Typical numerosity adaptation despite selectively impaired number acuity in dyscalculia

Giovanni Anobile[a],[*], Guido Marco Cicchini[b], Filippo Gasperini[a], David C. Burr[b],[c]

[a] Department of Developmental Neuroscience, Stella Maris Scientific Institute, Calambrone Pisa, Italy
[b] Institute of Neuroscience, National Research Council, Pisa, Italy
[c] Department of Neuroscience, Psychology, Pharmacology and Child Health, University of Florence, Florence, Italy

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ABSTRACT

It has been suggested that a core deficit of the "number sense" may underlie dyscalculia. We test this idea by measuring perceptual adaptation and discrimination thresholds for numerosity and object size in a group of dyscalculic and typical preadolescents (N = 71, mean age 12). We confirmed that numerosity discrimination thresholds are higher in developmental dyscalculia, while size thresholds are not affected. However, dyscalculics adapted to numerosity in a similar way to typicals. This suggests that although numerosity thresholds are selectively higher in dyscalculia, the mechanisms for perceiving numerosity are otherwise similar, suggesting that have a similar, but perhaps noisier, number sense.

1. Introduction

Dyscalculia is a severe neurodevelopmental disorder, strongly compromising the acquisition of school-level mathematical abilities. Its prevalence (3–7%) is similar to dyslexia, but despite its social and economic costs far less research has been done on this disorder (for review see Butterworth et al., 2011). A renewed and growing interest arose from evidence implicating impairment of the "number sense" thought by many to be the basic mechanism mediating the ability to estimate the numerosity of a group of visual items (Burr and Ross, 2008; Butterworth, 1999; Dehaene, 2011). Dyscalculic children often suffer severe difficulties with numerosity tasks, performing less precisely and showing higher sensory thresholds compared with non-dyscalculic peers (Mazzocco et al., 2011; Piazza et al., 2010).

The neural substrate of the number sense probably resides, at least in part, in the Intra Parietal Sulcus (IPS). IPS is activated by both mental calculation (Dastjerdi et al., 2013), and by numerosity tasks (Piazza et al., 2004), and shows both anatomical (Isaacs et al., 2001; Rotzer et al., 2008; Rykhlevskaia et al., 2009) and functional (Kucian et al., 2006; Mussolin et al., 2010; Price et al., 2007) abnormalities in dyscalculia. The width of neural tuning of IPS to numerosity (measured by fMRI habituation paradigm), which may be considered to be an index of neural sensitivity, correlates with numerosity discrimination thresholds measured behaviourally outside the scanner (Kersey and Cantlon, 2017). These and other findings suggest that dyscalculia may be characterized by a deficit affecting this basic function and its neural substrate.

While the link between the number sense and math is fascinating, it is still not clear whether numerosity discrimination plays a causal role in dyscalculia. And it is unclear whether the sensory discrimination deficit of dyscalculics is specific for numerical stimuli, or reflects a more general feature of visual coding (Braddick et al., 2016; Braddick, Atkinson, and Wattam-Bell, 2003). Besides discrimination thresholds (possibly reflecting the level of sensory noise), plasticity and adaptability may also be important (Iuculano et al., 2015). A well-known behavioural signature of experience-based plasticity is 'perceptual adaptation'. All sensory and perceptual systems are subject to perceptual *adaptation* (Thompson and Burr, 2009): prolonged exposure to a specific stimulus biases subsequent perception away from the adapter stimulus. These aftereffects are thought to be the perceptual result of adaptation-induced changes in activity of the system encoding that perceptual feature. It is thought adaptation reduces the activity of the channel preferring the adaptation stimulus so the post-adaptation stimulation will then activate an unbalanced system having weaker activity for mechanisms tuned to the adaptation stimulus and relatively stronger activity for those far from the adapter. In this way the post-adaptation stimulus will elicit stronger responses in those channels that usually respond to different magnitudes and it is misperceived (Blakemore and Campbell, 1969; Thompson and Burr, 2009).

Numerosity and size are both susceptible to adaptation: after

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participants inspect for few seconds a highly numerous ensemble (or a large object), the subsequent stimulus is usually perceived as containing less elements (or small) than they physical are (Burr et al., 2017; Burr and Ross, 2008; Pooresmaeili et al., 2013). fMRI studies have shown that while neural numerosity adaptation affects the balance of neural activation of IPS (Castaldi et al., 2016), size adaptation changes the activity pattern in areas as early as V1 (Pooresmaeili et al., 2013). Although not fully understood, adaptation reflects the malleability and the structural organization of the systems, and almost certainly plays an important functional role in keeping systems dynamically calibrated (Barlow, 1990a, 1990b; Webster, 2011). It has been shown to be dysfunctional in some clinical populations, including autism (Pellicano et al., 2007; Turi et al., 2015). In this study we asked whether dyscalculia may be associated with abnormal perceptual adaptation to numerosity, and also to other non-numerical dimensions of visual stimuli, such as size.

2. Methods

Stimuli were generated with the Psychophysics Toolbox for Matlab and presented at a viewing distance of 57 cm on a 23″ LCD Acer monitor (resolution = 1920 × 1080 pixels, refresh rate = 60 Hz). Participants were tested individually in a quiet room either at school or at the Stella Maris Research Hospital (Pisa, Italy). The study was approved by the regional pediatrics ethics committee at the *Azienda Ospedaliero-Universitaria Meyer* (protocol code: GR-2013-02358262). Parents signed the appropriate informed consent.

