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RESEARCH ARTICLE

Mathematical impairment associated with high-contrast abnormalities in change detection and magnocellular visual evoked response

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Abstract The cause of developmental dyscalculia, a specific deficit in acquisition of arithmetic skills, particularly of enumeration, has never been investigated with respect to the patency of the visual magnocellular system. Here, the question of dysfunction of the afferent magnocellular cortical input and its dorsal stream projections was tested directly using nonlinear analysis of the visual evoked potential (VEP) and through the psychophysical ability to rapidly detect visual change. A group of young adults with self-reported deficiencies of arithmetical ability, showed marked impairment in magnitude estimation and enumeration performance—though not in lexical decision reaction times when compared with an arithmetically capable group controlled for age and handedness. Multifocal nonlinear VEPs were recorded at low (24 %) and high (96 %) contrast. First- and second-order VEP kernels were comparable between groups at low contrast, but not at high contrast. The mathematically impaired group showed an abnormal lack of contrast saturation in the shortest latency first-order peak (N60) and a delayed P100 positivity in the first slice of the second-order kernel. Both features have previously been argued to be physiological markers of magnocellular function. Mathematically impaired participants also performed worse on a gap paradigm change detection for digit task showing increased reaction times for high-contrast stimuli but not for low-contrast stimuli compared with controls. The VEP results give direct evidence of abnormality in the occipital processing of magnocellular information in those with mathematical impairment. The anomalous high visual contrast physiological and psychophysical performance suggests an abnormality in the inhibitory processes that normally result in saturation of contrast gain in the magnocellular system.

Keywords Change detection · Contrast gain · Developmental dyscalculia · Magnocellular system · Visuospatial attention · Saturation · Surround suppression · VEP nonlinearity

Introduction

Developmental dyscalculia, a deficit in learning mathematics despite normal intelligence (Osmon et al. 2006; Price and Ansari 2013), has been related to the abnormal development of spatial and magnitude representations (Nieder 2005). Consistent with this view, neuropsychological investigations into abnormalities underlying deficits in learning mathematics have suggested impairments in spatial reasoning, particularly the attentional facilitation underlying grouping mechanisms necessary to perceive a "set" of items, manifesting as a deficit in visuospatial attention (Forrest 2004; Osmon et al. 2006).

Early work by Dehaene et al. (1993) noted that in making a speeded response to a set of numbers, smaller numbers elicited a faster left-hand response, while larger numbers elicited a faster right-hand response. This led to the idea of a relation between space and magnitude representation, and the notion of a mental number line emerged. Neuropsychological evidence for such an association comes

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from the disturbed internal representation of the mental number line that occurs in patients with unilateral neglect acquired from right parietal lesions (Zorzi et al. 2002). The nature of errors made by these patients in (mental) number line bisection resembles the rightward shift of the midpoint of physical lines, leading to the idea that the number line has a neural representation similar to that of physical space.

Neuroimaging literature (fMRI) has consistently implicated the right posterior parietal cortex posterior parietal cortex (PPC), particularly the horizontal intraparietal sulcus, in supporting magnitude estimation suggesting a potential brain locus for mathematical impairment (reviewed, Dehaene et al. 2003). Using fMRI, tasks involving nonsymbolic and symbolic targets Ansari et al. (2007) contrasted the enumeration of small sets allowing subitization and large sets requiring estimation. fMRI signal activation in the right temporoparietal junction for the small set > large set contrast correlated significantly with reaction time for the large set condition, and Ansari et al. interpreted their results as indicative that subitization and numerosity estimation require different mechanisms, while Burr et al. (2010) concluded that subitization requires attentional resources to a greater extent than numerosity estimation during dual-attention tasks. Enumeration of small number sets has been argued to share some of the same mechanisms as multiple object tracking (Trick and Pylyshyn 1994), a task that strongly activates the superior parietal cortex (Culham et al. 1998).

Abnormality in magnocellular processing has been implicated in a wide range of neurodevelopmental disorders such as autism, dyslexia and schizophrenia. Thus, in dyslexia, fMRI activation of motion-sensitive cortical regions (V5/MT+—magnocellular dominated) have been related to phonological processing ability, a consistent deficit in dyslexia (Ben-Shachar et al. 2007; Demb et al. 1998; Eden et al. 1996). Raised contrast threshold for phantom contours are also found, whether abrupt or ramped, comparing dyslexic with control children (Laycock et al. 2012). Also, visuospatial functions such as change detection and the ability to rapidly use cues to target location have been found to be significantly impaired in children with developmental dyslexia (Rutkowski et al. 2003).

