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Developmental dyslexia: A deficit in magnocellular-parvocellular co-activation, not simply in pure magnocellular activation

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ABSTRACT

The magnocellular deficit theory of dyslexia suggests a selective impairment in contrast detection of stimuli involving pure magnocellular response (e.g. Gabor patches of 0.5 c/deg, 30 Hz, low contrast). An alternative hypothesis is that, dyslexia may be associated with a reduction of typical facilitation that normal readers present for stimuli relying on low-level magno-parvo co-activation, relative to stimuli eliciting pure magno activation. According to this hypothesis, any advantage in contrast sensitivity, produced by either decreasing stimuli temporal frequency (from 30 to 10 Hz, Experiment 1) or using static stimuli of increasing spatial frequency (from 0.5 to 4 c/deg, Experiment 2), would be ascribed to the coexisting responses of the magnocellular and parvocellular systems. In the control group, this advantage in contrast sensitivity was found for a 0.5 c/deg Gabor (either static or flickering at 10 Hz) and for a static Gabor of 4 c/deg. In contrast to magnocellular deficit theory predictions, dyslexic individuals showed no deficit in the unmixed magnocellular response. However, they showed no advantage when the relative weight between magnocellular and parvocellular inputs was thrown off balance in favor of the latter. These results suggest that in order to interpret low-level visual deficits in dyslexia, it is worth considering that fast, feedforward low-frequency representations of spatial structures may result from the coexisting responses of two systems. Our results suggest that in dyslexia, the relative contribution of these two systems in visual processing is perturbed, and that this may have detrimental consequences in word processing, both within the parafovea and the fovea during fixation.

1. Introduction

Given the solid agreement on the presence of several neurobiological signatures of developmental dyslexia (Habib, 2000; Eckert, 2004; Shaywitz & Shaywitz, 2008; Mascheretti et al., 2018), recent psychophysical studies show that dyslexic individuals also manifest low-level problems in visual processing (see Walsh, 1995, Schulte-Körne & Bruder, 2010; Vidyasagar & Pammer, 2010, for reviews). In particular, these results suggest low-level problems in visuo-temporal information processing, as often showed by higher contrast thresholds for the detection and the discrimination of flicker and motion signals (Martin & Lovegrove, 1987; Cornelissen, Richardson, Mason, Fowler & Stein, 1995; Ridder, Borsting, & Banton, 2001; Slaghuis & Ryan, 1999; Hill & Lovegrove, 1993; Eden et al., 1996; Demb, Boynton, Best, & Heeger, 1998; Pammer & Wheatley, 2001; Buchholz & McKone, 2004; Ben-Yehudah, Sackett, Malchi-Ginzberg, & Ahissar, 2001; Laycock, Crewther, & Crewther, 2012). It has been suggested that these visual problems could arise from an inefficient processing within a part of the visual pathway known as the magnocellular stream (Stein, 2001; Stein, Talcott, & Walsh, 2000). The implication of this model is that the response of the visual magnocellular subsystem (M-system), more sensitive to low spatial (SF), high temporal frequencies (TF) and low contrast, should be reduced in dyslexia, whereas the response of the parvocellular subsystem (P-system), more sensitive to high spatial, low TF and color, should be unaffected. Consistent with this view is the evidence of a slower maturation of magno with respect to parvo functions during normal development, a divergence that makes this subsystem less efficient and more vulnerable to developmental changes (Coch, Skendzel, Grossi, & Neville, 2005). Skottun (2000), in reviewing the literature, focused on contrast sensitivity and observed that many results are not compatible with the predictions of a magnocellular deficit hypothesis of dyslexia. The author stated that the reason for this conflicting evidence relies upon the difficulty to psychophysically isolate the magnocellular response. Perhaps, the only appropriate stimulus

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Table 1
The table shows, separately for the two control groups (AC and adults) and for the DD group, means and Standard deviations of chronological age, Z scores of reading speed and accuracy and binocular and monocular (RE, right eye; LE, left eye; Bin, binocular) visual acuity for SLOAN letters (expressed in logMAR units) assessed before testing, using FrACT (Freiburg Visual Acuity and Contrast Test) Software (Bach, 2006). Z scores of four DD and five AC were not made available because of schools' internal privacy rules.

	Chronological age	Reading scores		Visual acuity		
		Speed	Accuracy	LE	RE	Bin
DD	10.8 (SD 0.5)	−2.4 (SD 1.2)	−1.7 (SD 0.38)	−0.13 (SD 0.03)	−0.05 (SD 0.4)	−0.21 (SD 0.04)
AC	11.3 (SD 1.9)	> 1	> 1	−0.14 (SD 0.02)	−0.11 (SD 0.02)	−0.19 (SD 0.15)
Adults	21.5 (SD 1.36)	> 1	> 1	−0.11 (SD 0.05)	−0.09 (SD 0.03)	−0.17 (SD 0.05)

to selectively activate the M-system is indeed the one possessing very low SF (lower than 1 c/deg), very high TF (15–30 Hz) and very low contrast (Merigan & Maunsell, 1990; Merigan, Byrne, & Maunsell, 1991). There is evidence that dyslexic individuals perform worse in these conditions than age-matched controls (Buchholz & McKone, 2004; Demb et al., 1998; Ben-Yehudah et al., 2001), but most results show a reduced sensitivity in a wider range of spatio-temporal conditions, in which an involvement of the P-system cannot be excluded.

