

## Reduced 2D form coherence and 3D structure from motion sensitivity in developmental dyscalculia

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### ABSTRACT

Developmental dyscalculia (DD) is a specific learning disability affecting the development of numerical and arithmetical skills. The origin of DD is typically attributed to the suboptimal functioning of key regions within the dorsal visual stream (parietal cortex) which support numerical cognition. While DD individuals are often impaired in visual numerosity perception, the extent to which they also show a wider range of visual dysfunctions is poorly documented. In the current study we measured sensitivity to global motion (translational and flow), 2D static form (Glass patterns) and 3D structure from motion in adults with DD and control subjects. While sensitivity to global motion was comparable across groups, thresholds for static form and structure from motion were higher in the DD compared to the control group, irrespective of associated reading impairments. Glass pattern sensitivity predicted numerical abilities, and this relation could not be explained by recently reported differences in visual crowding. Since global form sensitivity has often been considered an index of ventral stream function, our findings could indicate a cortical dysfunction extending beyond the dorsal visual stream. Alternatively, they would fit with a role of parietal cortex in form perception under challenging conditions requiring multiple element integration.

### 1. Introduction

Between 3 and 7% of the general population suffer from developmental dyscalculia (Lewis et al., 1994; Gross-Tsur et al., 1996; Rubinsten and Henik, 2009), a learning disability that prevents individuals from mastering numerical concepts and arithmetical procedures fluently, despite adequate neurological development, intellectual abilities and schooling opportunities (American Psychiatric Association, 2013). Although DD has been mostly studied in children, difficulties can persist into adulthood if not treated (Castaldi et al., 2020a; Kaufmann et al., 2020). Individuals with DD can be slower and less accurate in basic numerical tasks such as counting (Geary et al., 1992; Geary, 2004), numerical estimation and comparison of sets of items (non-symbolic numerosity) or Arabic digits (Rousselle and Noël, 2007; Iuculano et al.,

2008; Piazza et al., 2010; Mejias et al., 2012; Wilson et al., 2015). DD individuals hardly learn tables and simple calculation procedures (Geary, 1993; Butterworth, 2005).

The dorsal stream, and in particular the parietal cortex, is known to play a key role in numerical cognition (Eger, 2016; Piazza and Eger, 2016) and to present both structural and functional abnormalities in DD individuals. Structural alterations of both the parietal grey and white matter were found in DD children compared to controls (Isaacs et al., 2001; Rotzer et al., 2008; Rykhlevskaia, 2009). The parietal cortex of DD children also showed hypo- or hyper activation compared with controls during symbolic (Mussolin et al., 2010) and non-symbolic (Price et al., 2007) numerical comparison tasks, mental number line task (Kucian et al., 2011a), ordinality judgments (Kaufmann et al., 2009) and calculation tasks (Ashkenazi et al., 2012; Rosenberg-Lee et al., 2015;

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Iuculano et al., 2015), which normalized after tutoring (Kucian et al., 2011a; Iuculano et al., 2015). Also the pattern of neural activation elicited by numbers in different formats and by calculation tasks is peculiar and less precise: classifiers trained on the neural activation patterns read out from parietal areas were able to correctly categorize typically developing children from children with DD (Iuculano et al., 2015; Peters et al., 2018) and yielded lower accuracies when discriminating between non-symbolic numbers in DD adults compared to controls (Peters et al., 2018; Bulthé et al., 2019).

Nevertheless, studies in DD individuals have found that functional and structural abnormalities are not restricted to the parietal cortex, but can also extend to ventral stream areas. Abnormal functional activations in DD children were found in the fusiform gyrus and ventral occipito-temporal cortex during arithmetical (Iuculano et al., 2015; Rosenberg-Lee et al., 2015) and non-symbolic number comparison tasks (Kucian et al., 2011b). In addition to the parietal regions, Bulthé et al. (2019) identified a temporal region in which the classification accuracy for non-symbolic numbers was significantly lower in DD adults compared to controls. The same authors also reported increased functional connectivity from the occipital to the infero-temporal cortices, regions known to be involved in processing of complex visual objects (Grill-Spector et al., 2008). Decreased grey matter volume in ventral regions (fusiform and parahippocampal gyrus, anterior temporal cortex) and anomalies in the white matter projection fibers connecting the fusiform gyrus with the temporo-parietal cortex have been reported in DD children compared to controls (Rykhlevskaia, 2009).

Beyond core numerical and arithmetical abilities, cognitive difficulties in dyscalculia extend also to domain-general executive functions, such as attention, working memory and cognitive control (Ashkenazi et al., 2009; Fias, 2016; Iuculano, 2016; Szűcs, 2016). Deficits in visuo-spatial processing skills have also been reported: one study found that children with DD were slower in symmetry and mental rotation tasks, compared to their age-matched peers without DD (Szűcs et al., 2013). However, in how far alterations in more basic perceptual sensitivities (beyond numerosity) are also present in dyscalculia, and if so of which kind, remains much less documented and understood.

In the current study, we aimed at a precise psychophysical characterization of different types of higher-level perceptual abilities which can be considered to be associated with higher-order dorsal and ventral visual stream regions, in adult individuals with DD. We explored sensitivity to different types of global motion stimuli: translation on the horizontal plane and optic flow (containing expansion/contraction and rotation components). Translational motion was tested because this type of motion was evaluated in many other developmental disorders (Atkinson et al., 1997, 2006; Spencer et al., 2000; Hansen et al., 2001; White et al., 2006; Milne et al., 2006; Pellicano and Gibson, 2008; Conlon et al., 2009; Guzzetta et al., 2009; Koldewyn et al., 2010; Johnston et al., 2016). In typically developing children, one study found that children who were less sensitive to coherent motion when tested in kindergarten (5 years 8 months) were slower in solving subtractions in third grade (8 years 3 months) and this correlation remained significant even when controlling for nonverbal IQ and reading skills (Boets et al., 2011). In 5–12 years old typically developing children, another study found that global motion thresholds correlated with visuomotor and numerical skills (performance on calculation and non-symbolic number comparison tasks) and with the parietal lobe surface area (especially with the IPS area) (Braddick et al., 2016). Functional MRI studies in adult normal subjects showed that compared to random motion, translational and optic flow motion elicit stronger activation along the dorsal stream, specifically in segregated subregions of area MT (Morrone et al., 2000). In addition, optic flow perception elicits activations in regions of the parietal cortex that likely overlap with areas involved in numerosity perception (Harvey et al., 2017), including the putative homologue of the human ventral intraparietal area (VIP) (Sereno and Huang, 2006; Cardin and Smith, 2010).

We furthermore investigated 2D shape coherence/global form

sensitivity by means of Glass patterns (Glass, 1969), a class of stimuli that is constructed by randomly distributing dot pairs (called dipoles) according to a geometrical rule that induces the perception of a higher-level global shape. Compared to line segments – another type of stimulus often used to test global form perception (Atkinson et al., 1997, 2006; Spencer et al., 2000; Milne et al., 2006; White et al., 2006), Glass patterns can be generated using the same low-level elements (dots) as the ones employed to test global motion perception, and they differ only concerning the nature of the evoked higher-level percept. Sensitivity to Glass patterns requires local detection and integration of dots into oriented dipoles before the (paired) elements can be integrated into a global shape. Neurophysiological studies in macaques (Gallant et al., 1993; Smith et al., 2002, 2007), behavioral (Dakin, 1997; Dakin and Bex, 2001), neuroimaging studies in humans (Krekelberg et al., 2005; Ostwald et al., 2008; Mannion et al., 2009, 2013) and computational models (Wilson et al., 1997; Wilson and Wilkinson, 1998) suggested that Glass patterns are perceived through a continuum of form integration processes, from the local dipole orientation detection, presumably carried out by the primary visual areas, to the perception of global patterns, involving regions beyond the primary sensory ones.

In addition, we also tested sensitivity to 3D structure from motion (by using dot stimuli that elicit perception of a rotating cylinder), to evaluate sensitivity to shape extraction from dynamic information, and for 3D rather than mere 2D shape. A previous study reported elevated coherence thresholds in individuals with dyslexia compared to a control group when asked to judge the orientation of a temporally defined boundary (Johnston et al., 2016). fMRI and neuropsychological studies showed that perception of form and structure from motion involves areas along both the ventral and dorsal stream. Compared to 2D form from motion, 3D structure from motion elicits stronger activation along the dorsal stream and specifically in the parieto-occipital intraparietal sulcus, medial and anterior dorsal intraparietal sulcus (Orban et al., 1999; Vanduffel et al., 2002; Murray et al., 2003). All these regions are in close proximity and/or partial overlap with regions involved in the perception of non-symbolic numbers (Eger et al., 2015; Castaldi et al., 2019, 2020b) and with numerosity maps (Harvey et al., 2017).

In the current study we also aimed to establish whether potential deficits in any of these visual perceptual capacities specifically characterized DD independently of reading deficits. This is an important factor given the high comorbidity between dyscalculia and dyslexia (Wilson et al., 2015), and the fact that elevated global motion perception thresholds have been reported for dyslexic individuals (Talcott et al., 2000; Hansen et al., 2001; Pellicano and Gibson, 2008; Conlon et al., 2009; Johnston et al., 2016). Moreover, one previous study reported lower sensitivity to visual coherent motion, but not to form coherence, in 10-year old DD children compared to their age-matched controls with higher mathematics skills (Sigmundsson et al., 2010). However, this study was performed on a very restricted sample of six DD children and differences in reading abilities were not controlled between the DD and control group, thus more research seems needed to determine whether these results can be considered as characteristic of dyscalculia per se, independently of reading deficits.

## 2. Material and methods

### 2.1. Subjects

Participants included in this experiment were the same as those included in a previously published study investigating visual crowding (Castaldi et al., 2020c).

