing attention to detailed analysis of visual space for the parvocellular system (Vidyasagar & Pammer, 2010).

The role of magnocellular cells in lower visual areas and the separation of the magnocellular and parvocellular pathways into two distinct streams - ventral and dorsal has been established. Since magnocellular output is involved in areas beyond the LGN, it is expected that problems in these low-level regions would impact higher-level regions which rely on functional magnocellular input. For example, the parietal cortex receives mLGN afferents via areas V1, V3 and V5 which plays a central role in the process of visuomotor control (Sheth & Young, 2016). High-level regions selectively respond to complex shapes and objects (Tanaka et al., 1991; Desimone, 1991), so therefore high-level regions may disrupt processing of whole words and other large orthographic reading units in the lexicon (Glezer et al., 2009). Problems with font, resizing and repositioning that can transform an object’s structure or identity, suggests that visually presented words may rely on similar neural mechanisms to objects (Pegado et al., 2011; Zhou, Vilis & Strother, 2019). The flow of visual information to higher cortical areas from low-level visual areas depends on the type of information presented to the retina. Chapters 2, 3, 4, 5 and 6 will explain in further detail the low- and high-level processes responsible for the different types of visual stimuli.

### 1.6. Summary and Aims

In summary:

- The phonological deficit theory remains the most well-developed and supported theory of DD.
- The phonological theory, however, does not explain other neurological symptoms that a considerable proportion of dyslexic readers struggle with such as problems with visual processing, or dysfunction in higher-level mechanisms.
- Although a good indicator of reading ability, phonological tests are not suitable for measuring non-verbal ability and can be stressful and tedious for children with reading difficulties.
- A large body of evidence has suggested that when visual transient systems fail to develop properly reading is implicated.
- The magnocellular deficit theory proposes that the core deficit of DD is impairments in the magnocellular part of the visual system.
- The distinct properties of magnocellular and parvocellular cells enable the use of stimuli to separately engage the magnocellular or parvocellular pathways.

This chapter provides an overview of the central issues in dyslexia research and the different theories that may account for some of the remaining gaps in literature. The phonological deficit theory does not give insight to the mechanisms that cause reading problems in dyslexia or address other visual tasks that dyslexics seemingly struggle with. The purpose of this thesis is to test if performance in high-level visual tasks and reading ability is behaviourally measurable based on the proposed magnocellular deficit theory of dyslexia, i.e., diminished activity in the magnocellular pathway of dyslexic individuals has been established. The distinct aspects of the visual magnocellular and parvocellular pathways from the retina via the LGN to the visual cortex allows the use of visual stimuli to selectively drive them, since M cells are more sensitive to low contrast, low spatial and high temporal frequency. Previous behavioural and neuroimaging studies have reliably demonstrated that dyslexic readers responses are significantly reduced to magnocellular targeted stimuli compared to neurotypical readers. This account also rules out that dyslexics are generally worse at all visual tasks due to simply being disengaged. Since magnocellular outputs serve other areas outside the visual cortex, it is reasonable to assume that deficits in low-level psychophysical tasks which target the magnocellular system would impair performance in high-level tasks which rely on the function of this pathway via the LGN, e.g., mechanisms of visual attention trace back to magnocellular input to the dorsal stream which extends to the posterior parietal lobe (Merigan & Maunsell, 1993). Based on evidence for magnocellular dysfunction in dyslexics and the segregation of magnocellular-dorsal and parvocellular-ventral pathways, the following thesis focuses on employing stimuli designed to preferentially target low-level (magnocellular-biasing) regions and measure how this can affect high-level visual processing in different reading groups.

# Chapter 2: Visual Object Recognition and its Association with Reading

## 2.0. Chapter Overview

Efficient object recognition has been hypothesised to occur through rapid processing of LSF information by the magnocellular pathway (Bar, 2003). Top-down facilitation is triggered by magnocellular input which activates the orbitofrontal cortex (OFC), in turn activating visual representation of objects in the ventral temporal cortex through bottom-up processes. The link between early visual and high-level object recognition regions can be investigated in those with reading difficulties since it has been hypothesised that problems with reading, presented in disorders such as developmental dyslexia (DD), occur as a result of deficits in the magnocellular system. This chapter investigates the relationship between object recognition and reading ability measured by phonological and orthographic lexical decision tasks (LDT's). It begins with an introduction to object recognition, problems with magnocellular processing in dyslexic readers, and the reading process. Based on the research presented in the introduction, a psychophysical experiment was conducted to provide evidence for the links between low-level deficits in slow/poor readers and object recognition. The chapter will conclude with a summary and discussion of the findings.

## 2.1. Introduction

The human visual system enables us to recognise objects rapidly under a wide range of different viewing conditions, e.g., viewing angle, lighting level and direction, and scene context. Object recognition is commonly thought to undergo analysis by a hierarchy of functionally specialised areas situated along the visual ventral stream (Gross, 1994; Orban, 2008; Rolls, 2000). The structure and the functional maps of the visual cortex has aided the view that visual input is processed serially in a bottom-up analysis of complex information, a feedforward process. According to this view, visual information flows through low-level to high-level object recognition regions, after which activation of semantic analysis and object naming takes place.

This unidirectional view has been heavily influenced by the sequence of hierarchical processing stages from the primary visual cortex (V1) to the inferior temporal cortex (IT) (Bullier, 2001a, 2001b). However, a solely bottom-up architecture does not account for the noise and clutter of natural images, which has also been established in computer vision (Sharon et al., 2006; Ullman et al., 2002).

It is unlikely that bottom-up and lateral processes (those that depend on short-range horizontal connections) consider which edge should be allocated to one shape over another given the immense amount variation in occlusions, reflections, shadows, and lighting (Kveraga, Ghuman & Bar, 2007), making it difficult to process local details in a global manner. Furthermore, the visual field is large and the human eye spans over a wide region, which means V1 is too distant for local excitatory and inhibitory connectivity (Angelucci & Bullier, 2003). Consequently, this traditional view has been challenged by recent models which suggest a simultaneous bottom-up and top-down stream of information throughout the cortex (Bullier, 2001; Lamme & Roelfsema, 2000). The concept of top-down processing facilitating perception indicates that high-level visual information is processed earlier than some low-level information. Although functional imaging has supported the role of top-down signals from the pre-frontal cortex in visual processing, how such processing is initiated remains for further research (Ranganath, 2004).

In the early-mid 90's, positron emission tomography (PET) studies revealed selective activation of regions in the occipital and temporal cortex associated with the recognition of faces and objects, namely the fusiform gyrus and lateral occipital cortex (Malach et al., 1995). Studies have also proven the active role of the prefrontal cortex in the network that facilitates object recognition (Barr, 2001; Fenske et al., 2006). Providing that prefrontal regions have been shown to be involved in semantic analysis (Gabrieli, Poldrack & Desmond, 1998), one may predict based on the view that recognition is a purely bottom-up, feedforward process that activity in the prefrontal cortex which takes place during daily object recognition could be as a result of semantic post-recognition processing. However, this view does not consider orbitofrontal cortex (OFC) activity as a key site for object recognition (a prefrontal region involved in decision-making), but rather as a result of semantic processing which takes place after object recognition. Another possible view is that the network that mediates object recognition extends beyond typically defined regions of the visual cortex, in particular that OFC activation is the source of top-down facilitation in visual object recognition, and that this is magnocellular driven (Bar, 2003).

Top-down information should be activated prior to bottom-up processing and accessible to low-level areas to complete object recognition. Bar (2003) proposed a model for the mechanisms of such fast triggering of top-down facilitation (figure 2.1). According to this model visual input, in the form of low spatial frequency (LSF) information, is swiftly extracted and transferred from the early ventral (or object processing) visual stream to the OFC instead of directly through V2 and V4 areas to the inferior IT cortex (where representations of objects are found). Predictions (initial guesses) are then activated by LSF images in the OFC about what objects the visual input may have given rise to. The predictions then activate corresponding visual representations in the ventral stream (IT) where object processing takes place, which is postulated to facilitate recognition by biasing the bottom-up processes to focus on a small set of the most possible object representations (template matching). Functional magnetic resonance imaging (fMRI) integrating with magnetoencephalography (MEG) has provided strong evidence for this model in which the OFC was activated specifically by LSF information within the first 130ms of recognition, prior to activity in the IT (Bar et al., 2006). Along with the IT, the OFC also has reciprocal connections to the magnocellular (M) division of the medial dorsal nucleus and the pulvinar ('higher order thalamic relays') (Ongur & Price, 2000), and so is involved with decision-making, reward value, and emotional and cognitive control (Bechara et al., 2000; Freedman et al., 2003). Thus, the OFC is positioned for integrating and transmitting visual information rapidly, as well as general predictions (Bar, 2009).

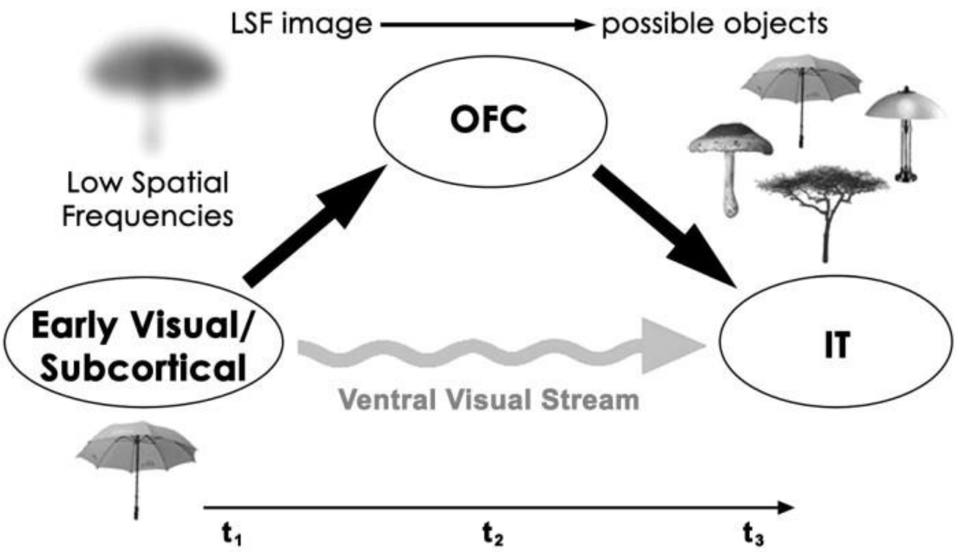

***Figure 2.1.*** *The top-down facilitation model (first proposed by Bar et al., 2003, image retrieved from Kveraga, Boshyan, and Bar, 2007). LSF visual input is projected rapidly to the OFC from early visual/subcortical regions. Simultaneously, analysis of image details occurs slowly along the ventral stream. Possible objects are predicted from the "gist" of the image (based on LSF information) and then fed back to object recognition regions in the IT where bottom-up processes begin.*

The projection of LSF images to the OFC is key to the top-down facilitation model. Bar et al. (2006) tested the theory that early recognition in the OFC is dependent on the spatial frequency of an image. This model considers only LSF to the OFC for the initiation of top-down facilitation of object recognition, as high spatial frequency (HSF) images are processed differently in the OFC site. In general, differences have been reported in spatial frequency processing, for instance, there are hemispheric asymmetries in the way visual stimuli with different spatial frequencies are processed and size differences in spatial-frequency tuning mechanisms (Fiser, Subramaniam & Biederman, 2001; Iidaka et al., 2004). Due to differential sensitivity in LSF and HSF images, Barr and colleagues used fMRI and MEG to compare OFC activation of LSF images of objects with HSF images of objects. They showed that LSF object images displayed higher fMRI signals in the OFC compared to HSF images. Additionally, an interaction was evident in LSF images between the occipital visual regions and the OFC and between the OFC and the fusiform gyrus but synchrony between these regions was significantly less in HSF stimuli. Altogether, these findings provide the foundation for the theoretically proposed model (Bar, 2003) for triggering top-down facilitation.

Early and rapid activation of the OFC has been hypothesised to be triggered by magnocellular projections to the OFC which generates the initial prediction based on magnocellular information. The magnocellular pathway is known to transfer low-resolution, achromatic (luminance defined) information rapidly, but the exact anatomical pathways which subserve magnocellular-driven facilitation remains poorly understood (Bullier & Nowak, 1995; Chen et al., 2006). One possibility relies on the dorsal visual stream which projects to the parietal cortex and connects with visual eye fields in the prefrontal cortex and with the OFC (Cavada & Goldman-Rakic, 1989; Fang et al., 2005). If top-down facilitation is triggered by magnocellular input, a prediction this theory can make is that dysfunction in the magnocellular pathway could in turn lead to impairments in activating predictions about potential objects higher up in the visual ventral stream, i.e., impaired (slower) object recognition. This prediction forms the foundation of the experiment presented in this current chapter which aims to reveal potential deficits in object recognition with stimuli designed to bias processing toward the magnocellular pathway and differentially activate the OFC.

The magnocellular system is involved in guiding visual attention and timing visual events during reading (Stein 2001). Reading involves a complex integration of skills concurrently with the involvement of fundamental cognitive processes (Polse & Reilly, 2015). The ability to read is crucial for knowledge acquisition and to succeed at all levels of formal education. It is also necessary for human communication and has substantial implications for human cognitive development (Darling-Hammond et al., 2019). The fundamental skill here is phonological processing which is defined as distinct units of sounds in a specified language (e.g., phonemes for alphabetic languages) used to process spoken and written language. This involves the awareness of what sounds are and how they combine to form words (phonological awareness), the storage and manipulation of verbal material (phonological working memory) and the ability to recall phonemes associated with specific graphemes (phoneme awareness skills) (Wagner & Torsen, 1987). Understanding the meaning of text heavily relies on phonological processing as this accelerates the decoding of written information, which in turn leads to word identification (Denton & Otaiba, 2011).

Within literature on dyslexia, there is extensive agreement on phonological deficits being a predominant cause for reading impairments for the majority of English speakers (Ramus, 2001; Snowling, 2000). The phonological deficit hypothesis states that dyslexic individuals have difficulty in analysing the sound structure of language which leads to failure in learning the semantic relationship between spelling and sounds (Snowling, 2000). The inability to acquire the skill to identify sounds associated with individual letters and letter combinations is ultimately considered to be the primary source for word recognition problems. However, the phonological deficit hypothesis alone cannot account for other comorbid symptoms of dyslexia, such as various deficits in visual processing, e.g., contrast sensitivity, coherent motion, contour detection (Simmers & Bex, 2000; Stein, 2014) and visual attention span deficit (Bosse, Tainturier & Valdois, 2007). Reading the western alphabet requires visual feature detection, letter identification, grapheme identification and then grapheme to phoneme translation, and word recognition. Disruption of any of these steps can lead to problems with linking stimuli to sematic information, and hence reading impairments unwind (Shovman & Ahissar, 2006).

Sigurdardottir and colleagues (2015) showed that dyslexics are also impaired in the recognition of faces and other complex non-word visual objects through a series of high-level visual processing tasks (see chapter 4), suggesting that problems with reading must be linked high-level visual processing in the ventral visual stream which receives magnocellular input. High-level visual deficits can be linked to problems with early low-level visual processing, i.e., the magnocellular system. The magnocellular-deficit theory suggests that reading impairments in dyslexia stem from deficits in the early visual system, specifically the magnocellular pathway which responds to luminance contrast differences, low spatial frequencies, high temporal frequencies, and motion (Stein, 2001). According to this theory, abnormal development of the magnocellular layers of the dyslexic lateral geniculate nucleus (LGN) can lead to problems in the subcortical processing of visual signals that have a measurable effect later in the visual hierarchy. This accounts for some of symptoms of dyslexia not explained by the phonological deficit theory. Some of the most direct evidence for the impaired development of the magnocellular system in dyslexic readers comes from Galaburda and Livingstone (1993) who examined dyslexic brains post-mortem. They found that magnocellular layers of the LGN were disarranged, and their neurones were 30% smaller than control brains (Galaburda & Livingstone, 1993). Talcott et al. (2000) found a behaviourally consistent result by demonstrating that when varying the number of dots per unit in random-dot-kinematograms, dyslexic reader's performance declined at higher densities suggesting that their receptive fields were effectively smaller (i.e., magnocellular neurons were under sampling the dots spatially).

There has been a history of attempts to classify reading disorders into different subtypes considering the complexity of reading (see Mitterer, 1982; Fletcher & Morris, 1986). Researchers have attempted to create explicit theoretical models of the reading system to account for these subtypes and make predictions about the particular patterns of reading that may be expected in specific populations (Olson et al., 1985; Coltheart et al., 1993; Plaut et al., 1996). First described in the 1970's, the dual-route model of reading aloud suggest two separate paths or routes involves in reading allowed: a lexical procedure which uses whole-word representations and involves accessing a mental lexicon of previously seen written words and a sub-lexical procedure that uses transitional rules for grapheme-to-phoneme conversion (Coltheart, 1978; Coltheart et al., 1993). While both routes rely on written inputs for activation, they vary in the types of input that can be read correctly. The lexical route will process familiar words in a skilled reader, but not recognise unfamiliar non-words (e.g., flit), while readers processing via the sub-lexical route will be able to "sound out" written non-words and words that act in accordance with typical grapheme–phoneme correspondences (e.g., market) but will struggle to read irregular words that do not follow typical correspondence rules (e.g., yacht). Castles and Coltheart (1993) tested phonological processing, lexical access and word knowledge/recognition in 53 poor readers based on their ability to read aloud sets of irregular words and nonwords. The results showed eight subjects were poor at reading non-words (classified as pure developmental phonological dyslexics), and 10 subjects showed difficulties in irregular word reading (classified as surface dyslexia). A further 27 subjects performed poorly in both tasks and were not classified as "pure" cases but showed significant differences, nevertheless. These results were best explained in terms of the dual route model and support subtype profiles representing different levels of development of the lexical and sub-lexical procedures.

English language especially, has an opaque orthography (i.e., grapheme-phoneme-correspondences are inconsistent) and therefore requires a greater contribution from phonological awareness skills for reading performance (Ziegler et al., 2003). There is empirical support for LDTs as a measure of reading ability, for example, Martens and de Jon (2006) demonstrated that reaction times (RTs) in classifying word and non-words in dyslexic children was significantly slower compared to neurotypically developed children.  Katz and colleagues (2012) examined LDTs in combination with naming tasks as predictors of standardised reading measures and found that average response times on LDTs had a strong correlation with reading ability composite scores, such as the Woodcock Johnson Basic Reading Skills (Woodcock, McGrew & Mather, 2001). Differences have been found between consistent and inconsistent orthographies in reading ability, for instance, after one year of reading instruction in both typical and poor German readers (a consistent orthography), reading accuracy is close to ceiling (Wimmer, 1993). Thus, in inconsistent orthographies such as English, reading problems are distinguished by problems with reading speed as opposed to reading accuracy (Bakos et al., 2018).

## 2.2. Aims

The aim of this experiment is to determine if slow readers are affected in their object recognition abilities based on two theories: (1) the magnocellular deficit theory which claims that issues with reading result from problems in the magnocellular pathway (2) the top-down facilitation model of visual object recognition which claims that top-down facilitation triggered by magnocellular projections to the OFC is required for object recognition in high-level areas. A comparison will be made in classification times of objects defined by luminance and LSF (magnocellular-biased) and LDTs which have been used to reveal deficiencies in word recognition skills in dyslexic individuals, i.e., poorer readers should take longer to process word stimuli in the LDTs due to lack of developed phonological and orthographic analysis skills. The proposal is that poor readers (defined by slow LDT performance) will have delayed bottom-up systematic analysis based on the proposed magnocellular deficit that may halt top-down facilitation, hence leading to slower object recognition.

## 2.3. General Methods

### 2.3.1. Participants and Ethical Approval

Ninety-four (45 females, 49 males) native English-speaking participants took part in the study. Within the subjects, five individuals claimed to have an official dyslexia diagnosis. The mean age was 36.5±11.2 (mean±SD) years and within the range of 18 to 64 years. Participants reported their education levels as follows: 13 secondary-school (or equivalent), 56 bachelor's level or technical school, and 25 achieving postgraduate level degrees. All participants were recruited via Testable Minds (testable.org/minds), an online platform used to recruit participants for behavioural studies, and received payment in return for taking part in the study (only 'verified minds' were permitted to take part). Ethical approval was given by the Brunel University's Research Ethics Committee (UREC).

### 2.3.2. Equipment

The online data collection platform Testable (testable.org) was used to host the experiment.  While viewing distance could not be precisely controlled, Testable's screen calibration function was employed to ensure stimuli were displayed similarly to each participant.

### 2.3.3. Stimuli

Three tasks were used in the experiment, namely an Object Decision Task, Orthographic Lexical Decision Task (LDT) and Phonological LDT. Details of stimuli used for each task is given below.

The rational behind using LDTs to measure reading ability comes from studies that have demonstrated these stimuli as a proxy measure for dyslexic readers (Marinelli et al., 2011; Marinelli, Traficante, & Zoccolotti, 2014; Burani, Marcolini, De Luca, &

Zoccolotti, 2008; Zoccolotti et al., 2008). It has been well documented that RTs for dyslexics are typically longer than those of neurotypical individuals, hence since face-to-face testing was restricted during the pandemic conclusions were drawn from slow readers defined using the lexical decision RTs and compared to the DD population. Additionally, dyslexic participants were identified in the slow reading groups throughout the experimental chapters in which all were included in the slow reading groups for larger effect sizes. Most research regarding speed in lexical decision making in DD include Italian dyslexics as they have transparent orthography, i.e., Italian dyslexic children "can read" but are slow at reading compared with their neurotypical controls. The participants in the experimental chapters are adults and hence were able to read, however, their RTs were longer than those of neurotypical controls, similar to that displayed in Italian dyslexics. Table 2.1 compares RTs for non-pseudohomophones (which were used for comparison in all chapters) in chapter 2, to mean decision times (in milliseconds) tested in lexical decision studies. However, it is important to consider that most studies in literature have been carried out in children and various LDT stimuli have been used, hence a variation in results may be obtained in adult dyslexics.

**Table 2.1.** Mean RTs (ms) of pseudowords for children with dyslexia and neurotypical controls in reading studies

| **Reference and conditions** | **Children with dyslexia** | **Typically developing children** |
|---|---|---|
| Marinelli et al. (2011)<br>*23 dyslexics and 42 controls; 4th grade*<br>Pseudowords | 2,876 | 562 |
| Marinelli, Traficante, & Zoccolotti (2014)<br>*17 dyslexics and 24 controls; 4th grade*<br>4-letter pseudowords | 2,086 – 2,789 | 581 – 705 |
| Burani, Marcolini, De Luca, & Zoccolotti (2008)<br>*17 dyslexics and 34 controls; 6th grade*<br>Simple pseudowords | 1,739 | 836 |

| | | |
|---|---|---|
| Zoccolotti et al. (2008)<br>*26 dyslexics and 81 controls; 6-7-8th grade*<br>4-letter psuedowords | 1,172 | 676 |
| | **Slow readers** | **Fast readers** |
| Object recognition (chapter 2)<br>*24 slow readers and 24 fast readers; educated to secondary school minimum*<br>4-letter pseudoword (non-pseudohomophones) | 2,091 | 558 |

#### 2.3.3.1 Object Decision Task

A set of 60 object and non-object stimuli were selected (30 of each) from Jennings and Martinovic (2014) (examples are depicted in figure 2.2). These stimuli are composed of Gabor patches, (see Jennings and Martinovic (2014) for full details on the method used to create and validate them). In brief, the object images are nameable (e.g., bike, tree, scissors), while the non-objects retain similar properties to objects, e.g., a closed structure, but are not recognisable as real objects and hence are not nameable. Low-level properties between objects and non-objects, e.g., mean number of Gabor patches, size, aspect ratio and complexity are equal. The Gabor patches were defined by luminance and are of relatively low spatial frequency (given typical screen-to-eye viewing distances ~1.5 cpd), hence are largely magnocellular biasing. The objects are on average ~300 (width) x 250 (height) pixels, the non-objects were created to match this size and aspect ratio on average. Based on an average viewing distance and monitor size/resolution the Gabor patches on screen were ~4 cycles per degree, with a contrast of ~25%.

The gist of this employed stimulus is that line versions of an object composed of LSF components is rapidly projected from early visual areas directly to the prefrontal cortex, via the dorsal magnocellular pathway. This coarse representation will activate predictions about the most likely version of the input image in object recognition regions within the temporal cortex. Any abnormalities in the magnocellular pathways proposed in impaired readers will be evident here as this will slow down bottom-up systematic analysis and hence object recognition.

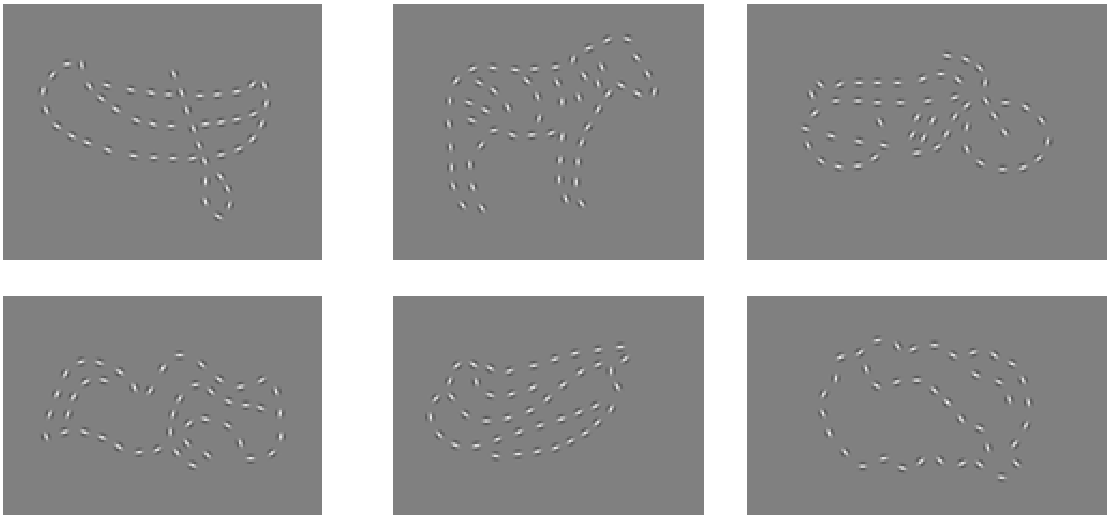

***Figure 2.2.*** *Top row: examples of object stimuli.*
*Bottom row: examples of non-object stimuli.*

#### 2.3.3.2. Orthographic LDT

Overall, 58 high-frequency (HF) and low-frequency (LF) words were retrieved from Plaut et al. (1996) and 58 high- and low-frequency non-words (i.e., nonwords derived from either real high- or low-frequency words, such as lare, foth and deak (HF non-words) and nowl, boad and fush (LF non-words)) were retrieved from Dobbs, Friedman and Lloyd (1985) (the stimulus sets can be found in the Appendix). Hence, the stimuli set consisted of four conditions, each containing 24 items: HF words, LF words, HF non-words and LF non-words. HF words occur in the range of 66 to 591 times per million words of text, with a median of 216 (Dobbs, Friedman & Lloyd, 1985). LF words are those not commonly used and ranged from <1 to 7 per million, with a median of 2. These were altered to create LF non-words (Dobbs, Friedman & Lloyd, 1985).

The rationale behind employing stimuli with frequency differences comes from studies that show variations in word processing between dyslexic and control children, specifically, differences in brain responses to LF words (lower evoked power amplitudes and a higher spectral frequency) (Paul et al., 2006). This might support the theory that poor readers are selectively impaired at reading words that require sublexical processing.

#### 2.3.3.3. Phonological LDT

Stimuli were retrieved from Seidenberg et al. (1996). In total 31 pseudohomophones (non-words that are pronounced as recognisable real words, e.g., gaim, staige and scul that sound like game, stage and skull, respectively) and 31 non-pseudohomophones (pronounceable non-words, e.g., waim, shaige and baije) were used for the experiment.

### 2.3.4. Testing Procedure

The object classification testing block was performed followed by the orthographic and phonological LDT blocks. Each block followed a 2-alternative forced choice design (2-afc), i.e., the guess rate was 50%. All stimuli were presented on a mid-grey background and in a random order to each participant.
For the object task each trial consisted of the presentation of an object or non-object. The participants' task was to classify the current stimuli (2-afc: object or non-object) via a key press.
For the orthographic LDT each trial consisted of the presentation of a high- or low-frequency word or non-word. The participants' task was to classify the current stimuli (2-afc: word or non-word).
For the phonological LDT each trial consisted of the presentation of a pseudohomophone or non-pseudohomophone. The participants' task was to classify the current stimuli (2-afc: sounds like a word or does not sound like a word).

All blocks were self-paced – participants were asked to respond as quickly and accurately as possible. Once a participant submitted a trial response the next trial commenced, after a blank, mid-grey, 800 m/s inter-trial-interval (stimuli staying on screen until a decision was submitted, however for the LDTs a cut-off of 4000 m/s was employed during analysis, classifications above this limit considered errors). Participants were asked not to read the stimuli out loud throughout the LDTs.

## 2.4. Results

For all conditions mean accuracy and median classification times were calculated. All classification times were based on correct responses, accuracy throughout was high, and no speed accuracy trade-offs existed (i.e., no significant correlation between accuracy and classification time existed for any condition, all ps>.05). The analysis is presented below in two sections. First a correlational analysis is presented, utilising all participants, to illustrate the relations between object classification ability and all LDT conditions. Second, the participants are split into the fastest (*n*=24) and slowest (*n*=24) object recogniser groups (i.e., quartile 1 (Q1) vs quartile 4 (Q4)) and the LDT performance is compared.

### 2.4.1. All Participants: Correlations between Object and Lexical Decision RTs

Overall significant and positive correlations were found in participants between object classification times and reaction times for all LDT conditions (considering correct responses only). The accuracy data showed insignificant differences between all conditions; hence analysis was conducted on RTs only which is affected in inconsistent orthographies such as English speakers with dyslexia. As this study was conducted on university students, some claimed to have dyslexia which means that their dyslexia may be compensated. The stimuli that were used in the LDTs were monosyllabic words/non-words which were not difficult to read, and hence as expected accuracy was retained here (Bakos et al., 2018). Similarly, Italian children with dyslexia have been characterised by their reading speed whilst retaining accuracy (Tressoldi, Stella, & Faggella, 2001; Zoccolotti et al., 1999).

Each of these correlations is depicted in figure 2.3.

All four orthographic conditions vs. object performance were found to be significantly correlated (Figure 2.3a-d). These relationships are: objects vs. HF words: r(92)=0.76, p<.00001, objects vs. LF words: r(92)=0.69, p<.00001, objects vs. HF non-words: r(92)=.737, p<.00001, and objects vs. LF non-words, r(92)=.70, p=.00001.

The two phonological conditions vs. object performance were also found to be significantly correlated (Figure 2.3e-f). These relationships are: objects vs. pseudohomophones: r(92)=0.60, p<.00001, and objects vs. non-pseudohomophones: r(92)=0.52, p<.00001.

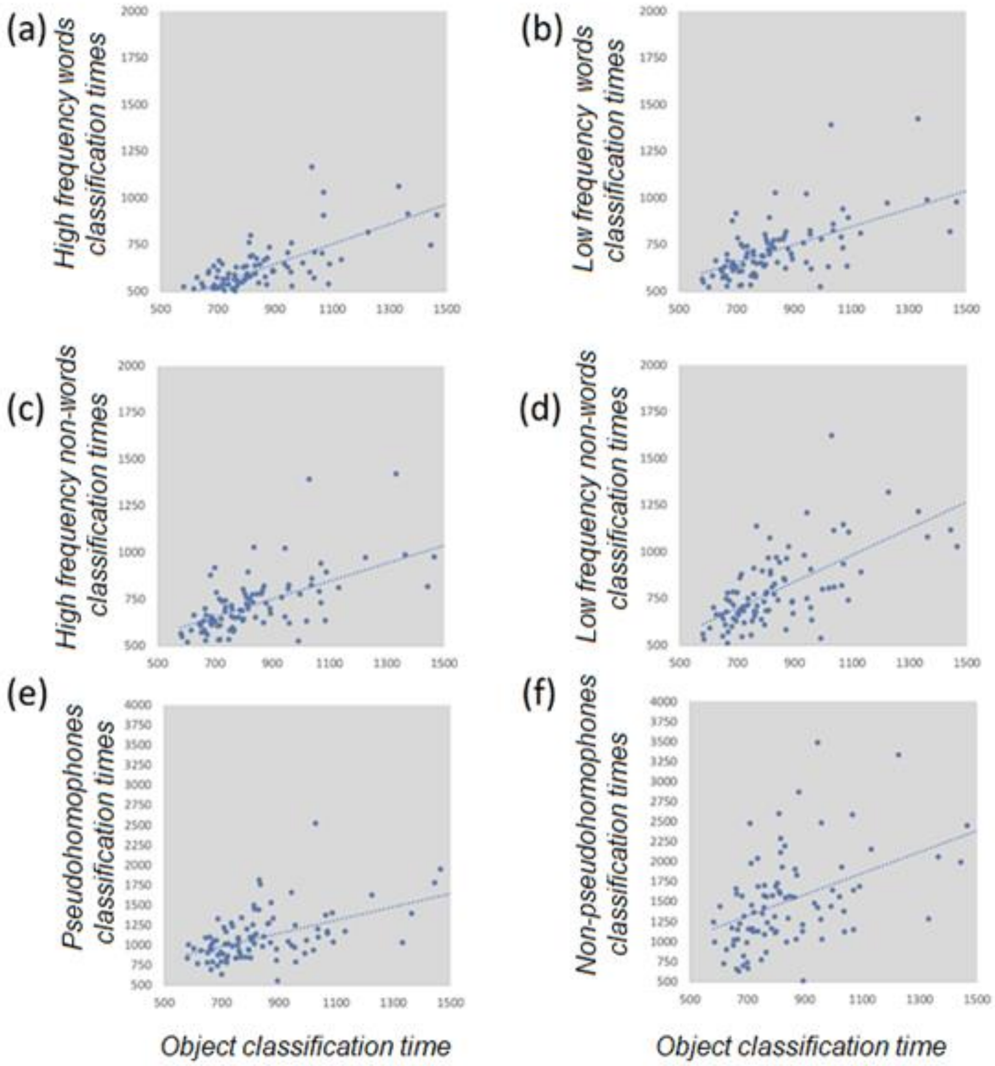

***Figure 2.3.*** *All panels show object classification times on the x-axis vs. the following classifications times for the orthographic LDT on the y-axis:* ***(a)*** *HF words,* ***(b)*** *LF words,* ***(c)*** *HF non-words, and* ***(d)*** *LF non-words – and for the phonological task:* ***(e)*** *pseudohomophones and* ***(f)*** *non-pseudohomophones (note the change of y-axis scale, and both axes start at 500 ms). All times are in ms, the dashed line represents the linear best fit.*

### 2.4.2. Fastest vs. Slowest Object Recognisers

Next, participants were split into quartiles according to their object recognition performance RTs, those in the top quartile were considered fast object recognisers (Q1), i.e., they had the fastest RTs, while those in the bottom quartile were considered as the slow object recognisers (Q4), i.e., slowest RTs. These two groups were compared based on the LDT performance. For all comparisons no differences in accuracy were found (all ps>.05). All data is summarised below.