To account for these inconsistencies, recent studies took a new root to address the issue of whether dyslexia relates to a deficit of the dorsal stream either at the lower (M-system) or at the higher level. In particular, recent models assume that efficient visual processing of objects and words relies on the information provided by feedforward processing and on information from recurrent connections, either horizontal or feedback (Hochstein & Ahissar, 2002; Lamme & Roelfsema, 2000).

More recent studies proved that horizontal connections in V1 provide joint magno-parvo inputs to extrastriate areas (Sincich & Horton, 2005; Nassi & Callaway, 2009). Sincich and Horton (2005) reviewed convincing anatomical indications that horizontal intra-cortical connections within V1 allow magno and parvo inputs to be intermingled extensively so that, the streams projecting to V2 commixture magno, parvo and konio signals. Nassi and Callaway (2009) extensively reviewed a piece of anatomic evidence that shows how the inputs from parvo and magno systems, originating from the retina and projecting to LGN, are recombined in V1, into multiple channels projecting to extrastriate areas.

The implication for these recent findings is that parvo-magno co-activation occurs as early as in V1 and would drive both feedforward central processing and feedback modulation from dorsal to ventral areas. In particular, the low frequency representation, extracted from fast feedforward inputs to the dorsal areas, may derive from this early magno-parvo co-activation, and can be suitable to execute broader spatial tasks.

This might be the case for a broad range of spatio-temporal stimulation, except for the few, exquisitely magnocellular, falling outside the P-system's response window. The psychophysical confirmation of this suggestion comes from the seminal work of Kulikowski and Tolhurst (Kulikowski & Tolhurst, 1973). They showed that observers perceive the flicker but not the spatial structure of a stimulus suitable for selective magnocellular activation (0.5 c/deg, 20 Hz). It was assumed that to allow the detection of the spatial structure of this stimulus, TF must be reduced so to add parvo to magno activation. Furthermore, this non-linearity of response is supported also by studies on transient and sustained channels, which match the anatomically defined magno and parvo systems. These studies used contrast detection rather than phenomenological reports (flicker vs. pattern threshold) and their results are highly compatible with a two-system co-activation hypothesis (Breitmeyer & Julesz, 1975; Tolhurst, 1975).

We distinguished prevalent magnocellular activation from magno-parvo co-activation by comparing contrast thresholds for detecting a stimulus of very low SF and very high TF with thresholds obtained with stimuli of either reduced TF or increased SF. Based on Lamme and Roelfsema (2000) model, recurrent processing promotes co-activation between the two systems, thus inducing an improvement in performance with respect to the condition in which stimuli selectively activate the magnocellular system. However, a deficit in recurrent processing should reduce this facilitation, so that contrast sensitivity should not be higher with respect to that obtained with stimuli inducing a pure magnocellular response.

2. Methods

2.1. Participants

Participants were nineteen children with Developmental dyslexia (DD) (7 females), average age 10.8 (SD 0.5), nineteen chronological-aged matched (AC) (14 females), average age 11.3 (SD 1.9) (see Table 1). Because a slower maturation of dorsal with respect to ventral stream functions cannot be excluded in AC (Coch et al., 2005), a group of nineteen adults (8 females), average age 21.5 (SD 1.36) was also included. Participants performed a contrast detection task with either flickering (Experiment 1) or static stimuli (Experiment 2). Informed consent was obtained from participants and/or from their parents. The work described has been carried out in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki). The study was approved by the Ethical Committee of the University of Padova (protocol n. 2571).

The children groups were recruited from local primary and secondary schools, whereas the group of adults were students of the University of Padova. Participation to the study was proposed by the teachers to the parents, following a written neuropsychological diagnosis of developmental dyslexia. As requested from a specific Italian law (Law 170, October 2010) that guarantee access to all the educational opportunities for students with Learning Disabilities (Al-Yagon et al., 2013; Losito, Cornoldi, & Tressoldi, 2014), the diagnosis for children who have Italian as their first languagecomplies with the following guidelines: dyslexia has to be assessed after the end of the second year of primary school, using psychometric standardized measures of accuracy and reading speed with a score cut-off below the 5th percentile (−2 standard deviations), in the absence of intellectual ability deficits, sensory impairments, attention/hyperactivity deficit (ADHD) or neurological or psychiatric disorders (Losito et al., 2014). The details about the sample are shown in Table 1.