Physiological identification of abnormalities in magnocellular function has been derived using nonlinear analysis of the cortical visual evoked potential (VEP). Klistorner et al. (1997) demonstrated that the second-order Wiener kernel responses to focal binary pseudorandom stimulation demonstrated two components distinguishable on the basis of contrast response, contrast saturation and latency. More recently (Jackson et al. 2013; Sutherland and Crewther 2010), using young adult neurotypical groups with varying levels of autistic tendency (measured with the autistic spectrum quotient AQ, Baron-Cohen et al. 2001) have shown strong segregation of major VEP peaks in terms of contrast gain and semi-saturation parameters with the putative magnocellular generated nonlinearities (high-contrast gain, with contrast saturation) also displaying a latency advantage of approximately 25 ms over the parvocellular (lower contrast gain, with little evidence of saturation).

With the focus in the developmental dyscalculia literature on the intraparietal sulcus, it is remarkable that there are no published studies investigating the patency of the magnocellular pathway in mathematical learning impairment.

Here, we aimed to directly measure contrast-dependent magno- and parvocellular contributions to the occipitally recorded VEP in mathematically impaired and number-normal controls and to relate this to psychophysical performance on change detection, known to invoke parietal cortical activation (Beck et al. 2001). Given the marked attentional abnormalities observed in dyslexia through measures of change detection (Rutkowski et al. 2003), we also aimed to examine change detection performance in participants with mathematical learning deficits, and in particular to determine whether stimulus contrast interacted with change detection performance on the basis that a hypothesized weaker magnocellular/dorsal cortical system would be more impacted by parvocellular inputs at high contrast.

The investigation of contrast dependence stems from recent observations of magnocellular dysfunction at high contrast in high autistic tendency (Jackson et al. 2013; Sutherland and Crewther 2010) and in contrast-dependent motion perception in autism (Foss-Feig et al. 2013) and schizophrenia (Tadin et al. 2006), where anomalies emerge at high contrast. In schizophrenia, this has been attributed to a contrast-dependent disruption of center-surround suppression and appears to be related to reduced GABAergic signaling (Yoon et al. 2010).

Materials and methods

Participants

The sample comprised of 19 females presenting with normal vision, recruited from university and wider communities. Written informed consent was obtained from each under an approval from the Swinburne University Human Research Ethics Committee. Experimentation was performed adhering to tenets of the Declaration of Helsinki. Fourteen of these participants formed the control group with a mean age of 24 years (SD = 2.70), 12 of whom were right hand dominant. The five mathematically impaired participants were females (19–33 years, four—right hand dominant) with well-documented histories of math learning difficulties as children. All participants undertook the Ravens Advanced Progressive Matrices test (Raven 2003) to measure nonverbal intelligence. Prior to analysis, however, an extreme value was removed from this data within the math learning impaired group. There were no significant group differences in mentation [Kruskal–Wallace test, $\chi^2(1) = .231, p = .631$].

Our approach was to test all individuals on three reference tasks (1) lexical decision, (2) magnitude comparison and (3) enumeration, in order to verify the relative degree of mathematical incapacity in mathematically impaired and control groups, and also to verify that any mathematical disability was not shared with reading disability.

All psychophysical tasks were designed using VPixx version 2.14 (www.vpixx.com). Psychophysical tasks were undertaken on a LCD display monitor with a 60-Hz refresh rate (mean gray luminance 75 cd/m^2). Participants sat approximately 40 cm from the monitor for all tasks, and in order to partial out practice effects, tasks were assigned in a randomized order across participants. Normal room lighting was employed.