### 2.4.3. Object Performance (RTs) vs. All Conditions (Accuracy)

As mentioned above, no differences exist in terms of accuracy for any conditions when splitting by fastest and slowest object responders, the data is summarised in figure 2.4. Slow object responders (grouped by RTs) had comparable accuracy to fast object responders in terms of object recognition, non-object recognition, word/non-word recognition (high- and low-frequency), and pseudohomophone and non-pseudohomophone recognition.

**Object task:** when comparing object and non-object accuracy (left two columns in figure 2.4) no differences were found between the fast and slow object responders (objects: t(42.8)=-0.17, p=.86, d=-0.048 and non-objects: t(42.9)=0.59, p=.56, d=.17).
**Orthographic task:** when comparing accuracy in the four orthographic conditions (four middle columns in figure 2.4) no differences were found between the fast and slow object responders (HF words: t(30.5)=-1.37, p=.18, d=-0.40, LF words: t(45.5)=-1.49, p=.14, d=-.43, HF non-words: t(41.2)=-0.69, p=.49, d=-0.20, and LF non-words: t(38.5)=-0.51, p=.62, d=-0.15).
**Phonological task:** when comparing accuracy in the two phonological conditions (right two columns in figure 2.4) no differences were found between the fast and slow object responders (pseudohomophones (sounds like a word): t(45.5)=-0.84, p=.042. d=-0.24, and non-pseudohomophones (does not sound like a word): t(46.0)=-0.52, p=.061. d=-0.15).

Multiple comparison correction has not been applied to the above p-values as without all are non-significant. Based on the magnitudes of the effect sizes the average effect is: 0.22±0.13 (mean±SD), i.e., in the small range.

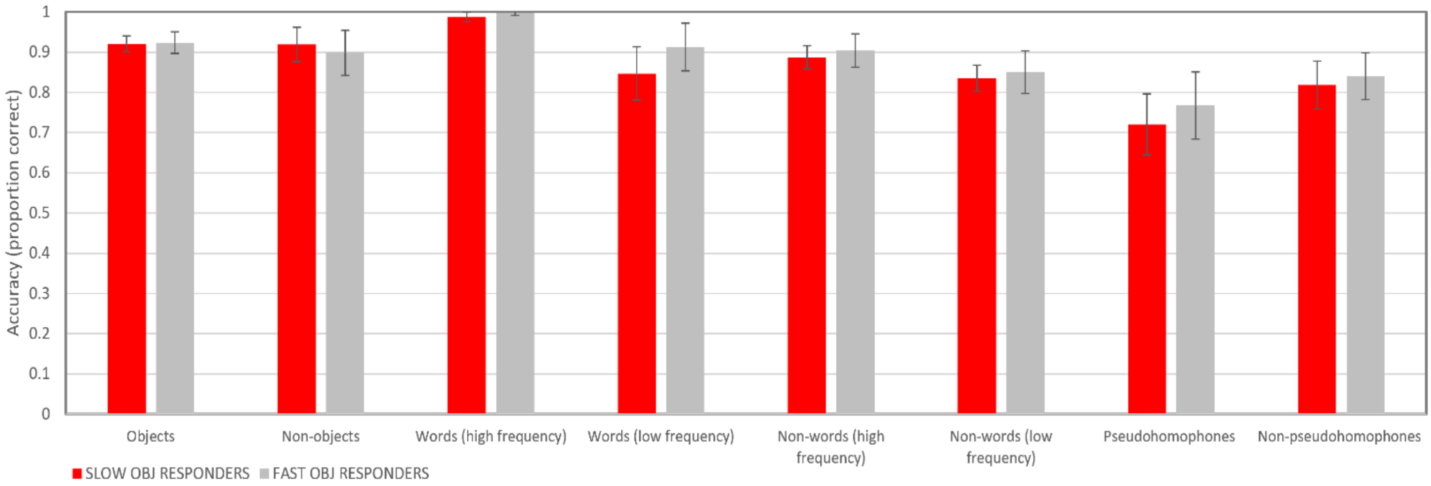

***Figure 2.4.*** *Accuracy for all conditions: based on Q1 fastest (grey bars) vs Q4 slowest (red bars) object responder groups. Error bars represent ±2SE.*

### 2.4.4. Object Performance (RTs) vs. All Conditions (RTs)

#### 2.4.4.1. Object Performance (RTs) vs. the Orthographic LDT (RTs)

An ANOVA was performed with the orthographic classification time data (Factor 1: Stimuli type (conditions: words / non-words), Factor 2: Frequency (conditions: high / low), and the between subject factor of object responder group (fast / slow). A significant main effect of Stimuli type (F(1,46)=33.5, p<.0001, $\eta_p^2$=0.42) and Frequency (F(1,46)=37.3, p<.0001, $\eta_p^2$=0.45), along with a significant interaction of Stimuli type X object responder group: F(1,46)=4.6, p=.037, $\eta_p^2$=0.091 was found. No other interactions were significant (frequency X object responder group (p=.74), frequency X stimuli type (p=.27), or Stimuli type X frequency X object responder type (p=.91)). The between subject effect was significant F(1,46)=18.6, p<.001, $\eta_p^2$=0.29.

Subsequent t-tests indicate significant differences between the fast and slow object responder groups for all conditions, with effect sizes in the large or very large ranges (Cohen, 1988; Sawilowsky, 2009). HF words: t(24.8)=4.37, p=.0002, d=1.26, LF words: t(29.9)=4.74, p<.0001, d=1.37, HF non-words: t(25.8)=4.92, p<.0001, d=1.42, and LF non-words: t(25.8)=3.15, p=.004, d=0.91. These differences are illustrated in figure 2.5.

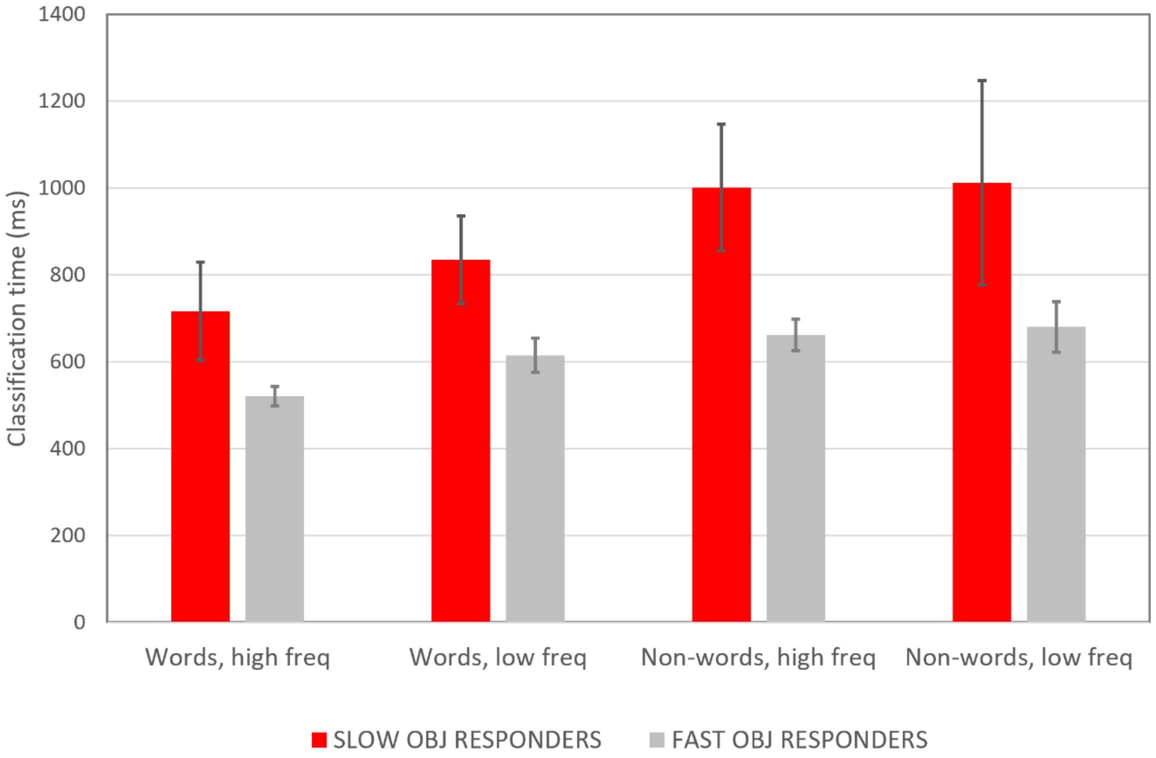

***Figure 2.5.*** *Classification times (in ms), for the orthographic conditions in terms of the Q4 slow (red) and Q1 fast (grey) object responder groups. Error bars represent ±2SE.*

### 2.4.4.2. Object Performance (RTs) vs. the Phonological LDT (RTs)

A second ANOVA was performed with the phonological classification RTs. Factor: Stimuli type (pseudohomophones / non-pseudohomophones) along with the between subject factor of fast / slow object responder. The main effect of Stimuli (F(1,46)=31.3, p<.0001, $\eta_p^2$=0.41), the interaction (F(1,46)=10.1, p=.0026, $\eta_p^2$=0.18) and the between subject effects (F(1,46)=25.8, p<.0001 $\eta_p^2$=0.36) were all significant.

Subsequent t-tests indicate significant differences between the fast and slow object responder groups for both pseudohomophones and non-pseudohomophones, with effect sizes again in the large or very large ranges.

Pseudohomophones*:* t(27.8)=-4.37, p=.0003, d=1.18 and non-pseudohomophones: t(33.7)=-4.85, p<.0001, d=1.40*.* These differences are illustrated in figure 2.6.

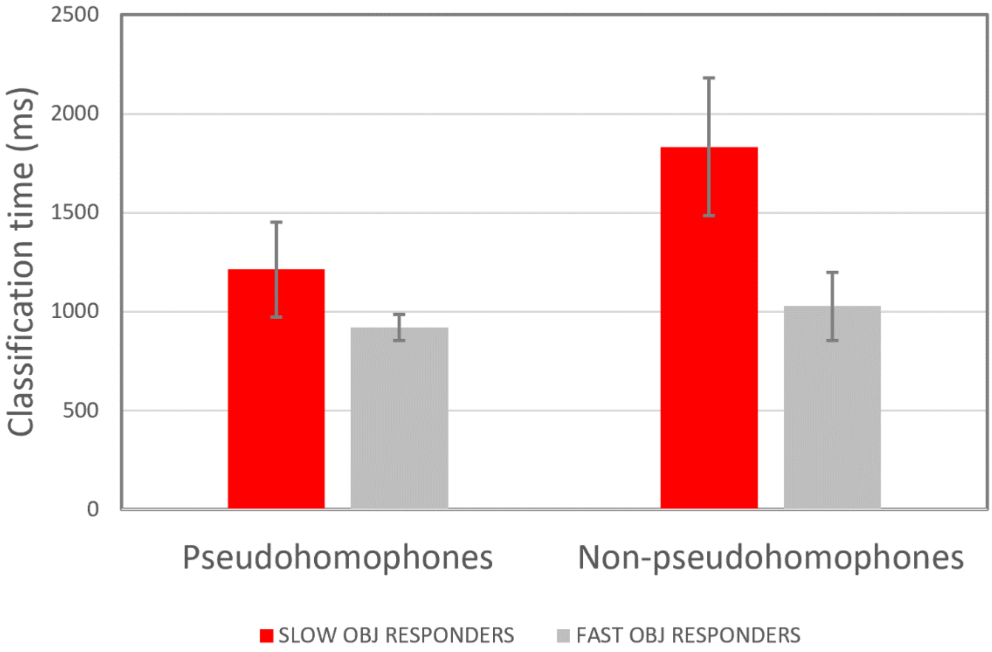

***Figure 2.6.*** *Performances, in terms of classification time (in ms), for the phonological conditions split by Q4 the slow (red) and Q1 the fast (grey) object responder groups. Error bars represent ±2SE.*

Overall, participants that had slower object recognition abilities also had slower phonological and orthographic analysis skills, while those with fast performance in recognition displayed faster orthographic and phonological analysis skills. A greater effect was seen when comparing phonological performance between the object responder groups.

*Note:* The following chapter contains a wide range of reading conditions (i.e., pseudohomophones, non-pseudohomophones, LF and HF words and non-words) hence, object recognition was compared to overall performance across the selected reading conditions. Based on the results from this current chapter, the phonological

LDT was compared to visual stimuli in chapters 2, 3, 4 and 5 as strong correlations were established in relation to visual object recognition. Slow object responders were clearly much slower at distinguishing non-pseudohomophones and pseudohomophones. This is consistent with literature which has shown poor phonological skills across dyslexics (Ramus et al., 2013; Share, 2021) and hence conclusions can be drawn in slow readers in comparison to the dyslexic population.

## 2.5. Discussion

The main findings of the study are summarised as follows:

- Object classification times correlate positively and significantly with all conditions from both LDTs (i.e., high- and low-frequency words, high- and low-frequency non-words, pseudohomophones and non-pseudohomophones). That is, slow object recognisers were worse at analysing all stimulus types compared to fast recognisers, albeit object or nonobject; high- or low-frequency words or nonwords, pseudohomophones and non-pseudohomophones.
- For every condition (objects vs non-objects and all conditions within both LDTs) no difference in accuracy existed between the fast and slow object recogniser groups. That is, the slow group was equally accurate to the fast group on all the stimulus types, albeit object or nonobject; high- or low-frequency words or nonword, pseudohomophones and non-pseudohomophones.

The fast projection of the magnocellular pathway linking early visual and object recognition with the OFC is essential for top-down facilitation of object recognition. This subsequently leads to activation of predictions for the most likely interpretation of the input image higher up in the visual ventral stream. The top-down “initial guess” combined with bottom-up processing facilitates recognition by significantly restricting the number of object representations that should be considered. Here we challenge the traditional view of the hierarchical feed-forward structure of the ventral visual stream and suggest top-down information is triggered earlier with magnocellular projections to OFC and subsequent feedback of predictions from the OFC to the IT based on the proposal that deficits in the magnocellular pathway are present in impaired readers (i.e., problems with the magnocellular system will impair top-down processing).

For the current experiment, line version of objects were manipulated using a custom written MatLab code to favour magnocellular processing in participants. By exploiting the high contrast sensitivity of magnocellular cells at low luminance and low spatial frequency, which parvocellular cells do not respond to, we were able to target and stimulate the magnocellular system. Strong interactions between LSF images and the OFC and between the OFC and fusiform gyrus have been shown with functional imaging (this effect was not seen with HSF images) (Barr et al., 2006), hence employing LSF stimuli is the key to triggering top-down facilitation. We assessed reading performance using LDTs that were able to give us a measure of reading by assessing phonological efficiency and visual-verbal access in sublexical and lexical word processing (Bakos et al., 2018). Participants were native English speakers (a phonologically inconsistent orthography characterized by deficits in reading speed rather than accuracy) and hence we were able to conduct analysis using LDT RTs (Bakos et al., 2018). Accuracy was retained across all conditions which confirms no speed accuracy trade-offs, i.e., participants were not sacrificing speed for accuracy. This was expected as monosyllabic words/non-words were used, in which English readers, including dyslexics, are able to read efficiently at first glance (Weekes, 1997). In the UK, a great effort is made in phonic decoding skills for impaired readers, thus everyone who took part in our study had mastered the letter-sound correspondences of English sufficiently, including reading non-words (Rose, 2009). This is not the same for reading speed, where poor readers remain substantially slower than controls which is a problem in those with reading disorders in higher education (Kwok & Elis, 2014).

The primary goal of this study was to test if object recognition varies in slow vs fast readers (defined by orthographic and phonological ability) based on two proposed theories: (1) that slow/poor reading is the result of problems in the magnocellular pathway (the magnocellular deficit theory) (2) that fast magnocellular projections to the OFC triggers top-down facilitation of object recognition (the top-down facilitation model). The current study provides support for impaired magnocellular processing in slow readers, and for the top-down facilitation model of object recognition, i.e., magnocellular input is necessary for high-level object recognition. Stimuli was employed to bias visual processing towards the magnocellular processing pathway – which led to correlations between the magnocellular-biased object stimuli and reading (based on both LDTs). According to the top-down facilitation model (Barr, 2003), LSF images are transferred via rapid activation of the magnocellular pathway. The current results suggest a deficit in the magnocellular pathway in slow readers who took longer to recognise magnocellular-biased object stimuli which can lead to delayed activation of the OFC, and consequently weaker performance in object recognition. This delayed activation is due to reduced magnocellular-driven top-down facilitation meaning the OFC is less efficient in triggering top-down facilitation, resulting in delayed bottom-up high-level object recognition regions in the fusiform cortex and ultimately slower object recognition. The opposite effect was seen for fast readers who recognised magnocellular-biased object stimuli much quicker than slower readers, leading to fast activation of the OFC and a speed advantage for object recognition. In other words, LSF information processed by magnocellular neurons is essential for the facilitation of recognition as it is required for fast triggering of the associated top-down processes.

Overall, the data presented here provides strong support for slow/poor reading skills co-existing with deficits in other non-reading-based tasks due to a potential magnocellular abnormality connecting early visual and object recognition regions with the OFC. When magnocellular projections are engaged early, speed of object recognition is improved as seen with positive signal changes in the OFC in a study by Kveraga, Ghuman and Bar, 2007. The OFC is generally known to participate in emotional development, reward, and decision-making, but it has also shown to have a more specific role than just value-based decision making and has been hypothesised to have major involvement in the analysis of visual information and memory. The OFC receives projections from multiple sensory modalities, with the lateral orbitofrontal regions specifically showing a greater role in analysing visual stimuli, including faces and expressions along with visually complex objects (Nomura et al., 2004; Strauss et al., 2005) leaving scope for further research in other visual non-object stimuli. Moreover, the OFC has strong feedback connections to the ventral temporal cortex and neuroscientific evidence has shown LSF projection extracted from the early ventral steam is swiftly projected to various regions in the prefrontal cortex via the dorsal magnocellular pathway (Barr, 2003). Studies have provided further evidence for the OFC projecting to object recognition areas in the ventral temporal cortex as impairment in object recognition are evident when connections between ventrotemporal regions and the prefrontal cortex are broken (Kveraga, Ghuman and Bar, 2007). Kveraga and colleagues demonstrated this when they used parvocellular-biasing stimuli that prevented magnocellular-processing. This led to impaired object recognition, providing further support for the importance of the magnocellular pathway in object recognition. It should also be noted that object recognition may also occur without magnocellular-driven top-down facilitation, but this mechanism is required in order for individuals to take advantage of top-down guidance which can lead to faster object recognition.

The dorsal visual stream was previously mentioned which receives strong magnocellular input that may support these anatomical connections. The dorsal stream also projects to the parietal cortex which connects to the frontal eye fields in the prefrontal OFC (Cavada and Goldman-Rakic, 1989; Fang et al., 2005). However, the OFC also has a reciprocal relationship with nuclei in the amygdala which also receive input from the temporal visual association cortex (Kravitz et al., 2013. The amygdala sends strong connections to neurons in the thalamic magnocellular mediodorsal nucleus (Timbie et al., 2020). Amygdala lesions have been shown to lead to impaired emotional face processing possibly from subcortical projections from the magnocellular pathway (Dolan and Vuilleumier, 2003; Vuilleumier et al., 2002). Strong BOLD signals have been found in magnocellular-biased stimuli compared to parvocellular-biased stimuli (Kveraga, Ghuman and Bar, 2007), which provides some speculation for this regions involvement in facilitating emotional facial recognition, but future studies are required to investigate how direct this relationship is.

Considering the entire sample, significant positive correlations were found between object classification times and all conditions in the LDTs (high- and low-frequency words and non-words, pseudohomophones and non-pseudohomophones). These effects were largest when comparing phonological lexical decision task classification times between the fast and slow object recogniser groups. This is perhaps expected as a phonological deficit has been established in the majority of poor and dyslexic readers. It is important to note that only five participants reported an official dyslexia diagnosis, and thus caution should be taken when generalising these results to individuals with DD. However, it is reasonable to assume that the effects seen in this experiment will be similar, and potentially greater, in those that present with reading difficulties such as DD based on their lack of developed phonological and orthographic analysis skills. The current study would benefit from being replicated on a large-scale population of dyslexic individuals, along with neuroimaging studies to compare the neural pathways involved in triggering top-down and bottom-up information processing in object recognition with typical readers.

The current results are consistent with previous research on impaired object recognition in poor readers and provide additional evidence that reading ability is directly related to cortical based visual ability. The presented data may be used to guide future imaging studies concerned with isolating relevant brain regions and differences in neural correlates for words and objects in poor compared to typical readers. Ultimately, this can lead to remediation programmes that assist with “strengthening” the magnocellular pathway (Gori et al., 2016; Lawton, 2016), in turn improving visual word recognition and other non-reading visual problems.

## 2.6. Conclusion

To conclude, the current results demonstrate differences in visual object recognition in slow versus fast readers as magnocellular projections to the OFC, which play a critical role in top-down facilitation of object recognition, is impaired in those with reading difficulties. LSF object stimuli that biased towards the magnocellular pathway took longer to identify in slow readers. This was expected since reduced magnocellular input to the OFC affects speed in object recognition. The current study establishes that the link between object recognition and reading is behaviourally measurable, based on the hypothesis that both processes rely on magnocellular input and a deficit in magnocellular functioning has been proposed to explain a host of non-reading deficits in poor readers. It was established that object recognition ability and poor/slow reading skills are co-morbid, in terms of both orthographic and phonological ability – indicators of general reading skill. The results provide further support for a magnocellular deficit in poor readers and top-down processing of object recognition and suggests that poor reading ability could be a symptom of a more generalised higher-level cognitive deficit, which cannot be fully explained by the phonological theory alone. Future imaging studies focusing on the ventral visual stream and its connections to low-level regions are required to add neuroscientific understanding to these results.

# Chapter 3: Reading and Visual Search: the Role of the Magnocellular Pathway

## 3.0. Chapter Overview

The previous chapter provided evidence for atypical object recognition in slow versus fast readers using object stimuli that preferentially biased the magnocellular pathway – diminished LSF magnocellular projections to the OFC impaired speed of object recognition in high-level regions. Object recognition and reading are therefore behaviourally measurable. Thus, this chapter aims to provide further evidence for a low-level magnocellular impairment by employing a high-level visual search task that entails the use of the frontoparietal attention network. The magnocellular pathway originates in ganglion cells of the retina, passes through magnocellular layers of the LGN and terminates at the parietal cortices (Gori et al., 2014a). Magnocellular input to the parietal cortex is therefore required for tasks that involve active scanning of a visual environment for a particular target. This chapter begins by introducing how the parietal cortex can be affected by problems with the magnocellular system and provides evidence for attentional processing deficits in dyslexic readers. The behavioural study in this chapter includes search stimuli that bias both the magnocellular and parvocellular pathways. The findings will be discussed in comparison to current research and how this can lead to therapeutic interventions to overcome reading difficulties.

## 3.1. Introduction

As previously discussed, there is increasing recognition that dyslexia is a heterogenous disorder that is associated with perceptual and cognitive weaknesses over the well-known modular deficit in phonology (Lovegrove, 1993; Eden et al., 1996; Stein, 2019). The magnocellular, parvocellular and koniocellular pathways constitute the three major parallel channels that transmit visual information from the retina to the striate cortex, i.e., V1, via the LGN (Solomon, 2021). The majority of previous studies have focused on the magnocellular and parvocellular pathways due to their opposing projections beyond the striate cortex; the magnocellular pathway is tuned to low spatial frequency, lower contrasts, and movement and is not sensitive to chromatic information, whilst parvocellular input in the ventral steam is sensitive to colour, high spatial frequencies, and low temporal frequencies (Merigan & Maunsell, 1993; Logothetis & Sheinberg, 1996). Multiple studies have confirmed reduced sensitivity to stimuli that bias the magnocellular pathway in dyslexic individuals relative to neurotypical readers (e.g., Conlon, Sanders, & Wright, 2009; Cornelissen et al., 1995; Demb et al., 1998; Slaghuis & Ryan, 2006; Wilmer et al., 2004; Wright & Conlon, 2009). However, a conclusive theory linking this physiological impairment to higher level cognition and reading is still pending. One theory that remains plausible has provided evidence for the magnocellular pathway projecting to the dorsal visual stream, which sequentially projects to the posterior parietal cortex involved in visuospatial attention (Vidyasagar & Pammer, 2010; Facoetti, 2012; Facoetti, Franceschini & Gori, 2019). Hence, the link between weakened magnocellular inputs to the parietal cortex suggests that optimal spatial visual attention performance may also be affected.

The role of visuo-attentional skills in reading acquisition has increased in popularity, with approximately 40% of children with reading difficulties displaying problems with visual attention (Franceschini et al., 2022). Specifically, orthographic processing of letter strings and grapheme parsing responsible for the conversion of a letter string into a grapheme, and subsequent phoneme blending (grapheme-to-phoneme mapping) involves visuo-attentional mechanisms (Franceschini et al., 2012, 2022). The fronto-parietal network has been shown to play a role in orthographic development and hence letter identification (Taran et al., 2022). Attentional processes are required to select relevant information and for the guidance of sensory processing, memory learning and perception (Facoetti, Franceschini & Gori, 2019). The concept of a magnocellular dysfunction to the fronto-parietal region in poor readers allows for the development of more practical methods for alleviating the symptoms of dyslexia, for example, through intensive spatial attention training before one begins to read. Evidence for weakness in visual attention in dyslexic readers comes from a variety of sources, including spatial cueing (Facoetti et al., 2006; Sireteanu et al., 2005), significantly prolonged attentional dwell times (Buchholz & Davies, 2007; Visser, Boden, & Giaschi, 2004), difficulties maintaining and focusing attention (Facoetti et al., 2003a; Facoetti, Paganoni, & Lurosso, 2000) and inhibiting irrelevant information from the periphery (Grabowska et al., 2004; Facoetti et al., 2000).

The visuospatial abilities of a group of impaired reading children compared to typical readers were evaluated in five-year follow-up study by Eden, Stein and Wood (1991). They classified participants as competent or poor readers based on the Woodcock Johnson standardised reading test (Woodcock, McGrew & Mather, 2001) and found that visual tasks which require children to localise and orientate small targets, predominantly on the left-hand side, were effective at predicting reading ability. Later, they assessed dyslexic children and poor readers by presenting them with a Clock Drawing Test (CDT) (Critchley, 1953) and found that these individuals tend to draw clocks with left-sided distortion more than competent readers (Eden, Wood, & Stein, 2003). This result is consistent with patients that have acquired right-hemisphere lesions (Friedman, 1991), and suggests that spatial construct deficits present in children with dyslexia may be attributed to right hemisphere dysfunction which can constitute phonological processing deficits in the left hemisphere. Right-hemisphere parietal dysfunction resulting from weakened magnocellular inputs provides a huge scope for further research. In a study by Facoetti et al. (2010), spatial attention and syllabic segmentation scores combined was a stronger predictor for identifying children at risk for dyslexia than either method by itself. In a cue size procedure, when a target is presented in a large cue (circle) compared to a small cue identification time is slower. Facoetti et al. (2003b) found that this effect is not present in dyslexics if there is a shorter cue-target delay (100ms), whereas the cue size effect is present when there is a longer delay of 500ms.The effect was not present at both times for typical readers, suggesting sluggish automatic focus of attention in poor readers potentially as a result of a magnocellular deficit. Using three labyrinths to measure focused visuo-spatial attention rather than typical visual search tasks that require working memory, Franceschini et al. (2022) showed clear visuo-spatial attentional deficits in poor readers compared to typical readers unrelated to motor coordination and procedural learning skills.

Visual search tasks are another popular method that have been employed to compare slow reading groups to normal-reading controls, and have yielded significant results i.e., slower visual search times for a target especially when a greater number of distractor items are present in dyslexic compared to typical readers (Buchholz & McKone, 2004; Sireteanu et al., 2008; Arguin, Joanette & Cavanaugh, 1993). Nevertheless, it remains uncertain whether visual attention difficulties are specifically due to magnocellular weakness (Wright, Conlon & Dyck, 2012; Vidyasagar & Pammer, 1999). One way of measuring the deployment of visuospatial attention is through serial search tasks. In a serial search task, multiple distractors with no distinct features are presented randomly in space around a unique target, for example, an image which contains the letter ‘L’ in a search array of inverted letter ‘T’ distractors requires each item to be evaluated in-turn, through an inefficient serial search employing focused attention. Search times are proportional to the number of distractors and the search slope gives a measure of the number of items per second that can be searched (Triesman & Gelade, 1980). When a search task is performed an individual focuses a ‘spotlight’ of attention around the search array, visual information outside of the spotlight is not processed as it is outside of the attentional window (McMains & Kastner, 2011). Prior to eye movements, an item is first identified in the visual field, and then focus on that specific item occurs from the definite binding of features from that item without interference from other objects. The mechanism which enables this restriction of space, allowing processing of stimuli within higher brain centres, has been proposed to be affected by weakened magnocellular inputs to the right posterior cortex (Vidyasagar, 1999, 2004). Studies which specifically look at magnocellular input in visual search are reviewed.

Neuroscientific evidence for magnocellular involvement in visual search comes from electrophysiological studies (Motter, 1993; Vidyasagar, 1998). In monkeys, visual discrimination of an object in a visual scene containing multiple objects triggers neuronal responses in the primary visual cortex as a result of attentional feedback (Vidyasagar, 1998). If neurons are suppressed in this region, attention has been shown to direct elsewhere. This is especially evident when multiple objects are cluttered across a scene, which leads to competition for limited attentional resources. Human psychophysical studies have also casted light on the ‘attentional spotlight’ (Treisman & Gelade, 1980; Treisman & Gormican, 1988), and evidence from fMRI studies have supported this early selection of attention, potentially due to magnocellular mediated input to the striate cortex (Brefzynski & DeYoe, 1999).

According to Vidyasagar and Pammer (1999), the magnocellular pathway plays a crucial role in visual search in a cluttered scene as this is required for focusing attention serially on objects in the visual field. Since dyslexia is associated with a magnocellular deficit, they compared children with dyslexia (*n*=9) with age-matched controls (*n*=11) in a search task. This required the identification of a target defined by form and colour (a yellow triangle surrounded by yellow circles and purples triangles). Participants were presented with four search conditions that consisted of 10, 24, 36 or 70 items. The dyslexic group performed significantly worse only in the condition with the greatest number of distractor items. They proposed that the neural mechanism involved in visual attention explains the pathophysiology of dyslexia, namely, the magnocellular pathway. However, the main limitations of this study, and with the majority of search studies, is that no test of magnocellular function was reported and a control stimulus was not used, thus definitive conclusions cannot be drawn on whether slow search times were due to a magnocellular deficit or whether this was due to a non-specific visual attention deficit, or other cognitive variables.

A later study specifically established magnocellular deficits in dyslexic participants based on performance in a coherent motion task, i.e., reduced coherent motion sensitivity was measured in the dyslexic groups compared to the age-matched control group (Iles et al., 2000). The dyslexic group had significantly slower search times than the controls overall. Specifically, the dyslexic group that did not present with a motion deficit performed significantly more slowly compared to normal readers in only one serial search task. When both dyslexic groups were compared against each other, the group with a motion detection deficit had much slower responses in most search tasks (as opposed to only one for the group without the deficit). Here, the authors were able to draw the conclusion that a magnocellular deficit affected the ability to allocate spatial attention efficiently during visual search leading to slower performance in this group. However, the study was limited by the finding that error rates were around 50 percent for a minimum of four out of eight tasks. Moreover, the two dyslexic groups had similar search times in two serial search tasks, thus, there is a possibility that poor ability to allocate visual attention in search may not purely be the result of a magnocellular deficit alone.

Studies using letters for serial search have shown that dyslexic groups are less efficient than controls when finding a target (Casco et al.,1998; Williams et al.,1987), but slower search times in these tasks cannot be interpreted as purely resulting from magnocellular impairments as alphabet characters are also processed poorly in dyslexic readers. A spatial cueing task is commonly used to study visual attention, in which a participant detects the target stimulus presented as quickly as possible after being prompted by an "exogenous" cue (the cue appears at the same location as the approaching stimulus) or an "endogenous" cue (the cue may appear as an arrow pointing to the location of the approaching stimulus) (Roach & Hogben, 2008). Roach and Hogben (2007) found that when dyslexic participants were presented with a cue to the potential target location, they had a significantly lower reaction times than controls. In contrast, no significant difference was found between the two groups when no cue was present. This indicates that the dyslexic group were less able to shift attention in response to the cue compared to the control group. Both groups took part in a coherent motion task to test magnocellular function and the dyslexic group showed poorer sensitivity than the control group. However, when presented with flicker contrast sensitivity task, which has low spatial and high temporal frequency stimuli to stimulate the magnocellular pathway, performance was similar between both groups. The authors concluded that a magnocellular processing deficit may not be the cause of poor reaction times, but a general poor ability to process in attentional areas in the parietal cortex and frontal lobe.

The substantial evidence for intervention programmes such as action videos games (AVG) has recently been documented (Facoetti et al., 2017; Franceschini et al., 2013, 2017a, 2019; Bertoni et al., 2021; Gori et al., 2013, 2014b). Franceschini et al. (2013) demonstrated that when children with dyslexia played video games for 12 hours (9 sessions, 80 minutes per day) they improved in reading speed without trading accuracy. This excluded the involvement of phonological or orthographic training and was more effective than a child's development in reading after one year of traditional reading treatments. Dyslexic children also showed improvement in attention skills indicating that improvements in attentional abilities from AVG can help direct attention during reading. The causal role of attention in reading displayed here also provides a novel, entertaining and engaging remediation programme for DD. Mapping English orthography with speech sounds can be especially challenging since English spelling is relatively inconsistent in terms of spelling matching the pronunciation of words, hence Facoetti et al. (2017) measured the extent to which AVG training would benefit English-speaking children (a deep orthography). The rapid shift of attention from visual letters to auditory speech sounds is essential for efficient reading acquisition. They found that after playing AVG only, English-speaking children had increased speed in phonological decoding and word recognition, and attentional shifting improved for visual-to-auditory and auditory-to-visual processing. Phonological short-term memory and phoneme blending deficits were also improved, emphasising the importance of strengthening the pathways involved in attentional control in poor readers. Similarly, a recent study by Bertoni et al. (2021) found that greater attentional control and phonological decoding speed was linked to high video game scores. However, the link between plasticity of the fronto-parietal and attentional control network with phonological decoding improvement was only established after efficient AVG training. Differences were not found in performance for non-alphanumeric rapid automatized naming (RAN) and word reading. This accentuates the importance of efficient training programmes for strengthening the neural pathways involved in reading acquisition. A systematic review by Peters et al. (2019) identified three types of visuo-attentional interventions. They found that each intervention benefited reading in different ways; visual perceptual training improved reading fluency and comprehension, AVG increased rate and fluency while visual-based reading acceleration programmes improved rate and accuracy. Importantly, they found evidence that indicates that these interventions can treat childhood dyslexia and improve reading skills equal to or greater than other non-visual interventions with effects lasting at least two months after intervention.