2.2. Stimuli

Stimuli were displayed centrally on a 19-inch LCD Asus monitor with a refresh rate of 60 Hz and a response time of 2 ms, and they were generated using Matlab Psychtoolbox-3 (Brainard and Vision, 1997; Pelli, 1997). Screen resolution was 1920–1080 pixels. Gamma correction for each color channel was applied through calibration with the Spyder 4 Elite colorimeter (DataColor). Calibration was further verified using a Minolta LS-100 photometer, which indicated that the mean luminance was ~50 cd/m^2. In order to represent 10.8 bits of luminance (1786 grey levels) on an 8-bit display, so as to reach a theoretical threshold value of 0.0011 Michelson contrast, we adopted a software

solution called “Pseudo-Gray”, also known as “Bit-Stealing” (Tyler, Chan, Liu, McBride, & Kontsevich, 1992), that was implemented via the Psychtoolbox built-in function.

Stimuli were Gabor patches consisting of a cosinusoidal carrier enveloped by a stationary Gaussian. Each Gabor patch was characterized by its wavelength (λ), phase (φ = 0, evens symmetric), and standard deviation (σ = 2 deg) of the luminance Gaussian envelope in the (x, y) space of the image. Formally, each Gabor patch can be expressed as follows:

$$G(x, y) = \cos((2\pi/\lambda)x + \varphi)e^{-(x^2+y^2)/\sigma^2}$$

Gabor stimuli were perceived either flickering (Experiment 1) or static (Experiment 2).

In Experiment 1, participants in all groups viewed a counterphase flickering Gabors, with SF of 0.5 c/deg that differed in temporal modulation: it could be either high (30 Hz), suitable for selective magnocellular activation, or medium (10 Hz), good enough to allow magno and parvo co-activation.

In Experiment 2 we measured contrast thresholds for static stimuli in each group. We used spatial frequencies of 0.5 and 4 c/deg. Both static stimuli involve parvocellular processing. However, whereas parvocellular processing is dominant for the high SF stimulus, a magno-parvo coexisting response more likely underlies detection of the static low SF stimulus. Contrast thresholds for a static 12 c/deg stimulus, selectively activating the parvo system, were also collected from a subsample of 15 participants. Stimulus duration was 250 ms in both experiments. In each trial, the participant viewed a fixation point (a white cross), followed by two stimulus intervals separated by 2 sec pause. One stimulus interval was blank (i.e., the screen background), whereas the other presented a Gabor stimulus.

2.3. Procedure

Participant had to report whether the Gabor was presented in the first or in the second interval (i.e., 2IFC task). The inter-stimuli interval was 1 sec while the inter-trials interval was varying with subject response speed with a minimum of 1 sec.

In the first trial, the Gabor had a Michelson contrast of 0.7. In the successive trials, the contrast was changed as a function of the participant’s response, according to a psychophysical adaptive procedure from the MLP toolbox (Grassi & Soranzo, 2009; Green, 1993, 1990). There were 30 trials in each block, a number sufficient to obtain a reliable and fast threshold estimate with this procedure (Leek, Dubno, He, & Ahlstrom, 2000; Amitay, Irwin, Hawkey, Cowan, & Moore, 2006). Each subject started with an easy practice dummy block, with high contrast stimuli, under the supervision of the experimenter. The order presentation of the four experimental blocks were randomized within the same day. Concerning threshold estimation, we used a logistic function defined by three fixed and a free parameter. The function’s slope (beta), the chance level (gamma) and the lapse rate (lambda), where set respectively to 20, 0.5 and 0. The free parameter corresponded to the displacement of the midpoint of the function along the abscissa (alpha) and could assume any value between 0.005 (the minimum contrast reliably produced by our setup) and 0.7 Michelson (detected 100% of the time by all participant). Accuracy level that defined the threshold was the 75% of the participant’s psychometric function. An important consideration regards the lapse rate. Since the presence of lapses in the very first trials can undermine the ability of this procedure to converge at threshold (Gu & Green, 1994), Grassi and Soranzo (2009) suggest starting with a first trial abundantly above the expected threshold and to repeat the procedure in case of errors in the “easy” trials. In our study the starting contrast was fairly above the threshold for all participants and this allowed us to monitor for the presence of lapses at the beginning of each block. If two subsequent lapses in the first five trials were spotted, the block was interrupted and repeated following a small break aimed at getting participant’s focus back. Overall, this procedure allowed for fast and accurate threshold estimations preventing tiredness and controlling for high variability in the lapse rate.

2.4. Statistical analysis

A three-ways ANOVA, with group as between-subjects factor (AC, adult normal controls and DD) and two within-subjects factors: stimulus type (flicker vs. static) and stimulus level (low vs. high SF/TF), was conducted to assess groups response to the modulation of either spatial or temporal frequencies. Repeated-measures ANOVAs was also conducted to assess group differences in threshold modulation. Threshold modulation was defined as the $\log_{10}$(10/30 Hz) and the $\log_{10}$(static/30 Hz), i.e. the variation of sensitivity produced by coexisting magno and parvo response, with respect to the predominant magnocellular response. Threshold modulation was also computed as $\log_{10}$(0.5/12 c/deg), i.e. the variation in sensitivity that a magno-parvo co-activation has with respect to selective parvo activation. Tukey correction was applied to pairwise comparisons. Threshold modulation effects were also assessed using Bonferroni corrected one sample *t*-test, based on the null hypothesis of 0 effect.