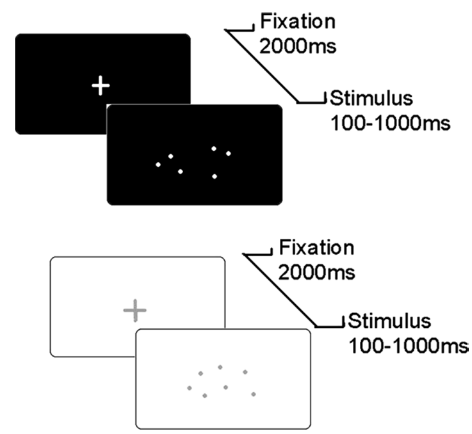

Fig. 1 A stimulus comprising 4, 5, 6 or 7 randomly distributed dots on a 30 × 30 array appeared in inspection-time paradigm for a variable duration. Participants indicated how many *dots* they saw by means of a four alternate forced choice (4AFC) rapid keyboard response. Two Michelson contrast conditions (24 and 96 %) were used in separate *blocks* of trials

Reference task: lexical decision

A lexical decision task was implemented as a control measure, in order to dissociate word recognition and reading skills from numeracy skills in the mathematics learning disabled. The task comprised of two blocks—orthographically irregular words/no-words (e.g., "quail"/"parbe"), and phonologically regular words/nonwords (e.g., "baker"/"tolst"). All stimuli were made up of five lower case letters presented in 72 point Apple Li Gothic Medium font (LCD display at 40 cm). Each trial commenced with a centrally presented fixation cross that remained on the screen for 500 ms. Participants indicated via key press whether the stimulus was a word or nonword, at which time the stimuli disappeared. The total number of trials for the task was 48, comprising two blocks each of 12 words and 12 nonwords.

Reference task: magnitude comparison

The stimuli comprised two-digit numbers (in 72 point Apple Li Gothic Medium font), presented centrally, and selected from a range from 11 to 99 (excluding the midrange 54, 55, 56). Participants were required to indicate via a left/right button response pad the magnitude or direction of numeric stimuli with respect to the midpoint of the mental number line. For the congruent block, participants indicated numbers <55 with the lefthand/left response button and numbers >55 were indicated with the right hand/right response button (i.e., congruent with the direction of the number line). For the incongruent block, participants indicated numbers <55 with the right hand/right response button and numbers >55 with the left hand/left response button, respectively, (Dehaene et al. 1993). The frequency of stimuli was arranged in such a way that numbers with double digits (e.g., 77) were likely to appear 20 % of the time. The other numbers preceded or followed the double-digit numbers (e.g., 76, 78). A total of 22 two-digit stimuli were used.

Reference task: enumeration

Enumeration (subitization) trials commenced with a centrally presented fixation cross that appeared for 2000 ms, after which a stimulus of 4, 5, 6 or 7 randomly distributed circular dots (30 × 30 pixels) on a 30°(W) × 20°(H) array (see Fig. 1) appeared for a duration (<1000 ms) set by a PEST routine. Participants indicated how many dots they saw (4, 5, 6 or 7) by means of a four alternate forced choice (4AFC) keyboard response. Two Michelson contrast conditions (24 and 96 %) were used.

Visual evoked potentials

A black and white multifocal visual stimulus was generated on a CRT screen using the VERIS Science system (EDI, San Mateo, USA, v3..1). A dartboard stimulus with 33 sections was used, each of which was flashed on and off in a decorrelated pseudorandom m-sequence at a 75-Hz frame rate. The responses from the central circular section (subtending 3.55° at 40 cm distance) were used for all subsequent analyses. Individual kernels were calculated using a cross-correlation of the digitized output signal with the input sequences (Sutter 2000). The stimuli were presented at two Michelson temporal contrast levels—low (24 %) and high (96 %), around a common mean luminance of 65 cd/m^2. Lighting in the room was dim during the 4-min recordings.

The multifocal visual evoked potentials were recorded using gold cup electrodes positioned at O_z referenced to F_z (impedances <5 KΩ). A ground electrode was placed on the left ear. The amplifier gain was set at 100,000× with band-pass filtering 3–100 Hz. A data sampling rate of 1 kHz was employed.

Change detection for digits

A 2AFC PEST procedure was implemented as part of the gap paradigm change detection task (Rensink 2000, 2002; Rutkowski et al. 2003), in order to determine the threshold duration of the initial presentation for correct detection of change for each group (math learning impaired and controls). Stimuli were four-digit strings presented either at 24 or 96 % contrast (in two blocks), surrounded by bordering figure eights located to the left and right of the screen (see Fig. 2). Following the appearance of the border stimuli, the first four-digit number was presented for a variable period (<1000 ms), followed by a random dynamic noise mask for 250 ms, and then followed by the second four-digit stimulus (either changed or unchanged with 50 % probability). Depending on correct/incorrect response, the initial presentation time was varied.

