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Review

Vision in developmental disorders: Is there a dorsal stream deficit?☆

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ABSTRACT

The main aim of this review is to evaluate the proposal that several developmental disorders affecting vision share an impairment of the dorsal visual stream. First, the current definitions and common measurement approaches used to assess differences in both local and global functioning within the visual system are considered. Next, studies assessing local and global processing in the dorsal and ventral visual pathways are reviewed for five developmental conditions for which early to mid level visual abilities have been assessed: developmental dyslexia, autism spectrum disorders, developmental dyspraxia, Williams syndrome and Fragile X syndrome. The reviewed evidence is broadly consistent with the idea that the dorsal visual stream is affected in developmental disorders. However, the potential for a unique profile of visual abilities that distinguish some of the conditions is posited, given that for some of these disorders ventral stream deficits have also been found. We conclude with ideas regarding future directions for the study of visual perception in children with developmental disorders using psychophysical measures.
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Contents

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In 2003 Braddick et al. [23] suggested that the dorsal visual stream is vulnerable during development. Supporting this claim was a body of evidence indicating that a variety of developmental disorders show anomalies in the detection of motion coherence in a field of dots, a function attributed to processing within the dorsal visual pathway. Often this anomalous motion perception was associated with normal performance on tasks requiring detection of coherent structure in stationary patterns, a capability attributed to processing in the ventral stream of the cortical visual system. These authors therefore posited that abnormalities in dorsal stream functioning are characteristic of developmental disorders. This conclusion was based predominantly on the psychophysical studies that measured coherence thresholds for global motion as an index of dorsal-stream functioning. However, as will be explained below, there are multiple stages within both of these cortical pathways and it is unlikely that a single task could capture processing at every level of either stream. While studies assessing the ventral pathway in Williams syndrome were outlined by Braddick et al., fewer studies examining multiple levels within the dorsal or ventral visual streams had been conducted for the other developmental disorders included in their argument. Much research assessing the visual capabilities of different levels within both visual pathways for several developmental disorders has occurred since then, and there have been advances in the way the visual system is conceptualised and measured. Accordingly, it is now pertinent to re-evaluate whether it is the case that developmental disorders can be characterised by a general vulnerability in the dorsal visual stream.

The aim of this review is to consider five developmental conditions for which early to mid level visual abilities have been investigated – developmental dyslexia, developmental dyspraxia, Williams syndrome, Fragile X syndrome, and autism spectrum disorders (ASDs) – to evaluate whether the pattern of performance on visual tasks is restricted to impairment in dorsal stream functioning. While there are studies of the anatomical development of the visual system (e.g. [100]), patterns of saccadic eye movements (e.g. [86]), and the involvement of the cerebellum (e.g. [158]), in visual perception (all of which involve the dorsal stream), the focus of this review is on psychophysical measurements of visual functioning in developmental disorders. The studies investigating visual functioning in this manner frequently use similar methods across different disorders. Therefore, following an update on recent theories regarding the pathways in the visual system and an outline of the visual paradigms most commonly used in investigations of early to mid level visual abilities, this review will summarise critical findings associated with each developmental disorder. We consider what contribution this research makes towards our understanding of these paediatric conditions in addition to evaluating whether performance on visual tasks is consistent with impairment in the dorsal stream. The advantage of considering the developmental disorders together is that we can evaluate whether this purported profile of anomalous dorsal stream processing is common to several disorders, or whether instead some of the conditions show certain visual anomalies not expressed in the other disorders.

1. The human visual system

1.1. Structure of the visual system

In the largest visual pathway in the primate visual system, information is transmitted from the retina to the lateral geniculate nucleus (LGN) and then on to the primary visual cortex (V1) via three distinct sub-pathways: the magnocellular (M), parvocellular (P) and koniocellular (K) streams[1] [33,113]. These sub-pathways account for the majority of the input to V1, although anatomical and physiological evidence shows other pathways containing fewer fibres exist [84]. The segregation of sub-pathways is very obvious within the LGN, which is composed of six prominent layers, the lower two consisting of large cell bodies known as the M (or magno) cells, and the upper four consisting of smaller cell bodies known as the P (or Parvo) cells, with the K (or Konio) cells interlaminar to each of these six main layers. These cells differ in their physiology as well as their anatomy [84,106].

The M cell population has relatively large receptive fields, is not systematically selective for colour, and has lower spatial resolution, higher temporal resolution and faster conduction speeds than the P cell population (although the populations do have considerable overlap on many of these dimensions; see [113,84]). The relative specialisation of function in the M and P cells led to the suggestion of specialised neural pathways [27,46,99]. In extra-striate cortical regions, the M cells provide the predominant input to the dorsal stream leading to the dorsolateral occipital cortex [105] and regions of the posterior parietal lobe [64]. This pathway responds well to rapidly changing stimuli such as flicker and motion [98,182]. Studies of primate physiology, lesions in humans and neuroimaging have identified an important role for the dorsal pathway in the processing of motion [38]. The P cells provide the predominant input to the ventral visual stream leading to inferotemporal areas of the temporal lobe [64]. This pathway is optimised for encoding information about shape and colour, and responds to slower moving or stationary stimuli [165]. Evidence from neuropsychology suggests the ventral stream is implicated in form perception [12]. Currently, it is understood that the idea that motion processing relies exclusively on the dorsal stream, and form processing relies exclusively on the ventral stream, is too simplistic [142] and that the cortical pathways show appreciable cross-talk [113,24,160].

Cortical projections from the visual pathways proceed in a hierarchical manner, from lower to higher cortical areas [20,107]. At the earliest stage of visual perception the neurons in the primary visual cortex (V1) extract information about the orientation, curvature, and spatial and temporal frequency of stimuli from small regions in the retinal image [48,79] (i.e. predominantly local processing). Higher visual areas combine the information from V1 to extract more global aspects of images. With respect to the ventral stream, it has been argued that V2 comprises an intermediate stage of angle processing by combining orientation information from filters in V1 [72], and by detecting implied and second-order contours [171]. V4 then encodes more complex object features than edge orientation, such as complex curved shapes [129]. Thus, V4 has been argued to have an important role in global form perception [180]. In the dorsal stream, direction sensitivity arises in V1 in primates [78], and the integration of information received from these cells, occurring in V3 and V5, results in preferential activation in response to fronto-parallel motion [25]. Higher up in the dorsal pathway, V6 cells are characterised by their preference for different types of pattern structures revealed only through large field motion such as rotation, and radial expansion or contraction of the retinal image [133,58]. Thus these areas have a central role in global motion perception.

While it was initially proposed that cortical projections proceed only in a feedforward manner, this idea has been revised following the discovery of an extensive network of feedforward and feedback

[1] The koniocellular pathway is currently thought to be concerned primarily with blue-yellow colour perception [157] and to have slower conduction velocities and more diverse response properties than the M and P cell responses [33]. Since it has not been a focus in research on developmental disorders, the koniocellular pathway will not be considered further.

interconnections [166,183]. The fact that conduction is faster for the larger M cells than for the smaller P cells allows for multiple cortical interactions via feedback or (in instances of masking) by M activity interfering with slower P activity at various levels of the visual system ([28,71,179], but see [93]). Thus, a 'magnocellular speed advantage' has been reported in the primate [106] and human [87] literature. Several theories of visual processing have been proposed (see [183,31,91]) in which this magnocellular advantage allows for the possibility of information carried by the M cells modulating the response to the later arrival of information carried by the P cells. The magnocellular advantage is thought to be very important in normal vision as it involves the initiation of attention mechanisms in the parietal cortex, allowing for a fast and automatic initial global analysis of a visual scene [143].