## 3.2. Aims

In aim to establish that impairments in reading dyslexic individuals experience results from problems with visual perception, specifically reduced sensitivity to the magnocellular visual dorsal stream, the theory that poor visual search in dyslexia is caused by a magnocellular deficit was investigated. As explained earlier, focusing on a target in visual search requires attention which is important for reading (Vidyasagar & Pammer 1999; Iles et al., 2000; Facoetti, 2012), and hence the pathway which leads to optimal search performance in higher level cognition may be defective in poor readers. If this is true, visual search tasks that targets form and colour may impair the access of stimuli to higher processing centres in the brain i.e., limiting the spotlight of attention to locate a target. The hypothesis for this experiment is that poor visual search performance in slow compared to fast readers is caused by specific dysfunction in the magnocellular pathway and by employing scrambled images designed to bias either the magnocellular (magno), parvocellular (parvo) or magnocellular/parvocellular (combined) pathway using colour manipulation, it is predicted that slower search times will be seen for conditions that require magnocellular input (i.e., required to allocate attention towards the search target) for the slow reading group (determined by phonological performance). In contrast, differences between reading groups are not expected in conditions which require use of the parvo pathway only.

## 3.3. General Methods

### 3.3.1. Participants and Ethical Approval

Ninety-four participants (45 females, 49 males) took part in the study. The mean age was 36.5±11.2 (mean±SD) years and within the range 18 to 64 years. Participants reported their education levels as follows: 13 secondary-school (or equivalent), 56 batchelor's level or technical school, and 25 achieving postgraduate level degrees. All participants were recruited via Testable Minds (see section 2.3.1) and received a small payment in return for taking part in the study (only 'verified minds' were permitted to take part). Ethical approval was given by the Brunel's University Research Ethics Committee (UREC).

### 3.3.2. Equipment

The online data collection platform Testable (testable.org) was used to host the experiment. While viewing distance could not be precisely controlled, Testable's screen calibration function was employed to ensure stimuli were displayed similarly to each participant.

### 3.3.3. Stimuli

#### 3.3.3.1. Phonological LDT

Similar to chapter 2 (section 2.3.3.3), phonological task stimuli were selected from Seidenberg et al. (1996). Overall, 31 common pseudohomophones (non-words that are pronounced like words, e.g., gaim, staige and paige, that sound like game, stage and page, respectively) and 31 non-pseudohomophones (pronounceable non-words, e.g., waim, shaige and baije) were selected (see appendix).

#### 3.3.3.2. Search Task

In order to create parvo- and magno-biasing stimuli chromatic and luminance defined search arrays were created based on a series of images of natural scenes selected from Olmos and Kingdom (2004). Phase-scrambling was achieved by employing the two-dimensional fast Fourier transform method outlined in Yoonessi and Kingdom (2008). The absolute phases of the R, G, and B layers of the images were scrambled, keeping relative phases intact, hence the scene structure is destroyed while chromatic information preserved as much as possible. The scrambled images then had a local “swirl” distortion applied at a random location. The amount of “rotation” within each condition the swirl contained was determined by a pilot experiment to estimate the amount required for the three conditions to produce approximately equal salience. Additionally, the size of the swirl was manipulated throughout each trial (large or small).

To produce the parvo- and magno-biasing conditions the scrambled images were decomposed into their chromatic and luminance components (layers). This was achieved by converting the images from the RGB to YUV colour space (based on the mean matrix from Boynton). The Y layer of the YUV space contains the luminance information, while the U and V layers contain the chromatic information. Hence, to create the magno-biasing stimuli the U and V layers were set to zero, and a lowpass Gaussian filter was applied, and to create the parvo-biasing stimuli the Y layer was set to its average luminance value. To allow subsequent presentation during the experiment the images were converted back, via an inverse matrix, to the RGB colour space. To create the combined (magno and parvo) stimuli, no further processing was required once the distortion was applied.

The justification for scrambling the images is that the chromatic isolating (isoluminant) images of natural scenes were found to not contain enough complexity, i.e., they are composed of large uniform regions, hence the applied distortions were not visible. As distorting a uniform area has no effect, the scrambling added complexity that could then be distorted.

The search stimuli were 576 (width) x 768 (height) pixels, after phase scrambling the magno- and magno+parvo stimuli had their contract reduced to 50%. The parvo stimuli was already low contrast, as expected due to the scene statistics of the chromatic layer, hence no further adjustment was made.

Examples of the combined (magno and parvo), and the magno- and parvo-biasing search arrays are shown in figure 3.1, the locations of the distortions are indicated by the red circles (for illustration only).

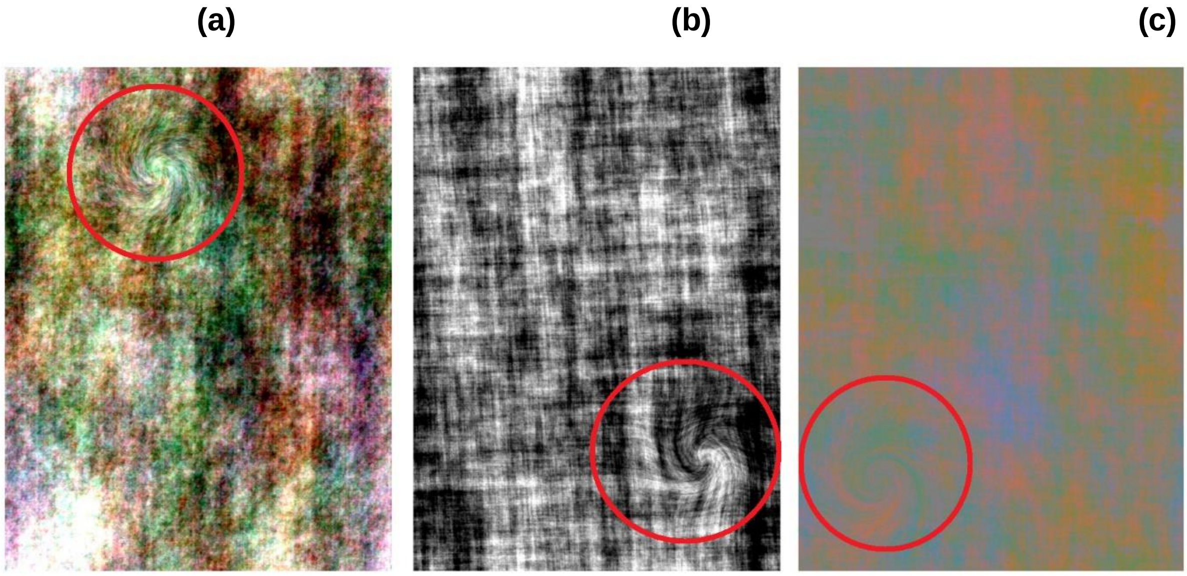

***Figure. 3.1.*** *Examples of visual search conditions for the scrambled scenes (a) magno- and parvo-biasing (b) magno-biasing and (c) parvo-biasing stimuli.*

### 3.3.4. Testing Procedure

The visual search testing block was performed followed by the lexical decision testing blocks. Each block followed a 2-alternative forced choice design (2-afc), i.e., the guess rate was 50%. All stimuli were presented on a mid-grey background and in a random order for each participant.

During the visual search task, participants were asked to search for the spatial distortion in the scrambled images for all three conditions (randomly presented). Two images appeared on screen during each trial side-by-side, one contained the distortion (the target) and the other did not contain a distortion (the distractor). The task for the participant was to report, as quickly as possible (while maintaining accuracy), which image was the target (left or right). On each trial there was a 50% chance the target image would appear on the left or right.

During the phonological decision task, similar to the chapter 2, each trial consisted of the presentation of a pseudohomophone or a non-pseudohomophone. Participants were asked to classify the stimuli (2-afc). Participants were asked not to read the stimuli out loud and to report whether the stimuli sounds like a real word or not, e.g., BRANE sounds like the real word BRAIN.

All blocks were self-paced - once a participant submitted a trial response the next trial commenced, after a blank mid-grey 500 ms inter-trial-interval (stimuli staying on screen until a decision was submitted).

### 3.4. Results

The following experiment and those that follow compares reading ability using the phonological LDT with visual stimuli based on the strong correlations observed in chapter 2, i.e., the phonological decision task provides a greater proxy measure for reading in comparison to orthographic lexical decision making. This result is expected as poor phonological skills are a common characteristic of DD.

For all blocks mean accuracy and median classification times were calculated from the raw data. All classification times were based on correct responses in each task. The analysis is based on comparing reading groups to performance in the visual search tasks. Two reading groups were defined based on slowest phonological decision reaction times (RT's) (bottom quartile (Q4 – *n*=24), slow readers), and fastest phonological decision RT's (top quartile (Q1 – *n*=24), fast readers) (see section 2.4.2).

### 3.4.1. Controlling for Age and Speed-Accuracy Trade-offs

For every comparison presented below no significant correlation between accuracy and age or classification time and age existed (all ps>.05). Also, no speed-accuracy trade-offs existed for any comparison (pseudohomophones, non-pseudohomophones, swirl identification in all conditions, figure 3.2) (again all ps>.05).

Since accuracy was retained across all groups, analysis was based on comparing overall phonological LDT RTs (Q1 and Q4) to search performance. This was motivated by the fact that children with dyslexia show very slow and effortful reading, while their accuracy is largely preserved (Tressoldi, Stella, & Faggella, 2001; Zoccolotti et al., 1999).

### 3.4.2. Phonological LDT (RTs) vs Search Performance (Accuracy)

Accuracy for visual search (swirl identification) between slow (Q4) and fast (Q1) readers (defined by phonological decision RTs) was compared for all conditions (combined parvo/magno, magno-only and parvo-only) using the Welch's t-test – no differences existed for any conditions (see figure 3.2).

**Parvocellular/magnocellular condition:** No differences were found when comparing parvo/magno (combined) visual search accuracy between the slow and fast reading groups (two left columns in figure 3.2). Small swirl: t(44.2)=-1.07, $p_{corrected}$=1 and large swirl: t(54)=1.6, $p_{corrected}$=1.

**Magnocellular condition:** No differences were found when comparing magno visual search accuracy between the slow and fast reading groups (two middle columns in figure 3.2). Small swirl: t(39.3)=-1.9, $p_{corrected}$=0.38 and large swirl: t(27)=-2.55, $p_{corrected}$=0.1.

**Parvocellular condition:** No differences were found when comparing parvo visual search accuracy between the slow and fast reading groups (two right columns in figure 3.2). Small swirl: $t(48.1)=-1.77$, $p_{corrected}=0.5$ and large swirl: $t(40.4)=-1.65$, $p_{corrected}=0.64$.

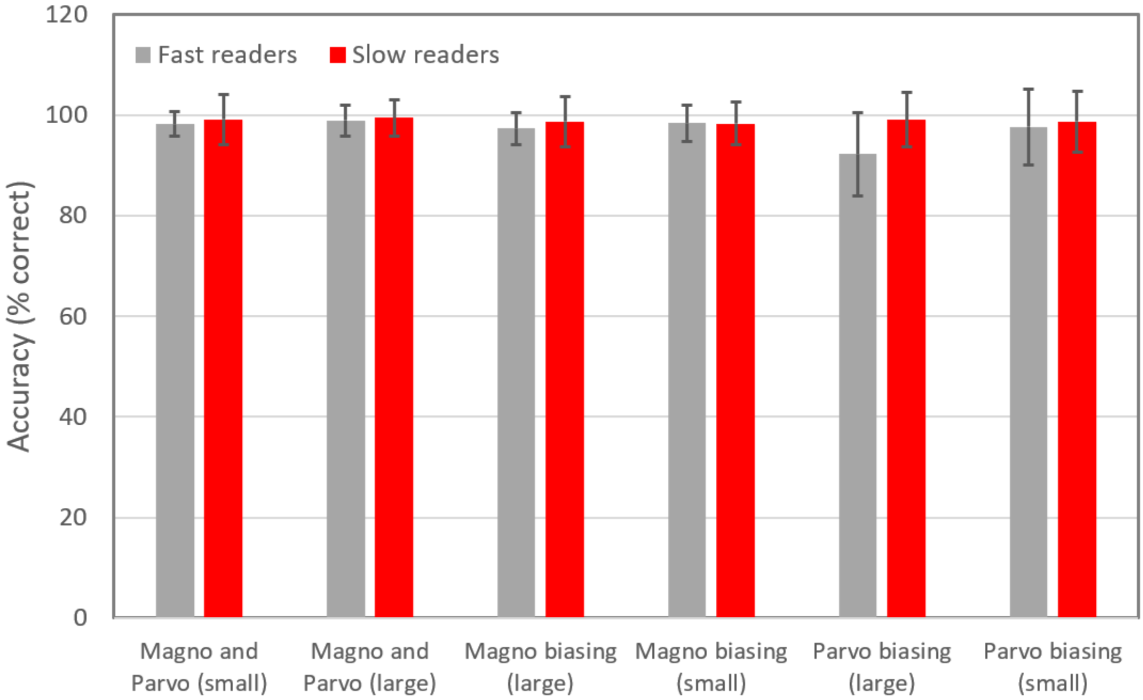

***Figure 3.2.*** *Accuracy (proportion correct) for each search condition (small and large swirl) split by fast and slow reading groups. No significant differences exist for any conditions.*

### 3.4.3. Phonological LDT (RTs) vs Search Performance (RT)

Reaction times for visual search between slow and fast readers (defined by phonological decision RTs – Q4 and Q1) was compared for all conditions using a Welch's t-test, i.e., a similar procedure as the accuracy analysis was performed. A significant difference existed for the magnocellular/parvocellular condition and the magnocellular only condition, whereas no difference was found in the parvocellular only condition. Corrected p-values are presented for each comparison (see figure 3.3).

**Parvocellular/magnocellular condition:** A significant difference was found when comparing parvo/magno (combined) visual search reaction times between the slow and fast reading groups (two left columns in figure 3.3). Small swirl: t(47)= -3.45, $p_{corrected}$=0.006, d=1.2 and large swirl: t(35.3)=-3.56, $p_{corrected}$=0.007, d=1.0.

**Magnocellular condition:** A significant difference was found when comparing magno visual search reaction times between the slow and fast reading groups (two middle columns in figure 3.3). Small swirl: t(53.5)= -2.78, $p_{corrected}$=0.042, d=1.2 and large swirl: t(39.1)=-3.27, $p_{corrected}$=0.012, d=0.92.

**Parvocellular condition:** No significant differences were found when comparing parvo visual search reaction times between the slow and fast reading groups (two right columns in figure 3.3). Small swirl: t(32.6)=-1.88, $p_{corrected}$=0.414, d=0.31 and large swirl: t(41.6)=-2.37, $p_{corrected}$=0.14, d=0.32.

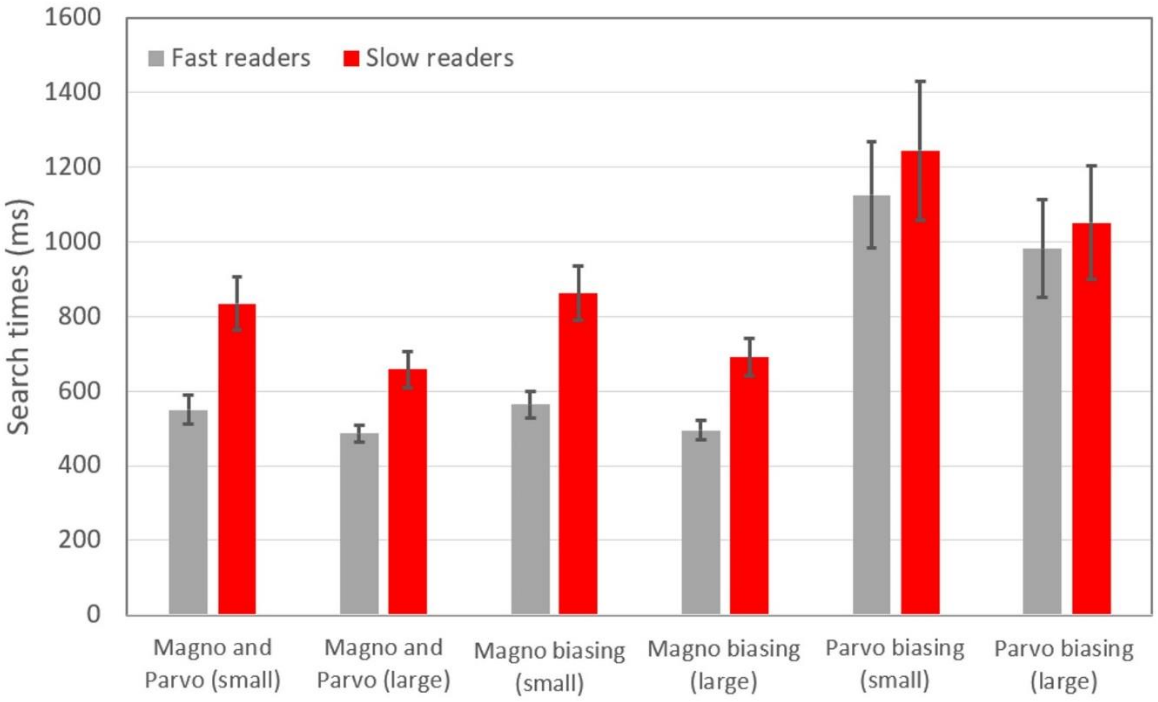

***Figure 3.3.*** *Reaction times (m/s) for each search condition (small and large swirls) split by fast and slow reading groups. Significant differences exist for all conditions that have magno-input (first four columns), while no differences exist for the parvo-only conditions (last two columns).*

## 3.5. Discussion

The main findings of the study are summarised as follows:

- Within all conditions, no differences exist between the slow and fast readers in visual search accuracy. All participants were equally accurate in identifying the swirl (small or large) in all conditions (magnocellular/parvocellular combined, magnocellular-biasing and parvocellular-biasing).
- Within the magnocellular-biasing and magnocellular/parvocellular (combined) conditions, significant differences exist in visual search reactions times. Slow readers took longer to identify the swirl (small and large) compared to fast readers.
- Within the parvocellular-biasing condition, no differences exist between the slow and fast readers in visual search reaction times. All participants were equally fast in identifying the swirl (small and large).

The aim of this experiment was to investigate if difficulties in visual search in slow/poor readers are exacerbated in conditions which require magnocellular input, ultimately providing support for the magnocellular theory of dyslexia. Magnocellular deficits have been found in a subset of dyslexic readers (Conlon et al., 2011; Talcott et al., 1998). Previous studies have proposed that visual magnocellular abnormalities are related to reading via the same attentional mechanisms required for visual search tasks, i.e., parietal cortical function is heavily associated with the magnocellular pathway (Vidyasagar & Pammer, 1999; Iles et al., 2000, Facoetti, 2012). For the current experiment, it was hypothesised that compromised visual search times in slow readers will be apparent in conditions which rely on magnocellular input - this was recorded in the current study. The slow reading group had significantly slower search times for both large and small swirls compared to fast readers in the magnocellular isolating and the magnocellular/parvocellular (combined) conditions with large effect sizes ($0.92 \leq d \leq 1.2$), indicating that slow and fast readers can be distinguished based on search times in agreement with other empirical studies (Vidyasagar & Pammer 1999; Iles et al., 2000; Casco et al.,1998; Williams et al.,1987). Previous studies have shown an overlap between groups with dyslexia compared to controls in terms of effect sizes for both visual (Ramus et al., 2003; Wright & Conlon, 2009) and auditory stimuli (Witton et al., 2002; Wright &

Conlon, 2009). The current data is consistent with the idea that a magnocellular deficit is the core characteristic of individuals with dyslexia (considered as slow readers in this current study (Tressoldi, Stella, & Faggella, 2001; Zoccolotti et al., 1999)) and is responsible for slower search times, rather than it being the result of a combination of different neural factors.

The current study compared the performance of slow versus fast readers in visual search tasks that employed stimuli composed of scrambled images of natural scenes in three different conditions: magnocellular isolating, parvocellular isolating, and a combination of both (magnocellular/parvocellular). Images were scrambled for a number of reasons, first in order to avoid fast reaction times in the chromatic (i.e., parvo) condition that would have resulted if a ‘traditional’ target was inserted. As these images have large low frequency regions the targets would have been rendered as efficient search “pop outs”. It was also not possible to add the distorting swirl pattern as the images did not contain enough structure to distort, scrambling created this ‘structure’ that the distortion could be applied to. No differences were subsequently found between reading groups in the parvocellular biasing conditions, although this group, overall, has slower search times for all participants with accuracy being equal across both groups. This result reflects the overall difficulty groups had in identifying the target when only isoluminant information is available. The likely explanation of the overall slower search times is that the lower isoluminant contrast simply reduced the relative target salience. Similar performance across both reading groups in this condition are conflicted with studies that generally show slower search times in dyslexic compared to typical readers (Sireteanu et al., 2008), perhaps highlighting a role for colour in search efficiency. Overall, comparable search times across participants for the parvo-biasing condition provides evidence for a specific deficit in the magnocellular pathway, i.e., deficits are not present in the parvocellular visual pathway. The magno/parvo RTs were similar to the magno-only condition as input from both pathways are required to increase the relative target salience, however poorer performance of slow readers in comparison to fast readers suggests that magnocellular signals dominate weak parvocellular cells as demonstrated by the increase in search times in the slow reading group.

The parietal cortex has several functions which can potentially explain deficits in visual search, such as problems with eye movements, focal attentional, crowding and failure to inhibit irrelevant stimuli (Das, Bennett & Dutton, 2011). All of these functions can be seen as contributors to impaired reading, e.g., visual crowding is another visual deficit which defies a purely phonological framework for reading impairments (Martelli et al., 2009). Spindelli et al. (2002) presented words alone or embedded inside other words to neurotypical and dyslexic readers. Vocal reaction times were slower in individuals with dyslexia, and they were more affected by the presence of surrounding stimuli compared to controls. Arrays and instructions may stimulate reading-like eye movements in these studies – it is unlikely, however, that eye-movements contributed to the deficits observed in this current experiment as the visual search tasks did not induce reading-like strategies. These types of tasks are better for determining basic visual processing differences between neurotypical and poor readers. Crowding affects have mainly been shown in studies with letters and letter strings (Martelli et al., 2009; Spindelli et al., 2002) and will not have been observed in our visual search experiment, especially since complexity (the probability of distractors being close to the target) was controlled for all images.

Generally, dyslexics have been shown to perform poorly in a range of tasks that require visual attention, i.e., the Posner task (Williams & Brannan, 1987), perceptual grouping (Williams & Bologna, 1984) and visual search (Vidyasagar & Pammer, 1999). Attention requires the inhibition of stimuli which takes away from focusing attention which dyslexics struggle to acquire (Rayner et al., 1989). This explanation broadens our hypothesis which focuses on the magnocellular theory to one which links these problems in the attentional system since magnocellular contributions dominate in the parietal cortex (Maunsell, 1992; Facoetti, 2012). Furthermore, controlling for chromatic vision by employing stimuli which targeted the parvocellular pathway affirms that other visual deficits are unlikely to account for the differences observed in our experiment as no issues in performance was present in slow readers compared to fast readers in this condition. This confirms there is relative segregation throughout the parietal cortex between the magnocellular and parvocellular pathways and both work independently of one another (Ungerleider & Mishkin, 1982; Maunsell & Merigan, 1993).

Previous studies have been criticised for not taking into consideration that differences in slow search time may be associated with simple motor reaction times (Roach & Hogben, 2007). However, in this current study slow readers showed similar performance to fast readers in the parvocellular condition, and no speed accuracy trade-offs were revealed. Therefore, the proposal that poor visual search in dyslexia occurs as a result of a weakened magnocellular stream (Iles et al., 2000; Vidyasagar, 1999, 2004; Vidyasagar & Pammer, 1999) is consistent with the current findings in the slow reading group. This data is also consistent with Iles et al. (2010), who report that dyslexic children with a known magnocellular deficit (as assessed with a coherent motion detection task) had significantly slower search performance than those with ‘normal’ coherent motion thresholds, however as mentioned this study was limited as elevated error rates suggest (some) participants may have been trading accuracy for speed.

The current data is not consistent with a study conducted by Wright et al. (2012) who aimed to link the magnocellular pathway to visual search performance. Here, it was reported that slow search times did not predict the dyslexic or controls participants (only small effect sizes were found between the groups), and when further splitting the dyslexic group into those with or without magnocellular deficit there were no differences between either group or controls in terms of search times.

The current results add new evidence in support for the magnocellular theory and provide data to guide future imaging studies concerned with the magnocellular pathway and its extension to the parietal cortex. These results can guide magnocellular-based interventions to increase speed in lexical-decision making over more generalised visual training that targets all visual pathways (Qian, 2015). This was demonstrated by Vialatte et al. (2023) who used a symbol search task for ten minutes per day on dyslexic individuals between four monthly reading sessions leading to improved visual search and enhanced reading performance. Additionally, the beneficial effects of AVG reported in both Italian and English dyslexic readers (Facoetti et al., 2017; Franceschini et al., 2013, 2017a, 2019; Bertoni et al., 2021; Gori et al., 2013, 2014b) leading to faster recognition of words, phonological decoding, and focused visuo-spatial attention has been appraised. Specifically, individuals that regularly play AVG display faster magnocellular-temporal processing leading to strengths in overturning distracting irrelevant information (Li et al., 2006). Peters et al. (2021) found that participants that had the greatest improvement in low contrast magnocellular-temporal processing after 10 x 30-minute AVG sessions also showed the most improvement in reading accuracy, emphasising the role of magnocellular-dorsal stream training for indirect improvement of reading skills by increasing visuo-attentional demands. This provides a more practical and motivational therapeutic intervention for reading disorders, compared to tedious and less engaging phonological awareness treatments. However, more research is required for the specific link between magnocellular and reading improvements following training with AVG (Gori et al., 2016).

Bertoni et al. (2023) recently demonstrated the direct effects of transcranial random noise stimulation (tRNS) on reading performance. The neuromodulatory effects of short-term bilateral stimulation of the posterior parietal cortex (PPC) were investigated by using active and sham tRNS in young adults whilst reading. They found word performance only improved after active bilateral PPC tRNS, providing direct evidence for neural connectivity between the PPC (involved in controlling visuo-spatial attention) and the ventral stream (involved in visual word recognition). The joint reduction in performance for the magnocellular biasing conditions seen in this current experiment provides evidence for a specific impairment in the magnocellular pathway involved in attentional mechanisms over a generalised visual processing disorder and suggests that problems with visual search are largely driven by magnocellular dysfunction.

### 3.6. Conclusion

The aim of this current experiment was to determine if poor visual search performance – in poorer readers - is due to impairments in the magnocellular pathway by comparing search times in slow versus fast readers determined by phonological performance. Deficits in visual tasks are unrelated to phonological processing and reflect processes in higher cortical regions. The results thus have shed further light on visual search deficits resulting from magnocellular dysfunction in poor/slow readers. Visual search times were not affected in the parvocellular pathway biasing conditions, where chromatic, i.e., isoluminant, information was presented. Magnocellular input is required for optimal search performance (Vidyasagar & Pammer, 1999), hence slow readers were affected in conditions which stimulated this pathway due to an impairment in attentional mechanisms. It is therefore suggested that poor/slow reading, such as that present in dyslexia, may be as a result of a general higher-level visual deficit projecting specifically from the magnocellular-dorsal stream. Future studies employing serial search tasks are proposed to determine if dyslexic groups, with specific magnocellular deficits, are linked to reading via the mechanisms of visual attention.

# Chapter 4: The Relationship between Emotional Face Perception and Reading

## 4.0. Chapter Overview

The previous two chapters found an association between reading with object recognition and visual search performance in magnocellular-isolating conditions. However, in contrast to visual search performance and object recognition, the majority of studies have agreed that dyslexic readers possess strength in holistic face processing, potentially due to a dissociation between holistic face processing regions (Sigurdardottir et al., 2015). In contrast, they display deficits in feature-based (local) processing of faces (i.e., similar to visual objects). Studies have also reported differences in holistic/local processing based on emotion type i.e., positive emotions are processed holistically, and negative emotions are processed analytically (Xie & Zhang, 2016). This chapter begins by reviewing face processing literature in dyslexia, and the perception of emotional faces. Psychophysical methods are employed to analyse emotional face classification in slow versus fast readers using emotional expressions that either induce holistic, or local face processing in normal and magno-biasing conditions. The findings of this experiment will be discussed in line with previous research including why faces are processed differently compared to other visually complex objects.

## 4.1. Introduction

Holistic (i.e., perceiving as a whole) and configural (i.e., the relationship between individual features) processing have been a cornerstone in face and word recognition research (Richler, Cheung & Gauthier, 2011). First-order facial configuration provides information about the basic attributes of a face and is used to distinguish faces from other visual objects, while second-order configuration refers to the geometric arrangement of the features of the face – allowing expertise in facial recognition (Tsao & Livingstone, 2008). Within the face perception literature, the term holistic processing is employed to describe the initial grouping of facial features as a whole which renders analysing individual features challenging (Taubert et al., 2001). In terms of reading, holistic processing has been shown to play a greater role in dyslexia, but as with face processing, results are mixed (for featural vs holistic word processing studies see Conway et al., 2017; Brady et al., 2021 and Sigurdardottir, Arnardottir & Halldorsdottir, 2021). Researchers have recently shown that holistic processing of faces appears to be intact in dyslexic individuals leading to the suggestion that dyslexic individuals may only be impaired specifically in part-based processing of words, faces and other visually complex objects (Brady et al., 2021). This is consistent with left-lateralized dysfunction of the fusiform gyrus and suggests a dissociation may exist with word and face processing in terms of global processing, whereas an association is present with word and face processing when feature-based processing is involved.

Sigurdardotti et al. (2015) investigated facial and object recognition in 20 dyslexic and 20 typical readers using a number of tests, the Cambridge Face Memory Test (CFMT) (Duchaine & Nakayama, 2006), the Vanderbilt Holistic Face Processing Test (VHFPT) (Richler, Floyd & Gauthier, 2014) and the Vanderbilt Expertise Test (VET) (McGugin et al., 2012). The CFMT consists of participants analysing six unfamiliar faces and recognising them in a three-alternative choice test (two distractor faces and one target face). The test was administered to assess the participants ability to match faces under ‘normal’ viewing conditions (i.e., non-inverted faces), followed by an inverted face condition, which triggers the inversion effect (when configural information can no longer be used to build a holistic representation of a face). The inversion effect was compared with the upright version under the hypothesis that recognition of faces suffers significantly in the inverted condition. This effect arises due to the processing of upright faces relying on both the processing of individual facial features and the processing of the face as a whole (holistic). Whereas inverted faces rely solely on the analysis of parts of the face (i.e., using local information such as the individual features of the face). The difference between performance when recognising upright vs inverted faces measures the extent to which a participant relies on holistic processing, i.e., if participants show significantly poorer performance when identifying inverted faces, holistic processing required for recognition of upright faces is abolished.

Dyslexics were more likely to have poorer memory for faces and were less accurate in the CFMT compared to typical readers for upright faces (Sigurdardotti et al., 2015). Although, the facial recognition abilities of dyslexics were generally lower, all participants with and without dyslexia had poorer performance for recognising inverted faces and the magnitude of the inversion effect was not significantly different between the dyslexic and typical reading groups. This indicated that holistic face processing abilities were equal between groups. However, studies have drawn conflicting conclusions on the reliability/strength of the face inversion effect as a measure of holistic processing (Richler, Floyd & Gauthier, 2014), hence the VHFPT (Richler & Gauthier, 2014) was conducted to assess the degree to which people use holistic face processing.

For the VHFPT, two different face parts were combined from two different identities (i.e., an upper half of face A and a lower half of face B) (Sigurdardottir et al., 2015). A composite face was shown, and one part of the face was outlined with a red box (target) in which participants were told to focus on. This was followed by the presentation of three composite faces, marked with a red box on the target region of each face. The target region was only correct for one of the faces and participants were tasked with choosing the correct target region of the composite face displayed previously. For congruent trials, the target part of the correct face was paired with the same distractor part as the study composite whereas the target part was combined with a different distractor part on incongruent trials. Holistic processing in this task is defined by the congruency effect where performance is impaired on incongruent trials relative to congruent trials. Comparable congruency effects in this experiment demonstrated that dyslexics employed equal amounts of holistic processing compared to typical readers.

In the VET test, Sigurdardottir and colleagues presented participants with six photographs of images belonging to a specific category (e.g., six birds or butterflies). On each trial, three images are subsequently shown containing only one of the same species from the original six objects. Participants are tasked with choosing the matching image, i.e., they are required to recognise objects within a particular category. Overall, the dyslexic group performed significantly poorer (65.3%) than typical readers (72.2%), hence the study concluded and affirmed that reading impairments may be the manifestation of a more general high-level visual deficit where part-based, or object processing occurs. Sigurdardottir et al. (2015) also included a colour control test and did not find any consistent differences between dyslexics and typical readers. This is consistent with the impairment dyslexics experience in facial and object recognition not being due to non-specific factors such as memory load.

In a later study Sigurdardottir et al. (2018) conducted two experiments requiring participants to match 3D images of faces and novel-objects. Experiment 1 showed a positive and significant correlation between face matching and reading ability in university students. In experiment 2, difficulties with face matching were shown to predict a dyslexia diagnosis, however performance in novel-object matching and noise pattern matching (stimuli designed to have similar low-level visual properties to faces) could not distinguish the dyslexic participants from typical readers. The authors speculated that reading difficulties present in dyslexia are partially caused by deficits in the high-level visual processing of words and faces for which participants require substantial experience, unlike the novel objects.

Gabay et al. (2017) reported a number of tasks finding significant effects when dyslexics matched faces over different viewpoints. Performance for upright and inverted faces was comparable between dyslexic and typical readers – again, indicating that holistic processing of faces may not be specifically impaired in dyslexic participants. Gabay and colleagues additionally evaluated the hemispheric organisation for words and faces, plus a control condition that included cars. Dyslexics had significantly lower accuracy than controls for both the face and word conditions, with a greater impairment on faces, while performance in the car control condition was equal between the groups.  Hence, this experiment provides evidence for the co-occurrence of word and face processing deficits in dyslexia but does not provide evidence for the expected atypical lateralization pattern in developmental dyslexia such as impaired object recognition in the left hemisphere (Sigurdardottir et al., 2015).

A theoretical proposal (Behrmann & Plaut, 2012; Plaut & Behrmann, 2011) suggested that specific constraints on neural and cognitive development led to the structural and functional interdependence of these domains. Words and faces therefore compete for representational space in both hemispheres in the region of extrastriate cortex adjacent to the higher-level retinotopic cortex which encodes central visual information (Levy et al., 2001), including both the visual word form area (VWFA) and fusiform face area (FFA). This view makes specific predictions for neurotypical readers, i.e., that word lateralization should precede face lateralization in development, and that the degree of face lateralization across individuals should be subject to reading skill.