Statistics

Due to the unequal sample size and unequal variances of the two populations, all psychophysical analyses were carried out using nonparametric statistical tests. Between-subjects comparisons were implemented by means of a multiresponse permutation procedure (MRPP) generated through the PASW statistical package as a syntax file developed by Cai (2006).

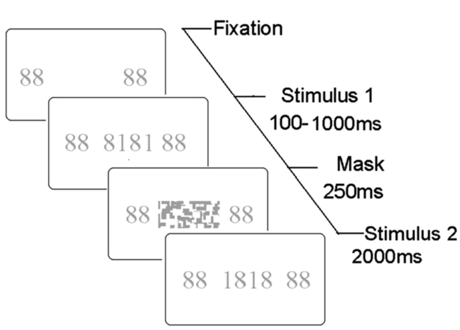

Fig. 2 Four-digit strings presented surrounded by bordering figure eights to provide a metacontrast mask for the peripheral digits. Following the appearance of the border stimuli, the first four-digit number was presented for a variable period adjusted via an adaptive staircase, followed by a random dynamic noise mask for 250 ms, and then followed by the second four-digit stimulus (either *changed* or *unchanged*). Two contrast levels (Michelson contrast 24 and 96 %) were used

Results

Reference task: lexical decision

The mean reaction times for orthographically irregular words/nonwords and phonologically regular words/nonwords are shown in Table 1 below for the control and mathematically impaired groups. Between-subjects comparisons of performance on the lexical decision control task (Kruskal–Wallis test) revealed no significant differences.

Reference task: magnitude comparison

A Wilcoxon signed-ranks test was run as preliminary analysis to investigate within-subject effects of magnitude comparison. During the congruent block, control participants responded significantly faster to numbers that were >55 compared to numbers that were <55 ($Z = -2.794$, $p = <.005$—see Table 2). During the incongruent block, there were no significant reaction time (RT) differences for numbers greater or <55 for the control group ($Z = -.094$, $p = .925$).

For the mathematically impaired group, when mean response times to numbers <55 during congruent and incongruent blocks were examined, no significant differences were found ($Z = -.282$, $p = .778$). However, when mean response times to numbers >55 during congruent and incongruent blocks were examined, right-hand

Table 1 Mean response times for lexical decision task

Stimulus	Control Mean ± SD (ms)	Math impaired Mean ± SD (ms)
Orthog. Irreg. Word	800 ± 119	920 ± 232
Orthog. Irreg. Nonword	925 ± 240	900 ± 115
Phonol. Irreg. Word	685 ± 81	704 ± 90
Phonol. Irreg. Nonword	745 ± 120	816 ± 85

Table 2 Magnitude comparison: mean (±SD) reaction times (ms)

Task	Control	Math impair
Congruent <55	547 ± 7	570 ± 50
Incongruent <55	550 ± 10	772 ± 180
Congruent >55	507 ± 7	567 ± 69
Incongruent >55	551 ± 9	714 ± 144

response times to numbers >55 were significantly faster than response times to numbers >55 with the left hand ($Z = -2.480$, $p < .01$).

Group analysis of magnitude comparison performance on the congruent block showed that there were no significant response time differences for numbers <55 [$t(17) = -.096$, $p = .402$] or >55 [$t(17) = -.525$, $p = .220$] between the math learning impaired and control groups. For the incongruent block, however, there were significantly different mean response times to numbers <55 with the right hand [$t(17) = -3.360$, $p < .01$] and numbers >55 with the left hand [$t(17) = -3.949$, $p = .006$] between the mathematically impaired and control groups.

Reference task: enumeration

As might be anticipated, the mathematically impaired group proved to be significantly slower at subitizing (see Table 3) than the controls.

This was true both for low-contrast [permutation test: 24 % contrast, $t(17) = -3.050$, $p = <.01$] and for high-contrast stimuli [96 % contrast, $t(17) = -3.237$, $p = <.01$]. The mean reaction time at threshold for each of the number sets (4, 5, 6, 7) showed no effect of set size.

Nonlinear VEP

At low contrast (24 %), the grand mean average visual evoked potentials (VEPs) from recordings showed little difference between the mathematically impaired and control groups, either for the first-order response (Fig. 3a), the first slice of the second-order response (K2.1—see Fig. 3b) or the second slice of the second-order response (K2.2—see Fig. 3c). A permutation test on the amplitudes and latencies of the major peaks at 24 % contrast did not reveal any significant differences.