The original pool of subjects included seventeen adults without mathematical impairment, recruited through a diffusion list provided by the French National Center for Scientific Research (CNRS), and seventeen adults with mathematical impairment. Participants with mathematical impairment were contacted either by our neuropsychologist collaborators or through an online screening questionnaire advertised

on social media and in universities. The first part of the questionnaire collected general information (such as age and schooling level), and whether the individual had received a formal diagnosis of dyscalculia or neurological disorders. The second part of the questionnaire explored the impact of the claimed math difficulties on the individual's everyday activities (such as when dealing with money) and the ability to perform some basic numerical tasks (such as reading/writing numerals, counting or solving simple arithmetical operations without using fingers or a calculator).

To be included in the experiment, all participants had to be compliant with the following criteria: (a) be between 18 and 50 years old, (b) present no neurological disorder, and (c) have completed at least secondary level education. In addition, participants were included in the math impaired group if they had received a clinical diagnosis of dyscalculia by a neuropsychologist or speech therapist or if they had claimed major difficulties when dealing with arithmetic and numbers according to the questionnaire. Participants fulfilling these criteria were contacted and tested with an extensive neuropsychological assessment. Participants were evaluated with tests of verbal and non-verbal intelligence, verbal and visuospatial working memory, visual attention, reading abilities, inhibitory skills and mathematical performance. Participants were then appointed to come back on a different day to perform a series of psychophysical experiments. Two subjects included in the math impaired group were not available for the proposed testing sessions and dropped from the study. An additional selection based on the results of the neuropsychological assessment was performed to define the final DD and control groups. Specifically, participants' results in the math tests were z-scored. The mean and standard deviation of the scores obtained by the subjects without math difficulty in each test was calculated and used for normalization: the mean of the group without math difficulty was subtracted from the score of each subject (including DD) and then we divided the result by the standard deviation of the subjects without math difficulty. If z-scores calculated from either accuracy or reaction time in two (of a total of four) or more math tests exceeded by more than 2 standard deviations the average z-scores of the control group, then mathematical performance was considered below the normal level. All DD participants were confirmed as such, as they all exceeded this cut off. Two participants in the control group also exceeded this cut off and were consequently discarded. The same procedure and criteria were applied to the accuracy and reading speed of a reading test in order to identify DD subjects with associated major reading deficits, potentially indicating associated dyslexia disorders. Three DD subjects exceeded the cut-off for reading abilities.

Overall, fifteen participants were included in the DD group (age  $27 \pm 11$ , 10 females), three of which with associated reading difficulties and fifteen participants were included in the control group (age  $31 \pm 10$ , 8 females). All participants had normal or corrected to normal visual acuity.

Written informed consent was obtained from all participants in accordance with the Declaration of Helsinki, and the study was approved by the research ethics committee of University Paris-Saclay.

## 2.2. Neuropsychological assessment

We briefly summarize the tests used during the neuropsychological assessment prior to the psychophysical experiments, but more information about these tests can be found in previous studies by Castaldi et al. (2018, 2020c).

Indices of verbal and non-verbal intelligence were measured with subtests Similarities and Matrix Reasoning from the Wechsler Adult Intelligence Scale edition IV (WAIS-IV). Verbal and visuospatial working memory were measured with the digit span subtest from WAIS-IV, and the Corsi Block Tapping test, respectively.

Reading abilities were evaluated with the French reading test "Alouette" (Lefavrais, 1967), which involves reading aloud a brief text composed of grammatically plausible sentences, but without a clear

overall meaning. The number of errors made while reading and the time needed to read the text were measured. Inhibitory skills were assessed with the Stroop-Victoria test adapted for francophone individuals (Bayard et al., 2009). The interference index was obtained by dividing the time needed to name the colour of words (whose meaning was incoherent the words' colour) by the time needed to name the colour of circles. Visual attention was assessed with a visual search test (Bells test) in which participants were shown a sheet containing silhouettes of different objects and were required to identify all the bells they could find. When the participant considered all the bells crossed, the time recording was stopped and the number of omitted bells was counted.

Mathematical abilities were measured with several subtests of the French battery TEDI Math Grands (Noël and Grégoire, 2015). This is a computerized battery which measures the individual's performance over various tests targeting different basic numerical skills. The tests included: 1) estimation of the number of briefly presented items (1–6 dots); 2) numerical comparison of two single-digit Arabic numerals; 3) single-digit multiplications and subtractions. Participants' accuracies and reaction times were collected by the software for most of these tests, except for the test measuring the ability to estimate small numerosities for which only the accuracy was measured. Participants were also tested with two subtests taken from an Italian battery for developmental dyscalculia (BDE, Biancardi and Nicoletti, 2004) which specifically target understanding of the semantic meaning of numerals. Subjects were asked to choose the largest of three Arabic numerals (one to three digits), or to place an Arabic numeral (one to four digits) in one of the four possible positions along a number line. Accuracy and overall response speed were measured.

Standard scores based on the norms for adults were calculated for the verbal and non-verbal IQ subtests, for the verbal and visuospatial working memory and for inhibition. For the TEDI-MATH the number of correct responses and the reaction time (in ms), when recorded, were analyzed. Reaction time and accuracy can often inversely trade off with each other, thus we reduced the number of variables by calculating the inverse efficiency score (IES, Collins et al., 2017), dividing the reaction time (RT) by the proportion of correct responses. From the TEDI-MATH scores, we obtained: 1) IES Digits – calculated from the results of the Arabic digits comparison test; 2) IES Calculation – calculated by averaging the results from the multiplication and subtraction tests together and obtaining the IES from the combined measure; 3) IES Math – calculated by averaging the IES Digits and IES Calculation to get an index of general math ability. From the BDE scores, we obtained the IES BDE from the combined measure from the two subtests.

Independent sample t-tests were used to determine differences across groups.

## 2.3. Psychophysical experiments

Participants were tested in a dimly lit room. Visual stimuli, generated and presented under Matlab using PsychToolbox routines (Brainard, 1997), were viewed binocularly from approximately 60 cm, displayed on a 15-inch Laptop (HP) LCD monitor with  $800 \times 600$  resolution at refresh rate of 60 Hz.

### 2.3.1. Global motion, global form and structure from motion tasks

Participants were tested with four tasks, with presentation order counterbalanced between participants. Two tests assessed different types of coherent motion sensitivity, one test assessed global 2D form sensitivity and another one assessed 3D structure from motion sensitivity. All tasks entailed identification of which out of two consecutive displays contained dots with a coherent pattern (either motion or form).

For the global motion tasks, we used random dots kinematograms eliciting either perception of horizontal motion (leftward or rightward translation) or flow motion (containing expansion/contraction and rotation components). In both these tasks, the visual stimuli comprised 200 dots, half white, half black on a grey background. Individual dots

had a diameter of  $0.25^\circ$ . The arrays covered an  $18^\circ$  wide squared or a circular area, yielding a density of 0.6 and 0.8 dots/deg<sup>2</sup> for the translational and flow motion, respectively. Dots moved at a local speed of  $14^\circ/s$  and had a lifetime of 167 ms (10 monitor frames). The target stimulus always contained some degree of coherent motion (translation or flow). The non-target stimulus contained solely dots moving in random directions. Task difficulty was modulated by changing the proportion of dots which complied with the global motion trajectory while the remaining dots moved in a random motion direction with the same velocity.

For the global form task we used Glass patterns (Glass, 1969). The overall perception induced was that of concentric circles. Stimuli comprised 400 dots (200 pairs), half black and half white, shown on a grey background. The array covered  $8.5^\circ \times 8.5^\circ$  with approximately 1.7 dots/degree<sup>2</sup>. Individual dots were  $0.25^\circ$  in diameter and were paired with their copy displaced by  $0.10^\circ$  (border to border dot distance). In the non-target stimulus, all dots were randomly paired. Task difficulty was modulated by varying the proportion of coherently paired dots in the target stimulus.

For the structure from motion task, stimuli were generated following a procedure similar to the one described by Treue et al. (1991). Individual dots (from 2 to 256 dots,  $0.35^\circ$  diameter, lifetime 133 ms (8 frames)) were projected onto the surface of a transparent rigid cylinder which rotated in 3D corresponding to a rectangular region of  $8.5^\circ \times 17^\circ$ , yielding a density range that varied between 0.01 and 1.8 dots/degree<sup>2</sup> when calculated considering 2 or 256 dots respectively. In the target stimulus the dots displayed corresponded to the 2D projection of the 3D object and gave the impression of a cylinder rotating around its vertical axis. The non-target stimulus comprised the same dots and motion vectors albeit assigned at random position and thus breaking the coherence of the display. Differently from the other tasks in which dot coherence was varied, in this case task difficulty was modulated by increasing or decreasing the overall number of dots in both stimuli, replicating a commonly used and established paradigm to study structure from motion (Treue et al., 1991).

For all four tasks, each trial began with a fixation dot which remained onscreen for the entire trial length. Two stimuli were then sequentially presented, lasting 500 ms each and separated by 500 ms inter-stimulus interval (ISI). After the presentation of the second stimulus only the fixation point remained onscreen and subjects indicated which one contained the coherent stimulus.

For all tasks, the experiment started at the easiest level possible (100% coherence or with maximal number of dots (256) for structure from motion) and was then adaptively changed according to the participant's responses, following a QUEST algorithm. On every trial, participants decided whether the coherent motion or form was presented in the first or second interval by pressing the left or right arrow respectively.

For each participant and task, we plotted the stimulus strength (number of dots for the structure from motion task or coherence for the others) in log-scale against percent correct responses. The data were fitted by a psychometric function spanning from 50% to 100% (corresponding to chance and perfect performance, respectively) and signal strength leading to 75% correct responses was taken as the threshold.

Sensitivity thresholds were compared across groups by means of t-tests and we reported Bayes factors alongside with classical statistics. The Bayes factor is the ratio of the likelihood of the two models H1/H0, where H1 assumes a difference between groups and H0 assumes no difference. By convention, when the base 10 logarithm of the Bayes Factor (logBF) > 0.5, it is considered substantial evidence in favor of H1, and when logBF < -0.5, substantial evidence in favor of H0. Correlation analyses and hierarchical regressions were performed with SPSS.

