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Review article

New insights into the role of motion and form vision in neurodevelopmental disorders

Richard Johnston*, Nicola J. Pitchford, Neil W. Roach, Timothy Ledgeway

School of Psychology, University of Nottingham, Nottingham, UK

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ABSTRACT

A selective deficit in processing the global (overall) motion, but not form, of spatially extensive objects in the visual scene is frequently associated with several neurodevelopmental disorders, including preterm birth. Existing theories that proposed to explain the origin of this visual impairment are, however, challenged by recent research. In this review, we explore alternative hypotheses for why deficits in the processing of global motion, relative to global form, might arise. We describe recent evidence that has utilised novel tasks of global motion and global form to elucidate the underlying nature of the visual deficit reported in different neurodevelopmental disorders. We also examine the role of IQ and how the sex of an individual can influence performance on these tasks, as these are factors that are associated with performance on global motion tasks, but have not been systematically controlled for in previous studies exploring visual processing in clinical populations. Finally, we suggest that a new theoretical framework is needed for visual processing in neurodevelopmental disorders and present recommendations for future research.

1. Introduction

Vision plays a critical role in human brain development. Even when babies are still in utero retinal cells fire spontaneously in preparation for the incoming stream of visual information that needs to be processed after birth (Ackman et al., 2012). Abnormal processing of visual information during infancy and early childhood initiates a cascade of events in the brain that have adverse affects upon motor, language, and cognitive development (Gori et al., 2016). Several studies have uncovered a visual deficit in various neurodevelopmental disorders and children born very preterm (Braddick et al., 2003; Grinter et al., 2010). What is interesting about this impairment is its apparent selectivity. Individuals with Williams Syndrome, Developmental Dyslexia, Autism Spectrum Disorder (ASD), Developmental Coordination Disorder (DCD) and children born preterm are all purported to have a deficit in the processing of global (overall) motion, relative to global form. Current theories for why such a pattern of impairment might arise are challenged by very recent research (e.g. Johnston et al., 2016, 2017). The aim of this review is to explore alternative explanations for why deficits in the processing of global motion but not global form might arise in neurodevelopmental disorders and children born preterm, by taking account of the new psychophysical evidence.

First, we will describe visual tasks that have been used to investigate the processing of global motion and global form in clinical populations. We will then critically evaluate studies that have administered these tasks to individuals across a range of neurodevelopmental disorders (Williams Syndrome, Developmental Dyslexia, Autism Spectrum Disorder, Developmental Coordination Disorder) and children born preterm. Some studies have only administered global motion tasks. However, we have chosen to focus our attention on those that have compared performance across both global motion and global form tasks, as these provide a more comprehensive assessment of visual processing and have a direct bearing on the selectivity of the underlying impairment. Table 1 presents a summary of the research we cite so as to facilitate comparisons across studies on key variables, such as matching criteria, age, the sex of an individual, and visual tasks used. We also calculate and report between-group effect sizes but this was only possible for ~40% of the studies we cite. We will then consider contemporary theories that have been proposed to explain why deficits in the processing of global motion, relative to global form might arise. These include the dorsal stream vulnerability hypothesis (Atkinson and Braddick, 2013; Braddick et al., 2003; Braddick and Atkinson, 2011), the anchoring-deficit hypothesis (Ahissar et al., 2006; Ahissar, 2007), and the noise exclusion hypothesis (Sperling et al., 2005, 2006). We will also review research that has suggested the origin of visual impairment in these clinical populations might reflect genotypic variation (Cicchini et al., 2015; Gori et al., 2015a; Morrone et al., 2011). We will outline each of these frameworks in turn and explain why they are

* Corresponding author at: Visual Neuroscience Group, School of Psychology, University of Nottingham, University Park, Nottingham, NG7 2RD, UK.
E-mail address: richard.johnston@nottingham.ac.uk (R. Johnston).

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Table 1
A summary of research that has used global motion and global form tasks to investigate visual processing in neurodevelopmental disorders and children born preterm. NVIQ: Non-verbal IQ; VIQ: Verbal IQ; FSIQ: Full-scale IQ; RDKs: Random-dot kinematograms; PVL: Periventricular leukomalacia. The symbol – indicates that the relevant information is unavailable.

		Age (years)		Sex ratio (m: f)		Visual tasks		Visual deficit		Effect size (Cohen's *d*)	
Study	Matching criteria	Disorder group	Control group	Disorder group	Control group	Global motion	Global form	Global motion	Global form	Global motion	Global form
Williams Syndrome											
Atkinson et al. (1997)	–	9.7	8.1	–	–	Segmentation	Line segments	Yes	No	–	–
Atkinson et al. (2003)	VIQ	4.7–15.3	4.0–10.0	–	–	Segmentation	Line segments	No	No	–	–
Atkinson et al. (2006)	FSIQ	28.3	27.5	–	–	Segmentation	Line segments	Yes	Yes	1.7	1
Palomares and Shannon (2013)	VIQ & NVIQ	8.3–35.8	4.7–27.7	–	–	RDKs & dynamic glass patterns	Static Glass patterns	Yes	Yes	–	–
Developmental Dyslexia											
Conlon et al. (2009)	FSIQ	22.8	22.1	–	–	RDKs	Line segments	Yes	No	–	–
Hansen et al. (2001)	NVIQ	28.9	24.0	–	–	RDKs	Line segments	Yes	No	–	–
Johnston et al. (2016)	NVIQ	22.5	21.9	17:26	16:27	RDKs	Oriented dot clusters	Yes	No	0.6	0.1
Kevan and Pammer (2009)	FSIQ	5.7	5.5	11:8	20:19	RDKs	Line segments	Yes	No	–	–
Tsermentseli et al. (2008)	FSIQ	23.4	28.4	12:8	11:9	RDKs	Glass patterns	No	No	–	–
White et al. (2006)	NVIQ	10.5	10.3	14:9	9:13	RDKs	Line segments	No	No	0.1	0.2
Autism Spectrum Disorder											
Koldewyn et al. (2010)	NVIQ	15.1	15.8	28:2	30:2	RDKs	Glass patterns	No	No	0.7	0.1
Milne et al. (2006)	NVIQ	10.1	10.3	22:1	10:13	RDKs	Line segments	No	No	0.6	0.6
Spencer et al. (2000)	VIQ	7.0–11.0	7.0–11.0	–	–	Segmentation	Line segments	Yes	No	–	–
Tsermentseli et al. (2008)	FSIQ	28.3	28.4	8:2	11:9	RDKs	Glass patterns	Yes	Yes	–	–
Developmental Coordination Disorder											
O'Brien et al. (2002)	VIQ	8.2	8.4	6:2	–	Segmentation	Line segments	No	Yes	–	–
Sigmundsson et al. (2003)	–	10.6	10.5	6:7	6:7	RDKs	Line segments	Yes	Yes	–	–
Children born preterm											
Taylor et al. (2009)	VIQ	7.3	7.3	11:12	10:10	RDKs	Glass patterns	Yes	No	0.6	0.3
Children born preterm (no PVL)											
Guzzetta et al. (2009)	–	10.7	10.1	4:9	6:7	RDKs Segmentation	Line segments	Yes	No	1.4 0.6	0.7
Children born preterm (with PVL)											
Guzzetta et al. (2009)	–	10.4	10.1	7:6	6:7	RDKs Segmentation	Line segments	Yes	Yes	1.9 1.6	1.6

challenged by recent findings. We will then describe four new visual tasks that can be used to elucidate the underlying nature of the visual deficit in neurodevelopmental disorders and children born preterm. We will then discuss the importance of non-verbal IQ and the sex of an individual on performance with these tasks, as these are factors that are known to be associated with performance on global motion tasks but have not always been systematically controlled for in previous studies exploring visual processing in neurodevelopmental disorders and children born preterm. This could explain discrepancies across studies and why some investigators have failed to uncover deficits in the processing of global motion, relative to global form. Finally, we propose a new theoretical framework that can account for visual processing in neurodevelopmental disorders and set out some recommendations for future research.

2. Visual tasks

It has been proposed that two anatomically distinct and functionally independent processing streams exist in primate cortex (Goodale and Milner, 1992; Milner and Goodale, 1995; Mishkin et al., 1983; Ungerleider and Mishkin, 1982). The dorsal stream originates in primary visual cortex (V1), passes through V5/MT and terminates in parietal cortex. It is thought to play a major role in processing the global motion of objects, spatial cognition and visual motor planning. The ventral stream also originates in V1 but passes through V4 before terminating in the temporal lobes. Tasks mediated by the ventral stream include global form perception, visual memory and object recognition. A common tool for studying the properties of these two processing streams are visual displays composed of an array of local elements that when integrated (combined, pooled or compared in some manner) create either the perception of global motion or global form. These stimuli have been used extensively to probe the functional organisation of the visual system and the origin of visual impairment in neurodevelopmental disorders.