It is the magnocellular pathway that feeds to the dorsal cortical stream that has been of particular interest to researchers investigating developmental disorders and that underlies Braddick et al.'s [23] dorsal stream vulnerability hypothesis. Specifically, it has been proposed that the larger M cells are more at risk early in the disease process than the P cells, since neurons with larger cell bodies and axon diameters are more susceptible to damage [135]. Additionally, magnocellular pathway loss might be more readily detected because there are far fewer M cells than P cells (approximately 80% of the retinal ganglion cell population is P cells, 8–10% M cells and 5–10% K cells [40]). Thus even if neurons were lost proportionally across all cell types, the sparser M cell system may demonstrate more readily detectable functional loss [112]. These factors are consistent with Braddick et al.'s [23] suggestion that measures of dorsal stream function may be more likely to show impairment or that the stream is "more vulnerable in development" (p. 1779) and therefore when a paediatric disorder is present, the likelihood of the magnocellular pathway exhibiting an abnormality may be increased, even if all cell types are affected. It is not yet clear whether this "magnocellular disadvantage" does indeed manifest across multiple developmental disorders. Therefore, investigating the evidence for dorsal stream impairment in these conditions forms the basis of the current review.

Much of the research investigating vision in the developmental disorders retains the conceptualisation of specialised but linked dorsal and ventral pathways, processing information hierarchically. Importantly, in order to determine the specificity of the purported magnocellular/dorsal pathway deficit in developmental disorders, the integrity of both the dorsal and ventral streams at both early and later visual processing stages must be assessed. In order to summarise the studies that have assessed functioning of this nature in the developmental disorders, we first describe a selection of ways in which different levels of both pathways are assessed psychophysically. This summary is by no means exhaustive. We focus on the methods most commonly used thus far to assess visual abilities in the developmental disorders. With respect to psychophysical studies, it is important to note that the whole visual pathway from retina to motor response is assessed. However, it is assumed that critical aspects of particular tasks are performed at specific points along the pathway and that failure on those aspects can identify the locus of a particular psychophysical effect [161]. Information gained from electrophysiological and imaging studies provides an important addendum to the psychophysical literature regarding physiological events or anatomical loci, and where relevant is included in this review.

1.2. Methodology used to assess visual functioning

1.2.1. Early visual processing

As outlined above, there are a variety of functions performed by the neurons in V1, and it is impossible to measure all these functions simultaneously. Thus, the most common psychophysical methods determine the minimally detectable presence of one stimulus attribute at a time. Predominantly, it is a contrast threshold that has been measured. Research has determined that, when presented at appropriate temporal frequencies, gratings with very low spatial frequencies, well below the peak of the contrast sensitivity function, can be used to assess M cell functioning, whereas those well above the peak may be used to address P cell performance [92,147]. One reason for using extreme values is that the peak of the contrast sensitivity function varies with display size and mean luminance [85,110,111]. Contrast sensitivity tasks assessing the parvocellular system generally employ high spatial frequency gratings with a low temporal frequency, whereas tasks assessing the magnocellular system typically use low spatial frequency gratings, or Gaussian blobs, with a high temporal frequency. For grating stimuli turned on and off gradually, M cells give little or no response at any spatial frequency [85] whereas P cells respond at various intensities depending on the spatial frequency and contrast [74]. Thus, the spatial and temporal characteristics of stimuli assessing the contrast sensitivity of M and P cells must be chosen carefully.

In a typical population, infants' contrast sensitivity is poor compared to that of adults; newborns can see stripes only if the spatial frequency is less than 1 cycle per degree and at high contrast, whereas adults can see spatial frequencies almost 40 times that amount (see [108,109], for reviews). Contrast sensitivity improves during early development, but takes approximately 7 years to reach adult levels [55].

1.2.2. Global processing

Global Dot Motion (GDM) stimuli provide a sensitive measure of dorsal stream capability [126] in that they assess global processing predominantly associated with areas V3a and V5 [25,29]. In one common form of GDM stimulus, a proportion of dots on a computer monitor move coherently and the remaining (noise) dots move in random directions at the same speed. Steps are taken to prevent observers detecting the signal motion direction by tracking the trajectory of a single dot. For instance, the lifetimes of single dots can be limited, with each disappearing dot replaced by a new dot at a different location [126], or the dot can continue throughout the lifetime of the display, but be assigned to signal or noise directions at random for each frame transition [53]. The ability to perceive global coherent motion therefore depends on successful detection and integration of local motion signals over both space and time [32,47,152]. The smallest proportion of dots that have to move coherently for the observer to perceive coherent global flow gives the threshold for coherent motion detection.

There are two ways in which global processing in the ventral stream has been assessed in the literature examining developmental disorders. The first presents a coherent form signal defined by short, high contrast line segments that are oriented according to a geometric rule (e.g. vertical, concentric), with all other line elements randomly oriented (see Fig. 1a). The smallest proportion of lines that have to be coherently oriented for the observer to discriminate a field containing the pattern from one that does not gives the threshold for coherent form detection. In V1, the response of orientation-tuned columns can be facilitated by long-range connections to other columns preferring the same orientations in adjacent parts of the visual field [101]. Recent investigations suggest that detectability of contours created by line segments can be enhanced in a similar way as that seen by the facilitation of long-range connections in V1 [59,96]. For this reason, global-form detection tasks that can be completed by detecting extended contours may well allow a grouping contribution from V1 and should therefore be avoided if the aim is to investigate global processing in V4. Instead, Glass patterns [63] provide a useful alternative as they specifically target high-level integrative processing in the ventral stream [180,163]. Glass patterns consist of randomly distributed

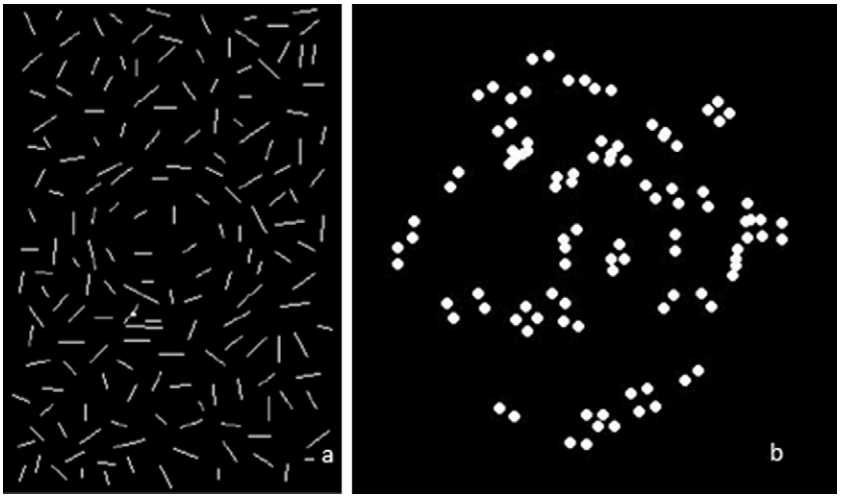

Fig. 1. (a) Example of a coherent line segment stimulus, taken from Milne et al. [118], and (b) example of a 100% coherent concentric Glass pattern.

dot dipoles, a proportion of which conform to a global structure, which is achieved by aligning the dots within pairs along contours of the desired global structure (such as concentric or parallel; see Fig. 1b). These stimuli minimise facilitation by long-range connections between orientation-tuned columns in V1 because random dispersion of the dot dipoles means there is no systematic alignment of any dot dipole with neighbouring dipoles, resulting in very few contours longer than a dot pair. The nature of the noise in the stimulus display (randomly oriented dipoles) means that long-range facilitation processes are less likely to link signal contours as selectively. In Glass patterns, an observer must combine the information from within multiple pairs of dots to perceive the overall structure.