### 3. Results

#### 3.1. Neuropsychological assessment

In the interview, all participants were confirmed to be compliant with the inclusion criteria described in the methods. Four DD participants had received formal diagnosis of dyscalculia during childhood and the others confirmed having always had major difficulties whenever dealing with quantities, numbers and arithmetic since the early school years. All subjects confirmed that these difficulties persisted over years. Seven out of fifteen participants reported having at least one relative with learning difficulty in arithmetic, reading, writing, or orthography.

The DD and control group were matched for age, verbal and non-verbal IQ, reading accuracy, inhibitory control as measured by the Colour- Stroop test, and visual search performance (all p-values > 0.05, see Table 1). Across group differences were found in reading speed ( $t(27) = 2.47, p = 0.02$ ), verbal ( $t(28) = -2.59, p = 0.01$ ) and visuo-spatial working memory ( $t(28) = -3.27, p = 0.002$ ), and most of the numerical and arithmetical tests. The DD group was slower with respect to the control group when comparing digits ( $t(28) = 3.97, p = 0.0004$ ), performing mental multiplication ( $t(28) = 4.34, p = 0.0002$ ), subtraction ( $t(28) = 4.79, p = 0.00005$ ) and the BDE test ( $t(28) = 5.87, p = 0.00005$ ). The DD group was significantly less accurate with mental multiplication

**Table 1**  
Descriptive statistics and tests across groups.

	Control group (N = 15)	Dyscalculic group (N = 15)	Statistical analysis
	Mean (STD)	Mean (STD)	t-value
Age	31 (10)	27 (11)	-0.93
IQ			
Similarities	13 (3)	13 (2)	0.42
Matrices	12 (3)	10 (3)	-1.83
Reading Ability			
Time (seconds)	89 (14)	106 (22)	2.47 *
N errors	3 (3)	4 (3)	1.43
Working memory			
Verbal (Digit span)	12 (3)	9 (3)	-2.59 *
Visuospatial (Corsi)	13 (2)	10 (2)	-3.27 **
Inhibition			
Colour Stroop Score	12 (2)	11 (4)	-1.15
Visuo-Spatial attention			
Time (seconds)	105 (45)	112 (37)	0.51
N omissions	1 (1)	2 (3)	0.53
Numerical skills/Arithmetics TEDI-MATH (no of items)			
Small numerosity estimation (36)	33 (4)	32 (3)	-0.75
Digit Comparison Accuracy (48)	46 (1)	47 (2)	1.04
Reaction Time (ms)	558 (51)	739(168)	3.97 **
IES Digit (ms)	578 (54)	754 (159)	4.03 **
Multiplication Accuracy (20)	18 (2)	15 (2)	-5.05 **
Reaction Time (ms)	1681 (403)	3617 (1681)	4.34 **
Subtraction Accuracy (20)	19 (1)	18 (2)	-2.18 *
Reaction Time (ms)	1572 (333)	3307 (1362)	4.79 **
Calculation (x and -) IES Calculation (ms)	3481 (727)	8365 (3559)	5.20 **
IES General Math (ms)	1166 (201)	2007 (1156)	2.77 **
BDE			
BDE Accuracy	33(1)	33(1)	-1.36
BDE Speed (seconds)	69(10)	110(25)	5.87**
IES BDE (seconds)	65 (10)	105 (24)	6.08**

DD differs significantly from controls at: \* $p < 0.05$ , \*\* $p < 0.01$ .

and subtraction (for multiplication:  $t(28) = -5.05$ ,  $p = 0.00002$ ; for subtraction  $t(28) = -2.18$ ,  $p = 0.04$ ). The DD and control group also differed for the IES for digit comparison ( $t(28) = 4.03$ ,  $p = 0.0004$ ), calculation ( $t(28) = 5.20$ ,  $p = 0.00002$ ), general math ( $t(28) = 2.77$ ,  $p = 0.009$ ) and BDE ( $t(28) = 6.08$ ,  $p = 0.003$ ).

### 3.2. Translational motion

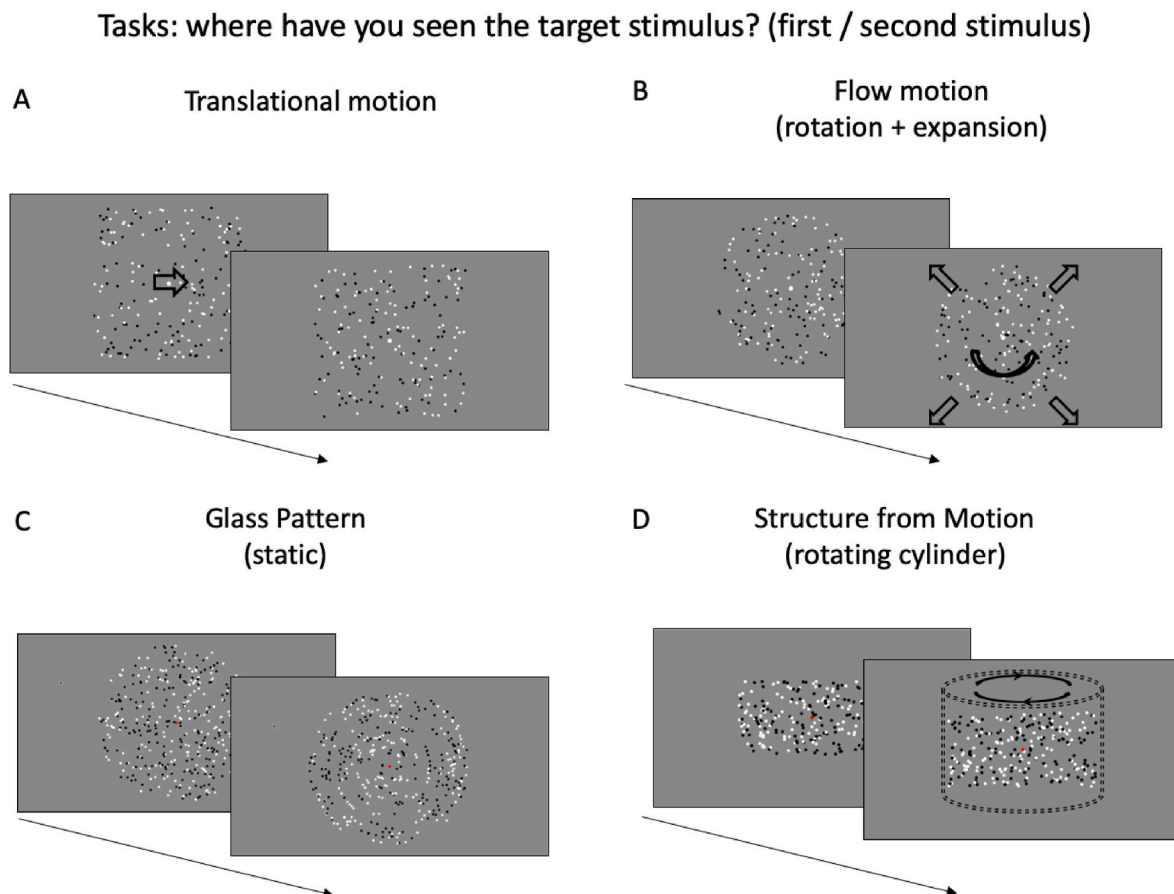
Participants were presented with two sequentially presented random dot kinematograms and were asked to decide whether the first or the second stimulus contained horizontally moving dots (moving either rightwards or leftwards) (Fig. 1A). On average, the percentage of coherent dots needed for the participants to yield 75% of performance was very similar across groups:  $5.4\% \pm 0.6\%$  for the DD group and  $5.7\% \pm 1.2\%$  for the control group (Fig. 2A). The difference was not significant, with Bayes factor suggesting strong evidence in favor of the null hypothesis of no difference between groups ( $t(28) = -0.24$ ;  $p = 0.81$ ,  $\text{LogBF} = -1.0$ ). Adult participants can sometimes compensate for their deficit and successfully maintain a similar sensitivity level, however with much longer reaction times. We therefore also analyzed reaction times which were nevertheless comparable between groups. To provide a response, the DD and control group needed on average  $0.70 \pm 0.21$  s and  $0.68 \pm 0.26$  s respectively, not significantly different ( $t(28) = 0.21$ ;  $p = 0.83$ ,  $\text{LogBF} = -1.0$ ). Overall, participants in the DD and control groups required the same proportion of coherently moving dots and the same integration time to correctly discriminate translational motion from random noise motion.

### 3.3. Flow motion

We also characterized motion discrimination sensitivity when participants were asked to identify which out of two sequentially presented stimuli displayed dots coherently moving simulating optic flow motion (Fig. 1B). The percentage of coherent dots needed to yield 75% correct performance were similar across groups also with this type of stimuli:  $20\% \pm 2\%$  for the DD group and  $17.1\% \pm 1\%$  for the control group (Fig. 2B). The sensitivity was not significantly different across groups, and Bayes factor suggested substantial evidence in favor of the null hypothesis of no difference between groups ( $t(28) = 1.26$ ;  $p = 0.21$ ,  $\text{LogBF} = -0.5$ ). Reaction times were also very similar across groups: the DD group performed the task in  $0.65 \pm 0.15$  s, and the control group in  $0.58 \pm 0.15$  s, not significantly different ( $t(28) = 1.21$ ;  $p = 0.23$ ,  $\text{LogBF} = -0.5$ ). Overall, as observed for translational motion, the DD and control groups discriminated flow motion from random noise motion with a very similar level of performance.