2.1. Global motion tasks

Random-dot kinematograms (RDKs) comprise a discrete set of images, each containing local dots, that when presented in succession create the perception of apparent motion (e.g. Albright, 1984; Barlow and Tripathy, 1997; Britten et al., 1992; Cavanagh and Mather, 1989; Newsome and Paré, 1988; Salzman et al., 1992). In a typical class of RDK, some of the dots move in the same direction on each image update (*signal* dots), whilst others move randomly (*noise* dots). Coherence thresholds are calculated to obtain a measure of perceptual performance and reflect the minimum proportion of signal dots needed to reliably detect or identify the global direction of motion. Evidence suggests that RDKs evoke a strong blood-oxygen-level-dependent (BOLD) response in hMT: the human homologue of macaque V5/MT (Braddick et al., 2000; Eden et al., 1996; Tootell et al., 1995; Zeki et al., 1991; Zeki, 2015). Neurophysiological studies have shown that directionally selective cells in this part of the brain are well equipped to integrate ("pool") the local responses of neurons in V1. They typically have larger receptive fields than their V1 counterparts and for this reason are thought to provide a global representation of object motion (see Born and Bradley, 2005 for review).

2.2. Global form tasks

In contrast, global form tasks typically comprise either Glass patterns (Dakin and Bex, 2002; Glass, 1969; Kim and Wilson, 1997; Smith et al., 2002, 2007; Wilson and Wilkinson, 1998) or static line segments (Burton et al., 2015, 2016; Hansen et al., 2001; Kevan and Pammer, 2009; Milne et al., 2006; Spencer et al., 2000; White et al., 2006). Some of the dots/lines are orientated to form a geometric pattern, usually depicting concentric, radial or translational structure, whilst others are orientated randomly. Coherence thresholds are measured in the same manner as RDKs and correspond to the minimum proportion of dots/lines needed to reliably detect the geometric pattern. Evidence suggests that global form tasks evoke a strong BOLD response in a region that might correspond to the human homologue of macaque V4 (Braddick et al., 2000; Ostwald et al., 2008). This part of the brain has been implicated in global shape perception but its precise functional role has yet to be elucidated (Roe et al., 2012). Single-cell recording studies have shown that up to one third of neurons in macaque V4 are directionally selective (Ferrera et al., 1994; Li et al., 2013; Schmid et al., 2013). It is possible that cells such as these might play a putative role in the processing of motion-defined boundaries (Mysore, 2006; Mysore et al. 2008; Chen et al., 2014; Sary et al., 1995).

3. Clinical populations

3.1. Williams syndrome

Williams Syndrome is a neurodevelopmental disorder caused by the deletion of approximately 25–28 genes on chromosome 7 (Ewart et al., 1993). It is primarily characterised by hyper-sociability but evidence suggests that individuals with this condition also have difficulty processing certain types of visual information (Anker and Atkinson, 1997; Braddick and Atkinson, 1995). To investigate the underlying nature of the visual deficit in Williams Syndrome, Atkinson et al. (1997) administered a global motion task and a global form task to fifteen children with Williams Syndrome (mean age = 9.7 years; range = 4–14 - years) and thirty typically developing controls (mean age = 8.1 years; range = 4–20 years). The stimuli in the global motion task comprised random-dot patterns that were spatially divided into horizontal segments. Adjacent segments contained dots moving in opposing directions (leftwards and rightwards). In the global form task, static line segments were orientated to form a concentric structure. Participants had to judge if the spatially segmented RDK or the geometric shape was located to the left or right of fixation in the global motion task and the global form task, respectively. Deviance analyses were performed to determine the proportion of children with Williams Syndrome who had coherence thresholds greater than 40% on the global motion task and the global form task. This criterion for deviance was chosen because it represents the maximum coherence threshold in the control group for both visual tasks. Seven out of the fifteen children with Williams Syndrome had coherence thresholds greater than the criterion for deviance on the global motion task, whereas only three out of the fifteen children with Williams Syndrome had coherence thresholds greater than the criterion for deviance on the global form task. These findings suggest that the processing of global motion is impaired to a greater extent than the processing of global form in some, but not all, children with Williams Syndrome. However, it is unclear if the participant groups in Atkinson et al. (1997) were matched for IQ. This is important because individuals with Williams Syndrome generally have a lower IQ than typically developing controls (Meyer-Lindenberg et al., 2006). Several studies have shown that non-verbal IQ is significantly and negatively associated with performance on global motion tasks but not global form tasks in the general population (Arranz-Paraíso and Serrano-Pedrazza, 2016; Johnston et al., 2016; Melnick et al., 2013). That is, individuals with a lower non-verbal IQ have higher coherence thresholds than those with a higher non-verbal IQ. This could provide an alternative explanation for why a greater proportion of children with Williams Syndrome had coherence thresholds above the criterion for deviance on the global motion task, relative to the global form task in Atkinson et al. (1997). Furthermore, the participant groups in Atkinson et al. (1997) were not well matched for chronological age. Evidence suggests that coherence thresholds on global motion tasks, and to a lesser extent global form tasks, are still maturing between the age of five and eleven in the general population (Braddick et al., 2016; see Hadad et al., 2015 for review; Meier and Giaschi, 2014). Atkinson et al. (2003) showed

that children with Williams Syndrome did not exhibit a selective deficit in the processing of global motion, relative to global form when coherence thresholds were converted into standard scores based on the mean and standard deviation of chronological age matched controls. These results highlight the importance of controlling for chronological age when measuring global motion coherence thresholds in neurodevelopmental disorders.

The results of Atkinson et al. (2003) suggest that children with Williams Syndrome do not have a selective deficit in the processing of global motion, relative to global form. However, it is possible that such a pattern of impairment could exist in adolescents and adults with Williams Syndrome. To explore this possibility Atkinson et al. (2006) administered the same global motion and global form tasks to forty-five individuals with Williams Syndrome (mean age = 28.3 years; range = 16–47) and nineteen typically developing controls (mean age = 27.5 years; range = 18–41). Significant group differences were found on both visual tasks but effect size was greater for the global motion task (Cohen's d = 1.66) than the global form task (Cohen's d = 1). These results suggest that global motion perception is impaired to a greater extent than global form perception in adolescents and adults with Williams Syndrome. However, Atkinson et al. (2006) did not control for marked differences in verbal, performance, and full-scale IQ. In addition, the participant groups were not well matched for chronological age. Several studies (Hutchinson et al., 2012; Billino et al., 2008; Snowden and Kavanagh, 2006) have shown that coherence thresholds increase across the lifespan meaning that older adults have higher coherence thresholds than younger adults on some, but not all (Hutchinson et al., 2014a; Pilz et al., 2017), global motion tasks. The maximum age of participants in the study by Atkinson et al. (2006) was higher in the Williams Syndrome group than the control group. Thus, it is possible that the mean coherence threshold for the Williams Syndrome group on the global motion task may have been elevated because of their older age. The fact that adults and adolescents with Williams Syndrome also exhibited higher coherence thresholds than typically developing controls on the global form task raises an important question regarding the selectivity of the visual deficit in Williams Syndrome, as it appears to affect the processing of both global motion and global form information.

Furthermore, the global motion task used by Atkinson et al. (1997, 2003, 2006) was spatially complex. It comprised "second-order" image cues in the form of motion-defined boundaries (Cavanagh and Mather, 1989) and subsequently necessitated a degree of spatial segmentation, as well as integration, of local visual cues (Braddick, 1993). Thus, one cannot be sure if it is global motion perception or motion-based segmentation that is impaired in Williams Syndrome. Whether or not this class of RDK can be relied upon to dissociate activity in brain regions that have been implicated in the processing of global motion is also debatable. Neurophysiological studies in non-human primates have shown that motion-defined boundaries may be encoded in area V4 (Mysore, 2006; Mysore et al. 2008; Chen et al., 2014; Sary et al., 1995). Thus, impaired performance on the motion task used by Atkinson et al. (1997, 2003, 2006) cannot be assumed to reflect a pure deficit in the processing of global motion *per se*. In addition, the neural correlates of motion-based segmentation have not been well explored in human observers, so strong claims about the cortical loci cannot yet be made.