Considering the evidence that magnocellular and parvocellular pathways converge significantly at the earliest level of processing in V1 (Nassi & Callaway, 2009), threshold modulation was used as an index of how varying spatio-temporal parameters of the target, resulted into a perturbation of the magno-parvo balance in favor of either systems. Threshold modulation computation, ($\log_{10}$ (X/Y), consists in normalizing contrast threshold for the target stimulus (X), with respect to that obtained in the baseline stimulus (Y). The $\log_{10}$(X/Y) computation may return a result not significantly different from 0, indicating that no threshold modulation, with respect to the baseline, occurred. Conversely, a threshold modulation < or > than 0 indicates that contrast thresholds for the target are either lower or higher with respect to the baseline (Y). If Y parameters are suitable for prominent magno activation (a 30 Hz and .5 c/deg Gabor) and X parameters introduce parvocellular activation that increases contrast sensitivity, then we predict threshold modulation to result into a negative value. On the other hand, little threshold modulation would be expected if Y produces a good response of the parvocellular system only (12c/deg, 0 Hz) and X co-activates both systems (.5 c/deg either static or flickering), considering that typical contrast sensitivity functions show similar contrast sensitivity at 12 and .5 c/deg.

3. Results

In these experiments we assessed performance of dyslexic children, age-matched controls and adults in a 2IFC contrast detection task. We compared temporal frequency (10 and 30 Hz, Experiments 1) and spatial frequency levels (0.5 and 4 c/deg, Experiments 2). Contrast thresholds for each group are reported in Fig. 1. Left panel shows thresholds obtained in Experiment 1, with temporally modulated Gabors. Right panel shows contrast thresholds from Experiment 2 obtained with static Gabors. The three-way ANOVA revealed that differences between static and flickering stimuli ($F_{(1,54)} = 40.4$, $p < .001$, $\eta_p^2 = .43$) and differences between low and high frequency ($F_{(1,54)} = 6.1$, $p = .017$, $\eta_p^2 = .1$) resulted significant, whereas the difference between groups did not reach statistical significance ($F_{(2,54)} = 1.6$, $p = .2$, $\eta_p^2 = .057$). Moreover, the interaction between stimulus type and stimulus levels was significant ($F_{(1,54)} = 69.9$, $p < .001$, $\eta_p^2 = .56$), showing that contrast thresholds differ significantly ($p < .001$) only between the stimuli of high spatial (4 c/deg) and high TF (30 Hz), hence supporting the absence of correlation (see Table 2) between these conditions. Most importantly, interaction between group and stimulus level was also significant ($F_{(2,54)} = 4.1$, $p = .022$, $\eta_p^2 = .13$), indicating a difference between DD and control

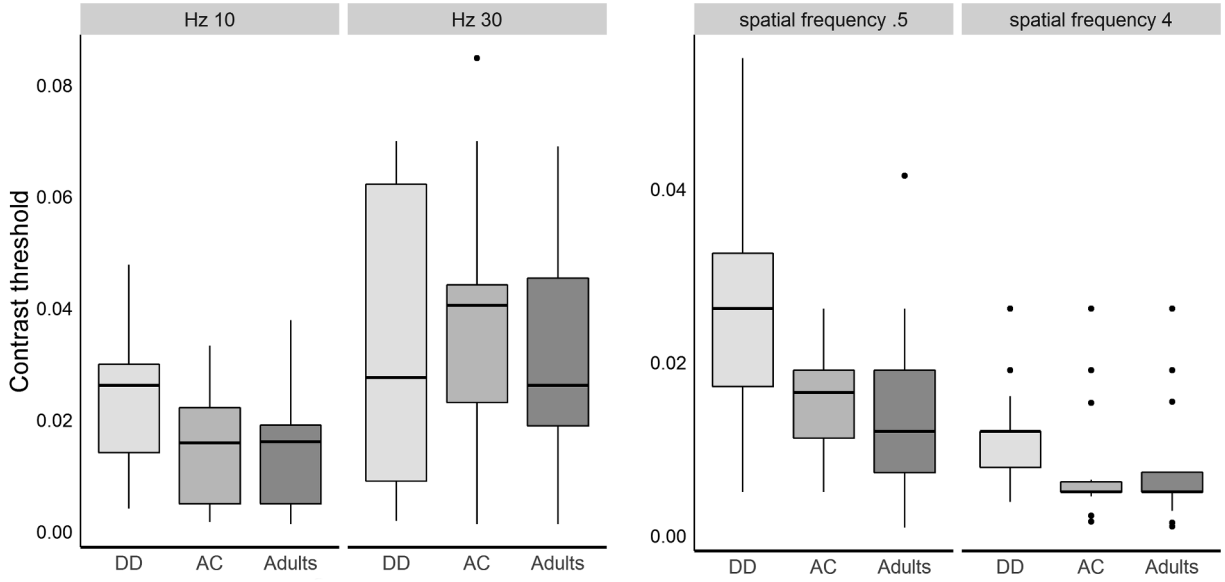

Fig. 1. Left panel: contrast thresholds for the three groups obtained with a 0.5 c/deg Gabor flickering at either 10 or 30 Hz (left panel) or a static Gabor with SF of either 0.5 or 4 c/deg (right panel). From bottom to top, boxes provide the 5th, 25th, 75th, and 95th percentiles of the distribution. Horizontal bold lines provide the median values of the distribution. Black dots correspond to outliers.

groups contrast thresholds: AC ($p = .004$) and Adults ($p = .004$), only when obtained with low frequency, either static (.5 c/deg) or flickering (10 Hz).