With respect to global processing in typical populations, for the dorsal stream Gunn et al. [68] reported that motion coherence thresholds for a task where observers were required to locate a target strip in which the direction of motion was opposite to the rest of the display does not reach adult levels until approximately 10–11 years. Conversely, Parrish et al. [128] concluded that the perception of coherent global motion reaches adults levels at approximately 6 years. Parrish et al. [128] also reported that performance on motion-defined form tasks improved up until approximately age 7 years, whereas performance on texture-defined form tasks continued to improve up to the oldest age group they assessed (11–12 year olds), suggesting that global abilities in the ventral pathway develop later than those in the dorsal pathway. In other work on ventral stream global processing, Lewis et al. [94] reported that thresholds for parallel and concentric Glass patterns were immature at 6 years of age, but were adult-like by 9 years of age (see also Porporino et al. [134], for an example of global form processing developing until 8 years of age using a non-psychophysical stimulus). Thus, most forms of global processing appear to mature prior to adolescence.

1.2.3. First- and second-order processing

Our visual world contains both luminance- (first order) and contrast- (second order) defined information [145]. Separate mechanisms for processing first- and second-order stimuli, both stationary and moving, have been demonstrated (see [34] for a review). Frequently, first-order motion and form stimuli are luminance-modulated noise patterns created by adding grey-scale noise to sinusoidal luminance modulation (e.g. a vertical sinusoid for translational motion; see Fig. 2a). Second-order motion and form stimuli are often texture-modulated noise patterns produced by multiplying rather than summing modulating sine waves with the grey-scale noise (see Fig. 2b). Critically, mean luminance level varies across space for first-order stimuli, and is therefore detectable by linear spatial operators. Second-order stimuli vary in contrast and not local mean luminance and are therefore intended to be invisible to the linear spatial operators operating at the signal frequency, such as those found in early vision [8]. Bertone et al. [20,19] refer to these first- and second-order stimuli as 'simple' and 'complex' stimuli, respectively, since the first-order stimuli are purported to be processed by linearly-summing output of simple cells in V1, whereas additional neural processing is required before second-order stimuli are perceived, and this processing occurs further along in the visual streams [181].

However, it is unclear whether the dynamic stimuli such as those described by Bertone et al. [19] are able to differentiate cleanly between simple and complex processing. For the dynamic second-order stimuli, it is possible that an observer can select one bar within the image and track its direction across space (known as "attentive tracking") rather than integrate information across the multiple elements of the display [44]. Derrington et al. [44] reported that this is most likely to occur at or near the contrast threshold, and thus provides a third mechanism (over and above the first- and second-order systems) by which these stimuli may be perceived. If attentive tracking can be used to perceive second-order stimuli, this may subvert the ability of such tasks to assess dependence on integrative capabilities at more complex levels. While stimuli are available that avoid this potential problem (see [9,11,54] for examples of first- and second-order Glass pattern and GDM stimuli), these have not yet been applied to the study of developmental disorders.

In investigating typical development, Lewis et al. [95] reported that first- and second-order perception of static stimuli was equivalent for 5 year-old compared to adults. These findings are consistent with those of Bertone et al. [18] who also reported no age differences in thresholds for first- and second-order static stimuli. Ellemberg et al. [56] reported that for both first- and second-order motion stimuli, thresholds for 5 year olds were higher than those for adults, but this was more pronounced for the second-order than the first-order stimuli. Bertone et al. [18] found a similar pattern of results in their 5–6-year-old age group, but reported that second-order motion perception reached adult levels earlier (7–8 years) than first-order motion perception (9–10 years) when assessing older children. These findings suggest that first- and second-order processing of form stimuli appears to mature earlier than first- and second-order processing of motion stimuli.

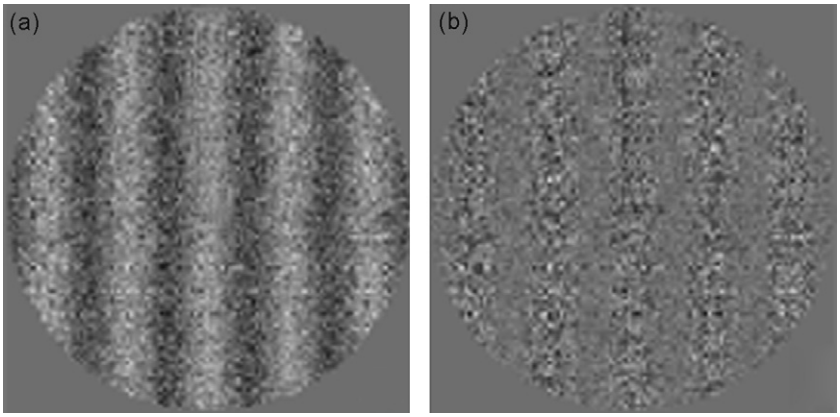

Fig. 2. (a) Example of a static first-order stimulus, and (b) example of a static second-order stimulus, taken from Bertone et al. [20].

2. Vision in the developmental disorders

Braddick et al. [23] present a body of evidence suggesting that functioning within the ventral visual stream matures earlier than dorsal stream functioning. They suggest that the later development of the dorsal stream provides a greater opportunity for anomalous development to impair functioning within this pathway. Thus, when a developmental disorder is present, the dorsal stream may be more susceptible to impairment. They suggest that this vulnerability is not specific to one particular condition, but rather is characteristic of many developmental disorders. Accordingly, they postulate qualitatively similar impairments in the dorsal stream across these conditions. For the psychophysical tasks of interest in this review, some of the summaries above are consistent with the suggestion that the ventral visual pathway develops earlier than the dorsal stream in typical development, as evidenced by performance on first- and second-order static tasks reaching adult levels earlier than is the case for equivalent dynamic tasks [18,95]. However, the evidence reviewed suggests that for global processing tasks the distinction may be more equivocal, with some studies reporting adult-like performance at similar ages for GDM tasks [68] and Glass pattern tasks [94], and one study even reporting that sensitivity to global form develops later than sensitivity to coherent motion [128,65]. Thus, the assertion that dorsal stream functioning develops later than the ventral stream, making individuals with a developmental disorder more susceptible on tasks designed to assess the dorsal pathway, requires further assessment. However, the purpose of this section is to test more generally the claim that the dorsal stream is especially at risk in the presence of a developmental disorder by reviewing the literature for those conditions in which visual performance has been assessed using the psychophysical methods outlined above. For each disorder, we first consider how impairment in the dorsal stream may relate to the symptomatology of the condition, and then outline the results of studies that have examined visual abilities in those affected by the disorder.

2.1. Dyslexia

Developmental dyslexia is a specific disability in which individuals do not acquire proficient reading skills, despite sufficient cognitive abilities and education [175]. Because reading is primarily a visual task requiring the integration of information from successive fixations [10], it is possible that some of the reading difficulties seen in dyslexia are the result of anomalies in processing visual information. In particular, initial proposals suggested a role for the magnocellular system in reading that involved the suppression of the parvocellular system during saccades [26]. In light of more recent evidence suggesting that it is the magnocellular system rather than the parvocellular system that is the target of suppression during saccades [4], other hypotheses have been explored concerning the role of the magnocellular system in reading problems in dyslexia. For example, Vidyasagar [168] argued that, when reading, sequential scanning of individual letters during fixation periods is necessary for effective letter identification. Since the large receptive fields of the ventral stream areas involved in object recognition do not code well for location, feedback from the dorsal stream could feed the location of the letters of each word in a temporal sequence to the ventral stream [169,170]. According to Vidyasagar, when learning to read, this attentional gating has to be trained to move sequentially across lines of text. Purportedly, difficulties in this process can happen even with small lesions affecting the M cells in critical parts of the visual field, preventing effective attentional spotlighting over the letters during each fixation.