To further investigate the underlying nature of the visual deficit in Williams Syndrome, Palomares and Shannon (2013) devised three visual tasks: a static global form task, a dynamic global form task, and a global motion task. The stimuli in the static global form task consisted of concentrically orientated Glass patterns, whereas those in the dynamic global form task were generated by presenting a new and temporally uncorrelated Glass pattern on each image update to create the perception of bistable apparent motion (Day and Palomares, 2014; Krekelberg, 2005; Krekelberg et al., 2003; Ross et al., 2000). In the global motion task, RDKs depicting "optic flow" patterns were used and were constrained to move in a clock-wise or anti-clockwise direction. Participants had to discriminate these static or moving patterns from stimuli containing randomly oriented elements (static global form task and dynamic global form task) or randomly moving noise dots (global motion task). Based on previous research, it was hypothesised that individuals with Williams Syndrome should be impaired to a greater extent on the dynamic global form task and the global motion task assuming that the neural mechanisms underlying the processing of global motion are equally activated by dynamic Glass patterns.

First, the performance of twelve Williams Syndrome participants (mean age = 17.71 years; range = 8–27 years) was compared to that of twelve typically developing controls matched for chronological age (mean age = 17.61 years; range = 8–27 years). Palomares and Shannon (2013) found that individuals with Williams Syndrome had significantly higher coherence thresholds than chronological age matched controls on the static global form task, the dynamic global form task, and the global motion task. Next, the performance of eight Williams Syndrome participants (mean age = 16.49 years; range = 8–23 years) was compared to that of eight typically developing controls matched for verbal and non-verbal IQ (mean age = 7.80 years; range = 5–10 years). A slightly different pattern of results was found as individuals with Williams Syndrome exhibited relatively impaired performance on the static global form task and the dynamic global form task, but not the global motion task. Taken together, these results suggest that the processing of global form is delayed to a greater extent than the processing of global motion in Williams Syndrome. The discrepancy between these findings and those of Atkinson et al. (2006) might reflect the fact that different stimuli were used to assess global motion perception. RDKs in Palomares and Shannon (2013) moved either in a clock-wise or anti-clockwise direction, whereas those in Atkinson et al. (2006) were spatially divided into horizontal segments by constraining dots in adjacent segments to move in opposing directions (see Table 1). Palomares and Shannon (2013) also controlled for non-verbal IQ, whereas Atkinson et al. (2006) did not address marked differences in IQ between participant groups.

In summary, some evidence suggests that the processing of global motion is impaired to a greater extent than the processing of global form in adolescents and adults, but not children, with Williams Syndrome (Atkinson et al., 1997, 2003, 2006). However, these results may have arisen because of incidental differences in non-verbal IQ between the participant groups (Palomares and Shannon, 2013), emphasising the need to control for this important factor in neurodevelopmental research. Furthermore, research using directly analogous visual tasks (i.e. in terms of demands and stimulus complexity) is needed to meaningfully compare global motion and global form perception in Williams Syndrome and typically developing controls matched for both chronological age and non-verbal IQ.

3.2. Developmental dyslexia

Developmental dyslexia manifests as a difficulty with reading despite adequate educational opportunities. It is primarily characterised by poor phonological decoding skills (Snowling, 2000) but several studies have observed difficulties with visual processing in individuals with developmental dyslexia which has resulted in different theories of visual processing in dyslexia being proposed including the magnocellular deficit hypothesis (Livingstone et al., 1991; Stein and Walsh, 1997). This theory assumes that anatomically distinct and functionally independent pathways can be discerned in a subcortical part of the primate brain called the lateral geniculate nucleus (LGN). The two major subdivisions of the LGN are the magnocellular and parvocellular pathways. A third koniocellular pathway has also been identified (Casagrande, 1994; Hendry and Yoshioka, 1994; Hendry and Reid, 2000; Kaas et al., 1978) but its precise functional role is yet to be fully elucidated (see Roe et al., 2012 for review). It is not uncommon for the subcortical magnocellular and parvocellular pathways to be conflated with the cortical dorsal and ventral processing streams (Skottun, 2015,

2016). For many years, the magnocellular and parvocellular pathways were thought to provide major feedforward input to the dorsal and ventral processing streams, respectively (Livingstone and Hubel, 1988; Merigan and Maunsell, 1993; Zeki and Shipp, 1988). However, more recent research in non-human primates has shown that this is almost certainly an oversimplification (Nassi and Callaway, 2009; Sincich and Horton, 2005; Vidyasagar et al., 2002). Magnocellular cells are thought to play a key role in the processing of relatively low spatial frequency stimuli, containing coarse scale details, which change rapidly over time, whereas parvocellular cells have been implicated in the processing of relatively high spatial frequency stimuli, containing fine scale details, which either remain static or change very slowly over time (Derrington and Lennie, 1984; Schiller and Malpeli, 1978). Determining the spatial and temporal frequencies at which human visual processing switches from the magnocellular to the parvocellular pathway is not trivial, but the magnocellular deficit hypothesis predicts that readers with dyslexia should exhibit impaired contrast sensitivity at relatively low spatial and high temporal frequencies (Livingstone et al., 1991; Stein and Walsh, 1997). The results of studies testing this hypothesis are very mixed (see Skottun, 2000 for review), suggesting that subcortical impairment of the magnocellular pathway is insufficient to fully characterise the visual perceptual difficulties experienced by individuals with developmental dyslexia. Indeed, the underlying nature of the visual deficit in dyslexia may instead reflect impairment at a relatively higher, cortical stage of visual processing where global motion and global form perception are thought to take place (Braddick et al., 2000; Eden et al., 1996; Ostwald et al., 2008; Tootell et al., 1995; Zeki et al., 1991; Zeki, 2015).

To explore if readers with dyslexia have a selective deficit in the processing of global motion, relative to global form Hansen et al. (2001) administered a global motion task and a global form task to fifteen adults with dyslexia (mean age = 28.9 years) and sixteen typically developing controls (mean age = 24 years) matched for non-verbal IQ but not chronological age. The stimuli in the global motion task were conventional RDKs. In contrast, the global form task consisted of static line segments that were orientated to create a concentric pattern. In the motion task, participants had to discriminate RDKs from stimuli containing randomly moving noise dots, whereas in the form task they had to discriminate geometric structure from stimuli comprising randomly orientated elements. Results showed that readers with dyslexia had significantly higher coherence thresholds than relatively good readers on the global motion task but not the global form task. These findings are indicative of a selective deficit in the processing of global motion, relative to global form. However, it is unclear if this impairment is confined to adult poor readers, or if it extends to children who are less skilled at reading.

To explore visual processing in children with dyslexia, White et al. (2006) used the same global motion and global form tasks as Hansen et al. (2001). They administered these tasks to twenty-three children with dyslexia (mean age = 10.5 years) and twenty-two typically developing controls (mean age = 10.3 years) matched for non-verbal IQ and chronological age. No significant difference was found between children with dyslexia and typically developing controls on the global motion task (Cohen's $d = 0.13$) or the global form task (Cohen's $d = 0.21$). These results are difficult to reconcile with studies that have uncovered global motion processing deficits in children with dyslexia (Raymond and Sorensen, 1998). This discrepancy might reflect the fact that different diagnostic criteria were used to identify reading difficulties. White et al. (2006) employed a six-point scale encompassing performance on a wide range of tests including reading, spelling, digit span, and speed of processing. In contrast, Raymond and Sorensen (1998) identified children whose reading skills were less than one standard deviation below the average expected for their chronological age. It is unclear if the reading tests used to diagnose dyslexia in White et al. (2006) and Raymond and Sorensen (1998) assessed the same, or different components, underlying reading skill e.g. sublexical or lexical processing. This is important because evidence suggests that deficits in the processing of global motion are more profound in readers who have a combination of poor phonemic decoding skills and whole-word lexical processing skills (Slaghuis and Ryan, 1999). How these distinct components underlying reading skill relate to performance on global form tasks is currently unclear but this could be explored in future research. We have already highlighted the importance of controlling for chronological age when exploring the processing of global motion in neurodevelopmental disorders and children born preterm. The discrepancy between White et al. (2006) and Raymond and Sorensen (1998) is unlikely to reflect differences in chronological age because the participant groups in both studies were matched on this variable. However, it is unclear if Raymond and Sorensen (1998) controlled for non-verbal IQ. Irrespective of the definitional criterion of developmental dyslexia adopted, careful matching of controls to dyslexic groups for non-verbal IQ, ideally on a case-by-case basis, is necessary.