Fig. 2 shows threshold modulation data. Threshold modulation scores increase as the co-activation of the two systems increases. Left panel of Fig. 2 shows the $\log_{10}$(10/30 Hz) modulation. A threshold modulation $\log_{10}$(10/30 Hz) < , > or not different from 0 indicates, each to each, that lower TF Gabor decreases, increases or does not affect thresholds, with respect to high TF Gabor. The ANOVA on TF $\log_{10}$(10/30 Hz) showed a significant group effect ($F_{(2,54)} = 3.77$, $p = .029$; $\eta_p^2 = .12$). One sample *t*-test based on the null hypothesis of 0 effect showed a threshold modulation < 0 for controls (AC mean: −0.30, $p = .006$; adults mean: −0.31, $p = .004$), yet not for DD (mean: −0.017, $p = .99$).

The right panel of Fig. 2 shows the $\log_{10}$(static/30 Hz) modulation. A threshold modulation log(static/30 Hz) < , > or not different from 0 indicates that static Gabors have lower, higher or not different thresholds than high TF Gabor decrease.

The ANOVA on threshold modulation for the static stimulus with respect to the high TF flickering Gabor (log(static/flickering 30 Hz), revealed a significant effect of SF ($F_{(1,54)} = 31.7$, $p < .001$, $\eta_p^2 = 0.14$), Group ($F_{(1,54)} = 4.8$, $p = .012$; $\eta_p^2 = .11$), but not a Group × SF interaction ($F_{(2,54)} = 0.02$, $p = .98$; $\eta_p^2 = .002$). One sample *t*-test based on the null hypothesis of 0 effect showed that threshold modulation was significantly lower than 0 for both control groups: AC (0.5 c/deg, mean: −0.30, $p = .004$; 4 c/deg, mean: −0.64, $p < .001$); adults (.5 c/deg, mean: −0.26, $p = .031$; 4 c/deg, mean: −0.57, $p < .001$). DD group showed no threshold modulation for the .5 c/deg grating (mean: 0.029, $p = .99$) and lower negative threshold modulation for the 4 c/deg Gabor (mean: −0.3, $p = .014$).

4. Control data

Our results clearly discarded the magnocellular deficit hypothesis (Stein, 2001; Stein et al., 2000). Instead, they support an alternative hypothesis of a magno-parvo co-activation deficit, which brings-up a corollary hypothesis, that is, this deficit would not have any effect on thresholds for stimuli mostly activating magno system, but also would not reduce sensitivity for stimuli mostly relying on parvo response (12 c/deg, 0 Hz). Considering that typical contrast sensitivity function shows similar contrast sensitivity at 12 and .5 c/deg, little threshold modulation ($\log_{10}$(low/high c/deg)) by magno-parvo co-activation for low SF stimuli either static or flickering at 10 Hz would be expected in controls.

We were able to retest 15 out 19 participants in each group, with a static stimulus of higher spatial frequency (12 c/deg), for which magnocellular activation may be excluded. Indeed, we found very similar contrast thresholds in all groups (average DD: 0.0095; average AC: 0.0094; average Adults: 0.0081). We then used these contrast thresholds to compute threshold modulation for .5 c/deg Gabors either static or flickering at 10 Hz (Fig. 3). The obtained values were positive indicating, for the low SF Gabors, higher thresholds than the high SF Gabors. There was no effect of stimulus ($F_{(2,42)} = 1.14$, $p = .29$, $\eta_p^2 = .027$) and no group × stimulus interaction ($F_{(2,42)} = 0.19$,

Table 2
Correlation index between the different stimuli used, separately for each group.

	DD			AC			Adults		
	SF.5 TF0	SF4 TF0	SF.5 TF10	SF.5 TF0	SF4 TF0	SF.5 TF10	SF.5 TF0	SF.4 TF0	SF.5 TF10
SF.5 TF0									
SF4 TF0	0.1			−0.53			−0.35		
SF.5 TF10	0.48	0.1		0.22	0.01		0.23	0.22	
SF.5 TF30	0.7	0.26	0.69	0.65	0.03	0.65	0.31	0.07	0.3