Much research has focused on determining whether dyslexic readers do indeed show impairment in the magnocellular pathway evidenced by reduced contrast sensitivity. This has already been the subject of an extensive review, and a detailed evaluation is beyond the scope of this paper; hence a brief summary is provided. In his review, Skottun [147] (see also [148,149]) reported that, of the 22 studies which investigated spatial contrast sensitivity in dyslexia, four found impairments at low spatial frequencies, suggesting a problem in M cell functioning (see also [155]), eleven studies found evidence of deficits of a nature incompatible with a deficiency in the magnocellular system, and seven studies were inconclusive (see also [178]). Similarly, of the seven studies investigating temporal contrast sensitivity, only two provided evidence consistent with an M cell deficit in dyslexia, while the other five were inconclusive. Skottun suggested that most of the research reviewed did not adequately distinguish between M and P cell functioning in that many studies did not involve spatial frequencies below the peak of the contrast sensitivity function. He thus concluded that further research needs to be conducted to establish whether the popular theory of a magnocellular deficit in dyslexia can be supported. However, contrast sensitivity is only one property of the neurons in V1. Not included in Skottun's review were those studies that demonstrate greater visible persistence at low spatial frequencies in individuals with dyslexia when compared to control groups [10,151,150], which has also been explained in terms of a magnocellular pathway deficit [104]. While the notion of a magnocellular deficit explaining the reading difficulties in dyslexia has been very popular, it appears that the evidence from measures of contrast sensitivity is currently unable to support the claim of a simple and consistent link between the two [147]. However, attempts have been made to explain why some studies find differences whereas others do not, based on subtle differences in task properties. For example, with respect to the attentional gating

hypothesis, Vidyasagar [169,170] suggested that the small lesions purportedly affecting the M cells might not always be detectable with the usual tests of M cell functioning, which may explain why some investigators (e.g. [147,3]) do not agree that there is a specific M cell impairment in dyslexia. This issue may be compounded by the fact that a uniform definition of dyslexia has not been used when selecting participants [76].

Also not included in Skottun's review were studies investigating high-level processing in the dorsal stream. While there are reports of equivalent performance [164,173], the majority of studies indicate that children with dyslexia are less sensitive than age- and IQ-matched controls to coherent motion stimuli [151,159,35,70,130,137]. Finally, all studies assessing higher-level processing in the ventral stream have found intact abilities when comparing individuals with dyslexia to matched controls [164,173,70]. Both Hansen et al. [70] and White et al. [173] used line segment stimuli, whereas Tsermentseli et al. [164] used Glass pattern stimuli. These studies are in agreement despite using different methodologies and the concern (outlined above) regarding the ability of line segment stimuli to tap global processes. Thus, were it to be the case that a magnocellular deficit affects contrast sensitivity and global motion processing in dyslexia, it does not appear that the underlying causes impact on the ventral pathway.

Overall, given that the ventral stream appears to be intact at both the earlier and later stages of visual functioning in dyslexia, it would appear that any visual deficits in this condition have the potential to be restricted to the dorsal stream, consistent with Braddick et al.'s [23] dorsal stream vulnerability hypothesis. Given the varied and conflicting results on contrast sensitivity measures, it remains to be clarified as to whether the reasonably consistent impairments in global motion processing in dyslexia are accompanied by deficits at the earlier levels of the dorsal stream. Considering the properties of the cells in V1 other than contrast sensitivity (such as direction selectivity or speed of processing) will be important in making this distinction. It has also been argued that future research assessing visual abilities would be facilitated by adopting an agreed and consistent definition of the diagnostic criteria for dyslexia [76], and examination of the profiles of subgroups within this population [22].

2.2. Autism spectrum disorders

Individuals with an ASD exhibit delays in language development, social and communication difficulties and repetitive, stereotypic behaviours and interests [2]. In this condition, anomalous visual abilities may impact on the perception of faces and body gestures essential for social communication (e.g. [45,132]). However, while not required for a diagnosis, it is the commonly reported motor functioning deficits in ASDs (see [140] for a review) that are most likely linked to specific difficulties in dorsal stream perception. The dorsal pathway has an important role in conveying information about the spatial relations between objects (see [120] for a review) and about their motion, and thus is purported to be involved in position coding and visually guided actions. Therefore, it is this pathway that is likely to be implicated in the abnormalities in co-ordination, gait, balance and posture that are frequently observed in children with an ASD. The potential for these anomalies to arise from visual deficits is highlighted by evidence that children with autism have a very weak postural reactivity to visually perceived environmental motion [62]. One possible explanation posited to account for these results was that children with autism have a deficit in the perception of motion and therefore experience less need to adjust their posture in response to environmental motion when compared to typically developing children. Thus, many studies have focused on determining whether children with an ASD exhibit a specific motion processing deficit, consistent with dorsal stream impairment.

Several researchers have reported higher motion coherence thresholds in individuals with high functioning autism compared to matched control groups on GDM tasks ([164,116,131,153,154,41],[2] but see [42]).[3] As an alternative to GDM stimuli in assessing global motion processing, Vandenbroucke et al. [167] employed plaid stimuli that can be perceived as a coherently moving pattern when integrated or, alternatively, as two transparent gratings sliding over each other. The proportion of time the plaid was seen as coherent rather than sliding did not differ for an ASD group compared to age- or IQ-matched control groups, suggesting no evidence of impaired global motion perception in ASDs with this task. However, the transition between transparency and coherence in plaids is a gradual one and the decision point between one percept and the next is open to subjective interpretation. Thus, this can result in variability in responses which may mask any group differences that may exist.

With respect to lower-level dorsal stream functioning, several studies have reported intact flicker contrast sensitivity thresholds in individuals with high functioning autism when compared to age- and non-verbal IQ-matched controls [20,131,41]. This suggests that the visual difficulties experienced by individuals with autism are not a function of deficient M cell contrast sensitivity. Rather, the favoured interpretation has been that impaired global motion thresholds in the presence of intact flicker contrast sensitivity thresholds is indicative of impairment in global processing at the higher levels of the dorsal cortical stream [20,131].

Regarding lower-level ventral stream processing, Davis et al. [41] and Sanchez-Marin and Padilla-Medina [144] reported that ASD groups, relative to controls, had lower contrast sensitivity thresholds (or better performance) for the detection of high spatial frequency gratings. However, de Jonge et al. [42] found no significant difference in ability to perceive orientation between a group with ASD compared to an age- and IQ-matched control group for high spatial frequency gratings. When higher-level functioning in the ventral pathway has been assessed, individuals with an ASD have been found to exhibit comparable performance on coherence thresholds for global structure in line segment tasks when compared to matched control groups [154,21,118]. In contrast, impaired Glass pattern thresholds consistent with anomalous global processing in the ventral stream have been found in subgroups of individuals with autism, but not the whole mixed ASD samples, when compared to control groups [164,153].[4] Thus, while

[2] Davis et al. [41] administered two GDM tasks, the first requiring children to identify the direction of motion and the second requiring identification of whether two stimuli were moving in the same or different directions. Short and long presentation-duration versions of these tasks were administered. Children with autism showed a deficit in identifying the direction of motion in the long presentation condition only.

[3] In this study, the ASD and control groups did not differ in motion coherence thresholds for a GDM task, however, the task had an unlimited stimulus presentation time, and the magnitude of the steps sizes was large (5%) compared to studies which have found a difference in coherence thresholds (e.g. [101,59]). These features may have limited the task's sensitivity to subtle differences between the two groups.