However, at high contrast (96 %), two marked divergences in the grand mean average waveforms were observed. The 95 % confidence interval fringes around the mean first-order responses (Fig. 3d) show clear separation in the range 55–65 ms. In the first slice of the second-order kernel (Fig. 3e), the mean waveform for the math impaired group showed a delay in the first positivity, which, while not reaching the 95 % confidence, strongly resembles the waveforms recorded in high autistic tendency (Sutherland and Crewther 2010) for this kernel slice. However, the lack of contrast saturation in the first-order N60 potential is in marked contrast to those recordings.

In terms of peak amplitudes and latencies, for the first-order response (Fig. 3d), the amplitude of the first-order (K1) early negativity (N60: latency ~60 ms) showed greater amplitude for the mathematically impaired compared with the control group [$t(17) = -2.610$, $p = .02$]. Significant differences were also seen in the first slice of the second-order response (K2.1) at high contrast, with the N60 latency significantly advanced [$t(17) = -3.235$, $p = .01$] and the P90 latency delayed (marginally) for the mathematically impaired compared with the control group [$t(17) = -2.115$, $p = .04$].

Table 3 Inspection times for subitizing of small number sets (4–7 elements) shown at low (24 %) and high (96 %) contrast (with standard errors)

Group	Contrast	Mean (ms)	SD
Mathematically impaired	High	841	123
	Low	839	161
Controls	High	413	97
	Low	413	91

Psychophysics: change detection

An interaction between experimental group and stimulus contrast for the presentation time to just detect change was observed in the mean thresholds at the two contrasts. While increasing contrast lowered presentation time for change detection for the control group, it caused the presentation time for change detection to increase for the mathematically impaired group (see Fig. 4). A Wilcoxon signed-ranks test showed that threshold estimates were significantly lower at 96 % contrast compared to threshold estimates at 24 % contrast for the control group ($Z = -2.23$, $p = <.02$), while the mean increase shown by the mathematically impaired group from 24 to 96 % was not significant. Comparison of performance between groups at 96 % contrast also showed a significant difference [MRPP permutation test: $t(17) = -9.321$, $p = <.0001$].

As nonparametric statistics are not particularly suited to investigate interaction statistics (relying on paired subtraction), a repeated-measures ANOVA was carried out to indicate the prediction of a parametric statistical approach. Despite the small population size, the Group*Contrast interaction showed a strong trend [$F(1,15) = 3.82$, $p = .071$].

Discussion

This study demonstrates abnormal magnocellularly driven visual function in a population with self-reported mathematical impairment, compared with the neurotypical population. More importantly, this physiological abnormality has an interesting feature—the difference between mathematically impaired and control groups only appears at high stimulus contrast. Inspecting this claim in more detail, the first difference observed—significantly greater amplitude of the