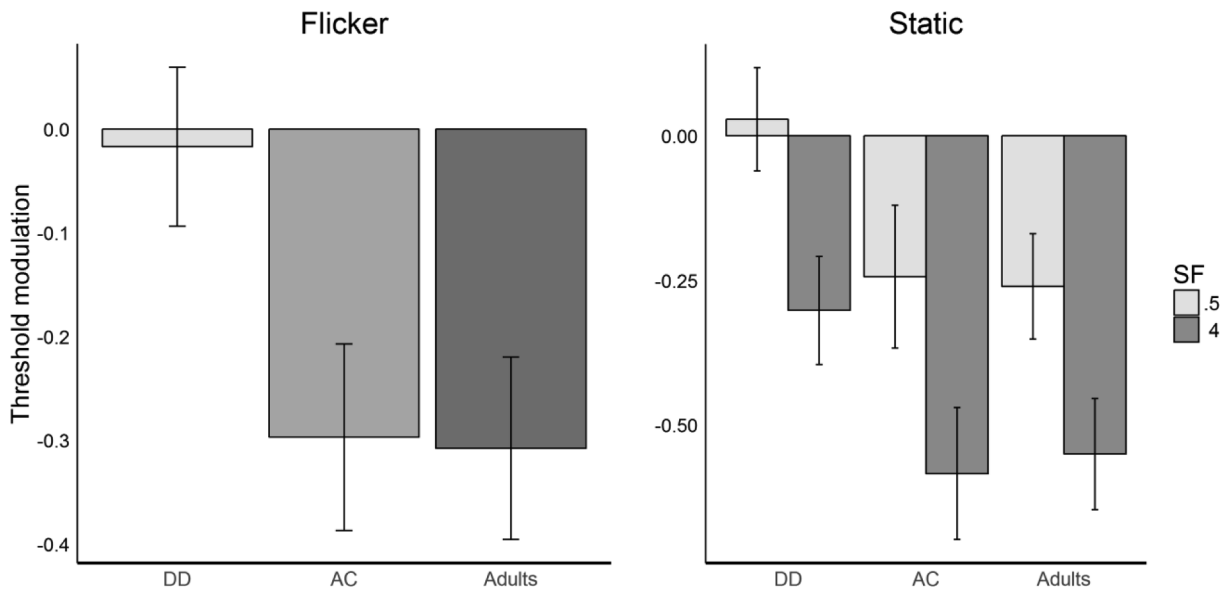

Fig. 2. Left panel: threshold modulation (log(10 Hz/30 Hz)) for each of the three groups. Right panel: threshold modulation, i.e. the log(static/30 Hz), for each of the three groups. Bars indicate standard errors.

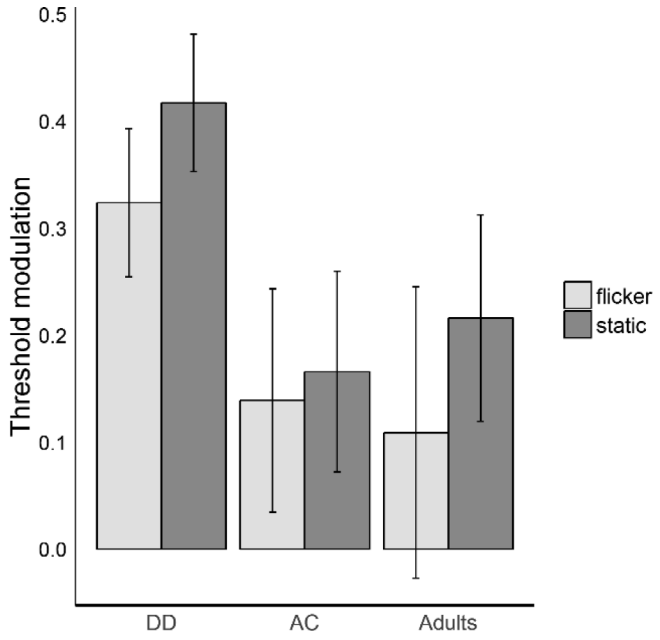

Fig. 3. Threshold modulation for the low spatial frequency static vs the high spatial frequency static (log_{10} (0.5 cpd/12 cpd)) and for the low spatial frequency motion vs the high spatial frequency static (log_{10} (0.5 cpd, 10 Hz/12 cpd)), for each group. Bars indicate standard errors.

p = .83, η_p^2 = .01]. As expected, a significant group difference was found ($F_{(2,42)}$ = 3.43, p = .042, η_p^2 = .14), with threshold modulation higher for DDs.

5. Discussion

The results of this study showed that, when detecting Gabors of low spatial frequency (0.5 c/deg), either static or temporally modulated at 10 Hz, thresholds were higher for DD than controls. No group effect for the 30 Hz flickering condition was found. In controls, when detecting a 30 Hz flickering Gabor, contrast thresholds were found to be higher than those obtained with a 10 Hz flickering Gabor as well as those for static Gabors of low and medium SF. However, DD group did not show facilitation with static or low TF Gabors with respect to high TF-Gabors, as thresholds modulation did not differ from 0. Moreover, when comparing stimuli involving magno-parvo co-activation (.5 c/deg either static or flickering at 10 Hz) with those mostly eliciting a parvocellular response (12 c/deg, static), dyslexic participants showed threshold enhancements higher than controls.