Another issue that has generated considerable debate is whether deficits in the processing of global motion, relative to global form, are the proximal cause, or merely a consequence of developmental dyslexia (Dehaene et al., 2015; Gori et al., 2015a, 2015b; Goswami, 2014; Olulade et al., 2013; Szwed et al., 2012). One way to address this issue is to explore if coherence thresholds measured before the commencement of formal reading training predict reading ability after formal reading training has begun. Kevan and Pammer (2009) administered a global motion task and a global form task to nineteen children (mean age = 5.7 years) identified as being at high-risk of dyslexia (i.e. who had a first-degree relative with dyslexia) and thirty-nine children who were selected from the general population matched for chronological age (mean age = 5.5 years). The visual stimuli were identical to those used by Hansen et al. (2001) and White et al. (2006). Results showed that coherence thresholds on both visual tasks, measured at the beginning of kindergarten (before formal reading training had commenced) did not significantly predict scores on standardised measures of reading ability at the end of grade 1 (after formal reading training had begun). Crucially, scores on the standardised measures of reading ability at the end of grade 1 were significantly associated with coherence thresholds on the global motion task also measured at the end of grade 1. However, this was not the case for the form task. No correlation was found at the end of grade 1 for performance on the global form task and reading ability. These findings suggest that deficits in the processing of global motion, relative to global form, are more likely to be a consequence, rather than the proximal cause of developmental dyslexia.

A criticism of the global motion and global form tasks described thus far is that they are not always comparable in terms of stimulus complexity or task demands. To overcome this problem Tsermentseli et al. (2008) administered two directly analogous global motion and global form tasks to twenty adults with dyslexia (mean age = 23.4 - years) and twenty typically developing controls (mean age = 28.4 - years) matched for full scale IQ but not chronological age. The stimuli in the global form task comprised an array of dot triplets that were orientated to form a concentric structure. Identical stimuli were used in the global motion task except the dots were displaced from the first position in the triplet to the last position, which created the perception of circular (rotational) motion. No significant difference was found between readers with dyslexia and relatively good readers on the global motion task or the global form task. These results do not corroborate those of Hansen et al. (2001) but there are at least two reasons why this might be the case. Firstly, research has shown that readers with dyslexia only have marked difficulty when local motion cues have to be integrated across extended trajectories, perhaps indicative of a temporal integration deficit rather than a pure motion perception deficit (Raymond and Sorensen, 1998). The global motion task used by Tsermentseli et al. (2008) comprised three frames, whereas that used by Hansen et al. (2001) comprised eighty frames. This raises the possibility that the global motion task used in the study by Tsermentseli et al.

(2008) might not have been sufficient to reveal significant between-group differences. Secondly, the participant groups in Hansen et al. (2001) were matched for chronological age. In contrast, the mean age of the control group was higher than that of the dyslexia group in Tsermentseli et al. (2008). As a result, the mean coherence threshold of the control group on the global motion task may have been elevated, which could have masked a significant between-group difference.

In summary, research suggests that at least some children and adults with dyslexia have a selective deficit in the processing of global motion, relative to global form (Hansen et al., 2001; Raymond and Sorensen, 1998). Although this finding has not always been replicated (White et al., 2006; Tsermentseli et al., 2008), discrepancies across studies could have arisen for at least three possible reasons: 1) a wide range of tests measuring different components underling reading skill (e.g. sublexical or lexical processing) have been used to diagnose dyslexia across studies; 2) research has not always controlled for factors that are known to be associated with performance on global motion tasks such as chronological age, sex, and non-verbal IQ; and 3) the global motion tasks administered may not have, at least in some cases, been sufficiently sensitive to reveal differences between readers with dyslexia and relatively good readers e.g. tasks in which the motion sequence comprised a relatively small number of frames. Another controversy is whether or not performance on global motion and global form tasks differentiates individuals with poor phonological decoding skills, consistent with the dyslexic profile, from generally poor readers. This issue is theoretically important, has implications for the definition of dyslexia (Fletcher, 2009) and will be addressed in more detail in Section 5.

3.3. Autism spectrum disorder

Autism Spectrum Disorder (ASD) is mainly characterised by social withdrawal and isolation but several studies have shown that individuals with ASD also exhibit impaired performance on a range of visual tasks (Manning et al., 2015; Smith et al., 2015; Simmons et al., 2009). For example, Bertone et al. (2003) reported that some individuals with ASD exhibit impaired detection of complex (second-order) motion and attributed this to a "decreased capacity to integrate complex perceptual information rather than a specific inability to efficiently process motion information as such" (Bertone et al., 2003, p.4). To explore the underlying nature of the visual deficit in ASD, Spencer et al. (2000) administered a global motion task and a global form task to twenty-three children with ASD (age range = 7–11 years) and fifty typically developing controls (age range = 7–11 years) matched for chronological age and verbal IQ. The visual stimuli in the global motion and global form tasks were identical to those used by Atkinson et al. (1997, 2003, 2006). Results showed that children with ASD had significantly higher coherence thresholds than typically developing controls on the global motion task but not the global form task. However, as previously mentioned, we cannot be sure that this particular class of RDK provides a sensitive measure of global motion perception as it requires some degree of spatial segmentation, as well as integration of local motion cues (Braddick, 1993). Hence, the visual deficit in ASD could either reflect a difficulty with global motion perception or motion-based segmentation. In addition, research has shown that both performance and non-verbal components of IQ are more strongly associated with thresholds on global motion tasks than verbal components (Melnick et al., 2013). A recent study did not find a significant correlation between verbal IQ and performance on a global motion task (Arranz-Paraíso and Serrano-Pedrazza, 2016). The participant groups in Spencer et al. (2000) were matched for verbal IQ but not non-verbal IQ. Children in the ASD group may have had lower non-verbal IQ than typically developing controls and this could explain why they had higher coherence thresholds on the global motion but not the global form task.

Milne et al. (2006) administered more conventional global motion and global form tasks to investigate visual processing in twenty-three children with ASD (mean age = 10.1 years) and twenty-three typically developing controls (mean age = 10.3 years) matched for non-verbal IQ and chronological age. The stimuli in the global motion task were RDKs, whereas the global form task comprised orientated lines that formed a concentric pattern (Hansen et al., 2001; Kevan and Pammer, 2009; White et al., 2006). No significant difference was found between children with ASD and typically developing controls on the global motion task (Cohen's $d = 0.61$) or the global form task (Cohen's $d = 0.57$). However, there was a marked imbalance between males and females in the participant groups. The group of children with ASD comprised twenty-two males and one female, whereas the group of children without ASD comprised ten males and thirteen females (Table 1). Evidence suggests that females have significantly higher coherence thresholds than males on global motion tasks (Billino et al., 2008; Hutchinson et al., 2012; Snowden and Kavanagh, 2006), which raises the possibility that a significant group difference on the global motion task could have been masked in the Milne et al. (2006) study because of sex differences in their sample. This important issue is often overlooked and will be discussed further in Section 6.

It is also currently unclear if the visual deficit sometimes found in ASD persists into adolescence. To explore this possibility Koldewyn et al. (2010) administered a global motion task and a global form task to thirty individuals with ASD (mean age = 15.1 years) and thirty-two typically developing controls (mean age = 15.8 years) matched for chronological age but not non-verbal IQ. The stimuli in the global motion task comprised conventional RDKs, whereas the global form task consisted of Glass patterns. Results showed that individuals with ASD had significantly higher coherence thresholds than typically developing controls on the global motion task (Cohen's $d = 0.71$) but not the global form task (Cohen's $d = 0.08$). However, the effect disappeared when non-verbal IQ was entered into the analyses as a covariate. These findings highlight the importance of controlling for intellectual ability when exploring the processing of global motion and global form information in groups with neurodevelopmental disorders and children born preterm.

In summary, research using conventional global motion integration tasks has not found reliable differences in coherence thresholds between children with ASD and typically developing controls, when both groups were carefully matched with regards to the sex of the participants and non-verbal IQ (Koldewyn et al., 2010). Further research is needed to explore if spatial segmentation, rather than integration, is impaired in children and adults with ASD when non-verbal IQ is taken into account. This issue forms the basis of a new theoretical framework of vision in neurodevelopmental disorders and will be addressed in more detail in Section 8.

3.4. Developmental coordination disorder

Developmental Coordination Disorder (DCD) affects approximately 5–6% of school-aged children and is characterised by a break down in the planning, organisation, and execution of physical movements (Zwicker et al., 2012). Two studies have been conducted to investigate if these difficulties reflect a deficit processing certain types of visual information. O'Brien et al. (2002) administered the same global motion and global form tasks as Atkinson et al. (1997, 2003, 2006) to eight children with DCD (mean age = 8.2 years) and fifty typically developing controls (mean age = 8.4 years) matched for verbal IQ and chronological age. Results showed that children with DCD had significantly higher coherence thresholds than controls on the global form task but not the global motion task. In contrast, Sigmundsson et al. (2003) administered the same global motion and global form tasks as Hansen et al. (2001) to thirteen children with DCD (mean age = 10.6 years) and thirteen typically developing controls (mean age = 10.5 years) matched for chronological age but not non-verbal IQ. They found that children with DCD had significantly higher coherence thresholds than controls on both visual tasks. The stimuli used in these

two studies differed and this might explain the discrepancy in results (Table 1). In addition, different criteria were used to identify individuals with DCD across studies. A formal diagnosis was required in the O'Brien et al. (2002) study, whereas Sigmundsson et al. (2003) used scores on the Movement ABC (Henderson and Sugden, 1992) to assess motor competency. Another factor that might have contributed to the discrepancy is sex. The ratio of males to females was well balanced across participant groups in the study by Sigmundsson et al. (2003). However, we cannot be sure that this was the case in O'Brien et al. (2002) as sex composition was only provided for the DCD group and not the control group (Table 1). In addition, the Sigmundsson et al. (2003) study failed to control for IQ, whereas participant groups in O'Brien et al. (2002) were matched for verbal IQ, the latter of which is not associated with performance on global motion tasks (Arranz-Paraíso and Serrano-Pedrazza, 2016). In summary, it is currently unclear if the discrepant results of Sigmundsson et al. (2003) and O'Brien et al. (2002) can be attributed to methodological differences between the two studies, or the control variables used to match participants with and without DCD. Disambiguating these possibilities is a promising area for future research.