Opposing the claim that the neural network for words and faces in the left and right hemisphere, respectively, are interdependent studies involving lateralized stimulus presentation have shown that the right hemisphere dictates holistic face processing only (Ventura et al., 2019). Research has shown that face perception can be holistic or part-based depending on the task in-hand and thus face analysis relies on different neural structures (Sigurdardottir et al., 2015; Collins et al., 2017). Supporting the claim that left and right face processing regions are not linked, Rossion et al. (2000) demonstrated a double dissociation between face processing in the right and left FFA, with the right side having more involvement in the analysis of the whole face, and the left side being more important for analysis of segments of the face i.e., facial features (see also Bourne, Vladeanu, & Hole, 2009). Functional magnetic resonance imaging (fMRI) studies investigating right and left hemisphere activation between individuals with dyslexia and typical readers in lexical decision tasks have shown expected hypo-activation in the left posterior areas of dyslexic individuals during reading-related tasks, such as the in left parietotemporal and occipitotemporal regions, but overactivation in areas of the right hemisphere have also been observed. Studies have consistently shown that dyslexic individuals possess higher activation when processing stimuli in specific areas of the right hemisphere, i.e., “right-brain dominant” (Vlachos, Andreou & Delliou, 2013; Waldie et al., 2013). Research has shown differences between neural pathways in dyslexic and typical readers which have led to improved use of certain right brain regions in dyslexics (Leonard & Eckert, 2008). An fMRI study has since confirmed that improved reading skills in dyslexic individuals were associated with greater brain activation patterns in the right side (Waldie et al., 2013) which was in line with right hemispheric asymmetry activation in a PET study for whole-word recognition (Gross-

Glenn et al., 1991). Right hemisphere compensation in dyslexia may therefore increase as there is an increase in phonological demand.

Although dyslexic individuals seem to depend on the same neural networks as typical readers, reduced activity in the left hemisphere and greater activation in right hemisphere regions are more robust in these individuals. In relation to face processing, an fMRI study by Waldie et al. (2013) showed an overactivation in various right hemisphere regions in dyslexic individuals including the inferior occipital gyrus (see also Puce et al., 1996). These results were exclusive to the dyslexic group. Dyslexic children display an over-reliance on right posterior regions during phonological processing tasks, perhaps to compensate for the dysfunction in the left posterior cortical areas, thus this indicates that impaired readers may rely on visuo-perceptual strategies, on the right side, for word recognition (Pugh et al., 2000). Relying on the right hemisphere, however, to compensate for reading pseudowords is not likely to result in successful reading as the processes involved in the learning of new grapheme-phoneme correspondences predominately occurs in left hemisphere regions. Studies have consistently shown left lateralised activation in the reading of pseudowords and typical reading. This does not dismiss the proposal that impaired readers show greater strength in other tasks involving hyperactive areas in the right hemisphere, such as holistic processing in the right FFA. These findings may point to an atypical activation in the right hemisphere of impaired readers. It is reasonable to assume that this enhanced activation is due to a compensatory mechanism resulting from increased attentional demand and cognitive effort during phonological processing (Grigorenko, 2001; Joseph, Nobel & Eden, 2001; Pugh et al., 2008).

The majority of facial recognition tasks in dyslexia focus on recognition of neutral faces and involves matching of faces to a sample face, i.e., comparing identities (e.g., Behrmann & Plaut, 2012; Sigurdardottir et al., 2015, 2021; Gabay et al., 2017). In previous studies there has been a limited focus on the perception of emotional facial expressions, a process that relies upon visual input (the face stimulus) and is vital to everyday social functioning, as our ability to interpret the emotional state of others, based on their face, provides us with valuable information upon which to base our future behaviour towards them for example. The limited studies that have been published, however, have shown elevated emotion-based right hemisphere activity in dyslexia, for example, emotional reactivity was measured in a task-free functional magnetic resonance imaging (tf-fMRI) study by Sturm et al. (2021). Here participants viewed emotion-based clips that induced either positive (i.e., love or amusement) or negative (i.e., sadness and disgust) emotions. Dyslexic participants were shown to have much stronger activation in the right hemisphere compared to typical readers when viewing these clips suggesting that lateralised dysfunction in the left hemisphere may facilitate functioning of certain areas in the right hemisphere as a compensatory strategy. The role of emotions in reading disorders have also been investigated in video games with findings showing that a positive emotional environment can lead to improved reading skills. A recent study by Franceschini et al. (2022) investigated visual perception, sensorimotor and reading skills in children with DD after taking part in shooting and puzzle video games. Visual perception was enhanced and reading difficulties and sensorimotor symptoms were reduced if the game was funnier and more interactive. A change in positive emotion correlated with greater contextual reading and induced biochemical activation enhanced single and pseudoword reading. The authors concluded that inducing positive emotion by play could prevent and treat reading disorders. This provides further evidence that poor readers use emotional context to compensate for reading ability.

There are conflicting findings in the literature as to whether the emotional context of face can influence holistic and analytic processing (e.g., Chen & Cheung, 2021; Curby, Johnson & Tyson, 2011; Murray 2019). Results from Curby et al. (2011) revealed that negative emotions trigger a local, as opposed to a global, visual processing style contradicting the assumption of automatic holistic processing that is resistant to outside factors. Hence, the types of emotions and their expressions, may interfere with, and influence visual processing style and potentially halt global processing. This was supported by Xie and Zhang (2016) who found greater holistic processing in a composite-face task for positive emotions as opposed to neutral facial expressions. In contrast, negative emotions decreased holistic face encoding leading to reduced accuracy for the discrimination of faces. Based on this, differences in accuracy can be predicted for emotional face classification in dyslexia/poor readers. For example, if negative emotions induce part-based processing, poor readers should perform worse than typical readers when classifying, for example, angry and sad expressions. This potential link between holistic face processing and emotion type has not been reported yet in the dyslexia literature.

As discussed in previous chapters, the magnocellular theory of dyslexia (Stein, 2018) postulates that dyslexia results from abnormalities in the magnocellular pathway that projects preferentially to dorsal visual stream (“where” system). The relationship between luminance contrast sensitivity and face discrimination points to neural mechanisms linking the magnocellular pathway to face processing regions. Perceptual studies have demonstrated this by showing face processing is more accurate when stimuli are presented under magnocellular isolating conditions compared to parvocellular isolating conditions (Bocanegra & Zeelenberg, 2009; Pourtois et al., 2005; Rassovsky et al., 2013; Vuilleumier et al., 2003; Zeev-Wolf & Rassovsky, 2020). In addition to luminance and chromatically defined stimuli, many studies have shown clear advantages for magnocellular biasing low spatial frequency (LSF) stimuli for identifying facial expressions in both young children and adults (Bocanegra & Zeelenberg, 2009; Pourtois et al., 2005), possibly as this induces holistic processing. In a series of five studies, Holmes and colleagues (2005a; 2005b) compared LSF and HSF biasing neutral and fearful expression faces and found a significant advantage for the LSF fearful faces, demonstrating the importance of the magnocellular pathways for rapid emotional processing.

Prior research has also shown that biasing the magnocellular pathway (associated with holistic processing) drives the face inversion effect (halts holistic processing) to a much larger extent relative to the parvocellular biasing stimuli. Grose-Fifer and colleagues found that children showed a larger face inversion effect for happy faces over fearful faces and showed greater immaturities in the face inversion effect for LSF images (Grose-Fifer et al., 2020). As positive emotions are associated with greater holistic processing, this may be a factor as to why the effect was stronger in this young sample. The magnocellular pathway is less ‘mature' during adolescence (Benedek et al., 2016), potentially explaining the observed effect.

## 4.2. Aims

In this current study, performance in emotional face classification will be compared between reading groups, this will be achieved via an objective face classification task and a phonological lexical decision task (LDT).  Importantly, for the first time, magnocellular-biasing faces (i.e., luminance defined, low contrast, low spatial frequency) will be employed in addition to the ‘standard’ high-contrast, full-colour, full spatial frequency face stimuli employed in previous studies. The prediction is that the slow reading group will have poorer accuracy for the full-face condition (i.e., the unmanipulated stimuli), specifically with negative emotions, and a pronounced reduction in accuracy for the magnocellular-isolating condition due to a hypothesised magnocellular deficit. In contrast, slow readers may display strength in processing positive emotions (i.e., happy) compared to fast readers in the full-face condition and will potentially not show measurable differences in the magnocellular-isolating condition. These predictions were made from data indicating that global processing is halted/reduced when emotional facial expressions are negative and heightened when expressions are positive (which poor readers prefer), and that deficits are shown in the magnocellular pathway of impaired readers, i.e., the magnocellular theory of dyslexia, which can impact global/local processing.

## 4.3. General Methods

### 4.3.1. Participants and Ethical Approval

One hundred twenty-five (71 female, 52 males and 2 others) native English-speaking participants took part in the study. The mean age was 25±8 years (mean±SD). All participants reported their education levels as finishing ‘high school’, with 90 completing university to at least bachelor’s level. Participants were recruited via Testable Minds (www.testable.com) and received payment in return for taking part in the study.  Ethical approval was granted by the Brunel University’s Research Ethics Committee prior to testing.

### 4.3.2. Equipment

The online data collection platform Testable (testable.org) was used to host the experiment.

### 4.3.3. Stimuli

#### 4.3.3.1. Phonological LDT

The phonological LDT was identical to that described in chapter 2, 31 pseudohomophones and 31 non-pseudohomophones were selected from Seidenberg et al. (1996).

#### 4.3.3.2 Emotional Face Task

Images were selected from the RADIATE face image database (Conley et al., 2018). Custom-written MatLab code was written to create the magnocellular-biasing condition stimuli.  The raw images were first converted in greyscale and then contrast was reduced by 50%. To isolate the magnocellular-pathway (LSF), images were filtered using a bank of log-Gabor filters, with four orientations (0, 45, 90, and 135°). The frequency ranges selected were based on previous studies (Vuilleumier et al., 2003; Bannerman et al., 2012) and correspond to a cut-off of ~6 cycles per face. For both conditions (unaltered and magnocellular biasing) the face stimuli were presented as 500 square pixel images. Examples are shown in figure 4.1.

***Figure 4.1.*** *Examples of facial stimuli 'full face' condition (left) and the magnocellular-isolating condition (right).*

### 4.3.4 Testing Procedure

For the emotional face classification task 168 trials were presented, in a random order per participant. These consisted of 12 identities, seven emotion-based conditions (anger, happy, sad, disgust, surprised, fear and neutral) and two image conditions (full-colour and magnocellular-isolating), i.e., for any specific condition there were 12 repetitions (with different identities on each trial). Images were on-screen for 400 ms after which participants submitted their choice of emotion by selecting from an array of on-screen buttons labelled with the types of emotion. This was followed by a blank, mid-grey, 800 ms inter-stimulus-interval before the next trail was presented. Participants were asked to make a guess if unsure as to which response to submit.

As depression and autism spectrum disorder (ASD) are known factors that can influence face and emotional face perception (Jelili et al., 2001), the PHQ-9 (Kroenke, Spitzer, Williams, 2001) and AQ-10 (Baron-Cohen et al., 2001) depression and autism multi-choice screeners were administered.

### 4.4. Results

Below, data analysis is presented in a series of sub-sections. First the LDT and hence the classification of participants as fast and slow reader groups are presented, followed by the control conditions (depression and autism). Finally, the main task is presented - first the individual conditions are compared, followed by an overall performance comparison between groups.

#### 4.4.1. Phonological LDT (Comparing Fastest to Slowest Quartiles)

Participants were grouped into the two upper and lower most quartiles (Q1 and Q4: the fast and slow reading groups, respectively). They contained *n*=30 participants each and were based on the median RTs for the pseudohomophone classification (correct responses only), i.e., they were based on the fastest vs slowest phonological performance. As expected, no differences were found between the groups for pseudohomophone and non-pseudohomophone accuracy (t(58.0)=-1.06, p=.29, d=0.27 and t(51.6)=-1.13, p=.26, d=0.29, respectively), but significant differences were found for RTs for both pseudohomophone and non-pseudohomophone classification (t(39.7)=-14.40, p<.0001, d=3.7 and t(51.5)=-6.18, p<.0001, d=1.6, respectively). This means participants were not trading speed for accuracy and hence RTs were used as a reliable measure of reading ability.

#### 4.4.2. Controlling Factors - Depression and ASD

No differences were found between the fast and slow reading groups in terms of depression (t(56.7)=1.32,p=0.19, d=0.34) or autism (t(58.0)=1.52, p=0.13, d=0.39). Hence, performance in the emotional face classification task is not affected by the following factors.

#### 4.4.3. Correlations between Face Classification and Lexical Decision RTs

First the data per emotion condition will be presented followed by the mean data (i.e., the average performance over all conditions per group).

##### 4.4.3.1. Individual Emotions (Accuracy) vs. Phonological LDT (RTs)

A Repeated measures ANOVA was performed with factor 1: emotion condition (e.g., fear, happy, etc), and factor 2: image information (full faces vs magnocellular isolating faces), this was combined with a between subject factor of reading group (fast and slow).

A significant main effect of emotion condition was found (F(6, 348)=73.27, p<.00001), however, this did not interact with the group (emotion condition x group: F(6, 348)=0.99, p=0.43). There was a significant main effect of image information (F(1, 58)=91.90, p<.00001), and a significant interaction with the group (frequency content x group: F(6, 58)=8.30, p=0.0056). A three-way interaction was also found (emotion type x frequency content x group: F(6, 348)=13.46, p<.00001).

Based on the above a series of post hoc t-test were performed. For the full face condition between the fast and slow reading groups a significant difference for the sad condition was found (t(52.4)=3.68, p=.00056, d=0.95), no other conditions were significantly different (all ps were in the range: .35≤p-value≤0.93, and all effect sizes were in the range: 0.023≤d≤0.25). For the magnocellular-isolating faces significant differences were found for surprised (t(54.4)=3.67, p=.00056, d=0.95), anger(t(50.3)=2.63, p=.011, d=0.68), fear (t(58.0)=2.48, p=.016, d=0.64) and neutral (t(38.5)=2.30, p=.026, d=0.59), corrected ps are presented. No other condition was significant (all ps were in the range: .17≤p-value≤0.88, and all effect sizes were in the range: 0.038≤d≤0.36). Figure 4.2 illustrates the data.

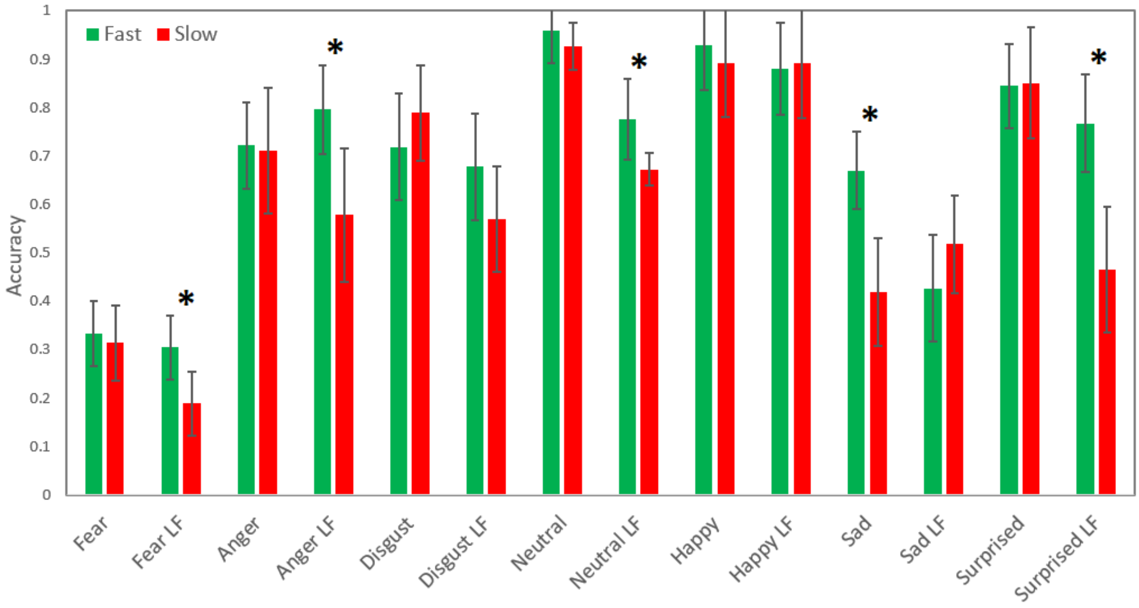

***Figure 4.2.*** *Accuracy for each emotion condition for the full-face and magnocellular-isolating (LF) conditions for both the fast (green) and slow (red) reading groups (significant conditions are indicated with an *).*

#### 4.4.3.2. Overall Performance (Accuracy) vs. Phonological LDT (RTs)

The overall performance for the entire testing block was analysed, i.e., determined by averaging over all emotion conditions. A repeated measures ANOVA with a factor of image information (full-faces vs magnocellular-isolating faces) and a between subject factor of reading group was performed. A significant main effect of frequency content was found (F(1,58)=67.7, p<.00001), along with a significant interaction of stimuli type with group (F(1,58)=15.3, p=0.0002), there was no significance between subject effect (F(1,58)=3.15, p=.08).

The post hoc t-tests indicated no significant difference between the fast and slow reading groups for the full-face condition (t(57.0)=-1.45, $p_{corrected}$=.15, d=0.37), but a difference did exist for the magnocellular-isolating face condition (t(55.8)=3.28, $p_{corrected}$=.00018, d=0.85), that is both reading groups had equal performance in emotional face classification in the full-frequency condition, but slow readers were

significantly impaired compared to typical readers in the magnocellular-isolating condition (throughout corrected ps are presented).
Additionally, comparing within the groups, the fast group differed in accuracy between the two images conditions (t(29.9)=-2.82, $p_{corrected}$=.0085, d=0.51), as did the slow reading group with a very large effect (t(29.0)=-9.27, $p_{corrected}$<.00001, d=1.69). Figure 4.3 illustrates the mean data.

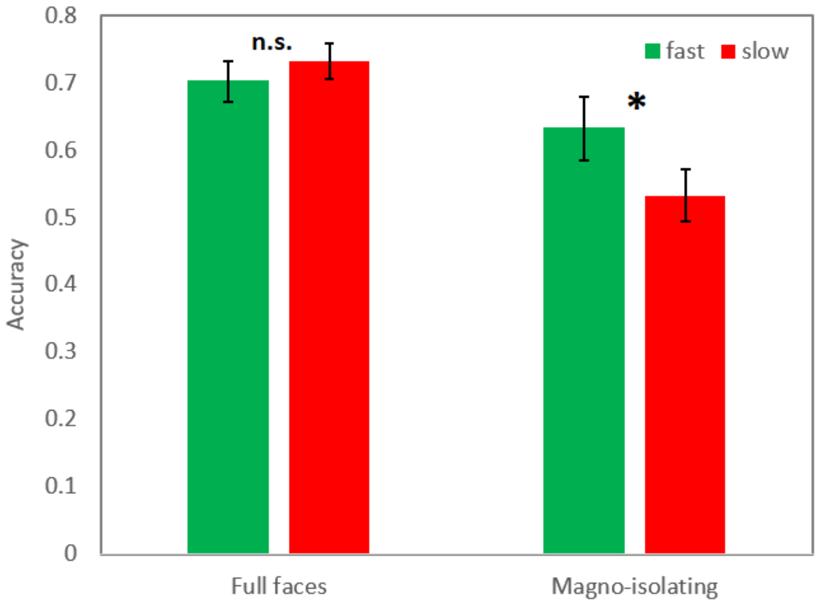

***Figure 4.3.*** *Accuracy for the full-face (n.s. = not significant) and magnocellular-isolating conditions for both the fast (green) and slow (red) reading groups.*

## 4.5. Discussion

The main findings of the experiment are:

1. Differences in accuracy were found between individual emotion conditions and slow and fast reading groups: sad (full-face condition), fear (magno-biasing), anger (magno-biasing), neutral (magno-biasing) and surprised (magno-biasing).
2. There were no significant differences in accuracy for emotional face classification overall between reading groups in the full-face condition.

3. Differences in accuracy were found between emotional face classification overall in the magnocellular-isolating condition between the slow and fast reading groups, with slow readers performing with significantly lower accuracy.
4. There was no difference in either non-clinical depression levels (as determined by the PHQ-9), or rate at which the autism screener (AQ-10) was positive (‘failed’).

The primary goal of this study was to investigate the link between emotional face classification and general reading ability, as determined by the LDT. Processing of words and faces has been linked to the ventral stream and are centered around the middle fusiform gyrus, i.e., the VWFA and FFA respectively. The rationale behind the current study was based on evidence that suggests specific dysfunction in the left fusiform gyrus of the ventral stream (Sigurdardottir et al., 2015) of dyslexic individuals which has led to impaired performance in feature-based tasks, such as configural face processing (an association between face and word processing areas in the left hemisphere), and evidence of a disassociation between left and right face processing regions which encourages holistic processing of faces in poor readers (Sigurdardottir et al., 2021).  Studies have established a link between emotional state and face-processing style (negative emotions engender greater local processing and positive emotions engender holistic processing); hence it was hypothesised that differences would exist between facial expressions of emotions depending on reading skills. Additionally, the data indicates face processing deficits are more apparent in the conditions which bias the magnocellular pathway; this is noticeable to a larger extent in poor readers compared typical readers (i.e., a magnocellular deficit is present in poor readers).

The current results indicate that emotional facial processing is comparable between poor and typical readers in normal conditions (i.e., the full-face condition), at least for the emotion conditions tested. It is possible that differences may exist in more complex emotional facial expressions (e.g., confused or embarrassed faces), however further testing is required to support potential differences across a range of different emotions. Emotional face classification under normal conditions in this current study support existing empirical studies that have found comparable performance in holistic facial classification between poor readers and controls (Brady et al., 2021; Sigurdardottir et al., 2015, 2021). However, differences are measurable when the magnocellular pathway is biased/isolated. Below the findings are compared to previous studies on visual processing in dyslexia, with the aim of providing possible explanations for the differences seen in the current study. Findings from this current study suggest normal-strength holistic processing in impaired readers when classifying emotional faces under normal conditions (i.e., when magnocellular use is not required), where holistic processing is defined as involuntary attention to a whole stimulus. It is then considered how deficits in the magnocellular pathway can override holistic processing leading to poorer performance, potentially guiding the conceptualization of visual deficits in dyslexia.

Overall, the current study indicates that facial expression classification (under normal conditions) in slow readers is equivalent to fast readers. The stimuli represent a wide range of emotional facial expressions: fear, disgust, surprise, happiness, sadness, and anger. A significant difference was shown in a number of emotions between slow and fast readers: sad (full-face), fear (magno-biasing), anger (magno-biasing), neutral (magno-biasing) and surprised (magno-biasing). Although no clear pattern between the negative emotion types were established in line with the first hypothesis (i.e., slow readers were predicted to be worse for negative emotions in both conditions), the results indicate that slow readers did not show any impairments in classifying happy faces in both the full-face and magnocellular-biasing conditions. This suggests poor readers tend to process happy emotions holistically, even in LSF magno-isolating conditions. Nonetheless, the same observation was recorded for classifying ‘disgust’, possibly as this emotion type displays similar attributes to happy emotions (i.e., scrunched nose, raised upper lip) and thus can be processed in a similar way to happy emotions.

The current results are not supportive of Curby et al. (2012) who revealed a local processing style with negative emotion types, which lead to our original hypothesis of worse performance in slow compared to fast readers in both full-face and LSF conditions since they struggle with local processing (Sigurdardottir et al., 2015). Differences in emotional face classification between slow and fast readers (excluding one emotion type, ‘sad’, which was worse for slow readers in the full-face condition) were mainly present in the magnocellular-biasing conditions, opening a new avenue for research. Comparable performance in emotional face classification between slow and fast readers overall in the full-face condition implies that facial expressions may be processed holistically, irrespective of emotion type. Although there are limited studies on emotional face classification in dyslexia, these results may provide support for Sturm et al. (2020), who found much stronger activation in the right hemisphere when viewing emotion-based clips. According to Murray (2019), ‘neutral’ faces are typically processed holistically, but expressing emotion can facilitate greater holistic processing regardless of the type of emotion expressed. Evidence from face inversion, composite and parts-whole experiments are in favour of holistic face processing over analytical processing for face identity, but much less is known about the nature of facial expression recognition. According to the results of this study, happy emotions may facilitate stronger holistic processing compared to other emotion types in slow readers, however further research on a greater number of dyslexic participants are required to confirm this.

Based on the current results, the hypothesis that negative emotion types trigger a local as opposed to holistic processing style can be rejected, instead a more probable explanation for these findings is the concept that emotions, overall, trigger holistic face classification in the right hemisphere. Supporting this theory, a study by Omigbodun and Cottrell. (2013) used composite paradigms to investigate holistic processing of facial expressions. Participants were presented with two composite faces and tasked to make a judgment on if top and bottom face halves were the same or not. The top and bottom face halves would generate the same answer in the congruent condition, whilst the incongruent condition would generate a different response. The difference in sensitivity between congruent and incongruent trials was indicative of holistic processing while sensitivity for incongruent trials was lower, hence, the conclusion was that all facial expressions were processed holistically. Tanaka et al’s. (2012) experiment also observed similar trends as it was demonstrated that facial expression processing did not show any analytic attributes.

As mentioned previously, most of the literature in face classification and dyslexia use neutral faces, thus the current results provide scope for further research on holistic emotional face classification in dyslexia. Providing evidence for strength in holistic processing in poor readers, the current results support a recent study in 2021 by Brady and colleagues who showed that holistic face and word processing abilities can foresee reading accuracy and speed in dyslexic individuals. Dyslexic and age matched typical readers took part in two perceptual tasks: the VHFPT and the Holistic Word Processing Task (HWPT). They firstly found that the overall error rare was similar between control (36.7%) and dyslexic participants (37.8%). Both tasks measured holistic processing by the congruency effect defined as “the difference in accuracy on incongruent and congruent trials”. This captured the extent to which individuals focus on neighbouring, but task irrelevant, spatial information. They showed that holistic processing of faces is easily distracted by irrelevant information, which in-turn leads to lower accuracy on the incongruent trials (higher congruency effect). Both dyslexics and typical readers showed comparable levels of holistic processing in the face recognition task, but a stronger effect was seen in the holistic word task for dyslexic participants compared to controls. In contrast, typical readers were less accurate in the reading of both words and pseudowords holistically. The current results, along with the finding from Brady et al. (2021) may have potential implications for specific reading programmes that will allow the processing of words in a more holistic style, and hence lead to improved reading performance (see also Wong et al., 2011). It is important to note that holistic processing of faces and words are processed by neurally distinct pathways, thus neuroscientific support is required to compare neural pathways during holistic face and word processing in dyslexic individuals.

The current results are also consistent with the conclusions drawn from Sigurdardottir et al. (2015) who showed that dyslexics did not show atypical holistic processing of faces. Results from their study showed that both dyslexics and typical readers were equally impaired by stimulus inversion in the CFMT and an advantage was not shown in typical readers over dyslexics for the congruent condition in the VHFPT, thus holistic processing was not affected in both tasks. Similarly, Gabay (2017) found that inverting face and cars led to comparable performance in dyslexics and typical readers, suggesting no holistic specific impairment. It is important to note the limitations when comparing the findings of the current study to those discussed above as different tasks and importantly stimuli (i.e., neutral faces) were employed to directly measure holistic processing in dyslexic and typical readers, as compared to emotion-based stimuli in the current study.

Since part-based processing of faces have been shown to be implicated in dyslexia, as opposed to holistic face processing (Sigurdardottir et al., 2015), the suggestion of a double dissociation by Rossion et al. (2000) is probable i.e., face classification relies on different neural structures depending on if they are processed locally or holistically. The current behavioural results are consistent with a double dissociation between the right and left FFA, with the right side being intact for analysis of the whole face (holistic style processing) (Bourne, Vladeanu, & Hole, 2009). Further behavioural studies are required to explore the advantages that dyslexics may display over typical readers when using a holistic processing style (Brady et al., 2021), alongside neuroimaging to see if overactivation in the right hemisphere can account for the differences seen between poor and typical readers, i.e., dyslexic participants may have right hemisphere compensation when processing face stimuli in the right hemisphere, otherwise known as “right-brain dominant” (Vlachos, Andreou & Delliou, 2013; Waldie et al., 2013; Collins et al., 2017). This perhaps compensates for the dysfunction seen in the left side of the brain involved in reading and part-based processing such as object recognition. The similar performance seen between participants in this current study, amongst others, suggests an adaptive neural compensation mechanism. Atypical activation of the right hemisphere in poor readers could mediate successful remediation in impaired readers to improve reading accuracy and speed scores.

Considering the current dataset and impaired object recognition (see chapter 2) those with reading impairments may specifically show dysfunction in part-based processing of words, faces and other visually complex objects processing in the left hemisphere. The findings provide support for the claim that impaired reading may be as a result of left-lateralized dysfunction of the fusiform gyrus, potentially leading to impaired part-based face processing as shown by Sigurdardottir and colleagues. Moreover, these finding are both in support of results from Dundas, Plaut, and Behrmann (2013) who concluded that word and face recognition do not develop independently and can be processed bilaterally (based on impaired part-based processing), and also a distinction between a shared processing mechanism for face recognition and the visual expertise of non-face stimuli, i.e., a double dissociation between the left and right hemisphere where holistic processing takes place.

In addition to measuring emotion-based face classification in unaltered full-frequency images (the full-face conditions), the current experiment contained a magnocellular biasing condition. By exploiting stimuli to the low contrast and LSF sensitivity of the magnocellular pathway (to which parvocellular cells do not respond to) the relationship between reading and the processing of faces was investigated. It was hypothesised that slow readers have atypical magnocellular processing, i.e., the magnocellular deficit theory for dyslexia (Stein, 2001), and will hence perform with lower accuracy in the magnocellular-biasing conditions (note here – the import role LSF play in the holistic processing of faces, objects, and scenes). However, since positive emotions engender greater holistic face encoding (Xie and Zhang, 2016), it was expected to see less of an effect here between the reading groups. The data in this experiment demonstrates that slow readers show a significant impairment in face classification overall (grouping all emotion types) when the magnocellular pathway is biased ('isolated') in comparison to fast readers; this was the case for most individual emotion types reported above. As expected, differences were not seen for the 'happy' face condition, indicating that this may encourage greater holistic processing in slow readers. Overall, the results indicate that reduced sensitivity in the magnocellular pathway can halt holistic processing of LSF faces leading to a significant reduction in emotional face classification performance. The advantage that typical readers have for magnocellular processing of facial expressions (Zeev-Wolf & Rassovsky, 2020) was not present. The results show that deficits shown in the magnocellular pathway overpower the adaptive neural compensation mechanism involved in holistic processing faces in the right hemisphere. In other terms, poor readers are potentially affected in tasks they are otherwise competent at, as a result of their magnocellular deficits.

It is worth mentioning the possibility that low-frequency faces that trigger fast activation of the OFC (see chapter two for the top-down facilitation model) was involved in the processing of emotional faces in this experiment. The OFC has multiple reciprocal connections with nuclei within the amygdala, specifically greater right amygdala activation has been seen with magnocellular-biased stimuli

(Ghashghaei et al., 2007; Bar et al., 2006; Kveraga et al., 2007). Since the amygdala and fusiform gyrus regions both play an important role in emotional face processing (Fairhall and Ishai, 2007), it is plausible that poor readers have a preference for holistic processing of emotional faces in the right FFA, but when in conditions which require analysis of LSF stimuli which triggers fast magnocellular projections to the OFC for top-down emotional face processing, impairments are revealed. This view implies that impaired magnocellular function can affect emotional face processing via the OFC. However, further studies are required to establish exactly what high-level regions can be triggered by top-down modulations such as neural fibre tracking with diffusion imaging of neural pathways.

Consequently, the evidence presented previously and the findings from the current study is consistent with the proposal that high-level visual dysfunction of the left fusiform gyrus proposed by Sigurdardottir and colleagues in poor readers is plausible. Dysfunction in this area may potentially implicate the parvocellular system as the fusiform gyrus forms part of the ventral stream which receives significant input from the parvocellular (as well as magnocellular) layers of the LGN (See Ciavarelli et al., 2021 for the magnocellular-parvocellular coactivation hypothesis). However, conflicting research in the contribution of these two systems in visual processing in dyslexia warrants further research (Ciavarelli et al., 2021; Contemori et al., 2019; Stein, 2001). Future studies are proposed that consider the intensity of emotions and holistic/local processing mechanisms.

### 4.6. Conclusion

The current experiment establishes a link between the classification of emotional faces and reading. Based on the hypothesis that a double dissociation exists between the right and left FFA, with the right hemisphere dominating holistic face processing, the data provides behavioural evidence consistent with the existence of a high-level abnormality arising from low-level regions. Although the slow reading group have poorer accuracy for the majority of the magnocellular-biasing conditions, there is also one full face condition for which they also have poorer accuracy for, while all other conditions show no difference, hence no clear pattern in terms of the valence of the conditions exists. However, when considering overall performance (figure. 4.3) similar accuracy exists between the slow and fast readers for the standard stimuli (i.e., the full-faces), while accuracy was reduced for both groups for the magnocelluar-biasing condition, this reduction is much greater (a very large effect vs a medium effect) for the slow reading group. This result is consistent with the magnocellular theory of dyslexia and a demonstration of it with a high-level visual task – i.e., the classification of emotional faces.

# Chapter 5: Natural Scene Recognition and Reading: Gist and Colour

## 5.0. Chapter Overview

The previous chapter highlighted the advantages that dyslexic readers display for holistic processing of emotional faces. However, the findings show that these advantages are overridden in magnocellular-biasing conditions for slow readers i.e., problems with emotional face recognition can arise due to a dysfunction in the magnocellular system. The concept of global and local processing also applies to visual scene analysis – researchers mostly agree that first the global aspect of a scene is processed in the right hemisphere, followed by local features in the left hemisphere (Olivia and Torralba's, 2001). The gist of a scene can be recognised within an 80 ms exposure, therefore at initial glance holistic processing is more important for scene gist recognition. The current chapter investigates scene gist recognition in full colour, luminance-isolating and LSF conditions in different retinal views (central, peripheral, and both). Additionally, a colour control test was employed to assess parvocellular function. Before presenting the associations between scene gist recognition and reading, an overview of scene gist analysis will be provided. The chapter will conclude with the significance of the findings in general and for intervention strategies.

## 5.1. Introduction

As discussed in previous chapters the phonological theory of dyslexia cannot account for other measurable visual deficits (e.g., elevated coherent motion detection thresholds, and atypical contrast sensitivity) observed in participants with dyslexia (Stein, 2001). The magnocellular theory attributes these deficits as being due to abnormalities in the magnocellular pathways, which processes low contrast information, low spatial frequencies, and high temporal frequencies (e.g., movement). In the current chapter a high-level natural scene recognition task (scene gist) is employed with stimuli that have been manipulated in size and shape and in terms of information content (i.e., colour, luminance, and spatial frequency content).

Studies have consistently shown that dyslexic readers struggle to processes low-spatial frequency conditions, i.e., magnocellular biasing. In contrast, the parvocellular pathway, involved in colour vision, seems to be intact. Contributions of parvocellular and magnocellular pathways are essential to dynamic conscious perception of scenes.