[4] Vandenbroucke et al. [167] recorded event-related potentials in response to figure-ground segregation of textured figures in order to examine the roles of feedforward, feedback and horizontal connections in visual processing in ASD. Horizontal connections are thought to play an important role in boundary detection and individuals with an ASD showed diminished cortical activity and had more difficulty on the figure-ground task that relied mainly on boundary detection. Vandenbroucke et al. therefore argued that deficient horizontal connections in low-level visual processing characterise ASDs. However, it is difficult to reconcile how impairment in early contour linkage, suggested by Vandenbroucke et al., in addition to impaired Glass pattern detection, can occur in the presence of intact perception in line segment tasks. Importantly, further study concerning the underpinnings of the line segment coherence task is required.

it appears that difficulties in higher-level global grouping in the dorsal cortical stream may be able to account for the elevated global motion thresholds in ASDs, it is currently unclear whether there is a comparable impairment in higher-level global processing in the ventral pathway. If it is the case that the contour detection tasks evoked by line segment stimuli can be processed by the cellular networks in V1 [101,59,96], then, with the exception of Vandenbroucke et al. [167], the results outlined above appear to be consistent with the notion that individuals with autism are unimpaired on tasks requiring lower level processing in the form pathway (with respect to both contour detection and contrast sensitivity), but exhibit difficulties on form tasks relying more heavily on higher-level integration, such as in detecting concentric Glass patterns.

Bertone et al. [19] assessed visual performance in ASDs with first- and second-order translating, radiating and rotating motion stimuli. The second-order stimuli are considered more 'complex' than the first-order stimuli as they require additional neural processing. No significant group differences in direction discrimination were found with first-order motion perception, but the autism group required higher modulation depths to discriminate the direction of motion for all second-order patterns, relative to an age-matched control group. To assess ventral stream processing, Bertone et al. [20] used first- and second-order form stimuli constructed in the same way as the motion stimuli in Bertone et al. [19]. Their autism group performed better than age-matched controls on the first-order form task (i.e. they required less modulation of contrast to determine whether a grating was horizontal or vertical), but the autism group performed more poorly than controls on the second-order form task. Bertone et al. [20] suggested that these results may reflect "atypical neural connectivity mediating the extraction of low-level orientation information within the visual processing hierarchy in autism" (p. 2436).

Other visually based abnormalities have also been demonstrated in individuals with autism in the form of superior performance in detecting embedded figures and in reproducing block designs relative to controls (see [67] for a review). Both these tasks require the ability to overcome the natural tendency to initially perceive the gestalt in order to focus on individual stimulus elements. In an attempt to account for both the strengths and weaknesses seen in ASDs, Weak Central Coherence theory was proposed [61]. Under this account, children with ASDs have difficulty combining local information to create a coherent global percept, a consequence of which can be their superior performance on tasks that require attention to details. The central tenets of Weak Central Coherence theory are consistent with Bertone et al.'s [20] suggestion that individuals with an ASD have difficulty processing complex information that requires the integration of information from multiple cortical regions. The findings within the dorsal visual stream in ASDs are also consistent with these hypotheses in that low-level processing appears to be intact, whereas individuals affected by these disorders display reduced sensitivity in global processing. Taken together these findings do not support an impairment specific to the dorsal visual system, but instead suggest a profile of visual performance characterised by difficulties in integrating information at the higher levels of both visual pathways.

To summarise, it does not appear that Braddick et al.'s [23] suggestion of impairment that is specific to the dorsal stream is characteristic of ASDs. Because sub-cortical dorsal stream processing remains intact in this population, it seems that any impairment in dorsal stream functioning in individuals with ASDs is restricted to the global level. While there is also some evidence of anomalous global processing in the ventral stream in autism, a comprehensive understanding of the capabilities of the ventral stream at both local and global stages in autism remains elusive.

2.3. Dyspraxia

Clumsiness, lack of coordination and poor balance are some of the most noticeable features of developmental dyspraxia [122]. Visual information has an important role in the planning and execution of coordinated movements [82], and thus it is possible that visual perceptual deficits also play an important role in dyspraxia. Many of the developmental milestones that children with dyspraxia struggle with, like catching a ball, jumping or tying shoelaces, are linked to visual perceptual deficits such as reduced gain in pursuit eye movements [90]. However, it is difficult to account for the visuo-motor deficits seen in dyspraxia without reference to the dorsal visual stream, given its role in conveying information about the spatial relations between objects and about their motion (see discussion in ASDs section above). Thus it is possible that impaired transmission of visual information, particularly within the dorsal stream, is implicated in the lack of co-ordination, poor balance and poor visuo-motor task performance seen in dyspraxia. Such deficits would be expected to affect visual processes that require the coding of information about the spatial positions of objects relative to the observer [120].

In an attempt to establish whether children with dyspraxia do demonstrate a disruption to the dorsal visual system, O'Brien et al. [127] measured thresholds on a GDM task, and compared them to thresholds on a line-segment contour detection task. Children with dyspraxia were impaired in the ability to detect coherent line-segment structure, but global motion processing ability was unaffected compared to an age and verbal mental-age matched control group. In another study, Sigmundsson et al. [146] applied the same GDM and coherent line segment measures as were employed by Hansen et al. [70] to test whether impaired visual function is characteristic of children with motor impairments. In contrast to O'Brien et al. [127], Sigmundsson et al.'s 'dyspraxic' group was not formally diagnosed; instead, it comprised the extreme 25% of scorers on the Movement ABC [73] test attending a regular classroom. Sigmundsson et al. [146] reported that developmental clumsiness was associated with difficulties in the detection of both global visual motion and the coherent organisation of static line segments.

While O'Brien et al. [127] suggested that the discrepancy in their results for tasks assessing the two visual pathways indicates that children with dyspraxia have a specific deficit in global processing in the ventral pathway, Sigmundsson et al. [146] clearly provide conflicting evidence. Of relevance here is the argument advanced earlier that the coherent line stimuli used in these two studies are likely to also assess visual abilities associated with the earlier stages in the ventral cortical pathway in addition to tapping global form processing mechanisms. The data from the two studies using these tasks to assess visual processing in dyspraxia indicate impairment at some level in the ventral stream, but given the possibility that processing in V1 may contribute to contour detection, the precise locus of the impairment remains unclear. Glass patterns would assist in clarifying this issue, since, as noted earlier, they more specifically target high-level integrative processing in the ventral stream. Furthermore, O'Brien et al. [127] matched their samples for chronological age and verbal mental age, and excluded any child with a comorbid diagnosis. Sigmundsson et al. [146], on the other hand, did not take IQ into account apart from noting that no child had any reported history of learning or reading disability. The failure to match samples may have impacted on the differences reported in the Sigmundsson et al. study.

A global motion processing deficit, when not associated with a deficit in early visual processing, signifies disruption to the visual processes in the later stages of the dorsal stream, and could be particularly central to the symptomatology of dyspraxia given the role the dorsal pathway plays in visually guided movement

[52,172,174]. However, both O'Brien et al. [127] and Sigmundsson et al. [146] used only translational motion to assess global motion perception. Translational motion can be encoded in V1 but is globally grouped in MT/V3a [1], whereas expansion/contraction and concentric motion are thought to be processed in MST [9,52,49,123]. Directly relevant to dyspraxia is that the optic flow that results from either self-movement or the movement of large objects near the observer is captured by expansion/contraction GDM stimuli. These critical global motion capabilities are yet to be assessed in individuals with dyspraxia. If, in clarifying the conflicting findings presented by O'Brien et al. [127] and Sigmundsson et al. [146], future research is unable to identify a global motion processing deficit for dyspraxia, this may suggest that a non-visual deficit is central to the symptomatology of this disorder, perhaps one arising from parieto-motor or cerebellar dysfunction [127]. Alternatively, if a dorsal stream deficit is found, the research must be able to additionally account for the ventral stream difficulties established in the current papers. Whether the dorsal stream is indirectly affecting the visual attention capabilities of the ventral pathway is still to be determined. Assessment of lower-level capabilities would provide important additional information regarding the integrity of both visual pathways in dyspraxia, particularly in identifying whether any GDM deficit arises as a result of impaired early input to the dorsal stream.