We found no higher thresholds in DDs with respect to controls for the 30 Hz stimulus. This results seems incompatible with the selective M-system deficit hypothesis, since it predicts a selective impairment in detecting this “pure” magnocellular stimulus (Skottun, 2000). However, the assumption that magnocellular and parvocellular responses can be psychophysically dissociated (Breitmeyer & Julesz, 1975; Kéri & Benedek, 2011; Pellicano & Gibson, 2008; Tolhurst, 1975; Skottun, 2000; Witton et al., 1998) does not always holds. For example, Goodbourne et al. (2012) found absent or no correlation between different magnocellular tasks.

To ensure that our stimuli differed with respect to the amount of magno-parvo balance, we computed a correlation index between the different stimuli we used, separately for each group.

As predicted by magno-parvo response dissociation, no significant correlation between the high-SF static Gabor and the two low-SF flickering Gabors was found in any group. Conversely, all groups showed high correlation between the stimuli eliciting “pure” magno (low SF-30 Hz Gabor) and co-existing magno-parvo response: (low SF Gabors of 10 and 0 Hz). In addition, the two static stimuli were negatively correlated (with high thresholds at low-SF going together with low thresholds at high-SF), only in controls. Taken together, these results suggest that, providing that task remains unchanged and stimuli are in all similar, except for either SF or TF modulation, it is possible to induce magno-parvo co-activation varying along a continuum, with a selective activation of either systems at the extremes.

Under the assumption that the 30 Hz stimulus of very low spatial frequency selectively activates magno system, our results challenge the anchoring deficit hypothesis (Ahissar, Lubin, Putter-Katz, & Banai, 2006; Ben-Yehudah & Ahissar, 2004). These authors proposed that readers with dyslexia have difficulties on tasks in which they must retain and compare information across two temporal intervals, when the information in either interval is repeated from trial to trial, as it does in the two-interval, temporal forced-choice task we have used. This hypothesis predicts that dyslexic children should have had higher contrast thresholds than CA matched controls, across all conditions in

Experiment 1 and Experiment 2. Results clearly showed that this was not the case. Instead, dyslexics individuals were selectively impaired in tasks that do not rely on "exclusive" contribution of either magnocellular or parvocellular system.

Hence, DDs difficulties seem to relay on an unbalance between magnocellular and parvocellular contribution to feedforward-visual processing. In normal vision, magno-parvo response coexists in detection of low and medium spatial frequencies. This is clear from the seminal studies that attempted to dissociate the response of transient and sustained channels, providing respectively inputs to magnocellular and parvocellular pathways. Breitmeyer and Julesz (1975) found that temporal transients increase contrast sensitivity, even for medium, parvo mediated, spatial frequencies. Tolhurst (1975) showed that response to a 2 c/deg grating is mediated by both transient and sustained channels activation. Most importantly, Kulikowski and Tolhurst (1973) showed that increasing parvocellular contribution, by reducing TF, leads to higher contrast sensitivity in the detection of either the temporal or the spatial structure of a flickering grating of very low SF, whereas only the temporal, not the spatial structure, is visible at the highest TF at which the magnocellular system responds alone.

In our study, the magno-parvo relative contribution in the detection of a spatial structure was derived by the threshold modulation index, that reflects how stimuli involving magno-parvo co-activation enhance stimuli detectability with respect to the 30 Hz flicker stimulus, assumed to selectively involve magnocellular processing.

On the bases of coexisting magno-parvo response hypothesis, we expected a negative log modulation index for all stimuli involving magno-parvo co-activation that indicates facilitation when these systems cooperate in stimuli detection. Indeed, controls' data showed a negative modulation index for both a 0.5 c/deg Gabor, either static or flickering at 10 Hz, and for a static Gabor of medium SF. Intriguingly, there was no facilitation in dyslexic participants for the .5 c/deg grating (either static or temporally modulated at 10 Hz) and it was reduced for the static stimulus of 4 c/deg, as threshold modulation did not differ from 0, when SF was low, or it was less negative, when SF was high.

In summary, our results indicate that DD participants, unlike controls, do not benefit from a change in the systems balance in favor of parvocellular inputs and they also exhibit a greater drawback when the balance is changed in favor of magnocellular inputs. Moreover, differently from other studies, we found similar performance in AC and adults in our tasks involving magnocellular activation, not supporting the suggestion of a slower maturation of dorsal with respect to ventral stream functions in typical population (Coch et al., 2005). This suggests that dyslexia is not simply an exacerbation of a neurodevelopmental difficulty but rather it may reflect a specific processing impairment.

It is worth discussing how well popular theories of recurrent processing, namely the Recurrent Processing theory (RPT) (Lamme & Roelfsema, 2000) and the Reverse Hierarchy theory (RHT) (Hochstein & Ahissar, 2002), account for DDs performance.