3.5. Children born preterm

Children born preterm experience unusually early post-natal visual stimulation and some researchers have argued that this might lead to deficits processing certain types of visual information (Birch and O'Connor, 2001). To explore this possibility, Taylor et al. (2009) administered a global motion task and a global form task to twenty-three children born less than thirty-two weeks gestation (mean age = 7.3 - years) and twenty full-term controls (mean age = 7.3 years) matched for verbal IQ and chronological age. The stimuli in the global motion task were conventional RDKs, whereas the global form task comprised Glass patterns. Results showed that children born preterm had significantly higher coherence thresholds than full-term controls on the global motion task and the global form task. Interestingly, the effect size between groups was almost twice as large for the global motion task (Cohen's d = 0.61) than the global form task (Cohen's d = 0.33), which suggests that children born preterm were impaired to a greater extent on the global motion task, relative to the global form task. A second type of analyses confirmed this finding. Mean deficit scores (i.e. the ratio between the coherence threshold for a single participant from the group of children born preterm and the mean coherence threshold for three typically developing controls who were closest to the preterm child in chronological age) were calculated for each task. They were larger than one for the global motion task but not the global form task. This pattern of results is consistent with the notion that global motion perception is impaired to a greater extent than global form perception in children born preterm. However, this type of analysis does not account for effects of variables such as sex and non-verbal IQ. For example, the mean deficit score on the global motion task for a female participant born preterm may have been severely overestimated if the three controls with the closest chronological age to her happened to be male. In addition, Taylor et al. (2009) opted to control for verbal IQ as opposed to non-verbal IQ. We have already alluded to the fact that coherence thresholds on global motion tasks are more strongly associated with both performance and non-verbal components of IQ than verbal components (Arranz-Paraíso and Serrano-Pedrazza, 2016; Johnston et al., 2016; Melnick et al., 2013). Hence, one cannot rule out the possibility that differences in non-verbal IQ between participant groups may have confounded the results of the Taylor et al. (2009) study.

It is known that children born preterm (especially those of birth weight less than 1500 g) are at greater risk of developing periventricular leukomalacia (PVL) and other neurological insults than children born at full term (Volpe, 2003). Hence, it is unclear if deficits in the processing of global motion, relative to global form, arise because of prematurity per se or increased susceptibility to white matter brain injury. To disentangle these two possibilities Guzzetta et al. (2009) devised three visual tasks: a global motion task, a global form task, and a motion-based segmentation task. They gave these tasks to thirteen children born preterm with PVL (mean age = 10.4 years; mean gestational age = 30.1 weeks, mean birth weight = 1528 g), thirteen children born preterm at low-risk of PVL who had normal ultrasound scans or minimal white matter abnormalities (mean age = 10.7 years; mean gestational age = 29.6 weeks, mean birth weight = 1466 g), and thirteen full-term controls (mean age = 10.1 years). All groups were matched for chronological age but not non-verbal IQ. The stimuli in the global motion task were conventional RDKs, whereas in the global form task static line segments were orientated to form a concentric pattern. In the motion-based segmentation task, RDKs were spatially divided into horizontal segments by constraining dots in adjacent segments to move in opposing directions (leftwards and rightwards). Participants had to judge the overall direction of the stimulus in the global motion task. In contrast, they had to discriminate concentric structure from stimuli comprising randomly orientated elements in the global form task. In the motion-based segmentation task, participants had to discriminate spatially divided RDKs from stimuli containing uniform motion that reversed direction periodically every 240 ms.

Results showed that children born preterm with PVL had significantly higher coherence thresholds than full-term controls on the global motion task (Cohen's d = 1.89), the global form task (Cohen's d = 1.57), and the motion-based segmentation task (Cohen's d = 1.61). However, a different pattern of results emerged when children born preterm at low-risk of PVL were considered. They had significantly higher coherence thresholds than full-term controls on the global motion task (Cohen's d = 1.37) but not the global form task (Cohen's d = 0.72) or the motion-based segmentation task (Cohen's d = 0.56). The only significant differences found between children born preterm with PVL and those at low-risk of PVL were on the global form task (Cohen's d = 1.4) and the motion-based segmentation task (Cohen's d = 1.57). These results suggest that children born prematurely with white matter brain injury have a more general visual deficit than children born prematurely at low-risk of PVL. It could be argued that the motion-based segmentation task used in this study did not provide a sensitive measure of object segmentation as participants could have based their decision strategy on each trial by identifying the stimulus containing uniform motion. However, this does not appear to have been the case at least for children born preterm at low-risk of PVL. They had elevated coherence thresholds on the global motion task and they would be expected to exhibit impaired performance on the motion-based segmentation task if this strategy had been adopted to identify the spatially divided pattern. In addition, Guzzetta et al. (2009) did not control for non-verbal IQ. This raises the possibility that the different pattern of performance observed in children born preterm with PVL and those at low-risk of PVL could be attributed to differences in non-verbal IQ. Although the two preterm groups were not well matched for birth weight, evidence suggests that birth weight is not significantly associated with performance on global motion tasks (Taylor et al., 2009). Hence, the different pattern of results observed in preterm children with PVL and those at low-risk of PVL is unlikely to reflect differences in birth weight across the participant groups.

In summary, global motion perception may be impaired to a greater extent than global form perception in children born preterm, but only when they are at low risk of PVL. Children born preterm with PVL appear to exhibit a more general deficit, which manifests as a difficulty on a wide range of visual tasks (Guzzetta et al., 2009). However there is a need for future studies to control for potential differences in non-verbal IQ, when comparing the visual abilities of preterm born children born with and without PVL, to confirm the robustness of these preliminary findings.

4. Why do selective visual deficits arise in clinical populations?

4.1. The dorsal stream vulnerability hypothesis

Approximately 40% of the studies cited in this review found that individuals with neurodevelopmental disorders and children born preterm have a selective deficit in the processing of global motion, relative to global form (Table 1). Arguably, the most popular theory that has been proposed to explain why such a pattern of impairment might arise is the dorsal stream vulnerability hypothesis (Atkinson and Braddick, 2013; Braddick et al., 2003; Braddick and Atkinson, 2011). As previously mentioned, this theory assumes that two anatomically distinct and functionally independent processing streams can be discerned in primate cortex (Goodale and Milner, 1992; Milner and Goodale, 1995; Mishkin et al., 1983; Ungerleider and Mishkin, 1982). The dorsal stream is thought to play a major role in processing the global motion of objects, spatial cognition and visual motor planning, whereas the ventral stream has been implicated in global form perception, visual memory and object recognition. The dorsal stream is thought to be more susceptible to damage and disruption during development than the ventral stream because magnocellular cells, which are thought to provide predominant input to the dorsal stream are larger and fewer in number than parvocellular cells, which are thought project to the ventral stream (Grinter et al., 2010). Even though there appears to be considerable mixing of magnocellular and parvocellular inputs in visual cortex (Nassi and Callaway, 2009; Sincich and Horton, 2005; Vidyasagar et al., 2002) it has been suggested that the primary origin of visual impairment across a range of neurodevelopmental disorders and children born preterm is the same and reflects vulnerability to dorsal stream processing (Atkinson and Braddick, 2013; Braddick et al., 2003; Braddick and Atkinson, 2011).