Therefore, to summarise, the assessment of visual capabilities in dyspraxia is currently incomplete. Two studies have focused on global processing in both visual streams. In assessing the ventral stream, both studies used stimuli that potentially rely on local processing rather than global grouping in this pathway. Regardless, the deficits reported suggest an anomaly in ventral visual stream processing in dyspraxia. Precisely what this means for our understanding of the condition is unclear, since Sigmundsson et al. [146] also reported impairment in global motion processing for their 'clumsy' group. Thus, impairment extending to the dorsal stream may also be implicated in difficulties in the coordination of space-based movements. Importantly, Sigmundsson et al. [146] introduced the possibility of studying a non-clinical sample with similar characteristics to dyspraxia to inform our understanding of the condition proper. Finally, assessing the perception of global motion for expanding and contracting stimuli would be beneficial since these capabilities are most directly related to movement, but they are yet to be studied in the dyspraxia population. Thus, it is yet to be clearly established whether deficits in the dorsal stream are present, consistent with Braddick et al.'s [23] hypothesis, and actually contribute to the poor visuo-motor processing seen in dyspraxia.

2.4. William's syndrome

Individuals with William's syndrome (WS; a congenital deficit resulting from a deletion on chromosome 7q11.23) experience difficulties in spatial cognition as well as delayed language and motor development [15,114]. Visuo-spatial ability [15] and motor function [75] are particularly affected in William's syndrome and neurobiological studies demonstrate atypical function and structure in posterior parietal, posterior thalamic (encompassing the pulvinar region, which provides direct input to the visual streams and MT; see [57] for a review) and cerebellar regions that are important in performing space-based actions [123,121,139]. Thus, it has been hypothesised that the visuo-spatial impairments in WS stem from developmental problems within the dorsal visual pathway [50]. Even though functional imaging [57,51] and post-mortem [77] studies have supported this hypothesis, there are relatively few psychophysical studies measuring the capabilities of the two visual streams in WS.

Nakamura et al. [125] outlined a case study in which a boy with WS demonstrated global motion perception thresholds similar to those reported in the literature for typically developing individuals. Reiss et al. [138] examined three different types of motion processing ability in WS. They used biological motion detection (animations of "lights" or dots attached to the joints of the body displayed in brief video sequences [83]), GDM stimuli and a 2-D form-from-motion task (discriminating which panel contained moving elements that formed a rectangular shape within a noise background). Individuals with WS performed at normal levels on both the biological motion and GDM tasks but had elevated thresholds on the form-from-motion task. In addition to GDM and coherent line segment tasks, Atkinson et al. [5] assessed performance on a visuo-spatial manipulation task expected to tap additional functioning subserved by the dorsal stream [119]. The task involved posting a card into a slot of variable orientation. Children with WS were less accurate on this task than controls, and demonstrated anomalies in posting behaviour not seen in any controls. In addition, the children with WS had higher GDM thresholds, but intact thresholds on the line segment task, compared to typically developing individuals. In further work, Atkinson et al. [7] again administered GDM and coherent line segment tasks, but this time to a larger group of WS children. When comparing their performance on these tasks to the age equivalent performance of typically developing children, Atkinson et al. [7] found a subgroup of WS children who were distinguished only in exhibiting high global motion thresholds, and an additional subgroup of WS children who demonstrated high thresholds for both global motion and line segment coherence. Given that similar patterns of performance are often seen in younger typically developing children, the authors posited that the difficulties seen in WS may be the result of immaturity in the visuo-spatial processing system that is more predominant in the dorsal stream. Later, Atkinson et al. [6] followed these initial studies by examining global motion and form sensitivity in adults with WS to clarify whether motion processing difficulties are a transient developmental feature or a persistent aspect of cerebral organisation in WS. The WS adults exhibited higher thresholds in both the global motion and the coherent line segment tasks when compared to matched controls. There was substantial variability within the WS group, with performance outside the normal range not being a feature of every WS individual.

The studies assessing global motion perception in WS provide a reasonably coherent profile of impaired GDM perception in this population, consistent with both the symptoms of impaired spatial abilities, and with the outcomes of imaging and post-mortem research concerning the dorsal stream in this condition. Regardless, it would appear that visual anomalies in WS are not restricted to the dorsal stream, as proposed by Braddick et al. [23]. While Atkinson et al. [7,6] report a *greater* deficit on GDM tasks than on line segment coherence tasks, a proportion of individuals with WS still displayed decreased sensitivity to coherence on the ventral stream task. It will be important for future research to determine whether the dorsal stream impairment stems from earlier stages of this visual pathway, and how it impacts, if at all, on ventral–stream functioning. A complete assessment of the local and global properties of the ventral stream, being mindful of the concerns raised above with respect to the line segment stimuli, in addition to an assessment of the local properties of the dorsal stream in WS, will assist in clarifying some of these issues.

2.5. Fragile X syndrome (FXS)

Fragile X syndrome (a disorder arising as a result of a trinucleotide repeat in the FMR-1 gene) is associated with weaknesses in attentional control [124], linguistic processing [16] and visuo-spatial cognition [36,37]. Decreases in the FMR1 protein product

result in neurons in the visual cortex having immature dendritic spines [81,80]. Kogan et al. [88,89] hypothesised that the impaired performance on visuo-motor tasks characterising the FXS phenotype may be the result of the magnocellular neurons being more susceptible to the loss of FMR1 protein.

In the first of two studies, Kogan et al. [88] evaluated the possibility of a perceptual dorsal stream deficit resulting from neurobiological changes in FXS by comparing individuals with FXS to both chronological age and mental age matched control groups on a variety of visual tasks. Global dorsal-stream processing was evaluated using a GDM task identical to that used by Atkinson et al. [5] and Spencer et al. [154], which required identifying the side of the screen containing a strip of dots moving coherently in a translational pattern. Sensitivity to coherent form was assessed using line segment stimuli that contained a target of concentrically aligned segments on one side. The functioning of the M and P cells was assessed using flicker contrast sensitivity tasks, whereby low and high spatial frequency stimuli, respectively, were modulated at both low and high temporal frequencies. The FXS patients had reduced sensitivity to global motion, but equivalent sensitivity to form stimuli, relative to both control groups. The individuals with FXS also showed significantly reduced M cell contrast sensitivity when compared to the chronological age matched group, but differed significantly from the mental age matched group only for low spatial frequency stimuli modulated at a high temporal frequency. The three groups displayed no significant differences in P cell contrast sensitivity. In their second study, Kogan et al. [88] examined performance on first- and second-order dynamic and static stimuli (as described by [19,20]). The FXS group had elevated contrast thresholds on both first- and second-order motion stimuli, for direction discrimination, when compared to chronological age-matched controls and controls matched for developmental age. The FXS group had significantly higher contrast thresholds on the first-order static stimuli, for orientation discrimination, when compared to the age-matched controls, but not relative to the developmental-matched controls. In addition, the FXS group was less sensitive to second-order static orientation stimuli when contrasted with both comparison groups.