RPT and RHT share many similarities but also present substantial differences. The two theories share the idea that vision is not accomplished by feedforward processing alone: recurrent processing through horizontal and feedback connections is reflected in the neural and perceptual response. Moreover, the two theories share the idea that difficult visual tasks involve recurrent processing via feedback connections, whereas easy tasks do not. Low-level processing (V1) via feedback from high-level visual areas occurs in visual task involving scrutiny (hard visual search, perception of letters into words and in crowded context). In addition, both theories posit that low-level processing via reentrant connections involves focal attention. However, the two theories differ on the role assigned to the highest levels of feedforward processing. For RPT, feedback processing is required for explicit attentive vision, and feedforward processing only mediates preattentive unconscious vision. According to RHT instead, the highest cortical levels of feedforward is responsible of forming explicit high-level representations with the involvement of distributed attention. This processing stage is rapid and uses implicitly information coming from both magno and parvo system, following their co-activation through intracortical lateral connections (Sincich & Horton, 2005; Nassi & Callaway, 2009).

Based on the aspects of convergence, both theories predict that the low SF representation of the image available from fast feedforward dorsal processing and back-projected to the ventral stream facilitates less delayed ventral processing during reading (Laycock & Crewther, 2008; Levy, Walsh, & Lavidor, 2010).

The specific RHT view of a more initial explicit perception is compatible with the hypothesis that fast dorsal processing at high cortical level mediates those tasks involving the extraction of a spatial structure without scrutiny. This would account for our phenomenal ability to consciously identify, after only few ms of exposure, a word but not the font or the letters composing the same word. This initial explicit percept is bound to facilitate the reading process. In particular, during parafoeveal previewing, feedforward-based high-level representation of words might allow to explicitly identify words before they are foveated.

Although RHT does not directly address lateral interactions, considering the evidence of magno-parvo intra-cortical connections as early as V1 (Sincich & Horton, 2005; Nassi & Callaway, 2009), it may be suggested that the explicit high-level representation, resulting from fast feedforward dorsal processing, might rely on both magno and parvo contribution, that mediate simple spatial tasks. Low frequencies representation, extracted at the highest level of fast feedforward processing to the dorsal stream, could be enough to execute a simple detection task, providing that TF is not too high (Kulikowski & Tolhurst, 1973). However, if the fast feedforward processing is deficient, as it is in the DD group, this representation of spatial structure would be unavailable, thence the detection would require the recruitment of lower level ventral mechanisms, that mediate detailed, attention driven analysis.

How a deficit in recurrent processing would affect reading? Several authors (Bullier, 2001; Laycock & Crewther, 2008; Levy et al., 2010; Vidyasagar & Pammer, 2010) suggested that inefficient fast processing of low SF information might compromise essentials components of reading process. First, low frequency representation of words within the parafovea, extracted at the highest level of the dorsal stream and projected backwards, would enhance processing of parafoveal words that have similar shapes and contours, which, if predictable, may be skipped from fixation and, in turn, may facilitate foveating saccades (Bullier, 2001; Levy et al., 2010). Moreover, the limited low-frequency information, obtainable from backward projection to earlier level of ventral processing, would be inadequate, during fixation, for a global word processing, so that high SF mechanisms need to be recruited to mediate attention driven, sequential recognition of single letters (Hochstein & Ahissar, 2002; Vidyasagar & Pammer, 2010). The obvious prediction that follows is that a relation between threshold enhancement scores and reading scores should be found. Although reading scores for four DD were unavailable for privacy reasons, we still computed the correlation between the accessible reading scores and the threshold enhancement data. Regarding reading speed, Z scores were negatively correlated with threshold modulation data obtained in the $\log_{10}$(10 Hz/30 Hz) condition ($R = -0.87$, $p = .002$) and in the two $\log_{10}$(static/30 Hz) conditions: .5 c/deg: $R = -0.70$, $p = .035$; 4 c/deg: $R = -0.87$, $p = .002$). Namely, in these conditions, the less negative the threshold modulation, the more negative the Z scores for reading speed. On the other hand, there is no correlation between reading accuracy and threshold modulation data. Before interpreting the data, it is worth to mention that the available data (15 out 19 participants) were obtained from the tables displayed within the written diagnosis presented by dyslexic participants. Since not all clinicians carried out the assessment of dyslexia through the same validated protocol, we cannot rely upon a unique, standardized analysis of reading error types, thus resulting into a little characterized sample in terms of dyslexia subtypes. Hence, although our correlational analysis might suggest that inefficient low spatial frequencies representation and reading speed

may both rely on inefficient magno-parvo co-activation, further studies are required to shed a light on the nature of the correlation between reading impairment and inadequate magno-parvo co-activation, within different subtypes of dyslexia (McArthur et al., 2013).

In conclusion, our results suggest that, to interpret visual deficit in dyslexia, rather than magnocellular inputs alone, it is fast feedforward processing conveying coexisting magnocellular-parvocellular inputs worth to be considered. Dyslexia may reflect a limitation into the balance between magnocellular and parvocellular processing contribution in feedforward processing of words, both in parafovea and in fovea during fixation.

Conflict of interest

The authors declare no competing financial interests.

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