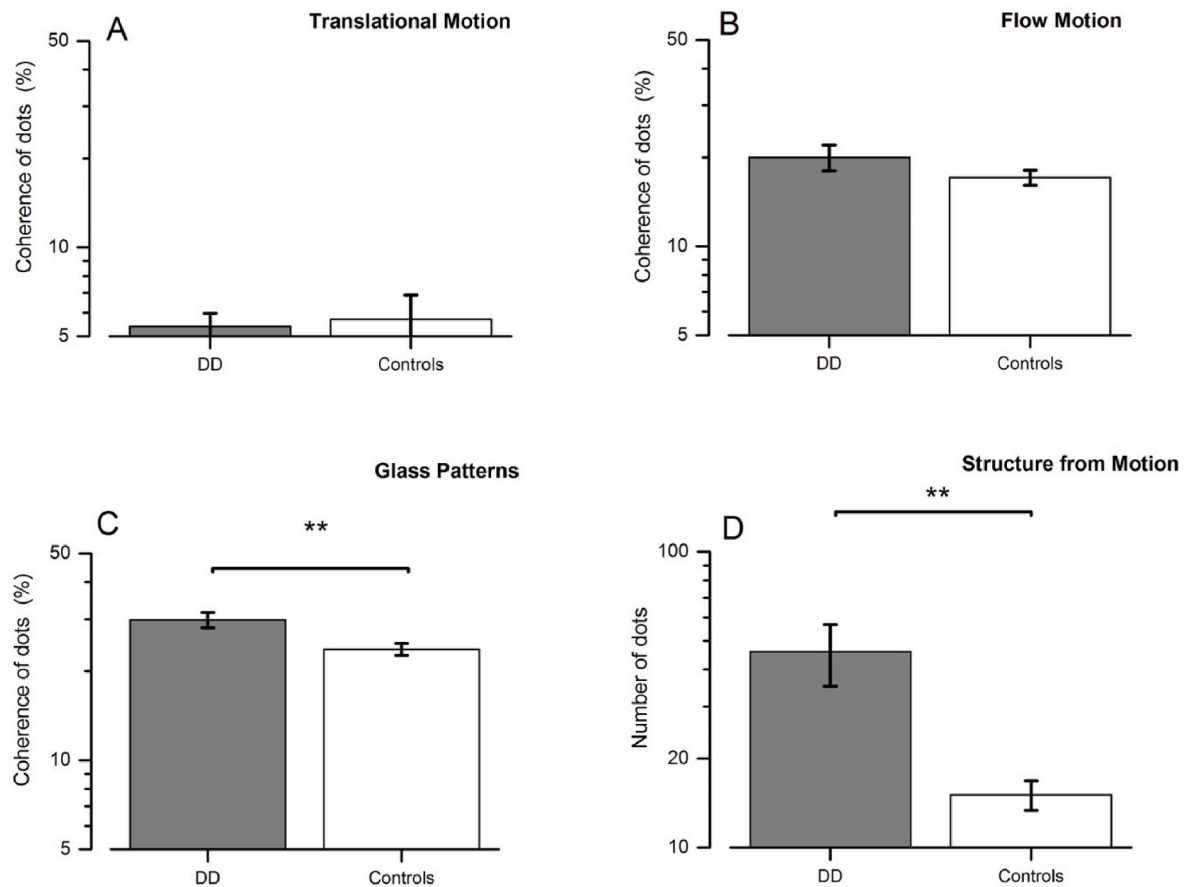
### 3.4. Glass patterns

To evaluate global 2D form perception without motion cues, participants were asked to identify which of the two intervals contained concentric circles in static Glass patterns (Fig. 1C). The DD group required more coherent dots compared to the control group to reach comparable level of 75% correct performance:  $29.8\% \pm 2\%$  compared to  $23.7\% \pm 1\%$ . This difference was significant and the Bayes factor provided very strong evidence in support of the alternative hypothesis of difference ( $t(28) = 2.88$ ;  $p = 0.007$ ,  $\text{LogBF} = 1.9$ ). Reaction times, on the



**Fig. 1.** Examples of stimuli used in the four tasks.

Example of stimuli shown to evaluate participants' sensitivity to translational motion (A), flow motion (B), Glass patterns (C) and structure from motion (D). Participants were asked to decide whether the stimulus containing the global motion or form signal was shown in the first or in the second interval by pressing the left or right arrow keys, respectively.



**Fig. 2.** Sensitivity in the global motion, global form and structure from motion tasks.

Bar graphs show the percentage of coherent dots required to yield 75% of correct responses in the translational motion (A), flow motion (B) and Glass patterns tasks (C) and the number of dots necessary to perform at 75% correct in the structure from motion task (D). Grey and white bars represent the DD and control groups respectively (bars and error bars depict the mean  $\pm$  SEM).

other hand, were not significantly different across groups (for the DD group:  $0.57 \pm 0.24$  s, for the control group:  $0.46 \pm 0.26$  s,  $t(28) = 1.26$ ;  $p = 0.21$ ,  $\text{LogBF} = -0.5$ ). These results were replicated even when discarding the participants with reading difficulties. The percentage of coherent dots was still higher in the DD group ( $29\% \pm 2\%$ ,  $t(25) = 2.70$ ;  $p = 0.01$ ,  $\text{LogBF} = 1.5$ ), while reaction times did not significantly differ ( $0.57 \pm 0.20$  s,  $t(25) = 1.23$ ;  $p = 0.22$ ,  $\text{LogBF} = -0.5$ ). In sum, the DD group showed less sensitivity to global form compared to the control group, when tested with static 2D Glass patterns.

### 3.5. Structure from motion

The ability to discriminate structure from motion from random noise was tested to study 3D form perception on the basis of dynamic cues. Participants were asked to identify whether a rotating cylinder was shown in the first or second of two sequentially presented intervals (Fig. 1D). On average, the DD group required a much higher number of dots compared to the control group to reach a 75% correct performance (for the DD group:  $46.9 \pm 11$  dots, for the control group:  $15.1 \pm 2$  dots, Fig. 2C). This difference was statistically significant and Bayes factor provided very strong evidence in favor of the alternative hypothesis of a difference ( $t(28) = 2.88$ ;  $p = 0.007$ ,  $\text{LogBF} = 1.9$ ). Reaction times on the other hand were very similar and not significantly different (for the DD group:  $0.63 \pm 0.1$  s, for the control group:  $0.67 \pm 0.09$  s  $t(28) = -1.68$ ;  $p = 0.10$ ,  $\text{LogBF} = -0.01$ ). To discard the possibility that this result might have been driven by the three participants who also had an associated reading deficit, we compared the across group performance once having discarded these participants. The results were replicated: the difference

in sensitivity between groups persisted and the average reaction times were largely similar – for the DD group sensitivity was  $41 \pm 11$  dots, still significantly different from the control group ( $t(25) = 2.53$ ;  $p = 0.018$ ,  $\text{LogBF} = 1.2$ ) and reaction times were  $0.62 \pm 0.10$  s, not different from the control group ( $t(25) = -1.34$ ;  $p = 0.19$ ,  $\text{LogBF} = -0.4$ ). Overall, the DD group required more moving dots to discriminate a motion-defined global shape from random noise compared to the control group.

### 3.6. Relationship with crowding

In a previous study we found that dyscalculic subjects were characterized by enhanced visual crowding, that is they showed higher orientation discrimination thresholds for a target in the presence of nearby flankers, compared to the control group (Castaldi et al., 2020c). The stimuli used here to measure global motion/shape thresholds had slightly different densities (higher in the Glass pattern condition), and this raises the possibility that visual crowding made the discrimination of denser stimuli harder. Since the participants included in the current study also took part in the one investigating visual crowding, we correlated crowding and global motion/shape thresholds. None of these correlations were significant (crowding vs translational motion:  $r(27) = -0.14$ ,  $p = 0.47$ ; crowding vs spiral motion:  $r(27) = 0.10$ ,  $p = 0.60$ ; crowding vs structure from motion:  $r(27) = -0.12$ ,  $p = 0.54$ ; crowding vs glass patterns:  $r(27) = 0.08$ ,  $p = 0.67$ ).

### 3.7. Relationship with math

As an explorative analysis we investigated whether sensitivity to

structure from motion and to Glass patterns, which were significantly different in the between group comparison, were predictive of numerical or arithmetical abilities. To reduce the number of variables we performed correlation analyses only between the psychophysical sensitivity measures and the IES scores for digit, calculation, general math and BDE. The correlations between the sensitivity to structure from motion and IES for digit ( $r(30) = 0.25$ ,  $p = 0.16$ ), calculation ( $r(30) = 0.40$ ,  $p = 0.03$ ), general math ( $r(30) = 0.38$ ,  $p = 0.03$ ) and BDE ( $r(30) = 0.36$ ,  $p = 0.04$ ) were all not significant after Bonferroni correction (which would require  $p < 0.0125$ , Figure S1). Sensitivity to Glass patterns was significantly correlated with the IES BDE ( $r(30) = 0.64$ ,  $p = 0.0001$ ) and it remained significant even when controlling for group ( $r(27) = 0.46$ ,  $p = 0.01$ ). Correlations between the sensitivity to Glass patterns and IES for digit ( $r(30) = 0.20$ ,  $p = 0.27$ ), calculation ( $r(30) = 0.40$ ,  $p = 0.02$ ) and general math ( $r(30) = 0.40$ ,  $p = 0.02$ ) were not significant after Bonferroni correction (Figure S2).

In the light of the enhanced visual crowding observed in DD in a previous study (Castaldi et al., 2020c) we asked whether shape perception sensitivity was an independent and specific factor predicting math performance or whether the relation between these two variables simply arose as a consequence of enhanced visual crowding. To this aim, we performed hierarchical regressions with orientation thresholds under crowding and sensitivity to Glass patterns as predictors and IES BDE as dependent variable to quantify the amount of variance explained independently by these two variables of interest. In a first set of models, the effect of each predictor of interest (sensitivity to Glass patterns or orientation thresholds under crowding) on top of the control variables (age, non-verbal IQ and reading abilities) was tested in isolation. Each predictor explained a significant portion of variance in IES BDE (sensitivity to Glass patterns:  $R^2 = 0.43$ ,  $R^2$  change = 0.31,  $p = 0.001$ ; orientation thresholds under crowding:  $R^2 = 0.34$ ,  $R^2$  change = 0.24,  $p = 0.01$  see upper half of Fig. 3). In a second set of models, each one of the predictors of interest in turn was added to the control variables in order to evaluate the portion of variance explained by the other left out predictor on top of it (see lower half of Fig. 3 and Figure S3). Sensitivity to Glass patterns continued to explain a significant portion of variance in IES BDE, even after controlling for orientation thresholds under crowding in addition to the other factors ( $R^2 = 0.70$ ,  $R^2$  change = 0.35,

$p < 0.0001$ ). In the same manner, the orientation thresholds under crowding explained a significant portion of variance in IES BDE when sensitivity to Glass patterns was controlled in addition to the other factors ( $R^2 = 0.70$ ,  $R^2$  change = 0.26,  $p < 0.0001$ ). Overall, these results suggest that the relationship between numerical skills and Glass pattern sensitivity could not be simply explained by visual crowding.