Dorsal stream vulnerability is claimed to manifest as a selective deficit on global motion tasks but not global form tasks (Atkinson and Braddick, 2013; Braddick et al., 2003; Braddick and Atkinson, 2011). However, we have shown that this pattern of impairment is not observed in all neurodevelopmental disorders and children born preterm, a finding that questions the generality of the dorsal stream vulnerability hypothesis. Even when selective deficits in the processing of global motion, relative to global form have been found it is often equivocal as to whether they can be directly attributed to neurodevelopment per se or other factors that are known to be associated with performance on global motion tasks such as sex and non-verbal IQ (Table 1). In addition, very recent research has cast doubt on whether global motion and global form tasks can be relied upon to clearly dissociate activity in the dorsal and ventral processing streams, respectively. Two studies have shown that coherence thresholds on global motion tasks and global form tasks are significantly and positively correlated in the general population (Braddick et al., 2016; Johnston et al., 2016). Although this relationship could arise for several reasons and/or be mediated by a third variable such as non-verbal IQ, sex, and attention, these results challenge the independence of the putative dorsal and ventral processing streams. They may be indicative of either some degree of cross-talk or a later common processing stage that serves to bind distinct object properties into a global percept. Indeed, evidence suggests that the dorsal and ventral processing streams interact in areas such as superior temporal sulcus, the fusiform face area, and potentially also at lower levels of visual processing (Cloutman, 2013; Freud et al., 2016; Giese and Poggio, 2003; Gilaie-Doton, 2016; Himmelbach and Karnath, 2005; Keizer et al., 2008). Hence, alternative explanations for why deficits in the processing of global motion, relative to global form, arise in several neurodevelopmental disorders and children born preterm need to be considered.

4.2. The anchoring-deficit hypothesis

The anchoring-deficit hypothesis (Ahissar et al., 2006; Ahissar, 2007) was initially proposed to explain the underlying nature of the sensory deficit in developmental dyslexia but it could also be applied to other clinical populations. This framework assumes that a perceptual anchor can be formed to reduce perceptual memory load on both auditory and visual tasks in which comparisons have to made across sequentially presented stimuli. In all the studies mentioned above, participants viewed RDKs and static form stimuli that changed coherence on every trial to determine a threshold level of performance. They had to discriminate these patterns from “noise” stimuli that only ever contained randomly moving dots or randomly orientated form cues. Across the duration of these tasks, participants could have learned these statistical properties and used the invariant noise stimuli to form a perceptual anchor. If individuals with neurodevelopmental disorders and children born preterm have a deficit forming or utilising a perceptual anchor to reduce the load of online retention they should exhibit impaired performance on both visual tasks. There is evidence to suggest that individuals with Williams Syndrome (Atkinson et al., 2006), DCD (Sigmundsson et al., 2003), and children born prematurely with PVL (Guzzetta et al., 2009) have elevated coherence thresholds on global motion and global form tasks (Table 1). An interesting question for future research is whether or not the underlying nature of the visual impairment in these neurodevelopmental disorders reflects a deficit forming or utilising a perceptual anchor.

4.3. The noise exclusion hypothesis

Another theory that has been proposed to explain the origin of the visual impairment in readers with dyslexia is the noise exclusion hypothesis (Sperling et al., 2005, 2006). Like the anchoring-deficit hypothesis, this framework can also be applied to other neurodevelopmental disorders and children born very preterm. The noise exclusion hypothesis assumes that visual deficits arise from a difficulty in segregating signal from noise elements. This would manifest as impaired performance on global motion and global form tasks in which stimulus coherence is varied, as high levels of external noise are present in both tasks. Hence, the predictions made by the noise exclusion hypothesis are similar to those made by the anchoring-deficit hypothesis. That is, individuals with neurodevelopmental disorders and children born preterm should exhibit impaired performance on both global motion and global form tasks. We have already shown that this may be the case in Williams Syndrome, DCD and children born prematurely with PVL (Table 1). Hence, the origin of the visual impairment in these neurodevelopmental disorders could reflect either a deficit with perceptual anchoring or external noise exclusion.

4.4. Genetic studies

A further explanation is that deficits in the processing of global motion might reflect genotypic variation (Gori et al., 2015a; Morrone et al., 2011). Cicchini et al. (2015) found that readers with dyslexia, for example, who had a deletion on intron 2 of the DCDC2 gene, were impaired to a greater extent on a motion discrimination task using drifting sinusoidal gratings than readers with dyslexia who did not have the genotypic deletion. A conventional global motion task was also administered and results showed that coherence thresholds were significantly higher in readers with dyslexia who had the deletion on DCDC2 than typically developing controls who did not have the deletion. However, the authors did not perform the critical comparison between readers with dyslexia who had the genotypic deletion and those for whom it was not present, so it is indeterminate if the behavioural result is indicative of DCDC2 deletion or dyslexia. No global form task was administered but these findings raise the possibility that visual deficits in various neurodevelopmental disorders and children born preterm might reflect genotypic variation. There has been a rise in the number of genetic studies exploring visual processing in neurodevelopmental disorders presumably because more is known about the

neural mechanisms underlying visual perception than other psychological and cognitive markers (Goodbourne et al., 2014). Although genotypical variation might explain why deficits in the processing of global motion arise in some clinical populations, at this point in time we know too little about this and further research is needed.

5. Recent psychophysical evidence

In order to gain a better understanding of why deficits in the processing of global motion, relative to global form, might arise it is important to consider carefully the demands that global motion tasks and global form tasks place on the human visual system. For example, global motion tasks require the precise registration and orchestration of temporal information in the brain, whereas global form tasks do not. Thus, a difficulty processing visual cues that are changing sequentially over time could underlie the visual deficit in some neurodevelopmental disorders or children born preterm. In addition, global motion tasks are traditionally more complex than global form tasks. In global motion tasks, local visual cues have to be integrated across two dimensions of space and over time, whereas in global form tasks local cues only have to be pooled across two dimensions of space. Hence, there are at least three possible reasons why a deficit in the processing of global motion, relative to global form, might arise. It could reflect a difficulty processing either motion, temporal information, or integrating local visual cues across multiple (> 2) dimensions.

To disentangle these possibilities in readers with dyslexia, Johnston et al. (2016) devised four, new, diagnostic global motion and global form tasks: a random-dot global motion task comprising conventional RDKs, a spatially one-dimensional (1-D) global motion task, a comparable static global form task, and a temporally-defined global form task (Fig. 1). These tasks were administered to a large sample (N = 106) of adults with a wide range of reading abilities. Participants had to judge the overall direction (upwards or downwards) of the stimuli in the global motion tasks, whereas in the global form tasks they had to judge the overall orientation (vertical or horizontal) of the stimuli. The visual tasks were specifically designed to reveal the underlying nature of the visual deficit in adults with developmental dyslexia. Thus, several predictions could be made (Fig. 2). Firstly, if readers with dyslexia have a general difficulty with the processing of global motion they would be expected to have significantly higher coherence thresholds than good readers on the two global motion tasks: the random-dot global motion task and the spatially 1-D global motion task. If, on the other hand, they have difficulty processing temporal information, they would be expected to have significantly higher coherence thresholds on the tasks necessitating precise encoding of time varying information: the random-dot global motion task, the spatially 1-D global motion task and the temporally-defined global form task. Finally, if readers with dyslexia have a difficulty with computationally demanding visual tasks, they would be expected to have significantly higher coherence thresholds than good readers on the tasks requiring local visual cues to be integrated across multiple (> 2) dimensions: the random-dot global motion task and the temporally-defined global form task.

Results were similar across a series of continuous analyses, conducted to investigate if general reading skills in the entire sample were associated with coherence thresholds on the four visual tasks, and a series of between-group analyses, conducted to explore if performance differed across readers with poor phonological decoding skills, consistent with dyslexic profile, and relatively good readers. In support of