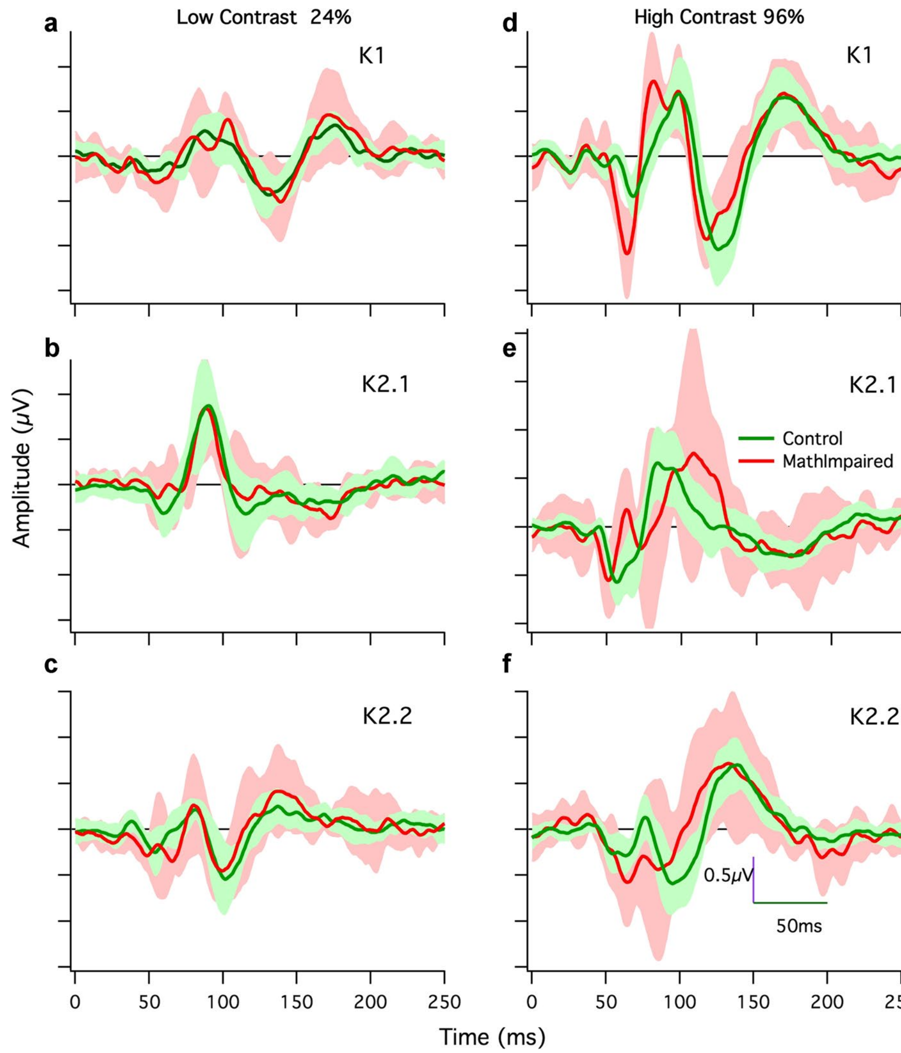

Fig. 3 Nonlinear VEP recordings from foveal visual field. The six figure elements show first order (K1) and the first two slices of the second-order kernel response (K2.1, K2.2) for recordings at low (24 %) contrast (**a**, **b**, **c**) and high (96 %) contrast (**d**, **e**, **f**). Mean waves are shown for mathematically impaired (*red*) and control (*green*) participants with the fringe around each mean representing 95 % Confidence Intervals. *Scale bars* are indicated at the bottom right for amplitude and time. Significant differences occur at high contrast in the K1 kernel response between 55 and 65 ms latency (color figure online)

first-order (K1) high-contrast response can be argued to be magnocellular in origin as this is the earliest cortical evoked response (latency: 45 ms; N1 implicit time around 65 ms). This latency measure is not much greater than the first neural spike times in V1 in primate (around 35 ms: Bullier 2001; Lamme and Roelfsema 2000), allowing for differences in brain size. Given the evidence in the literature of a "magnocellular advantage" (Laycock et al. 2007) of approximately 25–30 ms latency compared with parvocellular cortical activation in human (Baseler and Sutter 1997; Klistorner et al. 1997; Sutherland and Crewther 2010), the first 25–30 ms of cortical activity should be magnocellular in origin—this certainly covers the duration of the N1 peak. The increased K1 early peak amplitudes and shorter latencies also indicate that the mathematically impaired group shows abnormal contrast gain control compared with normal picture of magnocellular response saturation recorded both in primate (Kaplan et al. 1990) and human (Jackson et al. 2013; Klistorner et al. 1997).

In addition, a delay was observed in the completion of the second-order, first-slice (K2.1) response, previously identified as a nonlinearity of magnocellular origin (Klistorner et al. 1997). Despite the marginal significance, the delay in completion of the P1 peak for the mathematically impaired group is remarkably similar to that reported in a population of adults with high autistic tendency (Sutherland and Crewther 2010) who were assessed for autistic tendency on the Autism Spectrum Coefficient test (AQ) (Baron-Cohen et al. 2001). The High AQ group in that study showed a significantly reduced first-order response at low contrast but not at high contrast (compared with a low autistic tendency group). However, for the mathematically impaired group in the current study, low-contrast responses were in normal range, while at high contrast there was a significant increase in first-order amplitudes compared with controls.