In sum, both sensitivity to Glass patterns and orientation thresholds under crowding explained a significant portion of variance of IES BDE after controlling for age, non-verbal IQ and reading abilities and the third variable (Glass patterns sensitivity or orientation thresholds under crowding).

#### 4. Discussion

The aim of the current study was to characterize high-level visual processing abilities and more specifically different types of global motion and global form perception in DD adults. We found that while sensitivity to global translational and flow motion did not differ between the DD and control groups, both 2D Glass patterns and 3D structure from motion sensitivities were reduced in the DD compared to the control group.

Tasks measuring global motion and global form perception similar (though not entirely identical) to some of those employed here have often been used in clinical populations as a test for the functionality of the dorsal and ventral visual streams, respectively (for a review see: Johnston et al., 2017). Studies in individuals born preterm (Guzzetta et al., 2009; Taylor et al., 2009) or with developmental disorders such as autism (Spencer et al., 2000), Williams syndrome (Atkinson et al., 1997, 2006) and dyslexia (Hansen et al., 2001; Conlon et al., 2009; Johnston et al., 2016) found a common deficit in perceiving global motion while perception of global form appeared spared or much less affected. The most popular hypothesis advanced to explain this finding is the “dorsal stream vulnerability hypothesis”, according to which a common dysfunction of the dorsal visual pathway can explain the shared global motion perception deficit across these clinical conditions (Braddick et al., 2003; Braddick and Atkinson, 2011; Atkinson, 2017).

In the light of these findings, and given the known functional and anatomical correlates of dyscalculia in parietal cortex as reviewed in the introduction, the comparable sensitivity to translational and flow motion between the DD and control groups observed here may seem unexpected, but is unlikely to be explained by stimulus parameters. Several studies on dyslexia, reported elevated thresholds for global motion perception in affected adults using a quite variable range of stimulus durations, densities, dot sizes and lifetimes (Talcott et al., 2000; Hansen et al., 2001; Pellicano and Gibson, 2008; Conlon et al., 2009; for a meta-analysis see: Benassi et al., 2010) and the parameters used in the current experiment for the global motion task fit reasonably well into the range that previously yielded robust effects in dyslexia.

One possible explanation for the different result observed here compared to the study of Sigmundsson et al. (2010) which found elevated global motion thresholds in six dyscalculic children compared to age-matched controls may be the different attentional load across studies. Similar to many other studies investigating global motion perception in developmental disorders and children born preterm (Atkinson et al., 1997, 2006; Spencer et al., 2000; Hansen et al., 2001; Conlon et al., 2009; Guzzetta et al., 2009), Sigmundsson et al. (2010) presented the two stimuli simultaneously rather than sequentially, therefore putting heavier demand on the attentional system which can be deficient in DD individuals (Ashkenazi et al., 2009). Nevertheless, motion deficits have in some studies been observed in dyslexia even when presenting a single stimulus and asking for a directional up versus down response (Pellicano and Gibson, 2008; Cicchini et al., 2015), and we therefore opted for a central and sequential presentation of the stimuli to reduce the potential impact of abnormal visual crowding (Castaldi et al., 2020c). However, by presenting the stimuli sequentially, we might have decreased the attentional load and therefore the

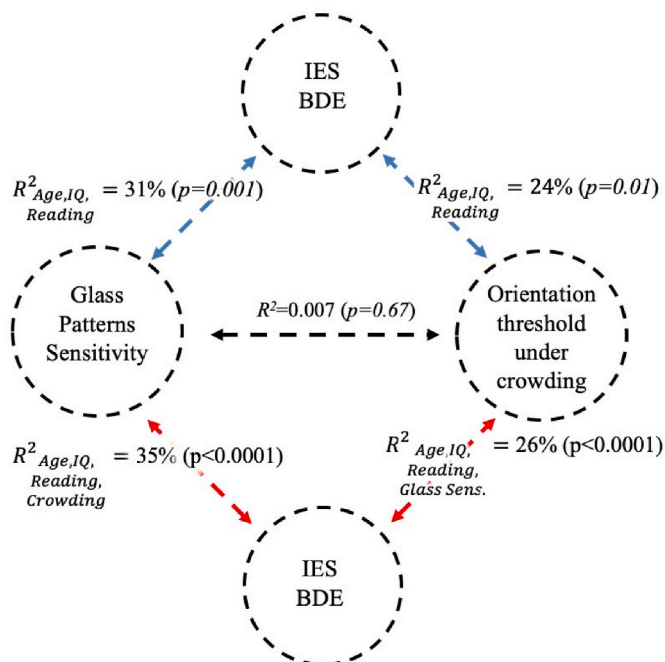


Fig. 3. Link between sensitivity to Glass patterns, orientation thresholds under crowding and IES BDE.

difficulty of the task compared to the study of Sigmundsson et al. (2010). Alternatively, differences in age and potentially in reading skills (not reported in Sigmundsson et al. (2010)) may have also contributed to the different findings.

Unlike Sigmundsson et al. (2010), we found a difference in sensitivity to 2D static global form in the DD group compared to the control group. However, the task used by Sigmundsson et al. (2010) and by other authors describing comparable sensitivity between individuals with developmental disorders and controls (Atkinson et al., 1997; Spencer et al., 2000; Hansen et al., 2001; White et al., 2006; Milne et al., 2006; Conlon et al., 2009; Johnston et al., 2016) differed from the one adopted here, in that they used line segments rather than Glass patterns. Among the few other studies that used Glass patterns (Tsermentseli et al., 2008; Taylor et al., 2009; Koldewyn et al., 2010; Palomares and Shannon, 2013), two found global form perception to be impaired or delayed in adults with high-functioning autism (Tsermentseli et al., 2008) and in children with Williams syndrome (Palomares and Shannon, 2013).

Perception of Glass patterns is thought to be achieved in two steps: first individual dots need to be locally paired to define oriented dipoles – a step not needed with line segment patterns – and then local orientations need to be pooled into a global percept of shape. Our visual system might be more sensitive to lines compared to Glass patterns (Dakin, 1997) and the developmental trajectory of global form perception by line segments also differs from the one mediated by Glass patterns: a VEP study found that 4–5.5 month-old infants were sensitive to global shape, but only when this was defined by line segments and not by Glass patterns (Palomares et al., 2010). The authors proposed that the integration fields might be larger and isotropic in infants compared to adults, who on the contrary, might successfully extract orientation signals in Glass patterns thanks to elongated integration fields sensitive to local collinearity. Therefore, the probability of spurious dots to elicit false pairings might be higher in infants compared to adults because the summation area of the infants' integration fields is larger and less spatially specific. Adding pixels connecting the dots (i.e., using lines rather than Glass patterns), makes the pairing explicit and might allow infants to detect global form as early as 4 months of age (Braddick and Atkinson, 2007). The time needed for the two mechanisms to fully develop is also different: while sensitivity to global forms defined by line segments is adult-like by 6–7 years (Gunn et al., 2002), Glass pattern sensitivity does not reach maturity before 9 years of age (Lewis et al., 2004). Following the model of Palomares et al. (2010), the global form deficit in DD participants observed in the current experiment could suggest that the integration fields might not sufficiently sharpen during development in DD individuals and remain relatively large and isotropic, similar to the ones characterizing the immature visual system. While this possibility may also explain the presence of abnormal visual crowding, it is plausible that difficulties in DD individuals are not restricted to local grouping processes, but also extend to the following stage of global pooling of this information. Computational models (Wilson et al., 1997; Wilson and Wilkinson, 1998) and neurophysiological studies in macaques (Smith et al., 2002, 2007) proposed that Glass pattern detection is achieved through multiple filtering stages, presumably carried out by simple and complex cells in V1 and V2, and a final pooling stage, hypothesized to be supported by the larger receptive fields of neurons in higher level areas as for example V4 that show selectivity for more complex structures, such as circular, radial or hyperbolic patterns compared to gratings (Gallant et al., 1993). In humans, a behavioral study estimated the spatial frequency tuning of the local and global grouping processes to be narrow and broader respectively, consistent with the receptive field properties of the hypothesized neural mechanisms (Dakin and Bex, 2001). Neuroimaging studies also suggested that early visual areas play an important role in detecting local orientation structure in Glass patterns, but that selectivity to global shape independently of local signals and sensitivity to Glass pattern coherence arise only in midlevel areas along both the ventral and the dorsal stream

(Krekelberg et al., 2005; Ostwald et al., 2008; Mannion et al., 2009, 2013). Overall, these studies suggest that Glass patterns are perceived through a sequence of integration stages that convert the selectivity for local signals in early visual areas into selectivity for global form which involve mainly, but not only, ventral areas.

In general, however, considering shape processing to be an exclusive property of the ventral visual pathway appears to be an over-simplification. Neurons in the lateral parietal area (LIP) for example, show selectivity for simple shapes of different forms (e.g. Sereno and Maunsell, 1998; Sereno et al., 2020), and one fMRI study found preferential activation to line segments forming coherent shapes compared to non-coherent ones in several areas along the ventral and the dorsal stream, including the intraparietal sulcus (Braddick et al., 2000). Other imaging and neuropsychological studies pointed at the involvement of the parietal cortex in perception of more complex objects, Gestalt perception, or in binding shape and surface details together (Humphreys, 2003; Eger et al., 2007; Himmelbach et al., 2009; Huberle and Karnath, 2012; Zaretskaya et al., 2013; Rennig et al., 2015). Medial and lateral parts of parietal cortex have been implicated in object recognition under challenging/impaired viewing conditions: their activity and functional coupling with fusiform cortex were increased when objects could be identified at more degraded stimulus levels due to congruent top-down knowledge (Eger et al., 2007). Glass-patterns as the ones used in our study, even though lacking higher-level semantic information, could be seen as placing a high demand in terms of such mechanisms for integration of partial information, especially when presented with low degree of coherence at near threshold levels. An impairment beyond the ventral visual pathway and at the level of parietal cortex is therefore a possibility that might be tested in future studies.