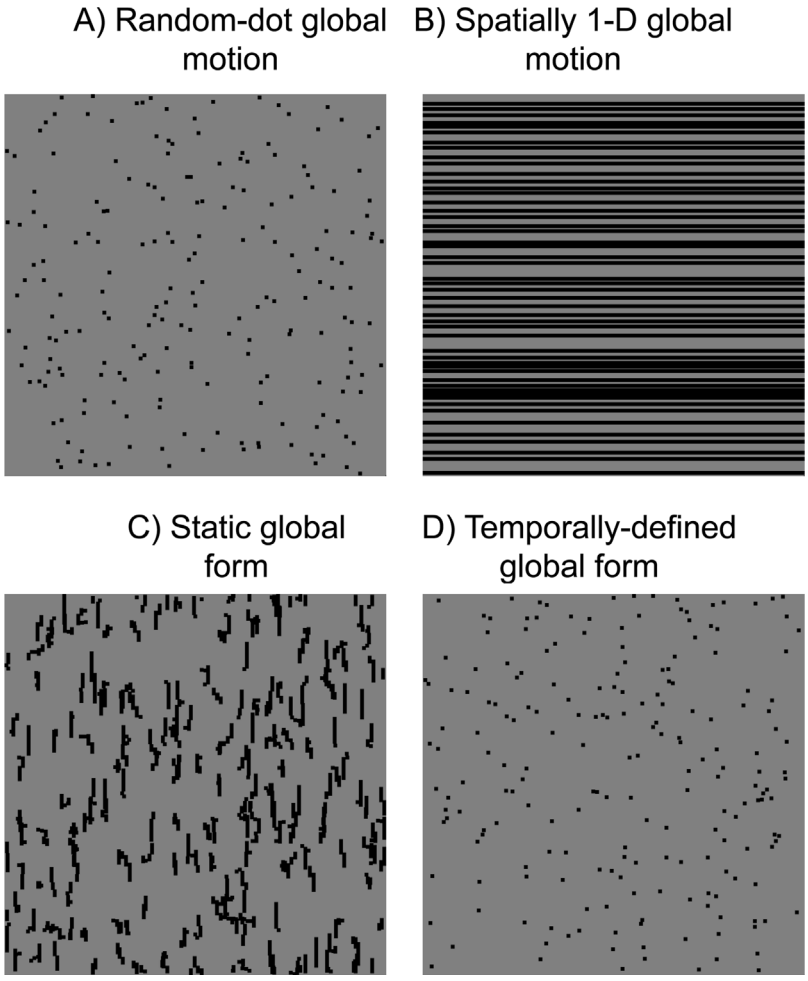

Fig. 1. Schematic illustration of the (A) random-dot global motion task, (B) spatially 1-D global motion task, (C) static global form task, and (D) temporally-defined global form task. Note that the spatial structure in the temporally-defined global form task arises from the asynchronous jittering of individuals dots over time giving rise to a perceptual boundary. Thus, it cannot be accurately depicted in this figure.
Adapted from Johnston et al. (2016).

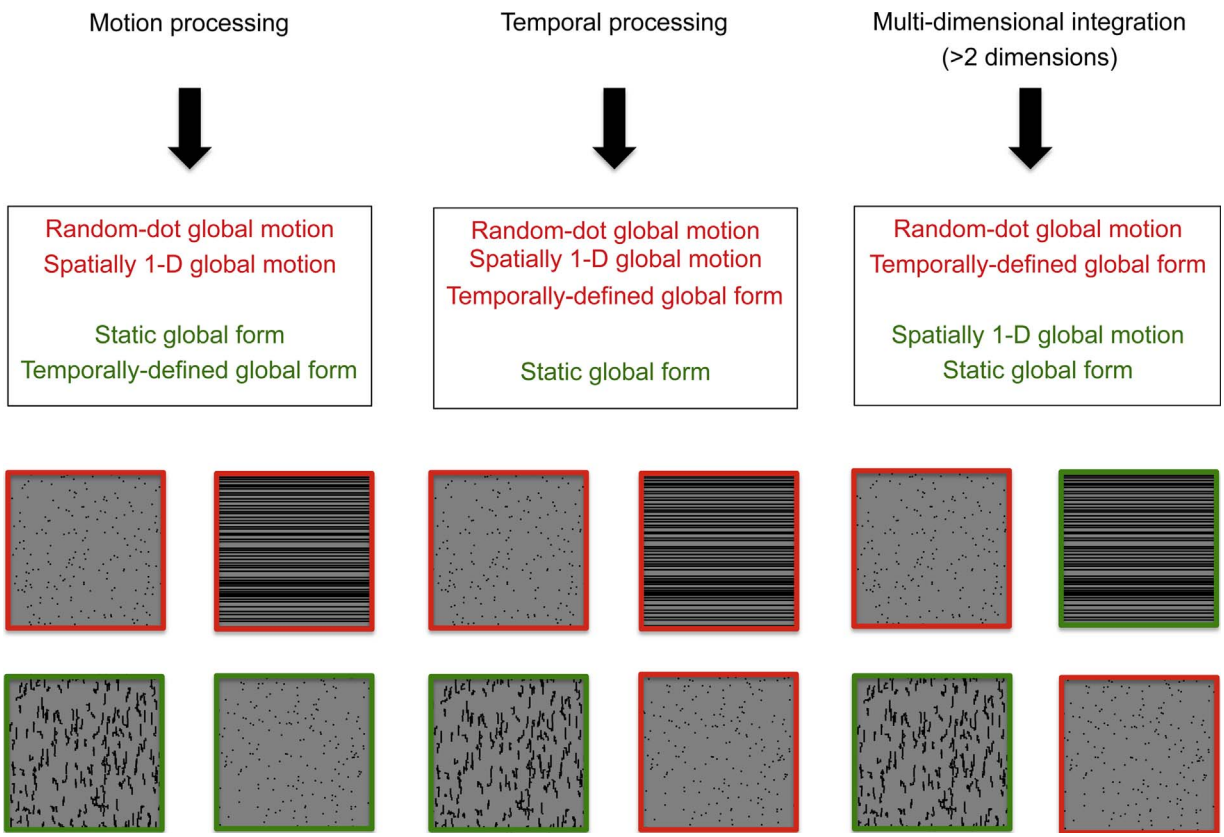

Fig. 2. Predicting performance on the four global motion and global form tasks in Johnston et al. (2016). Red = clinical population expected to have significantly higher coherence thresholds than controls. Green = no significant difference expected between clinical population and controls. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

previous studies, both generally poor readers and individuals who met conventional criteria for dyslexia had significantly higher coherence thresholds than relatively good readers on the random-dot global motion task (Cohen's $d = 0.59$) and the spatially 1-D global motion task (Cohen's $d = 0.42$) but not the static global form task (Cohen's $d = 0.06$) (Conlon et al., 2009; Hansen et al., 2001; Kevan and Pammer, 2009). However, crucially, and in contrast to previous research, both groups of poor readers also exhibited impaired performance on the temporally-defined global form task (Cohen's $d = 0.55$). These findings demonstrate that adult poor readers have difficulty processing temporal information rather than motion per se, consistent with some previous findings (see Famer and Klein, 1995 for review). They are theoretically important and speak directly to the debate as to whether dyslexia is best-defined as the lower-end of a normal distribution of reading ability or a distinct type of reading difficulty that is associated with poor phonological decoding skills (Fletcher, 2009). The similar pattern of results observed in generally poor readers and individuals with developmental dyslexia implies that performance on low-level visual tasks cannot differentiate these two groups of adult readers.

The underlying nature of the visual deficit in different neurodevelopmental disorders and children born preterm is unlikely to be the same. As the tasks developed by Johnston et al. (2016) have been shown to be effective in differentiating competing hypotheses as to the nature of the visual impairment observed in developmental dyslexia, their application to other neurodevelopmental disorders and children born preterm could be of similar value. In addition, comparing results of continuous and between-group analyses in each case could also help address similar, theoretically important questions of dimensionality/discreteness (Moreno-De-Luca et al., 2013). We suggest that some of the discrepancies in the literature that are highlighted above might reflect the wide range of diagnostic criteria that have been used across studies. Performing continuous rather than between-group analyses means that decisions regarding controversial definitional criteria and categorical assignment of participants do not have to be made. Adopting this type of experimental design might also enhance statistical power and increase the so-called positive predictive value i.e. the likelihood that a positive research finding represents a genuine effect. Low sample size has been put forward as a major contributing factor to the lack of reproducibility that currently abides in the neurosciences (Button et al., 2013; Loannidis, 2005; Munafò et al., 2017) and is prevalent in the studies reported here (see Table 1).

6. Sex

Throughout this review we have highlighted how the sex of an individual can influence performance on global motion tasks. There is some evidence to suggest that females typically have higher global motion thresholds than males but those studies that have investigated this issue have focussed primarily on the ageing visual system (Billino et al., 2008; see Hutchinson et al., 2012 for review; Snowden and Kavanagh, 2006). Interestingly, sex was a strong predictor of coherence thresholds on the random-dot global motion task used by Johnston et al. (2016), as results showed that for participants in early adulthood (mean age = 22.02 ± 5.21years) females overall had significantly higher coherence thresholds than males. However, no significant association was found between sex and performance on the static global form task, the spatially 1-D global motion task, or the temporally-defined global form task. These results extend those of previous studies as they show that sex differences on random-dot global motion tasks are not simply a consequence of differential visual decline in ageing. Several studies have sought to elucidate the origin of sex differences on low-level visual perception tasks (Hutchinson et al., 2014b) and it has been suggested that they might reflect left-right asymmetries in

hemispheric specialisation. To explore this issue, Kaufmann et al. (2001) asked participants to view flickering chequerboard patterns inside a magnetic resonance imaging (MRI) scanner. The BOLD response in right V5/MT was significantly larger in females than males. Hormonal differences might provide an explanation for this result as performance on low-level visual tasks fluctuates during the course of the menstrual cycle (Wong and Tong, 1974; Ward et al., 1978; Symons et al., 1990). However, no significant difference in BOLD response was found in right V5/MT when Kaufmann et al. (2001) compared women who took the contraceptive pill with those for whom it was not prescribed. This finding suggests that sex differences in visual perception reflect chromosomal sex composition rather than varying hormone levels. Research involving participants with complete androgen insensitivity syndrome (CAIS) could be used to further tease apart these possibilities (van Hemmen et al., 2014). Individuals with this rare genetic disorder have an XY karyotype but cannot respond to testosterone and subsequently develop a female phenotype (Oakes et al., 2008).