Kogan et al. [89] state that their results reflect a "clear pervasive impairment of motion perception in FXS" (p. 1638). This is consistent with Braddick et al.'s [23] notion of a general dorsal stream impairment arising in the presence of a developmental disorder, particularly given that both local and global processing within this pathway have been assessed using multiple techniques. However, this conjecture requires further examination considering that less than half of Kogan et al.'s [88] participants were able to complete the first- and second-order dynamic tasks. Alternatively, Kogan et al. [88] also posit that the form processing deficit seen clearly for only second-order stimuli is evidence of "a generalised cortical dysfunction in integrative mechanisms of early visual input regardless of its source" (p. 1638). It is possible that visuo-motor performance in this population may be related to impaired dorsal stream functioning as a result of the effects of decreases in the FMR1 protein as suggested by Kogan et al. However, it is critical that we keep in mind that the aforementioned studies have demonstrated a correlation between impaired dorsal stream functioning and losses in the FMR1 protein, but the genetic abnormality may not be the cause, given that other developmental disorders also demonstrate impaired dorsal stream processing without this particular genetic anomaly having been identified.

3. Evaluating the dorsal stream hypothesis of developmental disorders

Braddick et al. [23] argued that deficits in global motion processing in developmental disorders, specifically WS, dyslexia, autism and hemiplegic children, provide evidence for "an early vulnerability in the motion processing system of a very basic nature" (p. 1779). Consistent with this notion, each of the five developmental disorders considered above has a specific symptom profile that can potentially be related to impairments in dorsal stream functioning. However, while the physiological properties of the M cells may result in them being more at risk for damage during development, the results of the present review suggest that, in some instances at least, the problem in developmental disorders is not at the lower, M cell level but rather occurs further along in the dorsal stream. For instance, contrast sensitivity of M cells appears to be unaffected in ASDs ([20,131] although other properties of the M cells, such as speed of processing are yet to be assessed), whereas perception of GDM is impaired [164,116,131,153]. Similarly, the results from studies assessing M-cell contrast sensitivity in dyslexia are inconclusive [147], whereas studies investigating visible persistence provide more evidence for an M-cell deficit in this condition [10,151]. Additionally, there is a reasonably consistent pattern of impaired performance on tasks assessing integrative motion processing in the dorsal stream in dyslexia [159,35,130]. If impairment was to be found at the M cell level in any of the developmental disorders, then subsequent difficulties in global motion processing may be expected to arise as a result of flow-on effects from the earlier level. However, when global motion impairments occur without a corresponding deficit in M cell capabilities (provided all the capabilities have been assessed), then explanations other than a specific dorsal stream deficit must be considered. In ASDs for example, it has been suggested that while the early stages of cortical visual processing can extract local information adequately, difficulty is experienced when local information is accumulated in higher cortical visual areas to form a global percept [20,131]. While further research needs to be conducted concerning this pattern in the ventral visual stream, it is clear that this interpretation offers the possibility of ASDs exhibiting a profile that can be distinguished from dorsal stream impairment alone.

This review also suggests that it is still too early to decisively state that dyspraxia and WS have visual impairments arising from difficulties in the magnocellular pathway. The symptoms of dyspraxia suggest an important role of the dorsal stream; however the results of studies assessing GDM perception in this disorder are inconclusive. The lower levels of the dorsal stream, as well as sensitivity to expanding and contracting global motion, remain to be assessed for dyspraxia. Similarly, in WS, while GDM perception appears to be impaired [5,6], no study has evaluated whether the inputs from lower levels are also affected. However, the findings from dyslexia and FXS are more congruent with the dorsal stream impairment hypothesis [23]. Functioning in the ventral stream appears to be intact in these conditions, and while further work needs to be done to clarify the results at the lower levels of the dorsal stream in dyslexia, impairment is evident in the dorsal pathway in both dyslexia and FXS.

Some caution is warranted in that the conclusions of this review are based on comparisons of data across studies of the disorders investigated individually. While mostly the same methodology and test environments have been used, not all experimental factors have been controlled, which may have introduced some variability in results, necessitating a degree of assumption when comparing outcomes across studies. However, there are robust studies that have assessed two target groups simultaneously (e.g. ASD and dyslexia [164,13]) and have reported patterns of results consistent with the conclusions we draw in this review article.

Importantly, what this review highlights is that, while the dorsal stream does appear to be affected in some way in each of these disorders, there is the potential for the identification of unique patterns of abilities across the different levels of the visual pathways in some of the disorders. If a unique profile of visual ability could be

established for any of the disorders, these tasks might allow for the earlier recognition of such disorders when screening for problems early in childhood. However, while the research reviewed suggests promising possibilities (in particular, see Bertone et al. [20,17] for an attempt to characterise specific perceptual signatures as potential tools for dissociating condition-specific aetiology in ASD and FXS), unique profiles of visual processing for the developmental disorders are yet to be identified.

3.1. Methodological considerations and future directions

The summaries above highlight how information from a specialised area, vision research, can be applied to clinical populations to advance understanding of the symptoms and neurology central to these disorders (see also [66] for an example in schizophrenia). Psychophysical measurement is a useful way of assessing brain functioning in relation to vision because the processes invoked by such tasks are generally quite well understood relative to other cognitive processes, both functionally and neuroanatomically. Psychophysics allows us to see how local and global processing manifests in visual abilities, and thus may act as an indication of how specific cortical areas process information. However, as highlighted by the summary of recent developments in conceptualising the visual system hierarchy, it is important that clinical researchers incorporate the latest understanding of the processes assessed by certain tasks into the designs of their studies to ensure maximum progress. Therefore, the aim of the following sections is to briefly consider the methodological limitations of some of the studies considered above, and make suggestions for future research in this regard.

3.2. Ventral stream stimuli

The need to accommodate recent developments in our understanding of the visual system is particularly noticeable with respect to the line segment tasks designed to assess ventral stream functioning. The evidence regarding whether the identification of contours can be achieved by the neurons at stages earlier than V4 [101,59] is of particular significance. Future research may consider employing radial frequency (RF) patterns [177] as an alternative to coherent line segment tasks. RF patterns are closed contour shapes created by deforming a circle (see Fig. 3). The deformation is produced by sinusoidally varying the radius as a function of polar angle, and the number of cycles of modulation corresponds to the RF number. For RF patterns of high frequency, such as the RF24 pattern on the right of Fig. 3, performance for discriminating the whole shape from a circle is better than when only part of the closed shape is deformed [102], but only by an amount that can be explained by probability summation of the detection of independent local features. In contrast, there is evidence that curvature and position information is pooled along the entire circumference of the pattern for stimuli of low radial frequency, such as the RF3 pattern in the middle of Fig. 3 [102,13,14], consistent with global signal integration in shapes with up to about eight cycles of modulation [177,102]. Given that sensitivity to global versions of these shapes cannot be explained by local cues such as contour orientation or local curvature, RF patterns are ideal stimuli to examine local and global processing within the ventral visual stream, however, there is currently no equivalent stimuli that assesses the dorsal stream in a similar manner to the RF patterns. This is an important consideration, because if functionality in the ventral and dorsal visual streams is to be compared, the two streams should ideally be assessed using stimuli that have similar processing requirements at both the early and late levels in each pathway. While Glass patterns and GDM stimuli achieve this requirement at the later, global processing stages in the ventral and dorsal streams respectively, no study to date has compared performance on these global tasks with performance at the earlier, local processing stages. One way to do this may be to create stimuli designed to assess using dipole orientation discrimination and dipole motion direction discrimination. One advantage of the dynamic and static first- and second-order stimuli employed by Bertone et al. in atypical and typical populations [19,20,18] is that, despite the shortcomings outlined above, they represent the only paradigm that attempts to control for processing requirements while assessing different levels in the two processing streams.