### 5.1.1. Scene Gist Recognition

Recognising the gist of a scene requires the ability to determine the scene category from a brief presentation (e.g., Biederman et al., 1974; Castelhano & Henderson, 2008; Fei-Fei et al., 2007; Greene & Oliva, 2009; Oliva, 2005). Scene gist recognition has been formally defined in a variety of ways, but typically refers to categorising a complex, real-word scene, at their highest-level, for example, an image of a tropical beach at sunset, depicting adults and children relaxing, playing and drinking, surrounded by palm trees and sunbeds, with some people in the sea swimming and some in sailing boats, would simply be classified as “a beach” in a typical scene gist task. It has previously been shown, and widely replicated, that participants can correctly recognise scene gist with an 80 ms exposure of the stimuli with up to an 80% accuracy (e.g., Rensink et al., 1997, 2000).

The visual system facilitates holistic and sematic perception of complex natural scenes through the rapid grouping of elements, allowing gist recognition regardless of spatial complexity. The literature presented an array of theories underlying scene gist recognition, one being the notion that a scene is the organisation of a collection of objects – meaning the visual processing of global scene perception is the highest level of complexity of the hierarchal organisation of its local modules (edges, surfaces/shapes, objects and then scene). For example, typical models for this view are the probabilistic latent semantic analysis (pLSA) model and the latent Dirichlet allocation (LDA) model which entail that scene gist perception is grouped into a local semantic level so that scene classification occurs as several objects grouped together to create the final image representation (see Bosch, Zisserman & Munoz (2006) and Fei-Fe & Perona (2005) for the pLSA and LDA models respectively). However, other studies mainly agree that segmentation of objects happen at a later stage after scene gist recognition occurs, and that the initial fixation captures the global scene.

Vailaya, Jain, and Zhang (1998) showed that global edge features are useful in determining the classification of city and landscape views. Olivia and Torralba's (2001) model of scene perception proposed a global representation termed the "spatial envelope", which refers to the low dimension of the scene, i.e., the natural, roughness and openness that represent the central spatial structure of the scene. They suggest that the spatial envelope of an image can be determined though spectral and coarse localised information and that information about an object, shape or identity is not a necessity for the categorisation of a scene but rather a holistic representation of the scene can predict its semantic category. Colour information, however, was not included in their stimuli, leading to Zhou and Zang (2010) proposing the scene gist generative model based on evidence that has indicated scene gist is the visual percept of a natural image. They proposed that scene gist components rely on prior knowledge through the learning process and that these adapted components encode the spatial layout of the image when represented in the visual cortex. The model implies that scene gist representation is a global image descriptor that extracts the whole feature of the image and adapts it to the natural image statistics.

The view that the hierarchal organisation of a visual scene allows local details to be assigned once the useful context or 'gist' of a scene has been processed, requires rapid, coarse global processing (Franceschini et al., 2021). Future reading difficulties can be determined by problems with transitioning between global-to-local visual processing i.e., local-before-global processing suggests that issues with local processing are present in poor readers. The notion that humans first perceive a rapid, coarse representation of a scene allows human to take advantage of the whole context of a scene in which that can organise local details later, providing a much clearer representation of a scene (Kimchi, 1992; Vidyasagar, 1999, 2019).

In scene gist tasks, information is acquired within a short temporal window during a single fixation, hence this visual information has a fixed retinal position. The role of information at larger retinal eccentricities may therefore play and important role in scene gist accuracy. There has been debate over the role of central and peripheral vision and the contribution of these regions in recognising the gist of a scene; central vision (the fovea and parafovea, contained within 5° radius of fixation) is important for attention and object recognition due to its high visual acuity, while the periphery has an advantage in speed and is larger in size (it exceeds the central 5° radius). In terms of words recognition, central and peripheral views were investigated in Italian-speaking dyslexic children by Lorusso et al. (2004). Using the form-resolving field (FRF), they showed a higher identification of letters in the peripheral view for dyslexic readers compared to controls. Geiger and Lettvin (1999) also demonstrated that dyslexics struggle to suppress information in their periphery (lateral masking).

Based on differences in processing speed as a function of retinal location (peripheral visual information from the retina reaches the LGN and V1 before central information) it may be the case that peripheral information is relied upon more during these scene gist tasks (DeValois & DeValois, 1988; Carrasco et al., 2003). Alternatively, during these tasks central vision may be of greater importance, for example, if attentional processes dominate. Larson and Loschky (2009) found that within 5° radius of fixation participants were significantly worse in scene recognition compared to a full-view condition but had equal accuracy in the >5° radius condition compared to the full-view condition i.e., peripheral vision contributes more than central vision in scene recognition accuracy. Later, Larson and colleagues (2014) conducted an experiment to determine the relative contributions of central and peripheral vision to scene gist, using the “window/scotoma” method. This experiment involved participants (n=56) classifying 240 scenes into various categories presented in either the central or peripheral view. The results pointed to stronger performance in recognition for the central view. During a second experiment participants (n=85) repeated the same procedure but with presentation times varying from 24 to 376 ms. Similarly, within the first 100 ms accuracy was greater in the central view, affirming central vision is essential within the first 100 ms of image processing (analysing the “gist” of a scene) (Larson et al., 2014).

The role of spatial frequency, and hence the importance of the magnocellular pathway, has also been investigated in previous scene perception studies (e.g., Bar, 2003,  Kauffmann et al., 2014, Schyns & Oliva, 1994). The perceptual processing of natural scenes involves the extraction of scene information following a “coarse-to-fine” direction as a function of increasing time (Trouilloud et al., 2020). The low spatial frequency information is subsequently passed to higher-order areas (e.g., ventral and dorsal streams) where it is combined with high-frequency information and interoperation and recognition of the input is performed. Kauffmann et al. (2015) demonstrated this when reporting a significant coarse-to-fine advantage for accurate, fast, scene classification. Here, dynamic sequences were presented to participants that contained six filtered images of a scene either ordered from coarse-to-fine or fine-to-coarse order (i.e., low- to high-frequencies or the reverse were isolated, respectively). The data showed the important role of the magnocellular pathway as significantly faster classification for the coarse-to-fine condition existed.

### 5.1.2. Scenes and Dyslexia

There are limited studies that investigate dyslexia and reading in relation to scene gist performance, though some insights into high-level visual deficits which are in-line with the magnocellular theory of dyslexia exist. Ahmadi et al. (2015) investigated natural scene identification in 26 dyslexic and neurotypical (age-related level reading) children. The scenes were processed to isolate different pathways: the magnocellular, parvocellular and koniocellular (the koniocellular pathway is sensitive to both brightness and colour contrast corresponding to the “yellow-blue” S-cone direction). Scene identification was poorer in all conditions for the dyslexic group which indicates potential abnormalities in all pathways. However, it is questionable, based on their reported stimuli generation method, as to the extent their “magnocellular” isolating stimuli was actually magnocellular biasing, as high frequency information was preserved in this condition.

An earlier study by Schneps et al. (2012) investigated the time taken for dyslexic and non-dyslexics to identify the letter L or T in low frequency images. The location for letter identification stayed the same for each scene but the letters changed at random. The results indicate that dyslexic participants were less likely to find the correct letter by a significant 6.6% compared to typical readers, this was attributed to an impairment with the processing of low-frequency images. Although impairment in the magnocellular pathway was evident, the ability to recognise scenes was not considered. As scene gist performance is heavily reliant on magnocellular input – it follows that performance should be lower on these tasks for dyslexics/poor readers.

The concept of global and local processing of a visual scene in dyslexic readers was studied by Franceschini et al. (2017). They noted that initially scenes are processed in the right hemisphere, and later, local analysis of features are processed in the left hemisphere. In five behavioural experiments (n=353) they revealed that problems with initial global analysis of a scene characterised children with dyslexia compared to normal readers. After visual attentional and action video game (AVG) training (emphasising on peripheral and global processing) an increase in reading speed was found in children with dyslexia, along with less local interference in a global task. Additionally, they found that local before global perception can predict future poor readers. The findings hint towards deficits in the magnocellular pathway as the underlying neural mechanism preventing global before local perception and suggests that restoring global processing in dyslexic readers by targeting the right fronto-parietal network may help improve visual scene analysis and reading difficulties.

In addition, Gori et al. (2017) investigated global analysis of a visual scene where a “forest” is first analysed as a whole in the right hemisphere, followed by local features such as “trees” in the left hemisphere. They found that the reverse of “forest before trees” can characterise individuals with dyslexia and perceptual training on “forest before trees” (i.e., global before local processing) can improve reading skills in dyslexic children. The results suggest that the right neural network is essential for global analysis of a visual scene and thus disrupting this process can predict future poor readers.

### 5.1.3. Colour and Scene Recognition

While many studies on colour have focused on low-level objective measures, e.g., chromatic detection (e.g., Jennings & Barbur, 2012), others have been concerned with colour perception in the context of natural scenes. For example, it has been shown that when tasked with adjusting the chromatic gamut of a previously unseen image of a natural scene by expanding or contracting its limits (i.e., the colour gamut) participants’ setting were typically within 2% of the original image

(Nascimento et al., 2016). This is consistent with the idea that participants' have an implicit, unbiased, knowledge of the colour appearance (in this case the level of saturation) of natural scenes that they can rely upon to complete the task when no reference image is provided. This has also been shown to be the case for natural scene structure (Jennings et al., 2015).

The role of colour in scene recognition is also understudied in dyslexic individuals (Sperling, Lu & Manis, 2003; Pammer & Wheatley, 2001). Studies have mainly compared multiple visual pathways in dyslexic individuals which have confirmed low-level visual deficits, in conjunction with tasks that preferentially target the ventral stream showing preserved chromatic contrast sensitivity (Pina et al, 2017). Contrary to this claim, Ahmadi et al. (2015) reported abnormal chromatic contrast thresholds in children with dyslexia for natural scenes. Nonetheless, previous literature endorses the claim of a preserved chromatic pathway (i.e., parvocellular) in the dyslexic population, compared to other visual pathways such as the magnocellular pathway. Overall, differential low-level visual deficits argued in the majority of these studies is contrary to the notion of a generalised chromatic deficit.

In the current study, as colour is processed largely by the parvocellular pathway, and the magnocellular pathway is blind to it (Schiller et al., 1990), a high-level colour-based task will be employed to determine if any differences exist between the fast and slow reading groups based on a high-level chromatic task (details below).

## 5.2. Aims

The magnocellular pathway has relatively faster processing speeds compared to the parvocellular pathway and is much more sensitive to low spatial frequencies - this low-frequency information corresponds to the global shape (i.e., the "gist") of scene. As noted by Goodhew and Clarke (2016), for a particular stimuli or task, the relative balance of magnocellular vs parvocellular contributions can be "dynamically altered".

The above will be investigated via a scene gist task that employs three "image-information" conditions: full-colour, luminance isolating (i.e., the chromatic information has been removed), and a low-frequency isolating (the high spatial frequency and chromatic information has been removed, hence this condition will be magnocellular biasing). The prediction is that poor readers will have lower accuracy for the low-frequency condition. The stimuli will also be divided into three “image-type” conditions: small, large, and ring. As slow readers may have better recognition in the periphery, at least potentially for letter stimuli (Lorusso et al., 2004), scene gist performance will potentially be superior for the slow reading group in this condition. Additionally, a high-level parvocellular based experiment will be performed that aims to determine if judgements of the chromatic content of images of natural scene is perceived differently between fast and slow reading groups. The prediction here is that as the magnocellular is not involved in colour perception there will be no measurable differences between the fast and slow reading groups.

## 5.3. General Methods

### 5.3.1. Participants and Ethical Approval

161 (98 males, 63 females) participants took part in the experiment, all were recruited via the online Testable Minds participant pool (minds.testable.org), only verified “Minds” were recruited. Participants were compensated ($2.30 USD) for taking part. The inclusion criteria were as follows: 18 years or older and native English speakers. Participants were aged 36.4±13.0 years (mean±SD), with the majority (66.4%) reporting an education level of degree level or higher, the remaining reported completing either high school or college. Ethics approval was provided by the Brunel Ethics Committee.

### 5.3.2. Equipment

The online data collection platform Testable (testable.org) was used to host the experiment.

### 5.3.3. Stimuli

#### 5.3.3.1. Phonological LDT

For the phonological lexical decision task (LDT), 31 pseudohomophones and 31 non-pseudohomophones were selected from Seidenberg et al. (1996). The method was identical to that used in chapter 2, see section 2.3.3.3 for details.

#### 5.3.3.2. Scene Gist Task

The experiment used eight scene categories: 1. indoor (e.g., a room within a house), 2. train station, 2. city (i.e., large scale cityscapes), 4. shopping centre, 5. beach, 6. forest, 7. mountains, and 8. street. These were validated in a small (n=2) “focus” group to ensure they were accurate depictions of the intended scene category labels, no adjustments were required after this procedure, i.e., 100% of images were classified by both participants correctly.

Images were manipulated in MatLab to produce the final stimuli set. A third of the images, from each category, had their chromatic information removed to create a luminance isolating condition (the U and V layers of the YUV space were set to zero, see later), a further third, after the chromatic information was also removed, had their contrast reduced and a lowpass gaussian filter applied to create the magnocellular biasing condition, the final third was left unaltered (these formed the full-colour stimuli).

The images were further manipulated create the final stimuli set. The stimuli employed evaluates the relative contributions of central versus peripheral vision to scene gist. Hence the three image-type conditions were created: small, large window and ring.

The small condition was created by selecting small, circular central portions of scenes, while setting the surrounding region to a mid-grey. The large condition was created similarly but the circular scene region was larger, i.e., this would be viewable by both peripheral and central vision. The ring condition was the same size as the large condition, but a central, circular region was removed. Based on the estimated average viewing distance and screen sizes, the small scene images had a diameter of approximately 4 degrees of visual angle and the large scene images had 12.5 degrees of visual angle, the ring condition was the same size as the large condition with the central 9 degrees of visual angle removed, i.e., set to a mid-grey.

Hence, overall, nine stimuli conditions were created: small (full-colour, luminance isolating and low-frequency), large (full-colour, luminance isolating and low-frequency) and ring (full-colour, luminance-isolating, and low-frequency). Figure 5.1 illustrates examples of the stimuli.

For the magno-condition the cut-off frequency for stimuli was 2.5 cycles per degree. The large stimuli were 720 pixels in diameter, the small were 230 pixels in diameter, the ring condition was the same size as the large condition with the central 520 pixel circular diameter removed. The contrast was unaltered in the full-colour and luminance isolating conditions and the magnocellular biasing condition stimuli were reduced by 50%.

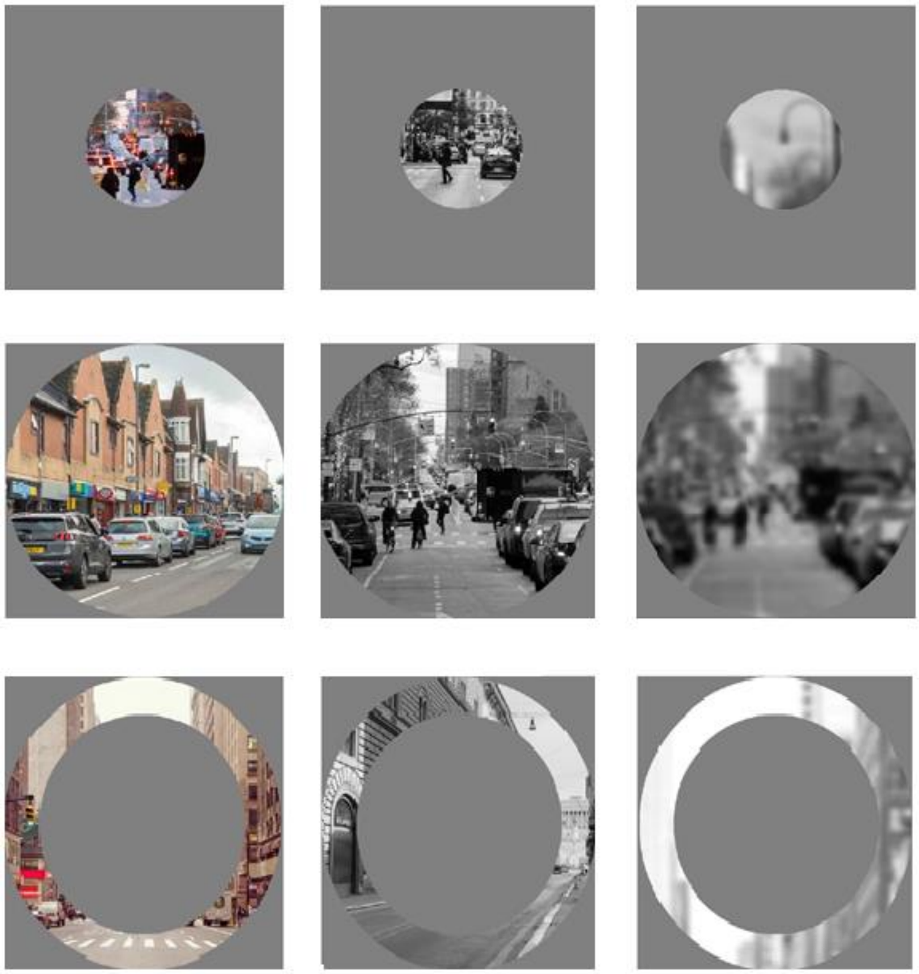

***Figure 5.1.*** *Examples of scene stimuli. From left-to-right: the full-colour, luminance-isolating and low-frequency (magnocellular-biasing) conditions are depicted. From top-to-bottom the small, large and ring conditions are depicted.*

### 5.3.3.3. Scene Colour Task

All stimuli were pre-generated using MatLab (Mathworks) prior to testing, one hundred digital photos were chosen from the McGill Calibrated Color Image Database (Olmos &-Kingdom, 2004), figure 5.2 provides examples of the range of scenes employed in the experiment, they were a mixture of urban and nature scenes, and scenes at different scales, e.g., zoomed in/out.

***Figure 5.2.*** *Example coloured scene stimuli (Olmos and Kingdom, 2004).*

The chromatic content of the scenes was manipulated while the luminance content was held fixed. This was achieved via the following procedure: for each image, each pixel's RGB triplet was converted to its corresponding YUV colour space triplet, by multiplying the RGB values by a 3×3 RGB-to-YUV transformation matrix. The Y layer of the YUV space contains the luminance information, while the U and V layers contain the chromatic information. Scaling factors were applied to the chromatic layers only to vary the colour saturation, this YUV 3d-image matrix was then transformed back into the RGB space via the inverse RGB-to-YUV matrix. The scaling factors applied to the chromatic layers were: 0.2, 0.4, 0.6, 0.8, 1.2, 1.4, 1.6, 1.8, 2.0, and 1 (i.e., no adjustment). An example image is shown in figure 5.3 after the scaling had been applied, for illustration only, at each factor. During the experiment no image was used more than once.

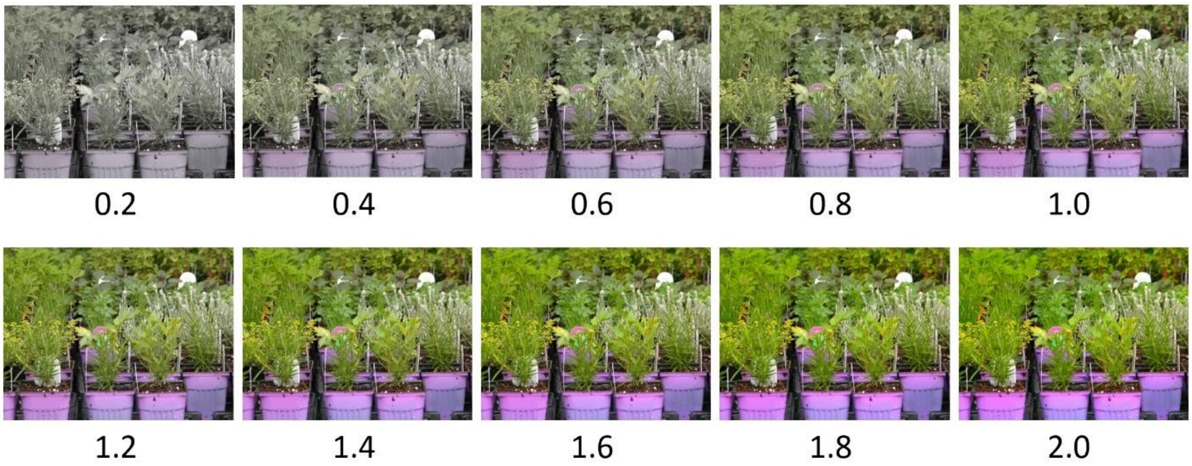

***Figure 5.3.*** *Each panel shows the result of applying the stated scaling factor to the chromatic information while keeping the luminance information constant, the top right image with a scaling factor of 1.0 shows the original unaltered image, scaling factors below 1 lower the chromatic saturation, while scaling factors above 1 increase it.*

### 5.3.4. Testing Procedure

First, the phonological LDT was performed (as per the procedure outlined in chapter 2). Secondly, participants completed the scene gist task, during which they were shown a series of images, one per trial, selected randomly from any condition. On each trial after the scene was displayed (100 ms), a scene name was displayed on-screen which was either congruent or incongruent with the previously displayed image (e.g., a forest scene was displayed followed by the word “Forest”, or an image of a train station was shown followed by the word “Beach”, respectively). The participants’ task was to report whether the word corresponded to the scene. The name and the scene were congruent 50% of the time (i.e., chance performance was 0.5), and on trials that were not congruent the ‘other’ scene names were counterbalanced evenly amongst the categories.

Finally, the scene colour task was performed, the method of constant stimuli was employed with the 10 stimulus “intensity” levels used (as given by the scaling factors above). The two-alternative forced choice task for the participant was on each trial to view the stimuli (presented on screen for 1000 ms and in a random order per participant) and report, via a key press, whether the colour content was too high (over saturated) or too low (under saturated). The testing block was self-paced with each subsequent stimulus appearing after an 800ms inter-trial-interval, starting at the point a response was submitted. Participants were instructed to make a guess if they were unsure as to how to respond in both tasks.

## 5.4. Results

### 5.4.1. Phonological LDT (Comparing Fastest to Slowest Quartiles)

Similar to previous chapters participants were split into fast and slow reading groups, defined by their phonological LDT reactions times (for correct responses only). The fast-reading group contained the 25% (i.e., Q1) of participants that had the lowest reactions time, and the slow-reading groups contained the 25% (i.e., Q4) that had the longest reaction times. One participant was excluded from each group based on Grubbs outlier test (in Q1 this participant had reaction times of <200 ms and an accuracy around chance level, and the Q4 participant had a median reaction time of over 6 seconds), this resulted in 39 participants per group.

No differences between the fast and slow groups were found in terms of accuracy for both pseudohomophones (t(75.6)=-0.87, p=.39, d=-0.20) and non-pseudohomophones (t(71.0)=-0.84, p=.41, d=-0.19). But, as expected (as the groups are defined by RTs), differences in RTs were present between the groups, pseudohomophones (t(54.0)=-16.23, p<.001, d=-3.70) and non-pseudohomophones (t(64.0)=-8.56, p<.001, d=-1.93).

### 5.4.2. Scene Gist vs. Phonological LDT (RTs)

A repeated measures ANOVA was performed with two factors: image-type (small, large, ring) and image-information (full-colour, luminance isolating and low-frequency isolating), along with a between-subject factor of reading group (fast or slow).
A significant main effect of image-type was found, (F(2, 154)=37.7, p<.00001, $\eta_p^2$=0.33), this did not interact with the fast/slow groups (F(2,154)=0.13, p=.88, $\eta_p^2$=0.002).
A significant main effect of image-information was found, (F(2, 154)=4.4, p=.013, $\eta_p^2$=0.055), this did not interact with the fast/slow groups (F(2,154)=0.25, p=.77, $\eta_p^2$=0.003).

Image-information and image-type did interact, ($F(4,308)=38.7$, $p<.00001$, $\eta_p^2=0.34$), however there was no three-way interaction between image-information*image-type and group ($F(4,308)=1.2$, $p=.31$, $\eta_p^2=0.015$). The between subject effect was significant, ($F(1,77)=7.5$, $p=.0078$, $\eta_p^2=0.088$).

Based on the above, post-hoc independent Welch's t-tests were performed to compare the individual conditions between the groups. The statistics are presented grouped for the three image-information conditions, see figure 5.4.

**Full-colour condition:** No differences were found between the fast and slow groups for the full-colour condition - for either the small (t(63.5)=-0.51, p=.61, d=-0.12), large (t(75.5)=-1.20, p=.23, d=-0.27) or ring condition (t(74.6)=-0.31, p=.76, d=-0.069).

**Luminance isolating condition:** No differences were found between the fast and slow groups for the luminance isolating condition - for either the small (t(75.3)=-3.01, p=.076, d=-0.069), large (t(75.6)=--2.15, p=.35, d=-0.49) or ring condition (t(74.3)=-2.37, p=.12, d=-0.42).

**Low-spatial frequency condition:** For the low-spatial frequency condition both the small and peripheral conditions showed no difference between the fast and slow groups: small (t(73.7)=-1.93, p=.057, d=-0.44) and ring (t(68.5)=-1.56, p=.12, d=-0.35), however a large effect was found with the large image condition, t(64.3)=-3.93, $p_{corrected}$=.0019, d=-0.91.

*Note*: the large image condition, with low-frequency information, is the only significant result and hence the only p-value above presented after Bonferroni correction has been applied (which it survives) and is accompanied with a large effect size, all other non-significant values are presented uncorrected.

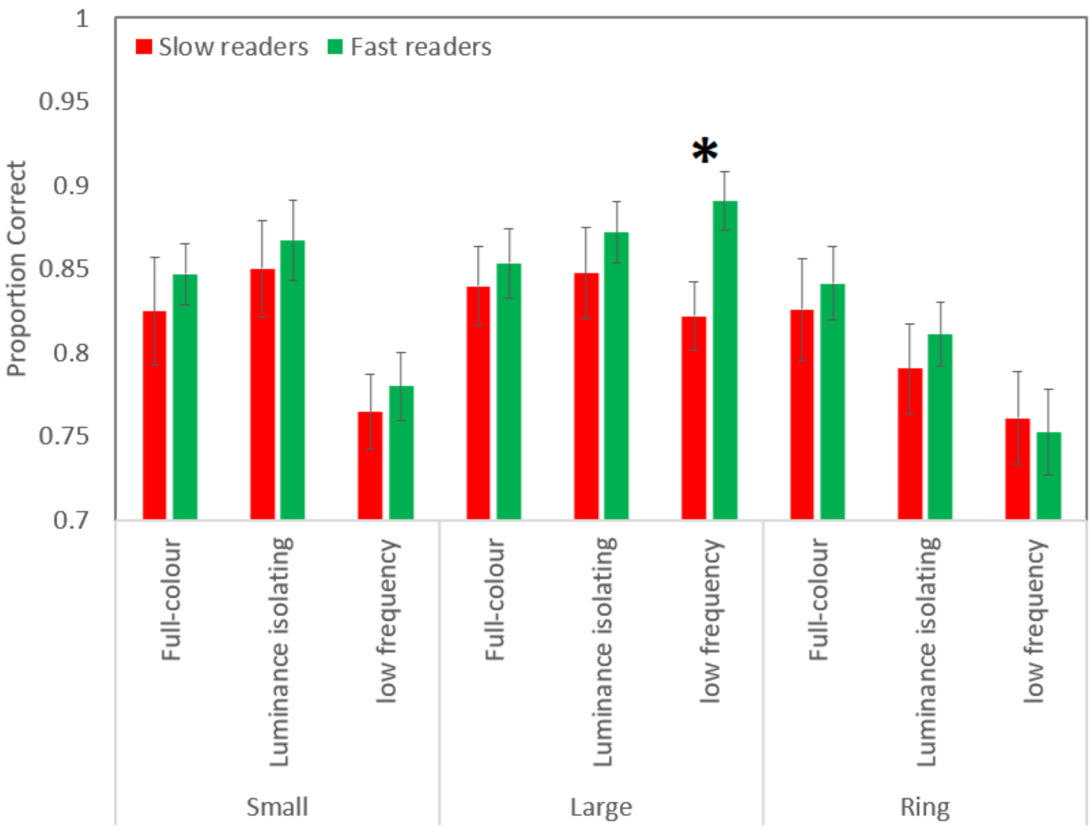

***Figure 5.4****. Accuracy for all the image-information conditions, grouped by image-type. The slow and fast readers are shown in red and green, respectively. Note the y-axis starts at 0.7 proportion correct.*

### 5.4.3. Scene Colour vs. Phonological LDT (RTs)

Psychometrics functions were fitted to the raw data for each participant, logistic curves were fitted using functions from the Palamedes toolbox (Prins and Kingdom, 2018). These employ a maximum likelihood method to fit the psychometric curves, and a bootstrapping procedure to estimate the standard errors of the perceptual-scaling-factor and function slopes they estimate. The individual perceptual-scaling-factors for each participant was defined as the point at which the fitted curves corresponded to a 50% chance of a participant rating the image as having either too high or too low a chromatic saturation (i.e., the factor on the x-axis that corresponds to 0.5 on the y-axis of figure 3). Hence, if a perceptual-scaling-factor was found to be less than or greater than 1 the participant was reducing or increasing the chromatic saturation in the image, respectively.

The following group averages were found (all values reported as mean±SD). Fast readers: perceptual-scaling-factor=1.09±0.21, slope=3.70±0.96. Slow readers: perceptual-scaling-factor=1.01±0.20, slope=3.63±0.95. All fitted functions and average functions for each group are shown in figure 5.5.

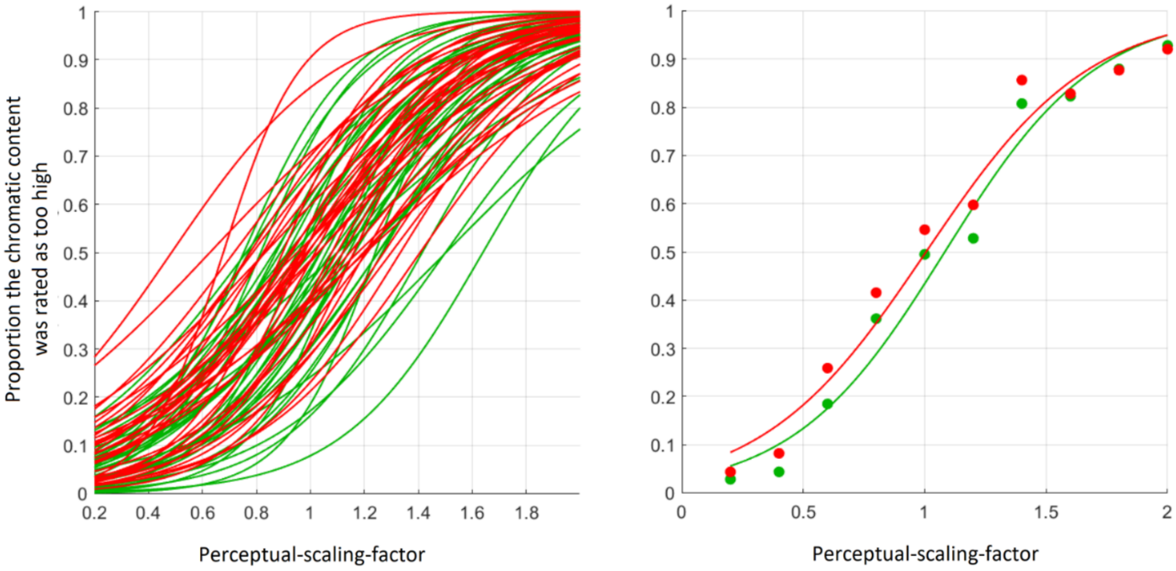

***Figure 5.5.*** *Psychometric functions for all participants: fast-readers (green) and slow-readers (red) are shown on the left, the right shows the mean functions per group. For both panels the x-axis indicates perceptual-scaling-factor, and the y-axis indicates the proportion of images that were judged as having a chromatic saturation that was too high.*

No differences were found between the fast and slow groups in terms of perceptual-scaling-factor (t(75.9)=1.73, p=.090, d=0.39), or function slope (t(76.0)=1.56, p=.12, d=0.35). Additionally, for both groups the mean perceptual-scaling-factor did not differ from 1, i.e., the scaling factor that would result in no adjustment to the chromatic content of the original image (p>.05 for both).

## 5.5. Discussion

The main findings of the experiment are summarised below:

1. The slow reading group shows poorer performance for only one of the three low-frequency conditions - the large image-type condition. For the small and ring image-type conditions, no differences were shown in performance between groups.

2. For the large, low-frequency condition the fast-reading group based on all conditions had the best performance.

3. There are no differences between the reading groups, or between the image-type (large, small and ring) when the stimuli were presented in the full-colour and luminance-isolating conditions.

4. Neither reading groups had a superior performance for any of the ring conditions, indicating no peripheral advantage for either group.

5. In the colour judgement task no difference in scaling factor, or function slope, was found between the two reading groups, moreover, neither of these groups scaling factors differenced from 1, i.e., participants on average matched the images chromatic content to the original images, without having access to the original, unaltered, reference image.

The primary goals of this study were to:

- Determine if manipulation of the image content, e.g., biasing the magnocellular pathway, or shape, e.g., to present the image foveal or peripherally, alters scene gist recognition as a function of reading ability.
- To investigate if differences in colour perception when viewing natural scenes exist as a function of reading ability.

For the current experiment a mixture of urban and natural scenes were employed and adapted so recognition of the scenes, in the gist task, occurred within the fovea, outside of the fovea and a mixture of both; a small condition (central view), ring condition (peripheral view) and large condition, respectively. The ability to comprehend the gist of a scene requires the processing and perceptual organisation of a complex visual scene. A holistic interpretation of a scene within a single fixation is essential for scene gist recognition, activating relevant information stored in long-term memory. This activated knowledge guides many additional essential processes such as object recognition (Bar & Ullman, 1996; Davenport & Potter, 2004), visual attention and visual search (Eckstein, Drescher & Shimozaki, 2006; Gordon, 2004; Torralba et al., 2006) and influences long-term memory access (Pezdek et al., 1989). Thus, the process of rapidly recognising the gist of a scene is essential for understanding how we perceive, interpret, and later remember the contents of the scene.