Another original finding of our study is that sensitivity to a different type of form information (3D structure from motion) was strongly impaired in the DD compared to the control group. Impaired form from motion sensitivity was previously reported in dyslexic adults (Johnston et al., 2016). However, in that case, the form from motion deficit coexisted with the motion direction discrimination deficit and was attributed to a more general temporal processing impairment. In the current study we found a deficit in structure from motion, but not in translational motion, despite the fact that the dots were moving horizontally in both cases. This is particularly striking as the structure from motion task we employ here implies the presentation of a sparse array of dots all belonging to a virtual cylinder with no other distractor dots presented, unlike the global motion tasks. Thus, of the two tasks, structure from motion is the one that taxes least mechanisms for attention and noise exclusion and the selective difficulty of dyscalculics in the structure from motion task can unlikely be ascribed to these factors. This also stands in contrast with what is observed in dyslexics who have marked difficulty in conditions that require teasing apart noise and stimuli in simultaneous presentations (Sperling et al., 2005, 2006). A particularity of the structure from motion task is that the 3D shape percept is achieved by changing the dots' speed at the edges of the cylinder. The structure from motion deficit observed can therefore be ascribed either to a global form deficit that is not only evident when shapes are defined by dipole pairing (as in the static Glass patterns), but also when they are defined by motion, or alternatively to a speed perception deficit. Future studies should disentangle these possibilities.

fMRI studies in individuals without DD reported that a network of areas along both the ventral and the dorsal stream are involved in structure from motion processing. A network including occipito-temporal, lateral occipital and parietal areas was reported to be activated by motion stimuli evoking 3D object perception when compared with 2D motion stimuli (Orban et al., 1999; Paradis, 2000; Vanduffel et al., 2002; Murray et al., 2003).

Given the reviewed evidence for a dorsal stream involvement in aspects of shape processing (also including both Glass patterns and structure from motion perception), the fact that we found global form



processing to be impaired in DD participants does not necessarily contradict the dorsal stream vulnerability hypothesis (Braddick et al., 2003). In addition, a central conceit of the dorsal vulnerability hypothesis is that motion abilities tend to show later development than form abilities, and that they are therefore more prone to disruption. In line with this reasoning, Glass pattern perception is maturing more slowly than simpler shape tasks, as reviewed above. There is at least some evidence that also structure from motion perception is maturing not before 7–8 years of age and thus somewhat later compared to global motion (Parrish et al., 2005), and parietal cortex responses to structure from motion were found to not yet be adult like at 6 years of age (Klaver et al., 2008). This fits well with the idea of more slowly maturing dorsal stream functions being more vulnerable in development compared to the ventral stream (Braddick et al., 2003), even if the cortical location of the impairments observed cannot be determined definitively based on behavioral measurements alone.

Interestingly, visual crowding, found to be enhanced in DD adults (Castaldi et al., 2020c) did not seem to be related with the global form impairments observed here. It can be argued that the enhanced visual crowding made perception of denser arrays more difficult. However, compared to global motion stimuli, only Glass patterns had higher density, while for SFM the total number of dots was hardly ever shown and, around the threshold (on average 45 and 15 dots for the DD and control group, respectively), the density was much lower. Therefore, density is unlikely to account for the combination of these impairments. In addition, stimuli were presented in the central visual field where crowding is generally weak, potentially explaining the lack of correlation between global form perception and visual crowding. Alternatively global integration and crowding might be at least partially independent processes.

Moreover, in our study the sensitivity to visual form (Glass patterns) predicted numerical abilities, even independently of visual crowding. Of course, correlation is not causation and on the basis of this admittedly somewhat unexpected finding we would not claim that the global form perception deficit is *the core* deficit in DD. On the other hand, recent studies found that the precision of numerical estimates and counting speed can be much increased when the items that have to be enumerated can be grouped, a phenomenon termed groupitizing (Starkey and McCandliss, 2014; Anobile et al., 2020; Maldonado Moscoso et al., 2020; Maldonado Moscoso et al., 2021). Importantly, this phenomenon occurs mostly when the number of groups and the number of items included within each group is comprised in the subitizing range i.e., without exceeding four items. This numerical limit corresponds to the number of vertices defining the most frequently encountered geometrical shapes: lines, triangles and squares. Thus, numerosity perception may be partially facilitated by a sort of shape-template matching. This possibility was suggested also by an ERP study reporting that shape perception may precede numerosity perception (Gheorghiu and Dering, 2020). The possibility that form perception can affect the development of numerical abilities more than commonly thought should therefore be tested in future studies.

The fact that only sensitivity to Glass patterns, but not the one to structure from motion, predicted numerical abilities, although all of these abilities have been found to recruit parietal regions (Orban et al., 1999; Vanduffel et al., 2002; Harvey et al., 2017), should not come as a total surprise. Indeed, although in the theoretical case of perfect cortical overlap of the regions supporting these abilities one could expect all the mentioned functions to be predictive of each other, the existing literature only suggests some degree of proximity within the dorsal stream (rather than perfect overlap). Indeed, the existing fMRI studies were performed in separate groups of subjects, making it hard to evaluate the exact degree of overlap between the regions found. It remains possible that at a less coarse scale some functions overlap more than others, determining a stronger relation between the respective behavioral sensitivities.

In sum, the present study provides evidence to suggest that on top of

known impairments in numerical and higher-level executive function skills, developmental dyscalculia can be associated with reduced perceptual sensitivity in some visual domains, in particular 3D structure from motion and 2D form coherence. An impairment in form but not motion processing sets our results apart from many previously published studies in other learning disabilities. We speculate that detailed task demands (as for example attentional load, or the degree to which stimuli challenge mechanisms for integration of partial information), rather than the mere distinction between type of feature processed (form vs motion), may have contributed to the patterns of findings observed. We believe that the current results are interesting in that they caution against the often-made oversimplification that evaluation of global motion and form perception would separately test the functionality of the dorsal and ventral stream, respectively. Future neuroimaging studies will be required to unambiguously identify the cortical locus underlying the differences in perceptual performance observed here between participants with and without DD. Moreover, the fact that the 3D structure from motion and 2D global form deficits can be observed in adult participants with DD motivates further studies in children to determine if and how aspects of form perception could be related to numerical skills.

### Author contribution

Elisa Castaldi: Conceptualization; Methodology; Formal analysis; Investigation; Resources; Writing – original draft; Writing – review & editing; Visualization; Supervision; Project administration; Funding acquisition. Marco Turi: Conceptualization; Methodology; Software; Validation; Formal analysis; Data curation; Writing – original draft; Writing – review & editing; Visualization. Guido Marco Cicchini: Conceptualization; Methodology; Software; Validation; Formal analysis; Data curation; Writing – review & editing; Supervision; Project administration; Funding acquisition. Sahawanatou Gassama: Investigation; Resources. Evelyn Eger: Conceptualization; Methodology; Resources; Writing – review & editing; Supervision; Project administration; Funding acquisition.

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### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.neuropsychologia.2021.108140>.

### References

- American Psychiatric Association, 2013. Diagnostic and Statistical Manual of Mental Disorders (Washington, DC).
- Anobile, G., Castaldi, E., Moscoso, P.A.M., Burr, D.C., Arrighi, R., 2020. "Groupitizing": a strategy for numerosity estimation. *Sci. Rep.* 10, 13436.
- Ashkenazi, S., Rubinsten, O., Henik, A., 2009. Attention, automaticity, and developmental dyscalculia. *Neuropsychologia* 23, 535–540.
- Ashkenazi, S., Rosenberg-Lee, M., Tenison, C., Menon, V., 2012. Weak task-related modulation and stimulus representations during arithmetic problem solving in children with developmental dyscalculia. *Developmental Cognitive Neuroscience* 2, S152–S166.
- Atkinson, J., 2017. The david a teller award lecture, 2016: visual brain development: a review of "dorsal stream vulnerability"—motion, mathematics, amblyopia, actions, and attention. *J. Vis.* 17, 26.
- Atkinson, J., Braddick, O., Nokes, L., Anker, S., Braddick, F., 1997. A specific deficit of dorsal stream function in Williams' syndrome. *Neuroreport* 8, 1919–1922.