3.3. Contrast sensitivity as a measure of magnocellular functioning

With respect to the dorsal stream, if M cells are adversely affected in developmental disorders, it is possible that measures of contrast sensitivity may not reveal these differences. Any impairment may become more apparent further along the dorsal stream, perhaps as a result of limited inputs for summation of movement direction information. The research summarised in the section on the human visual system above points to the need for future research to consider other properties of V1 that rely on input from M cells, such as the precision of direction coding [69,97], in addition to contrast sensitivity.

Additionally, as noted above, if any developmental disorder affects the M and P cells in similar proportions, less impairment might be observed with P cell functioning than for M cell functioning, given the relatively greater number of residual P cells [40,39]. This leaves open the possibility of impairment in P cells as well as in M cells, but where the former is not as apparent as the latter. The expression of a P cell impairment may depend on the number of P cells required to perform a task properly. An impairment that impacts both the M and P cells and flows through to affect higher levels of the dorsal and ventral streams respectively may

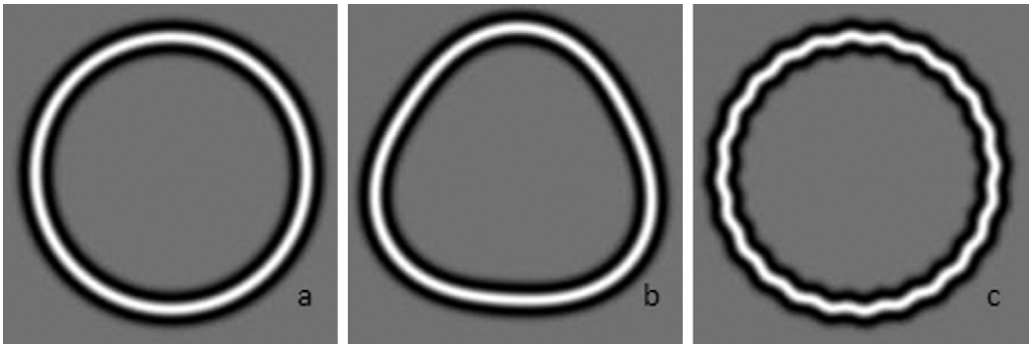

Fig. 3. Examples of (a) a circle (b) an RF3 stimulus and (c) an RF24 stimulus.

explain why the perception of global form along with the perception of global motion appear to be disrupted in dyspraxia and WS. Currently, P cell functioning in these two disorders has not been assessed, and it is unclear whether the deficits on the coherent line segment task reflect difficulties in local or global form processing.

3.4. Sample size and stimulus presentation methods

One key difference between vision research using experienced, neurotypical observers and research with children with developmental disorders concerns the reliability of the data collected. Vision research frequently uses designs in which smaller numbers of observers are assessed on many repetitions of the same stimuli. In contrast, and common to much clinical research, developmental researchers typically use larger samples with fewer trial repetitions. This is practical in that it reduces the amount of time one particular child is required to maintain attention on the task. The desire to use less time-consuming procedures means that staircase methods are often chosen. However, these methods can be susceptible to mistakes or inattentiveness early on in the staircase [141,156], thus affecting the capacity of the procedure to provide a reliable threshold estimate [162,176]. While there are more time consuming staircase methods that minimise this problem [60], they are not commonly employed. The method of constant stimuli is more robust in that it enables the entire psychometric function to be assessed, and while it also takes longer than staircase methods, it may ensure more reliable estimates of the individual's threshold, since the specific values tested later in the sequence are not dependent on early responses, and thus an attentional lapse affects only the specific trial on which it occurs. Within the literature cited above, only Bertone et al. [19,20], Kogan et al. [88], and Nakamura et al. [125] report using the method of constant stimuli. Additionally, while developmental studies may aim to have larger sample sizes to compensate for the fewer repetitions at each level of the psychometric function for individual observers, many studies do not obtain that larger sample size, so the generalizability of the results is unclear (e.g. [19,41,144,43] all used a sample size of 12 or less). Limited sample size can be particularly problematic in disorders where subtyping may be pertinent (e.g. dyslexia, [76]) and also where variability in the phenotype is common (e.g. in WS and ASDs). The reporting of effect sizes in the literature would assist in addressing this concern.

3.5. Variation in clinical samples

One other important issue concerns the fact that not all children within a clinical group may show atypical functioning with reference to a control sample. For example, Ramus [136] noted that 37 out of 128 children with dyslexia across seven different studies displayed elevated thresholds in tasks assessing dorsal stream functioning. Milne et al. [118,117] reported that not all children with autism showed elevated global motion thresholds, but rather that the difference in central tendency between the clinical and control groups reflected a skewed distribution in the group with autism (see also [7,141]). This suggests that researchers may be better advised to select those participants who show reliable performance differences to typical observers and investigate these individuals in detail. It is, of course, clear that if only a small proportion of participants show the differences then those visual performance factors are unlikely to be central to the developmental disorder. The reason why some children with developmental disorders show differences in visual perception compared to typically developing controls remains to be established. However, the variation within clinical groups does appear to indicate that such abnormalities might not have a causal role in these disorders, but rather may be an indication of wider neurological atypicalilties. It will be important for future research to consider the distributions of scores from the psychophysical tasks for the clinical groups. Perhaps differences within clinical groups on psychophysical task performance could relate to symptom severity, so it may be useful for future studies to collect data on symptomatology along with psychophysical data. Additionally, as briefly noted earlier, performance on the visual tasks covered in this review typically does not reached adult levels until the middle primary school years. Whether an impairment identified for a disorder represents a developmental delay or an enduring deficit then becomes an issue. This issue is informed by the use of developmental age-matched controls as well as chronological age-matched controls, and also by the assessment of adult samples. An ideal approach is to assess large samples varying in age that then enable the comparison of developmental functions for individuals with the disorder and those of typical development [30].

4. Summary and conclusions

To conclude, the application of psychophysical research methods to evaluate vision in developmental disorders offers the possibility of rigorously investigating the functional capabilities of specific brain regions in a manner that adds to what can be revealed through imaging and electrophysiological recording. Overall, the research has often been consistent with the hypothesis that the dorsal stream is particularly susceptible to damage during development [23,103] (see [112] for alternative possibilities), with individuals with developmental disorders exhibiting difficulty in visual tasks assessing this stream. However, several studies report ventral stream abnormalities, either in conjunction with dorsal stream impairment, or in isolation. Whether ventral stream abnormalities occur as the result of abnormal input from the dorsal stream or whether they can be impacted differentially is still to be determined. Advances in conceptualising the visual streams, the interconnectedness of the two, and the role they play in directing visual attention, in conjunction with more sophisticated and accurate methods of assessing visual functioning in developmental disorders, should assist with the resolution of some of these issues in the future. Overall, it seems that ASD is the most promising condition for demonstrating a unique profile of visual functioning that extends beyond the original "dorsal stream impairment" hypothesis of developmental disorders. In particular, impairment in developmental dyslexia and FXS appears to be restricted to the dorsal stream, and the assessment of the two pathways in developmental dyspraxia and WS is incomplete, whereas individuals with ASD appear to have difficulties in global grouping in the later stages of the dorsal visual stream. It will be important to clarify whether this difficulty in global processing extends to the ventral pathway in order to further elucidate the nature of any neurological deficit, as indicated by visual processing atypicalilties, associated with the disorder.

Conflict of interest statement

The authors declare that they have no competing financial interests.

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