According to the theory that scene gist recognition is a holistic semantic representation that occurs in a single eye fixation and studies that have shown strength in visual perceptual skills in dyslexic readers when operating predominantly in a holistic manner (see previous chapter), the similarities seen between slow readers versus fast readers in scene gist recognition may result from their strength in processing ideas and images globally. At initial glance, scenes require rapid holistic semantic recognition even without focal attention (Zhou & Zang, 2010). The holistic approach in scene recognition does not require explicit segmentation of image and objects which poor readers may struggle with, instead the image is considered as a whole. This is in line with Olivia and Torralba’s (2001) and Zhou and Zang’s (2010) model of global scene perception and suggests scene gist recognition does not occur as organisation of a collection of objects, as represented by the pLSA and LDA models. The advantage that a poor reader would have for processing the global shape (i.e., the “gist”) of scene diminished when deficits in the magnocellular pathways were exaggerated since this pathway is associated with holistic processing, as demonstrated by the highest performance in fast readers in the low-frequency condition compared to other conditions

Considering current data and the full colour condition, no differences were found over all three of the small, large and ring image-types, indicating that when the chromatic information is present both reading groups (slow and fast) can make use of this equally well. The luminance-isolating condition also had equal performance over the small and large image-types (potentially as high spatial frequency information is still preserved), but accuracy was reduced for the ring condition overall. However, similar to the full colour condition there were no differences between the groups for each condition. This is consistent with data from Jennings and Kingdom (in prep), that indicated a scene recognition advantage when colour information is present in periphery isolating presentations. For example, if a participant could not identify the scene structure, they potentially could rely on diagnostic colour in the stimuli instead to assist in classifying the scene, for example, perceiving green in the periphery may indicate a forest scene, etc. The importance of colour in recognising the gist of a scene was also noted by Oliva and Schyns (2000). as the coarse organisation of colour can be used to predict the scene category.

Overall, the only condition that displayed a difference between the reading groups is the large low-frequency (magnocellular-biasing) condition. Here the fast-reading group showed significantly higher accuracy, with a large effect ($p_{corrected}$=.0019, d=0.91). It is the case that for the small and ring image-types, as the task difficulty is high (these are the two lowest performing conditions overall), both reading groups struggled to identify scenes. As the large image-type is of a suitable size for scene gist recognition, the fast-reading group can take advantage of the isolated low-frequency global information which in turn leads to enhanced accuracy when catergorising the scene, while the slow reading group with magnocellular dysfunction could not (i.e., they did not present with the same advantage as fast readers for holistic processing), which led to a significantly lower average performance being observed. This highlights the importance of LSF information in holistic scene processing i.e., in normal readers holistic processing leads to more accurate scene recognition. In the large luminance isolating and full-colour scene conditions, slow readers were able to make use of colour and edge information hence the slight increase in accuracy in the slow reading group i.e., parvocellular information was used for scene recognition. Similar to fast top-down object recognition described in chapter 2, rapid projection of the LSF “gist” of an image to the OFC can activate fast predictions about scenes similar to the LSF appearance of the scene, leading to faster scene recognition. However, since this concept has only been explored in object recognition, further MRI evidence is required to add neuroscientific support to this theory.

The relative roles of central versus peripheral vision in recognising scene gist have been studied with inconclusive results (Loschky & McConkie, 2002; Parkhurst, Culurciello, & Neiburm, 2000). Previous studies, using similar stimuli to the current experiment, have shown that peripheral vision is more important than central vision for maximum performance. Specifically, Larson and Loschky (2009) showed that the “Scotoma” condition where the central portion of the scene was hidden and only peripheral information was available had almost equal performance to the entire information being available, providing that there is approximately twice as much area in the periphery. Nonetheless, they found that central vision was more efficient for scene gist recognition when measured based on a per-pixel scale. As mentioned, previous studies have demonstrated a peripheral advantage for dyslexic participants in reading (Larson & Loschky, 2009; DeValois & DeValois,1988; Carrasco et al., 2003). However, superior performance was not revealed in the current experiment. It is important to note, however, that caution needs to be taken when interpreting the ring condition data. As this is a web-based experiment, viewing distance was not tightly controlled, and hence it is only possible to estimate the average retinal position of the ring stimuli. Additionally, given the wide range of monitor resolutions reported, the variation in viewing distance this range is large. Future testing should be employed with controlled viewing distance.

Moreover, the second task, a non-magnocellular based colour judgment experiment showed no differences in terms of scaling factors between the fast and slow reading groups. The key result is that no differences in scaling factor was found between groups, and the mean perceptual-scaling-factor did not differ from 1 for both groups, indicating that both groups were able to classify chromatic content as too high or low reliably relative to the original image that they had no access to for reference. In other words, the point-of-subjective-equality matched the physical reality of the stimuli. The slopes of the psychometric curves were also identical, implying that the levels of (un)certainty between the groups was also equal. This result supports the hypothesis that no differences in high-level chromatic perception (i.e., colour perception in complex natural scenes rather than, for example, gratings) is correlated with reading ability, and is consistent with the overall conclusion that poor-reading is linked specifically to magnocellular and not parvocellular dysfunction (Bednarek & Grabowska, 2002; Pina et al., 2017).

The current findings indicate that restoring global perception in poor readers could therefore improve reading skills. This may be done through perceptual learning, transcranial electrical stimulation of magnocellular-dorsal stream or gaming programmes such as AVG (Heth & Lavidor, 2015; Lawton, 2016; Franceschini et al., 2017). These have been showed to play a role in strengthening the magnocellular pathway and hence magnocellular function which plays a critical role in global perception bias. In comparison to faces and words, research on global perception of scenes in dyslexia is limited. Studying the “gist” of a scene provides a great way of measuring perceptual differences related to the magnocellular pathway in dyslexic individuals. Future longitudinal studies are recommended to see the effect of magnocellular training in classifying scene gist in dyslexic readers.

### 5.6. Conclusion

This chapter presented two experiments that generally highlight the importance of colour information for scene gist recognition. Restricting the use of parvocellular-based information and biasing the magnocellular pathway resulted in poorer performance in the slow-reading group, consistent with the prediction of the magnocellular theory of dyslexia. It is suggested that the large, low-frequency condition is of the correct size to allow the fast-reading group to take advantage of the global information present. This elevated their scene gist recognition performance, something the poor-readers were not able to do. The advantage that poor-readers may have in peripheral scene recognition was not apparent in this study, however these results were limited by the fact that viewing distance was not tightly controlled, and thus accurate retinal position could not be confirmed. Finally, the high-level colour-based task that relied on parvocellular input showed no difference between the reading groups, again consistent with the idea that poorer-readers have a visual deficit specifically limited to the magnocellular pathway.

# Chapter 6: Visual Illusions and Reading

## 6.0. Chapter Overview

The previous two chapters demonstrated that biasing the magnocellular pathway can interfere with holistic processing mechanisms in slow compared to fast reading groups. This chapter aims to explore and develop the findings presented so far by employing visual illusions that trigger local processing (i.e., relative size perception), and targets luminance (i.e., perceived brightness). Visual illusions provide a unique way of investigating the neurobiology behind visual deficits by exploring subjective perceptual differences (Spillmann, 2009). This chapter will begin by reviewing the current literature on visual illusions in DD, followed by a study employing two visual illusions that have not yet been investigated in dyslexic readers: the Ebbinghaus and White's illusion. To conclude the final experimental chapter, a discussion about the findings will be provided and their contribution towards diagnostic and therapeutic approaches.

## 6.1. Introduction

As outlined in previous chapters, reading requires the processing of visual information where visual input is defined by contrast, shape/form and motion which requires processing at high speeds (Werth, 2021). The same processes are also required when perceiving and visually interpreting optical illusions (Grossberg, 2014), highlighting a potential use for illusions in revealing word processing deficits (Kristjánsson & Sigurdardottir, 2023). Visual illusions prevail the limitations of our visual system which can affect our perception of the external environment (Eagleman, 2001) and are defined as a misperception of an external stimuli that occurs due to a misconception of a physical stimulus (Todorović, 2020). Visual illusions provide a valuable method to investigate the neurobiology of visual deficits as they, by definition, induce large differences in perception versus their physical reality (Spillmann, 2009). As developmental dyslexia (DD) can be characterised by visual deficits in certain groups (Stein, 2019, 2021), the current experiment aims to provide new evidence demonstrating differences in the effectiveness (or ‘strength’) of visual illusions in slow compared to fast readers.

There are many sub-classes of visual illusions categorised based on their perceptual appearance, for example, colour (Pinna et al., 2001), size (Sperandio et al., 2010, 2012, 2013), brightness (Pinna et al., 2003; Gori & Stubbs, 2006; Todorović, 2006; Spillmann et al., 2010), shape (Axelrod et al., 2017), etc. Group differences are more evident when investigating visual stimuli that are “objective”. In cases where a “subjective” response is required, i.e., when an individual’s response is based on their own perceptual outcome and response criteria, the point of subjective equality (PSE, when the two stimuli (test and standard) look subjectively the same) has to be determined to investigate group differences (Todorović, 2020). Stimuli which display physical differences generate an “objective” response, and this assumption is otherwise known as “naïve realism” where perception of the world is exactly as it is, and others perceive it the same way as we do (Spillmann, 2009). Overall, using illusions to measure perceptual differences in individuals is equivalent to other behavioural studies using “typical” stimuli (Manning, 2001). Further limitations of the visual system may also be revealed due to unordinary stimuli triggering different neural mechanisms throughout the brain as opposed to standard stimuli (a review of how illusions provide an insight into brain processing to investigate neurobiological characteristics of the visual system can be found by Eaglemann, 2001).

Thus far, visual illusions have shown promising advances in the study of people with autism spectrum disorder (ASD) (Notredame et al., 2014; Happé & Frith, 2006; Chouinard et al., 2013). Similar to DD, there is a growing amount of evidence that demonstrates defects in low-level visual perception and attention in this population (Notredame et al., 2014; Happé & Frith, 2006; Dakin & Frith, 2005; Mottron et al., 2006; Simmons et al., 2009). The weak central coherence theory of ASD suggest that this group use a specific perceptual-cognitive style which leads to limited understanding of the context of an image (Tassini et al., 2022). This means that difficulties with global processing in individuals with ASD allows them to focus on local elements within a scene (Koldewyn et al., 2012). Happé (1996) first concluded that children with ASD were significantly less sensitive than control children to visual illusions (Happé, 1996). Later, Manning et al. (2017) compared autistic children to typically developed children and found that they were equally susceptible to the Ebbinghaus illusion (Manning et al., 2017), confirming their preference in local processing since this element is required in order to have accurate perception of the main target (see figure 6.3). Visual illusions are therefore a promising tool for examining perceptual processing in this population as several illusions can be applied to examine the weak central coherence theory (Frith & Happé, 1994; Happé & Frith, 2006; Chouinard et al., 2013). Since children with ASD appear to be less susceptible, or have similar performance to the general population based on the weak central coherence theory (Happé, 1996; Manning et al., 2017), it would be interesting to investigate susceptibility of illusions in groups that are impaired in their local perception, such as the dyslexic population.

Further research is required to determine the exact neural mechanisms involved in the susceptibility of illusions in DD, however throughout the years they have been shown to play a crucial role in revealing perceptual and attentional deficits (Slaghuis et al.,1996; Facoetti & Molteni, 2001). The Ternus illusion (Ternus, 1938) involves apparent motion interpretation, where two discs are shown adjacent to each other in a first frame followed by a blank frame for a short duration, and then a final frame where two adjacent discs are shown again in a shifted position (figure 6.1). The time interval between frames, spacing and layout can influence judgement on how the discs move. If one disc moves while the other is stationary “element motion” is reported, whereas if both discs move then “group motion” is reported. Evidence for a magnocellular deficit has been shown in individuals with DD using the Ternus illusion based on their reduced group motion perception (Slaghuis et al., 1996). This was due to an increase in the duration of visible persistence (continuation of perception after stimulus had diminished). These results were later confirmed by Slaghuis and Ryan (1999) in children with DD. The Ternus display was employed in a study by Cestnick and Coltheart (1999) where differences were shown between dyslexic individuals and controls. Here, they demonstrated differences in performance between the Ternus illusion and pseudoword reading but not exception word reading, i.e., issues were only reported in the phonological subtype. The authors explanation for this is based on the left-to-right distribution of visual attention across pseudoword reading which can also impact neural responses to the Ternus display. Alternatively, poor pseudoword was an indirect affect from neurodevelopmental disruptions that affected the LGN and in-turn altered Ternus performance, and the adjacent medial geniculate nucleus (MGN) which influences phonological ability, i.e., abnormal functioning of the MGN was the cause of poor non-word reading.

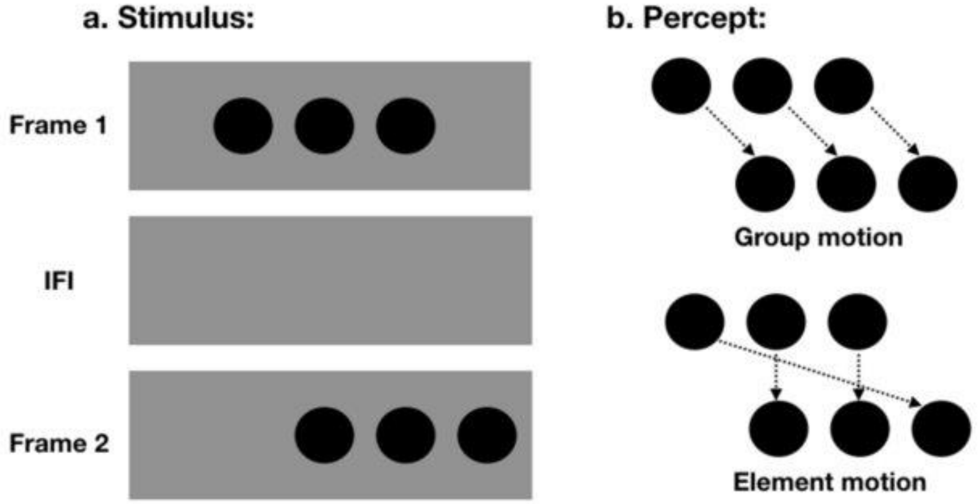

***Figure 6.1.*** *The Ternus display (Ternus, 1938). (a) The display consists of two frames separated by blank screen: frame 1 contains three horizontally aligned black discs, followed by a blank screen, and frame 2 shows the three black discs in frame 1 shifted by one inter-element spacing. (b) There are two possibilities for motion perception: all three elements seem to move as a group (group motion) or the two inner elements are stationary and only the last element seems to go back and forth between the outer positions (element motion).*

Contrary to Pammer and Lovegrove's (2001) theory that suggested the Ternus display as proxy in testing magnocellular pathway function in DD, Jones and colleagues failed to find differences in group motion between dyslexic participants compared to normal controls (Jones, Branigan & Kelly, 2008). They suggested that only when selective attention is required will magnocellular difficulties arise (Vidyasagar, 1999, 2013; Facoetti, 2012), which was not apparent in this study. Arguments for magnocellular involvement in DD mainly come from the frequency doubling (FD) illusion (Pammer & Wheatley, 2001). When modulated at low spatial and high temporal frequencies, the coarse sinusoidal grading patterns (figure 6.2) creates the illusion of a stable grating with a perception of having double the spatial frequency of the component gratings (i.e., double the stripes) (Kelly, 1981). FD occurs when a 0.1 - 4 c/deg grating is made to flicker at more than 15 Hz (Pammer & Wheatley, 2001). Since temporal frequency of the stimuli is very high, these can be detected by magnocellular neurons, which have been shown to be defective in the dyslexic population (Stein, 2019). The contribution of magnocellular Y-like cell (M(y)-cell) activity within the magnocellular deficit framework was investigated by Pammer and Wheatley (2001). Dyslexic readers were compared to neurotypical readers on their threshold detection for the FD illusion alongside a coherent motion and visual acuity task. Although poorer performance was observed in the FD illusion and coherent motion for the dyslexic group, both groups had comparable performance in the visual acuity tasks suggesting that visual deficits in dyslexia specifically originates from a retinal level in M-cell activity (Palmer & Wheatley, 2001). Not only did they display less sensitivity to the FD illusion, but they also demonstrated significantly decreased sensitivity compared to their standardised age cohort, as opposed to the control group who had similar sensitivity levels to their age group (for a comprehensive discussion between M(y)-cells and frequency doubling, see Maddess, Hemmi & James, 1992). Furthermore, Kevan and Pammer (2008) established significantly higher thresholds for the FD illusion in children with a familial risk of developmental dyslexia, even before reading acquisition (Kevan & Pammer, 2008). Later, in a longitudinal study, they importantly demonstrated that the threshold for the FD illusion at the pre-reading stage can predict reading skills in adulthood (Kevan & Pammer, 2009). This suggests a causal role for a magnocellular deficit in dyslexic individuals and highlights the importance of using visual illusions as a predictor of future literacy.

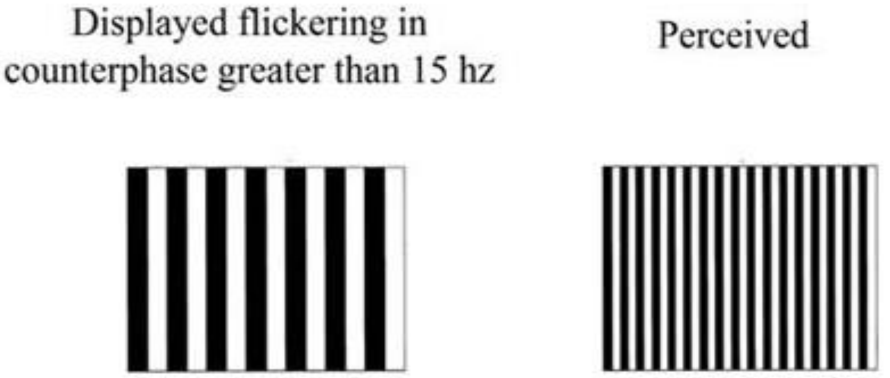

***Figure 6.2.*** *The FD illusion (Kelly, 1981). The display on the left shows the stimuli in its correct form. When the 0.1 - 4 c/deg grating is made to flicker at more than 15 Hz its apparent spatial frequency increases, giving the illusion that double the stripes are present (right display).*

The illusory line motion occurs when a line is perceived to extend away from a preceding attentional cue (Hikosaka et al., 1993). Differences have been observed between dyslexics and controls in line motion illusion which have been attributed to deficits in visual attentional mechanisms, dominated by magnocellular input (Steinman et al., 1998). In a later study, the role of attentional mechanisms conforming with the line motion illusion was confirmed using fMRI, i.e., brain patterns were in line with the attentional gradient model (Hamm et al., 2014). This emphasises the use of visual illusions as a proxy for measuring attentional processes, and hence magnocellular function in individuals with DD.

Given the recent methodological advances in measuring illusion susceptibility, it seems appropriate to revisit the question of whether poor readers are more susceptible to the effects of illusions compared to the neurotypical reading population. In this current study, susceptibility of two well-characterised illusions: the Ebbinghaus and White's illusion in two reading groups (slow vs typical/fast readers) is measured. To date, there are no recorded studies that have investigated the effect of these two illusions in a dyslexic/poor reading sample. The study allows the investigation of differences in brightness perception based on varying luminance, and size comparisons arising from the surrounding context in slow compared to fast readers. The main theoretical framework for the White's illusion accentuates the role of low-level mechanisms that activate on the 2D array of luminance values (Anderson, 2003). The Ebbinghaus illusion demonstrates how size perception can be manipulated by surrounding shapes (Rashal, 2020). Many factors can influence illusory effects including peripheral viewing, eye movements, global/local processing, and attention. Hence, visual illusions provide an appropriate method of indirectly measuring the association between perceptual, attentional, and subsequently magnocellular deficits in reading disorders.

## 6.2. Aims

The study aims to provide evidence for visual deficits in poor readers by investigating the susceptibility of two visual illusions in slow versus fast readers: the White's illusion and Ebbinghaus illusion. Based on the theoretical framework that low-level mechanisms (e.g., the magnocellular pathway) leads to the activation of luminance perception (Anderson, 2003), it was predicted that slow readers would be more susceptible to the White's illusion. Magnocellular cells are essential for detecting changes in luminance, hence in view of the proposed magnocellular deficit, the ability to distinguish luminance levels will be impaired in this group, i.e., slow readers may need more luminance contrast to perceive the bars as the same level of brightness due to their magnocellular weakness. Additionally, impaired readers are less likely to ignore the surrounding context and focus on a target, so are more likely to be deceived by the illusory effects. For the Ebbinghaus illusion, greater illusory effects were predicted for slow readers compared to fast readers since this illusion requires the analysis of local details (de Fockert et al., 2009). This is contrary to the effects seen in autistic children (Manning et al., 2017) who displays advantages for local processing, meaning they are less sensitive to the illusion. Hence, increased contextual integration could in theory lead to greater susceptibility to illusions in dyslexic individuals. Investigating susceptibility to visual illusions opens a gateway for the potential use of non-verbal stimuli as a measure of reading skills.

## 6.3. General Methods

### 6.3.1. Participants and Ethical Approval

A total of 151 participants took part in this study: 74 females and 77 males with a mean age of 30±9 years (mean±SD). Their level of education ranged from high-school education (22%) to batchelor's degree (67%), and master's and doctorates (11%). All participants were recruited from, and hence had previously signed up to, the Testable Minds participants pool (testable.org), they received a payment ($3usd) upon completion of the experiment. The study was approved by the Brunel University Ethics Committee.

### 6.3.2. Equipment

The online data collection platform Testable (testable.org) was used to host the experiment.

### 6.3.3. Stimuli

#### 6.3.3.1. Phonological LDT

Reading ability was assessed using a phonological lexical decision task (LDT), the pseudohomophone and non-pseudohomophone stimuli were taken from the same database as those used in previous chapters.

#### 6.3.3.2. Visual Illusions

##### 6.3.3.2.1. Ebbinghaus Illusion

Figure 6.3 demonstrates the Ebbinghaus illusion. The standard Ebbinghaus illusion consists of two grey circles of the same physical size, which are however perceived as different in size due to the context, i.e., neighbouring orange circles of different sizes (figure 6.3A). To determine the participant’s susceptibility to this illusion, the size of the left internal circle surrounded by the larger circles was manipulated, either increasing or decreasing its size relative to the reference circle on the right (see figure 6.3B for an example of the manipulated stimulus).

The target and test central grey circles were 90 pixels, the large flanking circles were 120 pixels and the small flanking circles were 40 pixels. The presentation time was 500 ms.

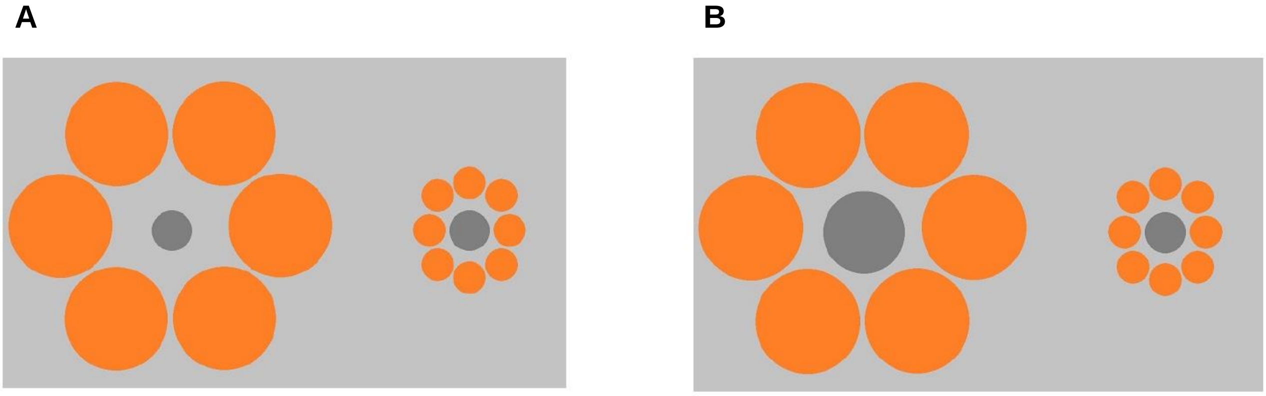

***Figure 6.3.*** *Image depicting the Ebbinghaus illusion (Ebbinghaus, 1902) (**A**) The standard Ebbinghaus illusion showing the two inner grey circles that are physically the same size but are thought to be different in size due to neighbouring orange circles of different sizes. (**B**) A manipulated example of the Ebbinghaus illusion, the left grey circle is physically larger than the right grey circle.*

### 6.3.3.2.2. White's Illusion

The White's illusion (figure 6.4) is a visual illusion consisting of two grey vertical 'bars' of equal luminance (i.e., grey level). However, due to the bars being in different contexts (i.e., embedded into either the white or black horizontal lines), they appear to be of different brightness. Susceptibility to the visual illusion is established by manipulating the luminance of the right bar so that it is physically darker or lighter than the reference bar on the left-hand side (see figure 6.4B for an example of the manipulated stimulus).

The black and white horizontal bars were 70 (high) X (wide) pixels, the internal grey "bars" were 175 pixels wide. The presentation time was 500 ms.

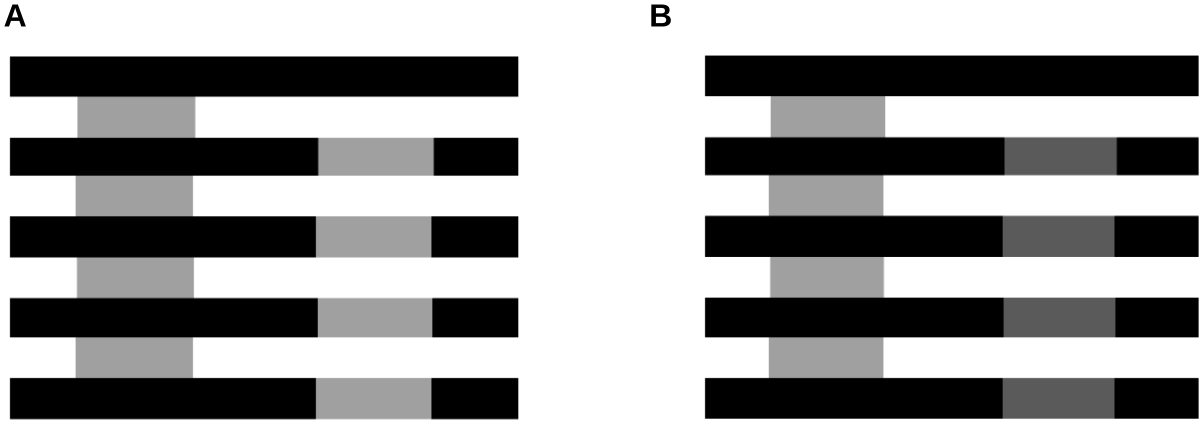

***Figure 6.4.*** *Image depicting the White's illusion (White, 1979, 1981). (**A**) The standard version in which two grey vertical bars of the same luminance are placed on either black or white horizontal stripes, giving the illusion that the right grey bar is brighter than the left. (**B**) An adjusted version of the standard White's illusion where the grey level of the right bar has been reduced rendering it perceptually darker than the left reference bar.*

### 6.3.4. Testing Procedure

First participants completed the phonological LDT, this followed the same procedure as previous chapters. The median reaction times (RTs) were calculated based on correct responses to the pseudohomophones - for analysis participants were grouped into quartiles, the fastest reaction times (the top 25%, Q1 – *n*=36) vs the slowest reaction times (the bottom 25%, Q4 – *n*=36).

Next, the Ebbinghaus visual illusion was presented to participants. Here the reference circle was fixed at 80 pixels (diameter). On different trials the left-hand circle, i.e., the test, was varied in size. The nine presented diameters were: 60, 80, 90, 100, 110, 120, 130, 140, and 160 pixels (presented in a random order). The number of presentations of each trial type ranged between 4-10, with 4 repetitions at the extreme sizes (60 and 160 pixels), 10 repetitions were performed for all other sizes. Participants took part in three practice trials with a stimuli set of 80, 100 and 160 pixels. The 2AFC task for the participant was to report which of the circles appeared larger, via a key press. If they were not sure, they were instructed to make a guess. Reaction times and responses were recorded for each presentation.

For the White’s illusion, each trial consisted of the stimuli being presented with the test (right) grey bar having a manipulated grey level of either: 60, 90, 110, 120, 130, 140, 150, 160 and 170. The physically matching reference was fixed with a level of 160. Each level was repeated 10 times. Three practice trials first performed with grey levels of: 90, 140 and 170. The 2AFC task was to report on each trial which bar appeared darker, via a key press. If the participant was not sure, they were asked to make guess. Again, reaction times and responses were recorded for each trial.

### 6.3.5. Psychophysical Data Processing

The raw data was processed in MatLab using the function PAL_PFLM.m, a curve fitting function provided in the *Palamedes* psychophysics toolbox (Prins and Kingdom, 2018). This function fitted the best fitting psychometric function (a logistic curve) to the data using a maximum likelihood method and extracted the PSE, i.e., the point at which the illusion stopped having an effect, and the slope of each fitted function, which provides a measure of the uncertainty. For example, for the White’s illusion, the PSE is the grey level required for the participant to perceive the two bars (the test and reference) as having perceptually equal brightness.

The dependent variable for each illusion was the PSE. For the White’s illusion the reference bar had a grey level setting of 160, hence as PSEs move further from 160 (downwards) a higher susceptibility can be inferred, as a larger difference between the bars is required to cancel the illusion’s affect. For the Ebbinghaus illusion, which had the reference circle size fixed with an 80-pixel diameter, as PSE values increase above 80 pixels a higher susceptibility can be inferred.

## 6.4. Results

### 6.4.1. Phonological LDT (Comparing Fastest to Slowest Quartiles)

After ordering the participants by RT and grouping into the fast and slow (upper and lower quartile) groups, no differences in accuracy was found for the pseudohomophone condition (t(59.7)=-1.94, p=.06, d=0.45) or the non-pseudohomophone condition (t(58.5)=-1.48, p=.14, d=0.34), and effects were small for both (see figure 6.5). As expected, large significant differences were found between the groups with respect to RTs, as this defined the groups. There was a significant difference for both the pseudohomophone and non-pseudohomophone conditions (t(59.7)=-17.30, p<.0001, d=3.97 and t(44.1)=-11.49, p<.0001, d=2.68, respectively), see figure 6.6.

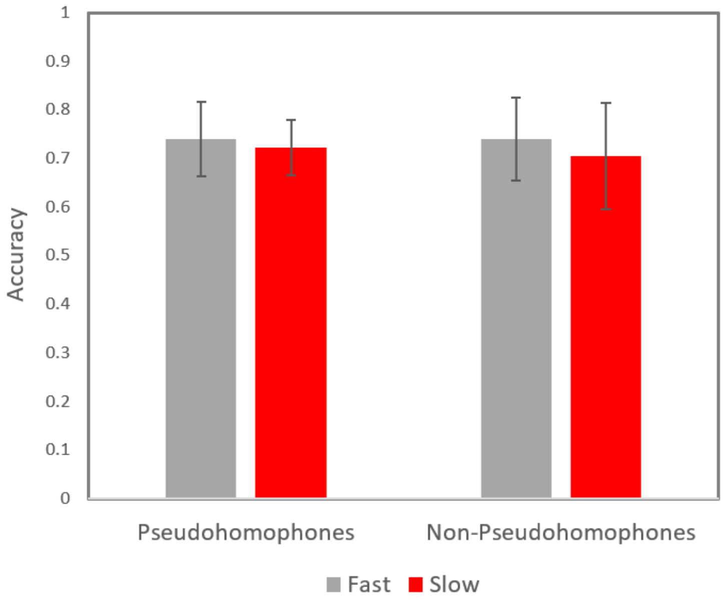

***Figure 6.5.*** *Accuracy between the fast and slow reading groups for the pseudohomophone and non-pseudohomophone conditions. Error bars represent ±2SE.*

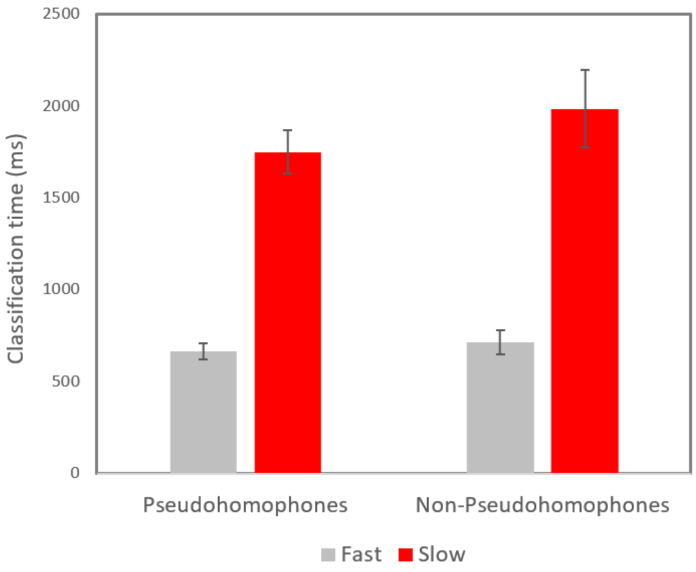

***Figure 6.6.*** *RTs between the fast and slow reading groups for the pseudohomophone and non-pseudohomophone conditions. Error bars represent ±2SE.*

### 6.4.2. Illusions Data

#### 6.4.2.1. Correlations over the Whole Sample (RT vs PSE and RT vs Slope)

For White's illusion no significant correlations between the RTs and PSEs or slopes was revealed (r(136)=0.17, p=.12. and r(136)=0.12, p=.15, respectively), see figure 6.7.

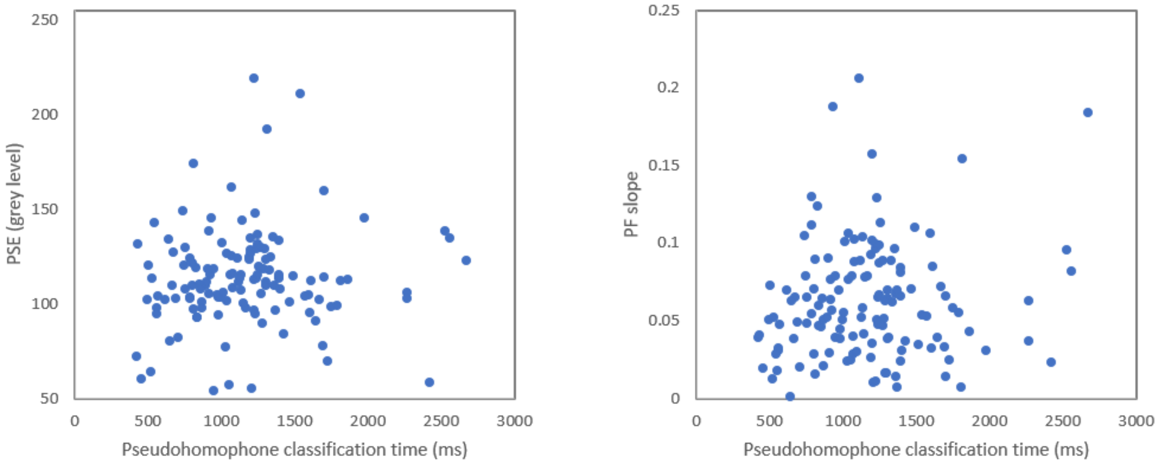

***Figure 6.7.*** *Scatter plots illustrating no significant correlations between the RTs and PSEs (left panel) or slopes (right panel) for the White's illusion.*

For the Ebbinghaus illusion significant correlations between the RTs and PSEs or slopes were found (r(146)=0.28, p=.00058 and r(146)=0.20, p=.016, respectively), see figure 6.8. Note that as not all functions for both illusion conditions converged, small differences in participants numbers have been reported.