- Atkinson, J., Braddick, O., Rose, F.E., Searcy, Y.M., Wattam-Bell, J., Bellugi, U., 2006. Dorsal-stream motion processing deficits persist into adulthood in Williams syndrome. *Neuropsychologia* 44, 828–833.
- Bayard, S., Erkes, J., Moroni, C., 2009. Test du Stroop Victoria-Adaptation Francophone. CPCN-LR, Gignac.
- Benassi, M., Simonelli, L., Giovagnoli, S., Bolzani, R., 2010. Coherence motion perception in developmental dyslexia: a meta-analysis of behavioral studies. *Dyslexia* 16, 341–357.
- Biancardi, A., Nicoletti, C., 2004. Batteria per la discalculia evolutiva (BDE) [Battery for developmental dyscalculia (BDE)]. Omega, Turin, Italy.
- Boets, B., De Smedt, B., Ghesquière, P., 2011. Coherent motion sensitivity predicts individual differences in subtraction. *Res. Dev. Disabil.* 32, 1075–1080.
- Braddick, O., Atkinson, J., 2007. Development of brain mechanisms for visual global processing and object segmentation. In: *Progress in Brain Research*. Elsevier, pp. 151–168.
- Braddick, O., Atkinson, J., 2011. Development of human visual function. *Vis. Res.* 51, 1588–1609.
- Braddick, O.J., O'Brien, J.M.D., Wattam-Bell, J., Atkinson, J., Turner, R., 2000. Form and motion coherence activate independent, but not dorsal/ventral segregated, networks in the human brain. *Curr. Biol.* 10, 731–734.
- Braddick, O., Atkinson, J., Wattam-Bell, J., 2003. Normal and anomalous development of visual motion processing: motion coherence and 'dorsal-stream vulnerability'. *Neuropsychologia* 41, 1769–1784.
- Braddick, O., Atkinson, J., Newman, E., Akshoomoff, N., Kuperman, J.M., Bartsch, H., Chen, C.-H., Dale, A.M., Jernigan, T.L., 2016. Global visual motion sensitivity: associations with parietal area and children's mathematical cognition. *J. Cognit. Neurosci.* 28, 1897–1908.
- Brainard, D.H., 1997. The psychophysics toolbox. *Spatial Vis.* 10, 433–436.
- Bulthé, J., Prinsen, J., Vanderauwera, J., Duyck, S., Daniels, N., Gillebert, C.R., Mantini, D., Op de Beeck, H.P., De Smedt, B., 2019. Multi-method brain imaging reveals impaired representations of number as well as altered connectivity in adults with dyscalculia. *Neuroimage* 190, 289–302.
- Butterworth, B., 2005. Developmental dyscalculia. In: *Handbook of Mathematical Cognition*. Psychology Press, Hove, pp. 455–467.
- Cardin, V., Smith, A.T., 2010. Sensitivity of human visual and vestibular cortical regions to egomotion-compatible visual stimulation. *Cerebr. Cortex* 20, 1964–1973.
- Castaldi, E., Mirassou, A., Dehaene, S., Piazza, M., Eger, E., 2018. Asymmetrical interference between number and item size perception provides evidence for a domain specific impairment in dyscalculia. *PLoS One* 13, e0209256.
- Castaldi, E., Piazza, M., Dehaene, S., Vignaud, A., Eger, E., 2019. Attentional amplification of neural codes for number independent of other quantities along the dorsal visual stream. *Elife* 8, e45160.
- Castaldi, E., Piazza, M., Iuculano, T., 2020a. Learning disabilities: developmental dyscalculia. In: *Handbook of Clinical Neurology*. Elsevier, pp. 61–75.
- Castaldi, E., Vignaud, A., Eger, E., 2020b. Mapping subcomponents of numerical cognition in relation to functional and anatomical landmarks of human parietal cortex. *Neuroimage* 221, 117210.
- Castaldi, E., Turi, M., Gassama, S., Piazza, M., Eger, E., 2020c. Excessive visual crowding effects in developmental dyscalculia. *J. Vis.* 20, 7.
- Cicchini, G.M., Marino, C., Mascheretti, S., Perani, D., Morrone, M.C., 2015. Strong motion deficits in dyslexia associated with DCDC2 gene alteration. *J. Neurosci.* 35, 8059–8064.
- Collins, E., Park, J., Behrmann, M., 2017. Numerosity representation is encoded in human subcortex. *Proc. Natl. Acad. Sci. Unit. States Am.* 114, E2806–E2815.
- Conlon, E.G., Sanders, M.A., Wright, C.M., 2009. Relationships between global motion and global form processing, practice, cognitive and visual processing in adults with dyslexia or visual discomfort. *Neuropsychologia* 47, 907–915.
- Dakin, S.C., 1997. The detection of structure in glass patterns: psychophysics and computational models. *Vis. Res.* 37, 2227–2246.
- Dakin, S.C., Bex, P.J., 2001. Local and global visual grouping: tuning for spatial frequency and contrast. *J. Vis.* 1, 4.
- Eger, E., 2016. Neuronal foundations of human numerical representations. In: *Progress in Brain Research*. Elsevier, pp. 1–27.
- Eger, E., Henson, R., Driver, J., Dolan, R., 2007. Mechanisms of top-down facilitation in perception of visual objects studied by fMRI. *Cerebr. Cortex* 17, 2123–2133.
- Eger, E., Pineda, P., Dehaene, S., Kleinschmidt, A., 2015. Spatially invariant coding of numerical information in functionally defined subregions of human parietal cortex. *Cerebr. Cortex* 25, 1319–1329.
- Fias, W., 2016. Neurocognitive components of mathematical skills and dyscalculia. In: *Development of Mathematical Cognition*. Elsevier, pp. 195–217.
- Gallant, J., Braun, J., Van Essen, D., 1993. Selectivity for polar, hyperbolic, and Cartesian gratings in macaque visual cortex. *Science* 259, 100–103.
- Geary, D.C., 1993. Mathematical disabilities: cognitive, neuropsychological, and genetic components. *Psychol. Bull.* 114, 345.
- Geary, D.C., 2004. Mathematics and learning disabilities. *J. Learn. Disabil.* 37, 4–15.
- Geary, D.C., Bow-Thomas, C.C., Yao, Y., 1992. Counting knowledge and skill in cognitive addition: a comparison of normal and mathematically disabled children. *J. Exp. Child Psychol.* 54, 372–391.
- Gheorghiu, E., Dering, B.R., 2020. Shape facilitates number: brain potentials and microstates reveal the interplay between shape and numerosity in human vision. *Sci. Rep.* 10, 12413.
- Glass, L., 1969. Moiré effect from random dots. *Nature* 223, 578–580.
- Grill-Spector, K., Golarai, G., Gabrieli, J., 2008. Developmental neuroimaging of the human ventral visual cortex. *Trends Cognit. Sci.* 12, 152–162.
- Gross-Tsur, V., Manor, O., Shalev, R.S., 1996. Developmental dyscalculia: prevalence and demographic features. *Dev. Med. Child Neurol.* 38, 25–33.
- Gunn, A., Cory, E., Atkinson, J., Braddick, O., Wattam-Bell, J., Guzzetta, A., Cioni, G., 2002. Dorsal and ventral stream sensitivity in normal development and hemiplegia. *Neuroreport* 13, 843–847.
- Guzzetta, A., Tinelli, F., Del Viva, M.M., Bancale, A., Arrighi, R., Pascale, R.R., Cioni, G., 2009. Motion perception in preterm children: role of prematurity and brain damage. *Neuroreport* 20, 1339–1343.
- Hansen, P.C., Stein, J.F., Orde, S.R., Winter, J.L., Talcott, J.B., 2001. Are dyslexics' visual deficits limited to measures of dorsal stream function? *Neuroreport* 12, 1527–1530.
- Harvey, B.M., Ferri, S., Orban, G.A., 2017. Comparing parietal quantity-processing mechanisms between humans and macaques. *Trends Cognit. Sci.* 21, 779–793.
- Himmelbach, M., Erb, M., Klockgether, T., Moskau, S., Karnath, H.-O., 2009. fMRI of global visual perception in simultanagnosia. *Neuropsychologia* 47, 1173–1177.
- Huberle, E., Karnath, H.-O., 2012. The role of temporo-parietal junction (TPJ) in global Gestalt perception. *Brain Struct. Funct.* 217, 735–746.
- Humphreys, G.W., 2003. Conscious visual representations built from multiple binding processes: evidence from neuropsychology. *Prog. Brain Res.* 142, 243–255.
- Isaacs, E.B., Edmonds, C.J., Lucas, A., Gadian, D.G., 2001. Calculation difficulties in children of very low birthweight: a neural correlate. *Brain* 1701–1707.
- Iuculano, T., 2016. Neurocognitive accounts of developmental dyscalculia and its remediation. In: *Progress in Brain Research*. Elsevier, pp. 305–333.
- Iuculano, T., Tang, J., Hall, C.W.B., Butterworth, B., 2008. Core information processing deficits in developmental dyscalculia and low numeracy. *Dev. Sci.* 11, 669–680.
- Iuculano, T., Rosenberg-Lee, M., Richardson, J., Tenison, C., Fuchs, L., Supekar, K., Menon, V., 2015. Cognitive tutoring induces widespread neuroplasticity and remediates brain function in children with mathematical learning disabilities. *Nat. Commun.* 6, 1–10.
- Johnston, R., Pitchford, N.J., Roach, N.W., Ledgeway, T., 2016. Why is the processing of global motion impaired in adults with developmental dyslexia? *Brain Cognit.* 108, 20–31.
- Johnston, R., Pitchford, N.J., Roach, N.W., Ledgeway, T., 2017. New insights into the role of motion and form vision in neurodevelopmental disorders. *Neurosci. Biobehav. Rev.* 83, 32–45.
- Kaufmann, L., Vogel, S.E., Starke, M., Kremser, C., Schocke, M., 2009. Numerical and non-numerical ordinality processing in children with and without developmental dyscalculia: evidence from fMRI. *Cognit. Dev.* 24, 486–494.
- Kaufmann, L., von Aster, M., Göbel, S.M., Marksteiner, J., Klein, E., 2020. Developmental dyscalculia in adults: current issues and open questions for future research. *Lern. Lernstörungen* 9, 126–137.
- Klaver, P., Lichtensteiger, J., Bucher, K., Dietrich, T., Loenneker, T., Martin, E., 2008. Dorsal stream development in motion and structure-from-motion perception. *Neuroimage* 39, 1815–1823.
- Koldewyn, K., Whitney, D., Rivera, S.M., 2010. The psychophysics of visual motion and global form processing in autism. *Brain* 133, 599–610.
- Krekelberg, B., Vatakis, A., Kourtzi, Z., 2005. Implied motion from form in the human visual cortex. *J. Neurophysiol.* 94, 4373–4386.
- Kucian, K., Grund, U., Rotzer, S., Henzi, B., Schönmann, C., Plangger, F., Gälli, M., Martin, E., von Aster, M., 2011a. Mental number line training in children with developmental dyscalculia. *Neuroimage* 57, 782–795.
- Kucian, K., Loenneker, T., Martin, E., von Aster, M., 2011b. Non-symbolic numerical distance effect in children with and without developmental dyscalculia: a parametric fMRI study. *Dev. Neuropsychol.* 36, 741–762.
- Lefavrais, P., 1967. Test de l'Alouette.
- Lewis, C., Hitch, G.J., Walker, P., 1994. The prevalence of specific arithmetic difficulties and specific reading difficulties in 9-to 10-year-old boys and girls. *JCPP (J. Child Psychol. Psychiatry)* 35, 283–292.
- Lewis, T.L., Ellemberg, D., Maurer, D., Dirks, M., Wilkinson, F., Wilson, H.R., 2004. A window on the normal development of sensitivity to global form in glass patterns. *Perception* 33, 409–418.
- Maldonado Moscoso, P.A., Castaldi, E., Burr, D.C., Arrighi, R., Anobile, G., 2020. Grouping strategies in number estimation extend the subitizing range. *Sci. Rep.* 10, 14979.
- Maldonado Moscoso, P., Greenlee, M.V., Anobile, G., Arrighi, R., Burr, D.C., Castaldi, E., 2021. Grouping modifies neural coding of numerosity. *Hum Brain Mapping*. <https://doi.org/10.1002/hbm.25694>.
- Mannion, D.J., McDonald, J.S., Clifford, C.W.G., 2009. Discrimination of the local orientation structure of spiral Glass patterns early in human visual cortex. *Neuroimage* 46, 511–515.
- Mannion, D.J., Kersten, D.J., Olman, C.A., 2013. Consequences of polar form coherence for fMRI responses in human visual cortex. *Neuroimage* 78, 152–158.
- Mejias, S., Grégoire, J., Noël, M.-P., 2012. Numerical estimation in adults with and without developmental dyscalculia. *Learn. Individ Differ* 22, 164–170.
- Milne, E., White, S., Campbell, R., Swettenham, J., Hansen, P., Ramus, F., 2006. Motion and form coherence detection in autistic spectrum disorder: relationship to motor control and 2:4 digit ratio. *J. Autism Dev. Disord.* 36, 225–237.
- Morrone, M.C., Tosetti, M., Montanaro, D., Fiorentini, A., Cioni, G., Burr, D.C., 2000. A cortical area that responds specifically to optic flow, revealed by fMRI. *Nat. Neurosci.* 3, 1322–1328.
- Murray, S.O., Olshausen, B.A., Woods, D.L., 2003. Processing shape, motion and three-dimensional shape-from-motion in the human cortex. *Cerebr. Cortex* 13, 508–516.
- Mussolin, C., De Volder, A., Grandin, C., Schölgel, X., Nassogne, M.C., Noël, M.P., 2010. Neural correlates of symbolic number comparison in developmental dyscalculia. *J. Cognit. Neurosci.* 22, 860–874.
- Noël, M.P., Grégoire, J., 2015. TEDI-MATH Grands: test diagnostique des compétences de base en mathématiques du CE2 à la 5e. Pearson.
- Orban, G.A., Sunaert, S., Todd, J.T., Van Hecke, P., Marchal, G., 1999. Human cortical regions involved in extracting depth from motion. *Neuron* 24, 929–940.