Computational models of thalamo-cortical synaptic depression (Carandini et al. 2002) generate saturation of contrast gain response through divisive gain attenuation mechanisms. The reduction in magnocellular response saturation observed here for the mathematically impaired

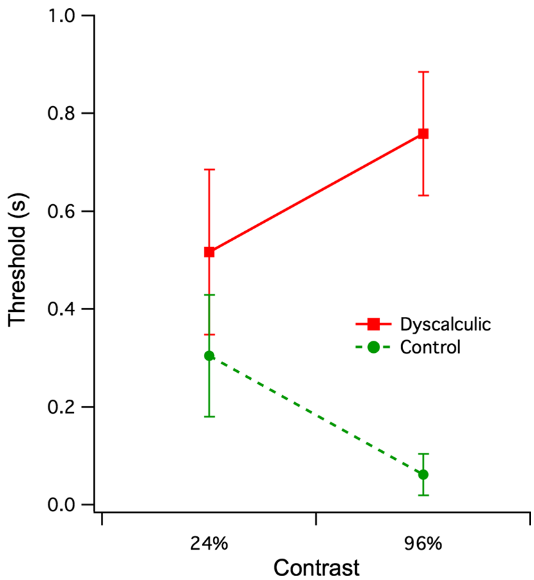

Fig. 4 Mean change detection thresholds (±1 SE) for mathematically impaired and control groups established at low (24 %) and high (96 %) contrast. These inspection-time thresholds, measured in seconds, represent the minimum initial presentation time of the first stimulus necessary to just detect change correctly. While there was no significant different observed at low contrast, the control group showed a reduction in threshold time for the presentation time of the first stimulus at high contrast, significantly less than for the mathematically impaired group who showed a mean increase in threshold presentation time

participants in this study would be explained within such models by functionally aberrant output modulation of inhibitory postsynaptic potentials and currents (Carandini et al. 2002)—a failure in inhibitory signal gating during periods of intense neural activity in the thalamo-cortical relay that occurs with high-contrast stimulation.

The contrast-dependent effects for change detection in dyscalculia are concordant with a psychophysical study where participants with negative symptoms of schizophrenia showed significantly elevated inspection times for a motion discrimination task at high but not low-contrast levels (Tadin et al. 2006). Such visual surround suppression abnormalities in schizophrenia have been associated with abnormal GABAergic inhibition (Yoon et al. 2010) and with altered gamma-band cortical oscillations (Uhlhaas and Singer 2010). These findings were proposed to be indicative of abnormality in contrast-dependent modulations of receptive field properties in the V5/MT+ cortical motion-processing areas (Tadin et al. 2006) dominated by magnocellular input and a major relay for the dorsal cortical stream. Our physiological recordings in this mathematically impaired population indicate an early source of this contrast-related anomaly—either subcortical, or in Area V1.

Receptive field response modulation such as surround inhibition has been suggested as a functional component of attentional filtering or sensory gating of redundant visual inputs (Anton-Erxleben et al. 2009; Schwartz et al. 2005), feature binding, and figure-ground segmentation (Tadin et al. 2006, 2003). Moreover, receptive field response modulations such as surround inhibition are influenced by context-dependent cortical feedback from higher-order areas in primates into V1 (Kapadia et al. 2000). Considered together, the prolonged initial stimulus duration to just detect change in the mathematically impaired participants, when stimuli were of high contrast, may be indicative of abnormal surround inhibition, affecting attentional gating and slowing cortical feedback mechanisms into V1. Feature-binding errors in dyscalculia may be explanatory of perceptual errors observed in dyscalculia, such as digit inversions/reversals and poor numerosity estimation judgements (Piazza et al. 2010). Moreover, aberrant receptive field center-surround interactions may affect the local and global grouping mechanisms at play when estimating number set size—perhaps creating greater noise levels than in neurotypical observers (Dakin and Bex 2001).

Conclusion

An association was found in a population measurably poorer in numerosity and magnitude judgement performance, with abnormalities in early cortical magnocellular functioning. Physiological delay in recovery of the cortical magnocellular system after firing, lack of magnocellular response saturation, as well as poor change detection of digits were apparent in the math learning impaired group, but only at high stimulus contrast. Representational neglect was evident from markedly delayed number decision response times in those with math learning difficulties, though their lexical decision performance was not significantly different from controls. We suggest that the delay in completion of magnocellular processing in combination with impaired contrast saturation mechanisms may lead to impaired transient attention at high contrast resulting in a propensity to errors in ordering numbers (as evidenced by poorer change detection at high contrast) and hence in numerical processing. The appearance of these effects at high rather than low stimulus contrast and the absence of contrast saturation in magnocellularly driven first-order VEP components suggest that magnocellular surround suppression mechanisms may be faulty, possibly indicating abnormal GABergic inhibition.

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