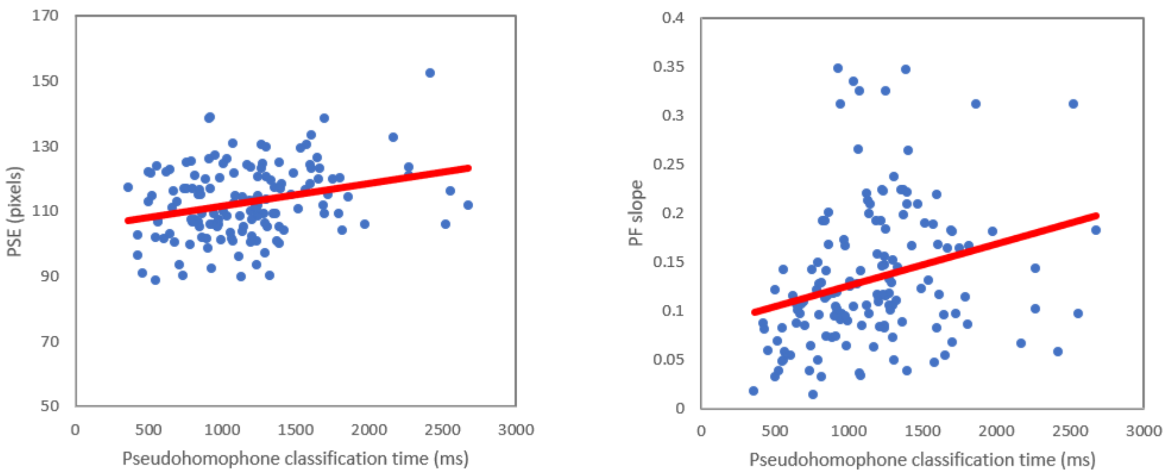

***Figure 6.8.*** *Scatter plots illustrating the significant correlations between the RTs and PSEs (left panel) or slopes (right panel) for the Ebbinghaus illusion, the red line indicates the line of best fit.*

### 6.4.2.2. Comparing Fast vs Slow Readers (Q1 vs. Q4) Illusion Susceptibility

No differences were found between the reading groups for White's illusion, both the PSEs and slopes revealed no significant differences (t(47.3)=-0.89, p=.37, d=0.22 and t(61.7)=-0.88, p=.38, d=0.21, respectively). However, significant differences existed for both PSE and slope for the Ebbinghaus illusion (t(72.3)=--3.41, p=.0011, d=0.80 and t(73.0)=-2.87, p=.0053, d=0.66, respectively). See figure 6.9 for the functions.

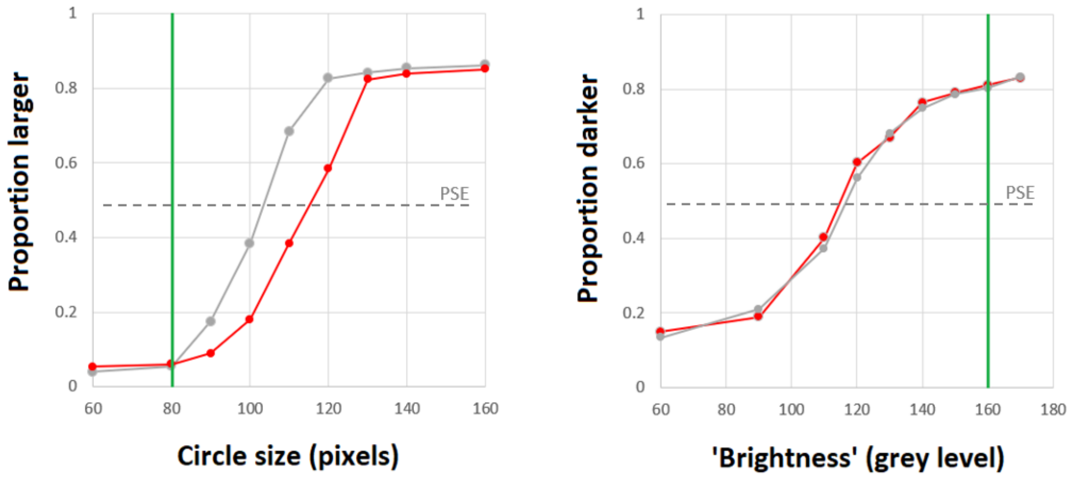

***Figure 6.9.*** *Psychometric data for the Ebbinghaus (left) and White's illusion (right). The green lines indicate the value of the fixed reference. The red and grey curves are the slow and fast reading groups, respectively.*

### Brief interpretation

**Ebbinghaus:** The shift to the right implies both groups were susceptible to the illusion, but the larger shift to the right in PSE for the slow reading group implies they were more susceptible, as a significantly larger difference in circle diameter was required for them to be perceived as equal in size.
**White's:** The shift to the left lower than 160 implies both reading groups were susceptible to the illusion, but to the same extent.

## 6.5. Discussion

The main findings of this study are summarised as follows:

- Both slow and fast reading groups were susceptible to the Ebbinghaus and White's illusion.
- No group differences were seen for the White's illusion in PSE and slopes between slow and fast readers, i.e., both groups were equally as susceptible to the illusion.
- Slow readers were more susceptible to the Ebbinghaus illusion compared to fast readers, i.e., a significantly larger increase (with a larger effect size,

d=0.8) in test circle diameter was required for the slow reading group to perceive the reference and test circles as equal in size.

The contribution of visual illusions to our understanding of DD is far from reaching its peak. The purpose of this study was to unveil the illusory effects in different reading groups based on evidence that has shown deficits in a range of tasks that require visual perception in the dyslexic population including brightness, size, colour, and motion, which can be investigated in numerous types of illusions (Pinna et al., 2001; Sperandio et al., 2013; Todorović, 2006; Axelrod et al., 2017). Researchers have mainly revealed visual illusion sensitivity in individuals with DD (Pammer & Lovegrove, 2001; Pammer & Wheatley, 2001; Slaghuis et al., 1996). Although visual illusions alter our physical reality, it is a useful tool in measuring adaptive brain mechanisms such as perceptual constancy (Spillmann, 2009). The use of visual illusions can lead to the early identification of learning difficulties such as DD, potentially even before early reading acquisition (Sanfilippo, 2020). This is because, in a typical population, illusions have shown a dissociation between the retinal image of an object and its perception (Takao, Clifford & Watanabe, 2018), and hence these effects may be more apparent in the dyslexic population who have consistently displayed poor visual perceptual skills. Current diagnosis can only theoretically be achieved once a child reaches 7 or 8 years of age and has sufficient vocabulary development (Snowling, Hulm & Nation, 2020). On the contrary, visual illusions are capable of testing for the disorder much sooner leading to earlier identification of children at risk of developing DD (Sanfilippo, 2020). Targeting the magnocellular pathway, or other visual deficits with visual illusions, may further unmask any irregularities in the visual pathway which can lead to therapeutic interventions to prevent or lessen negative outcomes associated with DD.

In the current experiment two visual illusions, the Ebbinghaus and White’s illusion, were employed and susceptibility to these illusions in slow versus fast readers (defined by phonological ability) was compared. The dependent variable for each illusion was the point at which the illusion stopped working for participants, i.e., the point of subjective equality (PSE). This White’s illusion had a setting of 160 for the physically matching stimulus, hence PSE values lower than 160 meant that participants had higher susceptibility to the illusion, which was the case in this current experiment - however, no differences were found between reading groups. For the Ebbinghaus illusion, which had a reference setting of 80 pixels for the test circle as a physical match, PSE values higher than 80 meant higher susceptibility to the illusion which again was apparent in all participants in this current experiment. However, it was revealed that PSE values were significantly different between reading groups; slow readers needed a greater difference in the test circle size in order to perceive the reference and test circle as equal. Significant differences were also observed in psychometric slopes for the Ebbinghaus illusion, i.e., the steep slope in fast readers demonstrates they were more certain in their decision of if the test circle was bigger or smaller than the reference circle. In contrast, no relationship between phonological reading ability and slopes were found in the White's illusion indicating that the variability in participants answers, i.e., the level of uncertainty between reading and grey levels were similar in both the slow and fast reading groups. Below, possible explanations for these findings are discussed.

Early theories for susceptibility to the White's illusion include low-level mechanisms that have suggested visual susceptibility occurs due to simple filters that implement lateral inhibition at early stages of the visual system (Anderson, 2003). Theoretically, considering local contrast or lateral inhibition, the target on the light stripe should appear darker than the target on the dark stripe, however the opposite is perceived, i.e., it is the opposite affect seen in simultaneous contrast illusions. As phasic ganglion cells of the magnocellular pathways are sensitive to luminance changes (Yoonessi & Yoonessi, 2011), it was hypothesised that slow readers would be less sensitive in detecting luminance contrast differences, and hence require more contrast (grey level) to perceive the test and reference grey bars as a physical match (i.e., the more the grey level of the right test bar is reduced, the more it is perceptually darker than the left reference bar). Additionally, poor readers have been shown to struggle with filtering irrelevant information and stay focused on a target. Fast/neurotypical readers were expected to be less susceptible to the differences in brightness due to their sensitivity to luminance contrast (i.e, normal magnocellular function) and their ability to focus on the target stimulus, however, no differences were recorded in perceived brightness between slow and fast readers (both reading groups were equally susceptible to the illusion). Equal performance may have occurred due to all participants using edge information to determine brightness. Betz et al. (2015) found that adapting to the orthogonal edges in the White's illusion decreases the lightness perception effect, hence, participants are likely to have made use of the parvocellular pathway to detect luminance contrast-based edges (Ringach, 2002).

Generally, adults have a temporal advantage in processing the whole compound of a visual stimuli (global processing) over the perception of elemental details (local details) (Primativo & Arduino, 2003). In the dyslexic population, it has been proven that local details of an object are especially difficult to process (Goldstein-Marcusohn et al., 2020). The Ebbinghaus illusion reveals how size perception can be manipulated by surrounding shapes, a stimulus that is surrounded by larger shapes will appear smaller than when surrounded by smaller shapes (Rashal, 2020). Although the majority of observers would agree that the circle flanked by larger shapes is smaller, in reality it is physically equal in size as the circle flanked by smaller circles. The shapes surrounding the circles are heavily related to this perceptual phenomenon. In the current study, Ebbinghaus illusion susceptibility is experienced by both slow and fast readers but is experienced more strongly by slow readers as they provided less accurate size judgment (a larger circle size was required for them to perceive the target as the same size). An excessive bias towards local information impairs perceptual performance in dyslexic individuals (Franceschini et al., 2017). For the Ebbinghaus illusion, correct identification of size requires participants to separate the local part of the object from its global whole (de Fockert et al., 2007). Since the Ebbinghaus illusion requires participants to pay attention to detail (analytical processing) over the context of the image (holistic processing), this explains the differences seen between reading groups in this current study. Problems with local processing, as seen in the dyslexic population, would therefore lead to a greater illusory effect caused by the surrounding inducers (the opposite effect has been recorded in individuals with ASD).

Furthermore, an alternative explanation for the results seen in this study may come from problems with selective attention. The way irrelevant distractors are processed is crucial to selective attention (van Moorselaar & Slagter, 2020), hence the circles surrounding the target can interfere with the attentional mechanisms required to process the target. The attention account suggests that longer fixation time on the target weakens the illusion because attention on the fixed target leads to exclusion of other distractor circles. Fixation restriction to the target thereby reduces the illusory effect (Whitewell et al., 2023). Since evidence has shown dyslexic individuals struggle to select relevant visual elements within a scene whilst ignoring the irrelevant visual elements (Hokken et al., 2023), attentional processing (which rely on magnocellular input) deficits can account for the difference seen here. This concept was applied to the Ternus display illusion in dyslexic children (Cestnick & Coltheart, 1999). Switching between the global and local elements in the Ebbinghaus illusion requires selective attention (Shedden et al., 2003). Since this process is automatic, problems with selective attention can interfere with global and the local levels of hierarchical image processing. This theory assumes that improvement in attentional selectivity can improve accuracy in visual illusions, hence training in guiding attention may influence perceptual organisation and improve accuracy in global/local tasks (Hübner, 2014). It has been proposed that the scheme of selective attention provides a neural mechanism that underlies reading, namely the magnocellular pathway (Vidyasagar & Pammer, 1999). Future studies should consider the link between perceptual organisation, visual attention and magnocellular processing. The behavioural results seen in this study are consistent with neuroscience-based evidence for left hemispheric dysfunction since the left hemisphere controls the shift of attention towards the right hemisphere (Mesulam, 1981) and is also responsible for local feature analysis (Fink et al., 1997).

It should be noted that the stimuli in the current experiment differed from those employed in other research such as Happé (1996), who presented the Ebbinghaus illusion in black and white whereas the current stimuli were presented in orange and grey (although for every circle the test, reference and the flankers all have a luminance defined edge relative to the background). Another important difference in the procedure seen in this experiment with other studies using the Ebbinghaus and White’s illusion is that a two-alternative forced choice paradigm was implemented, whereas other studies required physical manipulation of the circle (Mruczek et al., 2015) and lightness of bars (Betz et al., 2015), e.g., adjustment. Stimulus differences such as these may be contributing factors in determining the extent of illusion in impaired readers, for example, participants can adapt to the stimuli if the adjustment time is long. A limitation in the current study was that participants were not screened for ASD, which can heavily influence performance in illusion susceptibility (Manning et al., 2017), hence it is not possible to say if an ASD difference was present between the groups. It is also possible that susceptibility to illusions in the poor reading population may be attributed to atypical decision-making strategies, which means sampling differences can have a pronounced effect on performance. However, the relatively large sample size provides an advantage in confirming group differences along with the fact that deficits were only present in the task that had local processing bias, i.e., Ebbinghaus and not White's. The results are also consistent with previous research that has shown visual illusions can be used to distinguish between poor and typical readers (Slaghuis et al.,1996; Facoetti & Molteni, 2001; Pammer & Lovegrove, 2001). Moreover, the use of visual illusions can be seen as a child-friendly since younger participants would consider this to be a 'game' and hence would be engaged with the task and particularly motivated to complete trials, making this appealing for diagnostic purposes in children. This leads to the possibility of measuring age-related changes that may impact susceptibility to illusions, since the sample included adults only the current data cannot address this question.

Although more research is required on visual illusions for assessing differences in reading groups, the current results provide the first evidence that visual illusions demonstrated differences in different reading groups based on perceptual organisation. This can provide a crucial step in understanding brain patterns in the dyslexic population and indirectly tell us how their brain processes visual stimuli. The current data indicates that when processing a configuration of multiple objects, slow readers will struggle to process the local features of stimulus configuration and ignore the surrounding distractors. Thus, variability in local versus global processing can lead to differences in subjective size perception, at least in the context of this experiment.

## 6.6. Conclusion

In summary, visual illusions play a crucial role in the study of reading disorders such as DD and can provide new evidence for the possibility of visual deficits in this population. In particular, visual illusions can give more insight into magnocellular, attentional and perceptual deficits in DD. Here, it is demonstrated that performance in illusions is impaired when slow readers are required to segregate a target away from distractors (deficits in local processing). An element of attention may play a role in illusion performance which has been linked to the magnocellular pathway. Additionally, it was shown that slow readers had equal performance to fast readers in illusory brightness perception as participants were likely making use of edge information. The results suggests that perceptual organisation may impair judgment in specific tasks, i.e., poor readers are susceptible to illusions that trigger local as opposed to global processing. These results suggest group differences in susceptibility to illusions may emerge from high-level processes and provides a crucial step for the invention of early visual diagnostic and preventative tools for individuals with reading impairments e.g., global before local training to improve reading skills in children with dyslexia.

# Chapter 7: Overall Discussion and Conclusions

## 7.0. Chapter Overview

The following chapter includes a summary of the findings for each experiment and the significance of these results in terms of reading in general, and in those affected with DD. Dysfunction in low-level regions, i.e., the magnocellular pathway, and its impact on higher cortical levels of visual processing will be discussed along with the limitations of the presented experimental approaches and in dyslexia research overall. The thesis will complete with ideas for future research and final conclusions.

## 7.1. Participants and Rational

To compensate for restrictions in recruiting dyslexic readers, large sample sizes were collected in order to generalise findings to a wider population. Evidence from epidemiological longitudinal studies have confirmed that developmental dyslexia (DD) is a highly prevalent neurodevelopmental disorder, affecting approximately 5-12% of individuals worldwide. Considering these statistics and the large sample sizes present in experimental chapters, it is probable that participants with confirmed dyslexia diagnosis were present in the experiments conducted (i.e., the slow reading group). Additionally, all participants were native English speakers meaning it was possible to infer general reading ability using reaction times from lexical decision making (Bakos et al., 2018), i.e., English is a phonologically inconsistent orthography (characterised by reading speed over accuracy) (Ziegler et al., 2010; Martens & de Jon, 2006; Katz et al., 2012). Since accuracy remained relatively equal, across each sample, between the slow reading group (defined by those in the bottom quartile for speed in lexical decision making) and fast reading group (defined by those in the top quartile for speed in lexical decision making) throughout all experiments, it is possible to reliably draw conclusions based on reading ability and compare this to current research on DD. To test magnocellular function across slow and fast readers, visual stimuli were manipulated to produce low contrast, achromatic, low spatial frequency (LSF) images in order to bias the magnocellular system (parvocellular cells do not respond to these conditions).

The purpose of this thesis was to test if high-level visual tasks and reading ability are behaviourally measurable based on the magnocellular deficit hypothesis, i.e., that difficulties in reading arise from reduced sensitivity in the magnocellular system projecting to high-level regions. By comparing slow and fast reading groups in variety of different high-level visual tasks, as the previous literature typically uses low-level tasks, e.g., coherent motion detection, or stimuli that is not specifically designed to bias the magnocellular pathway, differences were found between reading groups.

## 7.2. Segregation of Magnocellular and Parvocellular streams

Although results from electrophysiological and lesion studies have revealed substantial overlap in the type of information the parvocellular and magnocellular pathway process (Solomon, 2021), it is feasible to identify specific characteristics of visual information processed by both pathways. In chapter 1.5, the distinctions between the magnocellular and parvocellular pathways were highlighted from the retina onwards based on differences in their connectivity and morphology (Underleider & Mishkin, 1982). Most researchers agree that although there is substantial overlap in tuning properties between the pathways, there are significant differences that make it possible to selectively drive them with caution. Hence, our ability to tailor visual stimuli to selectively stimulate these pathways can allow us to compare certain pathologies that have been linked to impaired functioning of these pathways, such as DD to neurotypical controls. The ability to measure their distinct contribution to visual perception has been demonstrated from anatomical, electrophysiological and lesion studies (Solomon, 2021).

The segregation of M and P cells continues to projection layers in V1 (M cells project to layers 4Cα while P cells to 4Cβ). Originally, it was thought that M and P cells project to the dorsal and ventral brain regions, respectively (Maunsell, 1987). However, it is now clear there is substantial overlap between the two pathways (Maunsell & Newsome, 1987). Although complete segregation does not occur beyond V1, there seems to be a high level of functional modularity that arises from V1 to V2 and extends to higher cortical areas such as V4 and V5/MT. M and P cell response vary in terms of luminance contrast, with the slope plotted on a graph represented as the contrast gain of the cell. M cells have a greater response and higher contrast gain at low contrasts, for example in a study by Kaplan and Shapley (1982), M cells only needed a contrast of 1.2% to draw a response of five impulses, while P cells required a contrast of 9.1% (Kaplan & Shapley, 1982).

The most obvious difference is in the frequency cutoff of the cells, with P cells being tuned to higher spatial frequencies than M cells. This was demonstrated by Kaplan and Shapley (1982) who measured spatial resolution in terms of the highest spatial frequency in which response to a drifting sinewave grating vanished. They recorded averages of 8.0 c/deg for P cells, 5.7 c/deg for sustained M cells, and 2.5 c/deg for transient M cells at matched eccentricities. Note, the spatial frequency a cell is tuned to correlates with the receptive field size, for example, higher spatial frequencies are processed by cells with smaller receptive fields as seen with P cells. In conjunction with how sensitivity to spatial information is manipulated, temporal sensitivity is expressed in terms of sensitivity to varied temporal frequencies (how quickly the stimulus or signal changes). M cells are tuned to high temporal frequencies whereas P cells are tuned to lower temporal frequencies (Derrington et al., 1984). Levitt et al. (2001) found that M cells required a temporal frequency of 31.6 Hz to drive macaque cells to half their maximum response, while P cells required a frequency of 21.9 Hz. In terms of the nature and latency of their response, M cells provide a transient response (brief response to stimulus) while P cells provide a sustained response over the whole duration of a stimulus (Kaplan, 2004). Additionally, M cells have shorter response latencies, for example, M cells have a latency of 28 ms and P cells 68 ms for cells in the central 5 degrees meaning that M cells fire 40 ms faster than P cells (Levitt et al. 2001). This is supported by the larger axons of M cells which result in quicker axon conduction speeds in comparison to P cells. Maunsell and Gibson (1992) found that this means M cells can transmit information to V1 10 ms faster than P cells.

Another crucial factor which makes it feasible to develop magno- and parvocellular based stimuli for online-based testing is their sensitivity to colour information. The difference in their relative tuning to the wavelength of light means that P cells are sensitive to colour differences, while M cells are colour-blind meaning that our perception of colour is mediated by P cells. Hence, it is evident that while there is a considerable overlap in the tuning properties of M and P cells, they show preferential differences in their sensitivity to specific visual properties. This makes it possible to preferentially drive these cells by the careful selection and design of visual stimuli, i.e., by using high temporal frequencies, low spatial frequencies and low luminance contrast to bias the magnocellular pathway.

### 7.3. Object Recognition

Traditionally, cortical processing of visual object recognition was thought to occur along a bottom-up hierarchy of ventral areas; however, such accounts do not consider the complexity of visual information such as noise and clutter (Sharon et al., 2006; Ullman et al., 2002). The hierarchal as well as parallel (magno- and parvocellular) features of the visual system transfer many types of visual information from the retina to the LGN and visual cortex. These pathways are combined in the cortex where functional subdivisions V1 (blob and interblob) and V2 have been found. Combination of these pathways guides the dorsal (magno-dominated) pathway which projects to the parietal cortex and is mainly involved with space, attention, and movement while the ventral (parvocellular pathway) projects to temporal areas and is associated with mainly object recognition and cognitive control of attention.

In bottom-up processing, analysis of new stimuli does not require the learning of processes and relies on one’s external environment (Gibson, 1972). According to this view, after an image is presented to the eye, successive stages are rapidly activated through feedforward connections. However, a solely bottom-up approach for analysis of objects has been criticised. Firstly, the number of differences in objects such as occlusions, reflections, shadows, and lighting make it difficult to allocate which edge belongs to which shape - global analysis is therefore not considered using this approach. The feedforward approach gathers the features of objects rapidly but is unable to yield visual awareness (Lamme and Roelfsema, 2000). The activity of cortical neurons provides evidence against a feedforward approach only, horizontal connections within areas and feedback provided by higher areas can lead to dynamic changes in tuning. Specifically, higher level areas send feedback signals to V1 and in turn back to the thalamus. This discovery led to the emphasis of top-down processing in recognition, but how a such process takes place remains unclear (Bullier, 2001; Lamme & Roelfsema, 2000).

Bar (2003) specifically proposed that top-down facilitation is triggered by magnocellular input, which is projected early and rapidly to the OFC. This was later confirmed using neuroimaging studies (Kveraga, Boshyan and Bar, 2007). Top-down processing requires previous knowledge, expectation and experiences which is essential in the perception of new stimuli (Gregory, 1974). Instead of a direct route for object recognition by a hierarchy of visual regions along the ventral visual stream (slower analysis), the top-down facilitation model considers that a LSF image is rapidly projected to the OFC from low-level visual regions (leading to faster recognition). It is in the OFC where the “gist” of an image is predicted based on prior knowledge about the LSF appearance and then fed back to the ventral temporal cortex where the most likely object representations are determined. Kveraga, Boshyan and Bar (2007) found that in contrast to magnocellular information, parvocellular-based stimuli were recognised much slower considering they had a higher contrast, although accuracy was similar in both magno- and parvo-biased stimuli. They concluded that magno-biased stimuli differentially activates the OFC, as opposed to parvo-biased stimuli. Moreover, a performance advantage was seen for magno-biased stimuli through OFC activity but not for parvo-biased stimuli (the opposite effect was seen in the fusiform gyrus). Hence, the role of magnocellular projections linking early visual regions and the inferotemporal cortex for object recognition via the OFC warranted further exploration, i.e., early predictions for object recognition relies on magnocellular input, which has shown to be defective in those with reading difficulties.

In the first experiment, it was hypothesised that slow readers would be compromised in their object recognition abilities based on weakened magnocellular projections to the OFC, required for the facilitation of object recognition. The use of low luminance and low spatial frequency object stimuli, composed of Gabor patches, targeted the magnocellular pathway – this method has been confirmed by magnocellular activation in electrophysiological and fMRI experiments (Demb 1998; Stein, 2019). The rational behind the study was based on research that has shown dysfunction in the magnocellular system of dyslexic individuals (Galaburda & Livingstone, 1993;

Skottun, 2000; Stein, 2001, 2019, 2021). It was predicted that since LSF visual stimuli (magno-biasing) is the key to triggering top-down facilitation, then an impairment in this system is likely to also affect object recognition, i.e., deficits in low-level vision can impair object recognition in higher cortical areas. The results of the first experiment provide support for both top-down processing of object recognition and potential deficits in magnocellular system of poor readers. These conclusions were drawn as stimuli used to preferentially target the magnocellular pathway led to much less efficient object recognition in slow compared to fast readers.

In Kveraga and colleagues' experiment, it was shown that speed of object recognition is improved for magno-biased stimuli, along with positive MRI signal changes in the OFC. Hence, training programmes designed to target the magnocellular pathway could potentially strengthen magnocellular-driven top-down facilitation, which can in turn engage bottom-up processes required for object recognition. Since the magnocellular pathway conveys information to the parietal cortex and has connections with the prefrontal cortex and the OFC, high-level tasks that target these areas may also be implicated – this was explored in later experiments. Overall, the current results provide evidence for poor object recognition in slow readers as a result of deficits in the magnocellular system.

### 7.4. Visual Search

Mounting evidence has confirmed the importance of the fronto-parietal network for attentional control in reading acquisition, along with other cognitively demanding tasks such as problem solving, and decision making (Taran et al., 2022; Ekstrand et al., 2020). The first phases of letter identification and orthographic development has been linked to the parietal network which is associated with visuo-attentional processing (Ekstrand et al., 2020). The ability to focus attention leads to appropriate extraction and selection of visual information and stronger visual word form representations (Finn et al., 2014). Sluggish attentional shifting (i.e., failure of automatic attentional processes to disengage effectively, leading to challenges navigating from one item to the next) could therefore interfere with rapid stimulus-sequence processing and lead to the difficulties in reading seen in dyslexics (Lallier et al., 2015; White, Boynton, & Yeatman, 2019; Franceschini et al., 2018). Visuospatial attention is a good predictor of future reading skills and strengthening the pathways that lead to better control of attention can enhance reading skills (Franceschini et al., 2012, 2013). For example, the substantial evidence for intervention programmes such as action videos games (AVG) has recently been documented (Bertoni et al., 2021; Franceschini et al., 2012; 2017). Franceschini et al. (2012) demonstrated that when children with dyslexia played video games for 12 hours they improved in reading speed without trading-off accuracy. This excluded involvement of phonological or orthographic training and was more effective than a child's development in reading after one year of traditional reading treatments. Dyslexic children also showed improvement in attentional skills indicating that AVG can help children focus visual attention which can translate onto reading. Similarly, improvements in reading skills using AVG were also noted by Franceschini et al., 2017 in English speaking children with dyslexia (a deep orthography), improving their shift of attention from visual to auditory modality.

Visual search tasks rely on sensory, perceptual, and cognitive processes. Visual search paradigms have therefore been used to investigate a range of phenomena such as attentional shift. Measuring the active scanning of the visual environment for a specific target in a particular location is a common method for measuring attention in general. The attentional spotlight theory has been used to describe how selective attention moves across the scene and selects important/target information. Surrounding stimuli in our peripheral view can distract attention away from the target prolonging the spotlight of attention from shifting. Studies on dyslexic readers have demonstrated poor visual search abilities in search conditions with a varied number of distractors (Vidyasgar and Pammer, 1999). Results from search tasks have mainly shown that dyslexics struggle to direct attention towards a target and simultaneously ignore irrelevant information, especially when a greater number of distractor items are present. The difficulties dyslexic readers exhibit during search tasks have been linked to the fronto-parietal network which receives input from the magnocellular pathway. Hence, a focus on strengthening the fronto-parietal attentional control network, such as with AVG training, can help improve shift of visual attention in search tasks.

Although studies have linked impaired visual search in dyslexics to dysfunction in the magnocellular pathway indirectly (i.e., guiding attention), there have been no documented cases that directly measure magnocellular function using LSF stimuli to preferentially engage the magnocellular pathway. In the current study, natural scenes were selected and scrambled across three different conditions: magnocellular isolating, parvocellular isolating, and a combination of both (magnocellular/parvocellular). Studies typically use traditional search tasks to investigate search times of those with dyslexia compared to controls (i.e., identifying a target amongst multiple objects), however, the current study used images of scrambled scenes (to avoid fast reaction times) and a swirl as the search target - other targets, such as letters, would be easily identified in such conditions. The findings, overall, indicate that search times are longer in parvo-biasing conditions for both slow and fast readers, at least for the task at hand (i.e., lower isoluminant contrast reduces the relative target salience). However, when comparing between reading groups, both slow and fast readers displayed similar search times in the parvocellular condition. Significant differences were measurable in magnocellular and magnocellular/parvocellular (combined) conditions, with large effect sizes, i.e., slow readers displayed significantly slower search times compared to fast readers. The current data suggests that defective magnocellular input to the parietal cortex may affect gravitating attention towards the target location. In conditions where magnocellular input was not required (i.e., participants made use of the parvocellular pathway), participants were able to direct attention towards the target stimulus, to the same extent as fast readers. The following findings provide evidence for specific magnocellular weakness as the core deficit in people with reading difficulties. This ultimately leads to inefficient control of attention, required for reading accuracy, reading fluency, and comprehension (Macdonald et al., 2021).

Overall, the data is consistent with deficits in magnocellular projection to the parietal cortex. This finding could potentially assist in developing intervention programmes that incorporate more specific magnocellular-based tasks (e.g., AVG) that focus on directing attention and strengthening magnocellular connection to the parietal cortex, as opposed to more generalised visual training programmes (Qian, 2015). The use of video games in improving magnocellular input to the parietal cortex provides a practical and engaging intervention for dyslexia, effectively reducing reading disorders.

### 7.5. Emotional Face Perception

Holistic processing is a cornerstone of facial recognition research. It is widely agreed across studies that dyslexic readers have abnormal facial recognition when analysing segments of a face (i.e., local processing). However, holistic processing of faces appears to be intact which can be explained neuroscientifically by a dissociation between word and face processing regions where global processing occurs (Sigurdardottir et al., 2021) – whereas an association is present when analysis is feature based, e.g., focusing on specific facial parts such as the eyes, nose, and mouth.

Featural versus holistic word processing has presented with mixed results in literature (Wang et al., 2016; Brady et al., 2021 and Sigurdardottir, Arnardottir & Halldorsdottir, 2021). Experiments that measure holistic face processing usually compare inverted faces to upright faces (the face inversion effect). Analysing upright (neutral) faces mainly requires a holistic approach, whereas inverting faces relies on local information, like objects (i.e, it cannot be perceived as holistically). The differences between recognising upright and inverted faces measures the extent to which one relies on holistic processing. A plausible explanation as to why holistic processing of faces in dyslexic individuals remains intact as opposed to configural face processing is the concept of a double dissociation between the right and left FFA. It has been proposed that dysfunction in face processing lies within the left FFA which is involved in analysing facial features (and is functionally connected with the VWFA), whereas the right FFA is involved in holistic analysis of the whole face and is functionally independent (Sigurdardottir et al., 2021). Overactivation in certain right hemisphere regions, such as the right FFA, could explain why many dyslexics possess strengths in specific tasks (Vlachos, Andreou & Delliou, 2013; Waldie et al., 2013). These findings are consistent with atypical activation of right hemisphere regions in dyslexic individuals.

An area which has not yet been explored in dyslexia research literature is the concept of local versus global processing in emotional face recognition – research has generally focused on facial recognition involving identities, rather than emotion-based, behavioural tasks (Behrmann & Plaut, 2013; Sigurdardottir et al., 2015, 2021; Gabay et al., 2017). Critical to socialisation, some studies have found that children with dyslexia are less accurate in interpreting emotions, specifically those that have scotopic sensitivity syndrome (Whiting & Robinson, 2009). In the neurotypical reading population, holistic and local emotional face recognition has been investigated, i.e., some studies have found that negative emotions induce local processing, while positive emotions which trigger global processing (Curby et al., 2011). Other studies have claimed that all emotions are processed holistically, irrespective of the type of emotion expressed (Murray, 2019). Considering the notion that emotion type influences global and local processing, accuracy in emotional face classification can, theoretically, be compromised if issues are present in global or analytic processing. Since dyslexic readers have shown problems with local processing (i.e., in faces, objects and words), poor readers may display difficulties when classifying negative emotion type which relies on local before global processing (Curby et al., 2011).

Prior to beginning the experiment, participants took part in two questionnaires (PHQ-9 and AQ-10) which showed, between the subsequently derived fast and slow reading groups, there was (1) no difference in non-clinical depression levels and (2) the fail rates of an autism spectrum disorder (ASD) screener were comparable. The reasoning behind employing these tests is that both depression and ASD can alter emotional face recognition (Jelili et al., 2001), and both conditions have a higher rate of co-occurrence amongst dyslexics.

Result from this experiment showed that, overall, emotional face processing is comparable between slow and fast readers in the full spatial frequency ‘full-face’ condition. Differences were found in accuracy between reading groups when classifying the following facial expressions: sad (full-face condition), fear (magno-biasing), anger (magno-biasing), neutral (magno-biasing) and surprised (magno-biasing). Although no clear pattern was seen in terms of negative emotions, participants were equally accurate in classifying ‘happy’ faces across full and magno-biasing conditions potentially due to an increase preference towards holistic processing for this emotion type. Considering all emotions grouped, a significant difference was found between slow and fast readers in the magno-biasing emotional face classification condition, but not in the full-face condition. The initial hypothesis, based on literature, that differences in face classification between slow and fast readers will be more apparent when viewing negative emotions (e.g., sad and disgust) due to a bias towards local processing was rejected as clear patterns were not observed.

Results indicate that, overall, emotions may induce a holistic processing style in slow readers (in normal conditions), irrespective of emotion type. Many studies also agree with the view that humans analyse all emotions holistically and local feature discrimination occurs at a later stage (Omigbodun & Cottrell, 2013; Tanaka et al., 2012). Poor readers may have a specific advantage for holistic face classification in the right FFA, with some studies even claiming overactivation in specific right hemisphere regions (Waldie et al., 2013). However, when sole use of the magnocellular pathway is required for emotional face classification, differences can be seen between slow and fast readers, with slow readers performing worse overall. A possible explanation for these findings considers low-frequency images, which are analysed through the OFC i.e., through magnocellular signals triggering fast activation of the OFC (see Bar et al., 2006), which plays a critical role in the emotional recognition of faces. Impaired magnocellular projections in slow readers can therefore affect emotional face processing.