- Ostwald, D., Lam, J.M., Li, S., Kourtzi, Z., 2008. Neural coding of global form in the human visual cortex. *J. Neurophysiol.* 99, 2456–2469.
- Palomares, M., Shannon, M.T., 2013. Global dot integration in typically developing children and in Williams Syndrome. *Brain Cognit.* 83, 262–270.
- Palomares, M., Pettet, M., Vildavski, V., Hou, C., Norcia, A., 2010. Connecting the dots: how local structure affects global integration in infants. *J. Cognit. Neurosci.* 22, 1557–1569.
- Paradis, A.L., 2000. Visual perception of motion and 3-D structure from motion: an fMRI study. *Cerebr. Cortex* 10, 772–783.
- Parrish, E.E., Giaschi, D.E., Boden, C., Dougherty, R., 2005. The maturation of form and motion perception in school age children. *Vis. Res.* 45, 827–837.
- Pellicano, E., Gibson, L.Y., 2008. Investigating the functional integrity of the dorsal visual pathway in autism and dyslexia. *Neuropsychologia* 46, 2593–2596.
- Peters, L., Bulthé, J., Daniels, N., Op de Beeck, H., De Smedt, B., 2018. Dyscalculia and dyslexia: different behavioral, yet similar brain activity profiles during arithmetic. *Neuroimage: Clinic* 18, 663–674.
- Piazza, M., Eger, E., 2016. Neural foundations and functional specificity of number representations. *Neuropsychologia* 83, 257–273.
- Piazza, M., Facoetti, A., Trussardi, A.N., Berteletti, L., Conte, S., Lucangeli, D., Dehaene, S., Zorzi, M., 2010. Developmental trajectory of number acuity reveals a severe impairment in developmental dyscalculia. *Cognition* 116, 33–41.
- Price, G.R., Holloway, I., Rashal, P., Vesterinen, M., Ansari, D., 2007. Impaired parietal magnitude processing in developmental dyscalculia. *Curr. Biol.* 17, R1042–R1043.
- Rennig, J., Himmelbach, M., Huberle, E., Karnath, H.-O., 2015. Involvement of the TPJ area in processing of novel global forms. *J. Cognit. Neurosci.* 27, 1587–1600.
- Rosenberg-Lee, M., Ashkenazi, S., Chen, T., Young, C.B., Geary, D.C., Menon, V., 2015. Brain hyper-connectivity and operation-specific deficits during arithmetic problem solving in children with developmental dyscalculia. *Dev. Sci.* 18, 351–372.
- Rotzer, S., Kucian, K., Martin, E., Aster, M. von, Klaver, P., Loenneker, T., 2008. Optimized voxel-based morphometry in children with developmental dyscalculia. *Neuroimage* 39, 417–422.
- Rousselle, L., Noël, M.P., 2007. Basic numerical skills in children with mathematics learning disabilities: a comparison of symbolic vs non-symbolic number magnitude processing. *Cognition* 102, 361–395.
- Rubinsten, O., Henik, A., 2009. Developmental Dyscalculia: heterogeneity might not mean different mechanisms. *Trends Cognit. Sci.* 13, 92–99.
- Rykhlevskaia, E., 2009. Neuroanatomical correlates of developmental dyscalculia: combined evidence from morphometry and tractography. *Front. Hum. Neurosci.* 3, Sereno, Huang, R.-S., 2006. A human parietal face area contains aligned head-centered visual and tactile maps. *Nat. Neurosci.* 9, 1337–1343.
- Sereno, A.B., Maunsell, J.H.R., 1998. Shape selectivity in primate lateral intraparietal cortex. *Nature* 395, 500–503.
- Sereno, A.B., Lehky, S.R., Sereno, M.E., 2020. Representation of shape, space, and attention in monkey cortex. *Cortex* 122, 40–60.
- Sigmundsson, H., Anholt, S.K., Talcott, J.B., 2010. Are poor mathematics skills associated with visual deficits in temporal processing? *Neurosci. Lett.* 469, 248–250.
- Smith, M.A., Bair, W., Movshon, J.A., 2002. Signals in macaque striate cortical neurons that support the perception of glass patterns. *J. Neurosci.* 22, 8334–8345.
- Smith, M.A., Kohn, A., Movshon, J.A., 2007. Glass pattern responses in macaque V2 neurons. *J. Vis.* 7, 5.
- Spencer, J., O'Brien, J., Riggs, K., Braddick, O., Atkinson, J., Wattam-Bell, J., 2000. Motion processing in autism: evidence for a dorsal stream deficiency. *Neuroreport* 11, 2765–2767.
- Sperling, A.J., Lu, Z.-L., Manis, F.R., Seidenberg, M.S., 2005. Deficits in perceptual noise exclusion in developmental dyslexia. *Nat. Neurosci.* 8, 862–863.
- Sperling, A.J., Lu, Z.-L., Manis, F.R., Seidenberg, M.S., 2006. Motion-perception deficits and reading impairment: it's the noise, not the motion. *Psychol. Sci.* 17, 1047–1053.
- Starkey, G.S., McCandliss, B.D., 2014. The emergence of “groupitizing” in children's numerical cognition. *J. Exp. Child Psychol.* 126, 120–137.
- Szűcs, D., 2016. Subtypes and comorbidity in mathematical learning disabilities. In: *Progress in Brain Research*. Elsevier, pp. 277–304.
- Szűcs, D., Devine, A., Soltesz, F., Nobes, A., Gabriel, F., 2013. Developmental dyscalculia is related to visuo-spatial memory and inhibition impairment. *Cortex* 49, 2674–2688.
- Talcott, J.B., Hansen, P.C., Assoku, E.L., Stein, J.F., 2000. Visual motion sensitivity in dyslexia: evidence for temporal and energy integration deficits. *Neuropsychologia* 38, 935–943.
- Taylor, N.M., Jakobson, L.S., Maurer, D., Lewis, T.L., 2009. Differential vulnerability of global motion, global form, and biological motion processing in full-term and preterm children. *Neuropsychologia* 47, 2766–2778.
- Treue, S., Husain, M., Andersen, R.A., 1991. Human perception of structure from motion. *Vis. Res.* 31, 59–75.
- Tsermentseli, S., O'Brien, J.M., Spencer, J.V., 2008. Comparison of form and motion coherence processing in autistic spectrum disorders and dyslexia. *J. Autism Dev. Disord.* 38, 1201–1210.
- Vanduffel, W., Fize, D., Peuskens, H., Denys, K., Sunaert, S., Todd, J.T., Orban, G.A., 2002. Extracting 3D from motion: differences in human and monkey intraparietal cortex. *Sci. New Series* 298, 413–415.
- White, S., Milne, E., Rosen, S., Hansen, P., Swettenham, J., Frith, U., Ramus, F., 2006. The role of sensorimotor impairments in dyslexia: a multiple case study of dyslexic children. *Dev. Sci.* 9, 237–255.
- Wilson, H.R., Wilkinson, F., 1998. Detection of global structure in Glass patterns: implications for form vision. *Vis. Res.* 38, 2933–2947.
- Wilson, H.R., Wilkinson, F., Asaad, W., 1997. Concentric orientation summation in human form vision. *Vis. Res.* 37, 2325–2330.
- Wilson, A.J., Andrewes, S.G., Struthers, H., Rowe, V.M., Bogdanovic, R., Waldie, K.E., 2015. Dyscalculia and dyslexia in adults: cognitive bases of comorbidity. *Learn. Indiv Differ* 37, 118–132.
- Zaretskaya, N., Anstis, S., Bartels, A., 2013. Parietal cortex mediates conscious perception of illusory Gestalt. *J. Neurosci.* 33, 523–531.