Post-mortem studies have also been carried out to explore the neurophysiological correlates of sex differences in visual processing. Amunts et al. (2007) obtained measurements of volume and surface area in a cytoarchitectonic area known as hOc5 (Malikovic et al., 2007). This brain region might correspond to extrastriate area V5/MT (Barnikol et al., 2006; Wilms et al., 2005). Results showed that hOc5 was significantly smaller in the right hemisphere of females than males, consistent with some previous findings (De Lacoste et al., 1991; Kovalev et al., 2003). It was suggested that this left-right asymmetry might provide males with additional neural resources or 'space' for the processing of computationally demanding visual stimuli. A direct prediction of this hypothesis is that females should exhibit better performance on RDK tasks when the stimuli are presented in the right visual field (left hemisphere) than the left visual field (right hemisphere). This interesting hypothesis is currently untested but it could be explored in future research.

Regardless of the neural substrate, that females have significantly higher coherence thresholds than males on global motion tasks has important implications for research exploring visual processing in clinical populations. It could explain discrepancies between studies and in particular why some research has failed to uncover deficits in the processing of global motion, relative to global form, in some neurodevelopmental disorders, as many studies have neglected to take sex into account. We have already suggested that a significant group difference between children with dyslexia and relatively good readers in the study by Milne et al. (2006) may have been masked by a marked imbalance between males and females in the participant groups. However, the opposite could also be true. Effect size is likely to have been exaggerated if the ratio of males to females is markedly higher in the control group than the clinical population. Half of the studies cited here that have uncovered deficits in the processing of global motion relative to global form, have failed to report sex ratios in participant groups (Table 1), which means this possibility cannot be ruled out and is a promising area for future scientific study.

7. Non-verbal IQ

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

The fact that non-verbal IQ is a significant predictor of coherence thresholds on global motion tasks but not global form tasks has further implications for studies investigating visual perception in clinical populations. As previously mentioned, Koldewyn et al. (2010) found that adolescents with ASD had significantly higher coherence thresholds than typically developing controls on a global motion task but not a global form task. The effect disappeared when IQ was entered into the analyses as a covariate. Some argue that it is "misguided and unjustified" to partial out IQ when studying neurocognitive function in developmental disorders (Dennis et al., 2009). It has been suggested that IQ represents a global outcome measure that is directly attributable to, and confounded by, the neurodevelopmental disorder. When investigating the processing of global motion and global form, we believe it is critical to control for non-verbal IQ because recent research has confirmed that a strong link exists between this variable and performance on global motion tasks even in the general population (Arranz-Paraíso and Serrano-Pedrazza, 2016; Cook et al., 2016; Johnston et al., 2016; Koldewyn et al., 2010; Melnick et al., 2013). Half of the studies that have found deficits in the processing of global motion, relative to global form, either did not control for non-verbal IQ, or only matched groups on the basis of verbal IQ, the latter of which is not associated with performance on global motion tasks (Arranz-Paraíso and Serrano-Pedrazza, 2016). This is likely to have confounded results and contributed to the inconsistencies reported across the studies we have cited in this review (Table 1).

8. The need for a new theoretical framework

In light of new psychophysical evidence it appears that a novel theoretical framework of visual processing in neurodevelopmental disorders is needed. Although deficits in the processing of global motion, relative to global form, have been found in some neurodevelopmental disorders and children born preterm, there is a great deal of inconsistency in the literature. In addition, it is unclear if the results of studies that have uncovered such a pattern of impairment reflect differences in factors that are known to be associated with performance on global motion tasks such as sex and non-verbal IQ. Task and stimulus parameters also differ between studies to an extent that makes a proper comparison difficult. To operate effectively in the world the visual system has to satisfy the competing constraints of integrating features that belong to a common object, whilst segmenting those arising from different objects (Albright and Stoner, 1995; Braddick, 1993; Nakayama, 1985). Integration and segmentation are thus opposite ends of a continuum and may well be mediated by distinct mechanisms that are differentially susceptible to impairment during development. Five of the studies we have reviewed administered a motion-based segmentation task, rather than a straightforward motion-integration task (Table 1). In those studies, participants had to discriminate spatially divided random-dot stimuli from patterns containing uniform motion that reversed direction periodically. That individuals with Williams Syndrome (Atkinson et al., 1997, 2006), ASD (Spencer et al., 2000), DCD (O'Brien et al., 2002), and children born preterm with PVL (Guzzetta et al., 2009) exhibited impaired performance on this task, relative to typically developing controls implies that the underlying nature of the visual deficit in these neurodevelopmental disorders

might extent to object segmentation. However, segment size was fixed in all of the studies mentioned above and research has shown that coherence thresholds on motion-based segmentation tasks are dependent upon segment size (Burr et al., 2006; Johnston et al., 2017; Watson and Eckert, 1994; van Doorn and Koenderink, 1982). In addition, participants could have based their decision on each trial by identifying the uniform pattern, leaving open the possibility that impaired performance might reflect the known difficulty with global motion (integration) rather than segmentation. A recent study by Johnston et al. (2017) addressed these issues in developmental dyslexia. Two motion and form tasks, designed to provide a sensitive measure of object segmentation, were administered to thirty-eight adults with a wide range of reading abilities. Participants viewed a random-dot display divided spatially into horizontal segments. Adjacent segments contained either local motions in opposing directions or analogous static form cues depicting orthogonal orientations. They discriminated this stimulus from one containing identical motion or form cues that were spatially intermingled. Results showed that generally poor readers and individuals with dyslexia exhibited a different pattern of performance to relatively good readers on the motion-based but not the form-based segmentation task. Specifically, coherence thresholds decreased as segment size increased, but for the motion task the rate of improvement was shallower for the poorest readers and the segment size at which performance became asymptotic was larger. Johnston et al. (2017) showed, using a biologically-motivated model of spatial segmentation, that this pattern of impairments is consistent with a deficit involving spatial scale selection. That is, there is a mismatch between the spatial scale of the visual mechanism used to solve this task and the movement information available in the stimulus. An important avenue for future research is to explore whether visual perception in other neurodevelopmental disorders, and children born preterm, is also limited by sub-optimal scale selection.

The neural mechanisms underlying spatial scale selection are currently unknown but neurophysiological studies have shown that receptive field size of cells in extrastriate visual areas including V5/MT and V4 is dynamic rather than hard-wired (Womelsdorf et al., 2006, 2008; Treue and Martinez-Trujillo, 2012). These neurons also exhibit centre-surround antagonism, a property that has been implicated in object segmentation (Allman et al., 1985; Born and Tootell, 1992; Born et al., 2000; Cox et al., 2013; Pack et al., 2005; Tadin, 2015). How these adaptive receptive field properties mediate scale selection is a promising area for future scientific study in non-human primates. Research is also needed to explore if scale selection operates in a bottom-up manner or whether it is mediated by top-down signals from attentional control sites (Hopf et al., 2006).

9. Summary and future directions

In this review, we have shown that some individuals with neurodevelopmental disorders and children born preterm have a selective deficit in the processing of global motion but not global form. However, there are discrepancies in the literature, which might reflect the fact that research exploring visual processing in these disorders has often neglected to control for factors that are known to be associated with performance on global motion tasks such as sex and non-verbal IQ. Several theories have been proposed to explain why deficits in the processing of global motion, relative to global form might arise but these are difficult to reconcile with recent psychophysical evidence that we have brought to the forefront. In addition, we have described four new, global motion and global form tasks that have been successful in elucidating the underlying nature of the visual impairment in dyslexia. We believe that their application to other neurodevelopmental disorders and children born preterm is timely and could be of similar value. The lack of consistency across studies that have explored the processing of global motion and global form in neurodevelopmental disorders and children born preterm implies that a new theoretical framework is needed. Recent work has shown that visual perception in readers with dyslexia is limited by sub-optimal scale selection and we have proposed that a similar impairment might arise in other clinical populations. Although sub-optimal scale selection would manifest primarily as a difficulty with object segmentation, it could also explain why deficits in the processing of global motion have been found in neurodevelopmental disorders and children born preterm. Elucidating the neural and computational mechanisms underlying scale selection would greatly enhance our knowledge of visual processing in clinical populations. We believe this is an exciting area for future scientific study. It has wide-reaching implications and will help elucidate the critical role played by vision in human brain development.

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