Overall, the results provide a step towards distinguishing between slow and fast readers based on emotional face processing. Targeting the magnocellular pathway does not affect emotional face classification in fast readers, but slow readers appear to struggle in these conditions. Dysfunction in the left hemisphere, which is well-established for speech and language, may lead to compensatory mechanisms in certain right hemisphere regions in slow readers such as holistic processing in the right FFA. This may also link to their remarkable artistic and creative talents in comparison to typical readers (Stein, 2019). Overall, it seems that superiority that some slow readers may exhibit in creative visuospatial contexts and holistic processing can be used to help assist in creating remediation programmes.

### 7.6. Scene Gist

Research presents a selection of theories on how one recognises a scene – some studies claim that scenes are initially recognised as a group of objects with global perception at the highest level of processing, i.e., local before global processing (Bosch, Zisserman & Munoz, 2006; Fei-Fe & Perona, 2005). However, scenes can be recognised at their highest level after only a brief exposure, i.e., their “gist” can be identified quickly and accurately. Olivia and Torralba’s (2001) model of scene perception suggest that a visual scene is first processed in a global manner based on a “spatial envelope”, and that the holistic representation of a scene is more important than localised information for categorisation. Analysing the local details of a scene first can lead to delayed scene recognition. The following experimental chapter considers the effect of scene gist recognition when presented in full-colour, luminance-only, and in magnocellular-biasing conditions, in different retinal “image-type” views (central “small”, peripheral “ring”, and central/peripheral “large”). The role of colour in scene gist has been shown to have an advantage when the colour is diagnostic and presented peripherally, this condition was included since dyslexic readers have been shown to have preserved chromatic contrast sensitivity (at least centrally, Rodrigues et al, 2017).

Retinal position plays an important role in scene recognition and can affect accurate classification. Central vision is contained within a ~5° radius of fixation and its high visual acuity is essential in directing attention towards objects, whereas peripheral vision takes up the vast majority of the visual field and exceeds the central 5° radius. Peripheral information reaches the LGN and V1 before central information - and as the gist of a scene is acquired in a single fixation, peripheral information may be considered as more important (DeValois & DeValois,1988; Carrasco et al., 2003). If attentional processes are required in scene recognition, central vision will dominate. To test the relative contribution of peripheral and central vision in scene gist a “ring” and “small” condition was employed, respectively. These conditions were used in an experiment by Losky and Larson (2009), who found that the periphery was more useful than central vision for maximum performance in scene gist identification, more or less equal to viewing the entire image.

Here, it was hypothesised that scene recognition will be compromised in the magnocelluar-biasing condition as deficits in the magnocellular pathway can potentially halt holistic scene recognition in slow readers, i.e., a holistic representation of a scene is important for single "gist" fixation. Additionally, a peripheral advantage was predicted for classifying the gist of a scene as poor readers have been shown to have an advantage for stimuli presented in their periphery (Loressu et al., 2004). It was shown that classifying scene gist is impaired in the "large" magnocellular condition, but not when scenes are presented in colour, i.e., when parvocellular input existed, or in the luminance-only condition for slow compared to fast readers. Although the magnocellular pathway is colour-blind, similar performance between reading groups in the luminance-only condition may have been attributed to parvocellular input (i.e, participants were making use of high spatial frequency information). A peripheral or central viewing advantage was not seen for the reading groups in this study (methodological limitations have previously been discussed).

Research has suggested that the right temporo-parietal junction plays an important role in global processing. As magnocellular information is projected to the parietal lobe, global processing of scene-related visual information can be affected if the magnocellular pathway is not functioning properly. In literature, a global over local processing style has been demonstrated across individuals for scene "gist" recognition, however, in conditions where sole use of the magnocellular pathway is required these benefits may be diminished in impaired readers since they exhibit dysfunction in their magnocellular system (involved in holistic processing). The current results have implications in the development of training methods to encourage a global processing style for visual scene recognition and, hence improve reading skills. This can be achieved by strengthening magnocellular connections, for example, global before local processing can be encouraged with the use of visual attentional and AVG training, which leads to improved reading skills such as pseudoword repetition (Franceschini et al., 2017).

Finally, studies have shown that viewers are able to set the chromatic gamut of an image of a natural scene to within 2% of the original image (Nascimento et al., 2016). This implies that individuals have an unbiased knowledge of colour appearance in natural scenes without the need of a reference image. A similar task was included in this current study (i.e., as a parvocellular control), participants were tasked with judging whether the saturation of a previously unseen scene was too high or too low. Both reading groups has similar judgments of scene saturation in this task (equal PSEs were measured between the groups) providing further evidence for sufficient function of the parvocellular pathway in slow readers.

### 7.7. Visual Illusions

The use of visual illusion allows psychophysical measurements of perceptual differences which provide an insight into the neural mechanisms involved in perceived reality. Both reading and understanding optical illusions require processing of visual information in the form of shapes, contrasts, and motion (Werth, 2021). Therefore, visual illusion ‘performance’ potentially correlates with reading deficits, since both rely on some shared neural mechanisms (Kristjánsson & Sigurdardottir, 2023). The majority of evidence for the role of the magnocellular pathway in visual illusions comes from the motion Ternus display (Ternus, 1938), where children with DD show a significant reduction in group motion perception. Illusions are therefore a great way of identifying limitations in the visual system of dyslexic readers since it can prevail how they perceive the world in an engaging, non-invasive way.

In contrast to most literature on DD which agrees that dyslexic readers prefer a holistic processing style for certain visual stimuli, studies on patients with ASD have found a unique perceptual-cognitive style that enables them to analyse local aspects of an image accurately (Koldewyn et al., 2012). The Ebbinghaus illusion is ideal for analysing global/local preferences since it requires the analysis of local details (inner circle surrounded by circles of varying size). The tendency of individuals with ASD to prioritise analysis of local details means that they are able to have more accurate size judgements of the inner “test” circle compared to the reference circle, i.e., they are not as misled by the surrounding “distractor” circles that can interfere with size perception. Since the opposite has been seen in those with dyslexia (they are impaired in analysis of local details), a comparison was made between slow versus fast readers on their relative size perception using the Ebbinghaus illusion, i.e., the extent to which they perceive the test circle surrounded by larger circles as being smaller/larger than the reference circle surrounded by smaller circles. As there is subjective variability in participant responses to illusions, measuring the point of subjective equality (PSE) is essential for comparisons (the point at which the test and standard stimuli appear the same). For the Ebbinghaus illusion, a greater shift in PSE was displayed for slow readers compared to fast readers, i.e., slow readers needed a greater difference in the test circle to perceive it as equal in size to the reference (they were more susceptible to the illusion). This was the predicted result as dyslexics find it difficult to ignore the context of an image (Hokken et al., 2023) - large interference from local features in the Ebbinghaus illusion means that slow readers prioritised local details and were not able to separate the local from the global image (i.e., the surrounding circles). Another explanation for these results involves problems with attention in the parietal cortex. The inability to focus attention on the target (reference circle) will increase susceptibility to the illusion as participants will struggle to inhibit irrelevant information, i.e., surrounding circles in this case. Therefore, poor readers are likely to perceive illusions more ‘strongly’ if they are unable to focus attention on a relevant target and ignore distractors. This account considers magnocellular projection to the parietal cortex which is crucial for focusing attention.

Another illusion which has not been investigated in dyslexia literature is the White’s illusion, here the same physical luminance can elicit different perceptions of brightness, i.e., stripes of a black-and-white grating are embedded by grey ‘bars’ of the same luminance. The grey bar placed into the black grating (surrounded by white) is perceived to be lighter than the grey bar placed into the white grating (surrounded by black). In this current experiment, both slow and fast readers were equally as susceptible, i.e., they both perceived the grey bars placed on the black stripes to be lighter than the grey bars placed on the white stripe, and importantly by the same amount.

The main theoretical framework proposed to explain the White’s illusion considers low-level mechanisms that activate luminance values which generate perceptions of brightness. According to this theory, it was predicted that slow readers would be more susceptible to the illusion (i.e., require greater differences in luminance contrast to perceive equal brightness between the grey bars). The prediction was made as according to the magnocellular deficit theory, sensitivity in detecting changes in luminance is impaired in poor readers, hence their brightness perception could be altered. Furthermore, they are less likely to ignore the surrounding context (i.e., in this case, the white stripes neighbouring the grey-on-black bar and the black stripes neighbouring the grey-on-white bar) and focus on the target. However, the current experiment indicates that differences in perceived brightness between the grey bars are equal across slow and fast readers. Potentially, this may have resulted from participants taking advantage of high spatial frequency information (i.e., the parvocellular pathway), corresponding to sharp edges. Luminance contrast across the edges, therefore, influences perceived lightness in White's Illusion which slow readers are able to make use off (Betz et al., 2015).

Overall, visual illusions provide a powerful and non-invasive tool for understanding how the brain processes unordinary visual stimuli. This method is more engaging for children compared to standard reading tests and hence could potentially be used to identify those at risk for reading impairments, such as DD, before reading skills develop. Remarkably, there are limited studies investigating illusory perceptual organisation in DD, although many of these individuals display visual deficits in the way information is grouped. Thus, further research is proposed to test the efficacy of different types of visual illusions for early identification of DD.

### 7.8. Experimental and Research Limitations

Restrictions in conducting the initial set of in-person lab-based experiments during the COVID-19 pandemic resulted in the conversion of experiments to online versions where possible. Participants were consequently categorised based on reading speed, rather than a formal diagnosis of dyslexia. However, these limitations were overcome by using a larger sample size and by using LDTs as a measure of reading ability which has been used to classify dyslexic individuals/slow readers based on reaction times (Martens & de Jon, 2006). Additionally, other studies have persuasively categorised dyslexics based on reading speed deficits (Tressoldi, Stella, & Faggella, 2001; Zoccoletti et al., 1999). Throughout all the experimental chapters, no speed-accuracy trade-offs were found in participants for lexical decision making, this in-turn allowed for meaningful groups to be formed based on RTs (slow versus fast readers).

It is also noted that since testing was online, it was not possible to control for external variables, for example, participants' surroundings, and importantly viewing distance and screen sizes, hence in retrospect meaningful conclusions could not be drawn in terms of the peripheral versus central view contribution to scene gist (chapter 5).

Another limitation that should be considered is testing of magnocellular function, i.e., isolating or biasing the pathway. This raises the question as to what extent using stimuli to "bias" this pathway excites magnocellular cells only. Despite the large body of evidence in support of colour-blind, low contrast information for measuring magnocellular deficits, Skotton (2000) suggested that achromatic contrast sensitivity loss may not be a good measure of magnocellular function as this in part uses high spatial frequency information, with some studies showing no differences in contrast sensitivity loss between dyslexics and normal readers. At certain eccentricity, magnocellular and parvocellular neurons in both pathways practically have the same spatial resolution (Crook et al., 1998). Interestingly, red light via coloured filters on text have been shown to lead to improved reading. Since red light is thought to inhibit the magnocellular pathway (Chase et al., 2003), this provides support for lack of magnocellular input in reading. However, red light is not specific to the magnocellular pathway and these improvements may result from other visual factors such as alleviating visual stress (Skottun, 2005; Denton & Meindl, 2016). Moreover, the use of coloured filters in dyslexia has mixed results (Razuk et al., 2018; Skottun & Skoyles, 2007; Chase et al., 2003). Nevertheless, studies using VEP has confirmed that low-contrast rapidly moving stimuli used to target the magnocellular pathway can be used to distinguish between typical and dyslexia readers. However, this may be consistent with other aetiologies such as a temporal processing deficit (the ability to process rapidly presented sounds) (Ben-Yehudah et al., 2001). Borsting et al. (1996) reported that reduced sensitivity to LSF (at 10 Hz) is only specific to a subgroup of dyslexic individuals, and this may not be because of a magnocellular deficit. A subgroup of dyslexic readers had visual problems that were attributed to magnocellular problems in a study by Amitay et al. (2002), but they also found issues in other visual tasks that were not related to magnocellular function.

This brings us to the degree of ventral stream involvement and its interference with reading skill. It is possible that participants in the luminance-isolating condition, specifically when classifying scene gist (chapter 5) and interpreting the White's illusions (chapter 6), may have been able to utilise HSF information from the ventral stream. Thus, the degree in which participants may have benefited from parvocellular involvement in experiments and the degree to which the magnocellular and parvocellular pathways are segregated is questioned.

Another important point to consider is the level of reading skill. All participants selected for the experiments were educated adults that have a sufficiently developed language and reading system. Testing school aged children before they start reading or while they are in the processes of learning to read would likely enhance the findings seen in the current experiments since immaturities in the magnocellular system are seen in young children (Benedek et al., 2016), regardless of if they have a dyslexia diagnosis. Participants with lower education level are likely to have more severe reading impairments and thus this could lead to worse performance in visual tasks. For example, research by Sigurdardottir et al. (2019) suggested that education levels of dyslexia readers are correlated to severity of the visual deficits.

An alternative proposal for the visual problems that dyslexic individuals experience is due to general lack of experience with letter and text stimuli due to simple lack of exposure, as individuals with dyslexia are less likely to read. However, this view does not consider non-word visual stimuli, i.e., impaired recognition of objects in dyslexics are unlikely to be the result of lack of reading experience. Gosawami (2015) stated that visual deficits in dyslexia are a consequence of problems with the linguistic process, rather than a direct cause. Phonological recoding involves the combination of phonological and orthographic knowledge of words; the mapping of sounds (phonemes) onto visual information (graphemes). He disputes that there have not been any recorded credible arguments against the idea that visual deficits result from reduced reading experience. This view was also proposed by Galaburda (1999) who claimed that changes in low-level processing in the brain may be the consequence of developmental changes occurring in higher-order cortical areas, quoting that “we can be reasonably certain that there are cognitive deficits and perceptual deficits, but we cannot support the idea that the perceptual deficits are causally related to the reading". A more recent review and meta-analysis, however, suggests brain differences in the right parietal lobe of pre-reading children predicts those at risk of dyslexia, suggesting that visual deficits may not be the consequence of lack of reading experience (Vandermosten, Hoeft & Norton, 2016). Additionally, Gori et al. (2015) showed visual motion perception correlated with future reading skills (irrespective of auditory or phonological skills), and training specific to the magno-dorsal pathway (not targeting auditory or phonological stimulation) lead to improved reading skills in children and adults with dyslexia – disproving the symptom over causal claim.

### 7.9. Magnocellular Deficit – Cause or Effect?

The magnocellular theory remains one of the most well-established and accepted neurobiological theories explaining the experiences encountered by dyslexic individuals. However, as demonstrated by researchers such as Gosawami (2015) and Galaburda (1999), there is disagreement in literature on whether a weak magnocellular system in dyslexics is a consequence of inadequate practice in reading skills, or if it is a direct cause of reading difficulties. More recently, emerging evidence has pointed to magnocellular deficits as a cause, not a consequence, of reading difficulties. If the cause of dyslexia relates to the magnocellular system then training magnocellular-dorsal functions, such as that seen in attention-focused video games, can improve reading skills in dyslexic individuals (Gori et al., 2016; Qian, 2015, Peters et al., 2021).

The magnocellular-dorsal pathway locates and accurately detects and times the order of visual events such as scanning letters in a word during reading. Thus, a functioning magnocellular pathway is essential for the correct sequencing of letters and to memorise the visual form of words. Additionally, analysing the phonological structure of words is impacted because of the indirect effect of orthographic problems caused by the magnocellular pathway on learning the representations of letters in a word. However, one cannot conclude that impaired magnocellular function is the sole cause of dyslexia. The majority of studies measuring magnocellular function in dyslexics agree that a magnocellular deficit is present in most dyslexics with Gori and colleagues claiming that this causal relationship “virtually closes a 30-year long debate’ (Gori et al., 2015). However, the controversial debate of magnocellular processing as the root cause of has been argued against by many researchers (Skottun & Skoyles, 2005; Gosawami, 2015). These have been challenged by perceptual differences in poor compared to neurotypical readers that rely on magnocellular processing, such as performance in coherent motion and Ternus illusions. Furthermore, there are a large number of dyslexics that do not present with a phonological deficit (Castles and Coltheart, 1993; Peterson et al., 2014), hence this cannot account for all cases of DD and does not justify why children fail to learn letter-sound correspondence. Successful sequencing of letters also relies on accurate timing of auditory events, i.e., temporal processing. Attention to the order of sounds in words is largely dependent on ‘transient’ systems involved in timing sensory and motor events, a process medicated by magnocellular neurons (Vidyasagar, 2013). This has consistently proven to be impaired in dyslexic individuals, supported by anatomical evidence showing smaller and more disorganised magnocellular layers within the LGN of dyslexics (Livingstone et al., 1991).

The main difficulty presented in literature is that “correlation does not necessarily prove causation”. Although unlikely given the evidence presented, the point that magnocellular sensitivity may be the outcome of reading failure, i.e., less practice of visual skills, has been argued. This theory can be challenged by comparing magnocellular sensitivity of dyslexics to typically developing children matched in terms of reading age, to prevent additional visual training that older dyslexics have been exposed to. Gori et al. (2015) was able to demonstrate that typically developing younger children that had similar reading experience to dyslexics had stronger visual magnocellular function. Studying pre-reading children, along with using controls such parvocellular stimuli that targets static and form, will allow arguments such as “general lack of concentration” to be rejected, especially as some studies have proven that dyslexics may actually have increased contrast sensitivity at high spatial frequencies (Lovegrove et al., 1982) and stronger colour discrimination (Dautrich, 1993).

Although the current thesis is consistent with a magnocellular deficit as a cause of reading difficulties, these results should be replicated on aged-matched children before and after reading acquisition i.e., further longitudinal studies are required. This will prevent other variables from explaining reading difficulties, such as reading experience. Furthermore, the control experiments throughout this thesis provide further evidence for a magnocellular-specific deficit, as opposed to a general visual deficit or lack of exposure to visually presented words. In chapter two, slow readers had comparable search performance to fast readers in the parvocellular only condition. In chapter three and four, emotional face recognition and scene gist recognition was comparable in both reading groups when parvocellular input was required. Additionally, a colour control test showed similar scene colour judgment. Opposingly, consistent differences were seen between slow and fast reading groups across all experiments that required sole use of the magnocellular pathway. Overall, these results are collectively in line with causal links between the magnocellular-dorsal pathway and reading difficulties. Randomised controlled trials showing improvements in reading following magnocellular, compared to other interventions are essential on a larger scale i.e., improvements in reading accuracy and fluency were seen in dyslexics after magnocellular training in comparison to phonological training which had little impact in a study by Lawton, 2016. Further long-term studies are also required to draw definitive conclusions and to identify children at risk of developing DD.

### 7.10. Are Magnocellular Deficits Brain-wide or Brain-specific?

Another question which remains for further research is whether magnocellular deficits are a brain-specific or brain-wide problem. As mentioned in previous chapters, the magnocellular-dorsal pathway begins in the ganglion cells of the retina and ends in the parietal cortices where attentional mechanisms occur (Facoetti, 2012). The development of the visual magnocellular system directly and indirectly effects motion sensitivity, binocular fixation (hence visual localisation) and perceptual stability, all of which has been shown to be impacted in dyslexic individuals. Thus, good magnocellular function is required for high motion sensitivity, stable binocular fixation and effective development of orthographic skills. The following thesis demonstrates potential routes in which weak magnocellular signals can impact vision beyond the magnocellular layers of the LGN. Magnocellular projection to the OFC provides connections to the inferior temporal cortex where bottom-up processes for object recognition occur. The OFC also has multiple reciprocal connections within the amygdala with fMRI showing activation in the right amygdala for magnocellular-biasing emotional stimuli (Kveraga et al., 2007); this implies that poor magnocellular function may impact high-level decision-making processes. Further research such as neural fibre tracking with diffusion imaging is required to study magnocellular connections to brain-wide regions. The current results collectively suggest that poor magnocellular function can impact wider high-level brain regions as opposed to just early subcortical levels involved in motion and colour.

## 7.11. Future Directions

There has been increased recognition on visual accounts to explain the symptoms associated with dyslexia (Bosse, Tainturier & Valdois, 2007; Stein 2001, 2019, 2021). There is no clear cut-off point for being classified as dyslexic and symptoms appear to be influenced by many factors. It is important to identify these risk factors before negative effects of reading are felt, and hence high-level visual performance could play an important role in identifying those at risk of developing reading difficulties before learning to read. It is important to establish which group of dyslexics possess visual deficits and the pathways involved in higher visual processing. The current thesis provides unique evidence for magnocellular specific issues that feed high-level vision, but studies are required that compare and assess different structural and functional brain-related factors specifically in individuals with dyslexia. This is critical in moving forward with dyslexia research.

The possibility of multifactorial accounts of dyslexia disregards many researchers views on one cause for DD. However, it is necessary to extend the experiments conducted here to a large group of participants to assess if similar patterns emerge across all poor readers or if only a subgroup of dyslexics are affected, possibly with exacerbated RTs, for example. This could be achieved by a cross-sectional study to analyse data across subjects to see if dyslexics show consistent deficits in specific modalities in comparison with others, for example, some may have cognitive impairments while others may have sensory and motor deficits. This can help determine whether non-phonological deficits such as magnocellular impairments are specific to only a subgroup of impaired readers. Large-sample longitudinal studies are necessary to draw robust conclusions regarding sub-types of dyslexia and identifying overlap with other theories, i.e., a combination of neural and behavioural studies are required to classify subtypes. These suggestions are in agreement with Goswami (2015) who suggested that the only way of clearly addressing the causality of DD and determining if training programmes can alleviate symptoms and improve reading is through longitudinal studies.

Current results should be replicated in pre-reading children. Children who display problems with visual tasks should be followed up with appropriate training to assess if visual deficits subside, and if reading skills are affected, alongside a control group. A longitudinal study has recently shown that stronger neural response to faces in children was positively correlated with reading performance after two years (Liebig et al., 2021). Lower activity in specific brain regions can therefore be used to predict future reading skill prior to formal reading instruction. Research into critical periods is required to measure various visual functions that could be impaired before a child learns to read as fast identification of those at risk of developing reading conditions before learning to read could help improve future reading skills.

There has been a vast amount of research on the effect of visual-based training programmes on reading fluency, however the contribution of the magnocellular pathway to these improvements requires further investigations. For example, a visual symbol search training programme for only one month (10 minutes a day) can be used to stimulate superior parietal lobules (which receive magnocellular projections), leading to enhanced reading performance (Vialatte et al., 2023). As mentioned previously, the role of video game-based training has been established in improving visuospatial attention and enhanced reading fluency in children with dyslexia and that the duration of these benefit can last for weeks (Ren et al., 2023) – these improvements have been indirectly linked to the magnocellular system. Participants that had the greatest improvement in magnocellular-temporal processing (measured using a flicker fusion task) also had the greatest improvements in reading (Peters et al., 2021). Future studies would benefit from parvocellular-based control tasks to see if improvements are specific to magnocellular function. Additionally, electrophysiological evidence alongside psychophysical testing would strengthen conclusions, for example, investigating N2 amplitude in the right hemisphere before and after magnocellular-based training programmes. Stronger connectivity in the dorsal fronto-parietal network regions has been linked to faster perceptual decisions (Brosnan et al., 2020), thus neuroimaging studies in these regions in people with DD could reveal dysfunction related to psychophysical tasks.

Another route for further exploration involves comparing global versus local processing preference across objects, faces and scenes. For example, some studies demonstrate an advantage in global processing of faces, while other researchers have demonstrated no such advantage in the analysis of certain scenes and objects (Franceschini et al., 2017; Sigurdardottir et al., 2018). The relative contributions of magnocellular input should be investigated in these regions. The right FFA, involved in holistic processing, seems to be intact in dyslexic individuals and MRI studies have revealed activation in right face processing regions (Gerlach et al., 2022). It is possible that there are different perceptual mechanisms underlying holistic processing (Tso, Chung & Hsiao, 2020) which could explain why dyslexics prefer global processing styles in certain visual tasks. Future studies should focus on the neural mechanisms behind holistic processing in different high-level tasks, which may guide intervention programmes for holistic processing of words and hence, encourage faster reading.

## 7.12. Significance of Research

Much of the research between dyslexic and neurotypical readers suggest differences in feature detection, stimulus detection, visuo-spatial attention and object recognition which appear to affect both visual and auditory domains. The present findings support behavioural, psychophysical, electrophysiological and neuroimaging research regarding high-level deficits in impaired readers. The current thesis links deficits in low-level regions, specifically the magnocellular pathway, to high-level cortical areas which can affect attentional and cognitive processes. Markedly, treatment programs for dyslexia have mainly focused on targeting phonological difficulties (Torgesen, 2005). Although there is evidence for impaired phonological learning, phonemic awareness and phonemic fluency in dyslexic readers, the phonological deficit theory has little explanatory power and it is unlikely to be the only determining factor behind reading difficulties (Stein, 2018). Since reading requires a fully developed sensory system to accurately process and interpret written words, and approximately half of children with dyslexia have reported issues with their vision (Wilkins 1995), visual deficits provide an appealing explanation for the cause of dyslexia. These complications exist in children with DD despite their phonological symptoms (Lallier et al., 2013).

One of the major issues in dyslexia research is the degree of specificity and its association with other learning difficulties. The discussion surrounding the definition of dyslexia and whether different ‘subtypes’ exist have led to arguments about a single underlying cause, or whether there is a distinction between sensory and phonological subtypes of dyslexia. The current research supports the argument that difficulties with reading are not specific to language only. This is crucial for the treatment and diagnosis of DD, for example, by understanding the neural pathways behind reading difficulties it will allow the development of a non-language based diagnostic method for dyslexia that can be administered before a child reaches reading age. The identification of children at risk for future reading impairments can lead to early interventions and support and potentially prevent the spiral of negative consequences that follow with reading impairments, such as low self-esteem, low academic achievement, anxiety and behavioural problems (Zuppardo et al., 2023). Specific magnocellular-based training, for example, could improve reading in children with visual deficits and improve high-level visual perceptual activities.

### 7.13. Overall Conclusions

Overall, the following thesis demonstrates that individuals with poor (slow) reading skills display strong differences to neurotypical (fast) readers in their visual abilities in a number of high-level visual tasks: object recognition, emotional face perception, scene gist recognition, visual search and visual illusion susceptibility. In contrast, control experiments/conditions showed that slow and fast readers do not have measurable differences in parvocellular reliant tasks, i.e., when colour and HSF information is available.

Overall, the visual deficits displayed by slow readers in the experimental chapters were directly linked to low-level magnocellular processing deficits, impairing projection to high-level regions. The main findings of the studies are summarised as follows:

- Study 1 showed, using objects of low luminance and LSF, impaired activation of the OFC for fast visual object recognition in slow readers, i.e., magnocellular input is the key for initiating top-down processes in object recognition.
- Study 2 showed that slow readers are less efficient in visual search in conditions that require magnocellular input, i.e., magnocellular projections to the parietal cortex are required for guiding attention in search tasks.
- Study 3 showed that the advantages that slow readers have for holistic processing of emotional faces is impaired in magnocellular-isolating conditions, i.e., magnocellular input is required for emotional face processing.
- Study 4 showed global scene “gist” recognition is impaired in slow readers when the magnocellular pathway is stimulated, i.e., participants were not able to make use of global information required for scene gist classification.
- Study 5 showed that slow readers were more susceptible to the Ebbinghaus illusion, i.e, magnocellular input is required for attention to local details.

Overall, considering the evidence presented in literature, the current results provide additional evidence for an underlying deficit in the magnocellular pathway effecting high-level visual processing. The differences seen between fast and slow readers in the current studies are proposed to be as a consequence of impaired top-down facilitation, weakened signals to the parietal cortex and disturbed holistic processing; all of which trace to problems with the low-level visual magnocellular system. The current results, and published research, have indicated that individuals with reading difficulties have problems with a number of visual tasks – impaired reading, such as in individuals with DD, is therefore not restricted to phonological skills. Evidence suggests that strengths poor readers display in specific visual tasks, such as holistic face processing, may reflect segregated and intact neural mechanisms. The current results provide support for the magnocellular-deficit theory of dyslexia, beyond the low-level and mid-level previously reported evidence, e.g., motion/contrast/contour/flicker detection. These results provide a crucial step towards the development of future diagnostic and remediation programmes in dyslexia research by targeting and strengthening the magnocellular pathway before a child begins to develop reading skills, i.e., by using practical and engaging tools such as visual illusions or video games. It is recommended that pre-reading children and suitable control groups, ranging in age, are employed in future longitudinal studies based on the current thesis, with the inclusion of neuroimaging techniques, to further our fundamental knowledge of dyslexia and reading disorders, and with the additional practical aim of developing a robust method to identify at risk children.

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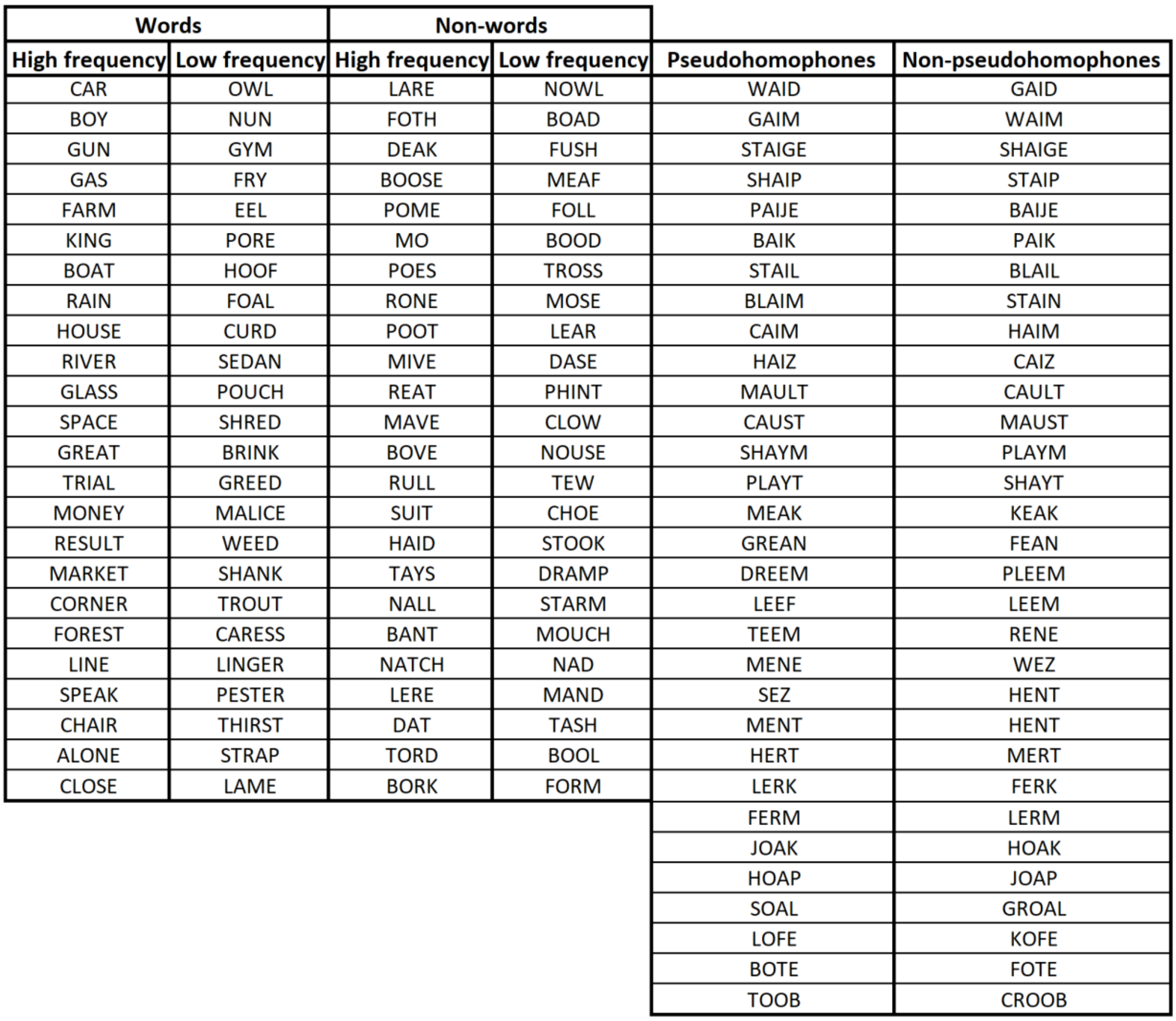
# Appendix

Word, non-word, pseudohomophones and non-pseudohomophones stimuli used in the orthographic and phonological LDT's.



| Words | | Non-words | | | |
|---|---|---|---|---|---|
| High frequency | Low frequency | High frequency | Low frequency | Pseudohomophones | Non-pseudohomophones |
| CAR | OWL | LARE | NOWL | WAID | GAID |
| BOY | NUN | FOTH | BOAD | GAIM | WAIM |
| GUN | GYM | DEAK | FUSH | STAIGE | SHAIGE |
| GAS | FRY | BOOSE | MEAF | SHAIP | STAIP |
| FARM | EEL | POME | FOLL | PAIJE | BAIJE |
| KING | PORE | MO | BOOD | BAIK | PAIK |
| BOAT | HOOF | POES | TROSS | STAIL | BLAIL |
| RAIN | FOAL | RONE | MOSE | BLAIM | STAIN |
| HOUSE | CURD | POOT | LEAR | CAIM | HAIM |
| RIVER | SEDAN | MIVE | DASE | HAIZ | CAIZ |
| GLASS | POUCH | REAT | PHINT | MAULT | CAULT |
| SPACE | SHRED | MAVE | CLOW | CAUST | MAUST |
| GREAT | BRINK | BOVE | NOUSE | SHAYM | PLAYM |
| TRIAL | GREED | RULL | TEW | PLAYT | SHAYT |
| MONEY | MALICE | SUIT | CHOE | MEAK | KEAK |
| RESULT | WEED | HAID | STOOK | GREAN | FEAN |
| MARKET | SHANK | TAYS | DRAMP | DREEM | PLEEM |
| CORNER | TROUT | NALL | STARM | LEEF | LEEM |
| FOREST | CARESS | BANT | MOUCH | TEEM | RENE |
| LINE | LINGER | NATCH | NAD | MENE | WEZ |
| SPEAK | PESTER | LERE | MAND | SEZ | HENT |
| CHAIR | THIRST | DAT | TASH | MENT | HENT |
| ALONE | STRAP | TORD | BOOL | HERT | MERT |
| CLOSE | LAME | BORK | FORM | LERK | FERK |
| | | | | FERM | LERM |
| | | | | JOAK | HOAK |
| | | | | HOAP | JOAP |
| | | | | SOAL | GROAL |
| | | | | LOFE | KOFE |
| | | | | BOTE | FOTE |
| | | | | TOOB | CROOB |