2.1. Participants

We tested 35 Italian children diagnosed with developmental dyscalculia (DD) aged 8–16 y (mean 11.9 y, SD 1.8) and 36 typically developing (TD) children (mean 12.3 y, SD 0.9) matched for age ($t_{(69)} = 1.39$, p = 0.17). DD met Diagnostic and Statistical Manual of Mental Disorders, Fifth Edition (DSM-V) criteria for dyscalculia (severe difficulties in math reasoning and calculation, severe school difficulties below those expected by the chronological age, early onset and math difficulties that cannot be explained by intellectual disabilities, sensory and/or neurological deficits as well as by psychosocial adversities, lack of language knowledge or inadequate education). Two TD had a current diagnosis of dyslexia. All the others had no medical or psychiatric diagnosis, as reported by parents and teachers.

DD performed a full IQ scale (WISC-IV) with total IQ average score 91.3 (SD 9.8, min 75, max 113). In three cases the total IQ was equal to 75 but at least two out of the four aggregate indexes provided by the battery (ICV, IRP, IML, IVE) were higher than 80. TD IQ was assessed by Progressive Raven Matrices (non-verbal IQ) and all scored above 10th percentile (mean 76, SD 19.4, min 14, max 98). In order to statistically compare the two groups for IQ, we first transformed the performance obtained by the typical group in the Raven test and those obtained by the dyscalculic group in the non-verbal reasoning index of the WISC-IV into z-scores (by normative data provided by the tests manuals). An independent group *t*-test (two tailed) revealed that TD had higher scores compared to DD ($t_{(67)} = 5.46$, p < 0.001, mean difference 1 SD). For this reason, non-verbal IQ was used as covariate where group differences were detected (see results).

Math abilities were assessed by a comprehensive Italian battery for the diagnosis of dyscalculia (BDE2). The dyscalculia group completed the full version (10 sub-tests), while the matching group performed a shorter version (6 sub tests). Average math z-scores were: mean −2.13, SD 0.79, and mean 0.84, SD 0.52 for the DD and TD groups. Reading decoding abilities were also assessed. The DD group performed a full battery, which includes word-list, non-word-list and text reading aloud. The TD group performed the word-list sub test. Average z-scores collapsing both speed and accuracy for the shared word-list sub-test were: mean −2.12, SD 3, mean −0.13, SD 1.29 for the DD and TD groups

respectively ($t_{(67)} = 3.57$, p = 0.001). As often reported in the literature, and well known in clinical practice, most of the dyscalculic patients also met criteria for developmental dyslexia (18 out of 35, 51%). However, reading abilities were found to be uncorrelated with all the perceptual measures (see results), and any other variable (numerosity and size thresholds, math skills, age, non-verbal IQ, numerosity and size adaptation magnitudes, min p-value = 0.26). Two DD participants also met criteria for ADHD. Two DD did not perform the word reading test. Two DD did not have available data for the WISC scale because, at the moment of this experiment, they already received diagnoses of dyscalculia from other clinics and previous raw data were not consultable. However, one of those performed four subtests of the WISC-IV (SO, VC, DC, RM) and the other two performed the Raven matrices test. Finally, two DD and two TD did not perform the size discrimination task. DD were recruited and tested at the clinical centre IRCCS Stella Maris (Calambrone, Pisa), while TD were tested in a local school. We employed different IQ tests as well as a reduced math-battery in TD in order to reduce testing time and minimise interference with school activities. Missing values were left empty and data excluded with pairwise deletion method.

2.2. Numerosity-adaptation task

Stimuli were patches of dots presented on either side of a central fixation point (Fig. 1 B). Dots were 0.25° diameter, half-white and half-black (to balance luminance), 80% contrast on a grey background of 40 cd/m². They were constrained to fall within a virtual circle of 10° diameter, centred at 12° eccentricity. Non-numerical parameters (except luminance) were not controlled. The numerosity of the probe stimulus (on the left) was 24, while the test (on the right) adaptively changed following a QUEST algorithm. During the adaptation phase the adapter comprised a patch of dots with a numerosity that could be 0 (control, no dots), 12 (adapt to half the numerosity of the probe) or 48 (adapt to twice the probe). Each session started with 3000 ms of the adapter presented on the left of central fixation point, then 500 ms after the adapter disappeared the test and probe were simultaneously presented for 250 ms. Participants indicated by appropriate key-press the side of the screen with more dots. All participants performed 1 session of 45 trials for each adaptation condition (135 trials in total). The proportion of trials where the test appeared more numerous than the probe was plotted against the test numerosity (on log axis), and fitted with cumulative Gaussian error functions (Fig. 2). The 50% point of the error functions estimates the point of subjective equality (PSE), and the difference in numerosity between the 50% and 75% points gives the just notable difference (JND), which was used to estimate Weber Fractions (JND/PSE) (for similar procedures see Anobile et al., 2018; Anobile et al., 2014). To sustain attention, during the adaptation phase a colour change-detection task was placed. Subjects were asked to quickly report any change in colour (black/white) of the fixation point by pressing the spacebar (1:3 of trials).

2.3. Size-adaptation task

All procedures were identical to the numerosity task, but here stimuli were luminance-modulated sinusoidal gratings windowed within an annulus. Spatial frequency was 2 c/deg, and Michelson contrast 90% (Fig. 1 B). After stimulus presentation, a 100 ms full-screen random noise mask was displayed to annul possible afterimages. The diameter of the probe stimulus was 5°. Adapter stimuli were annuli of diameter either 2.5° (half the probe size) or 10° (twice the probe).

2.4. Data analysis

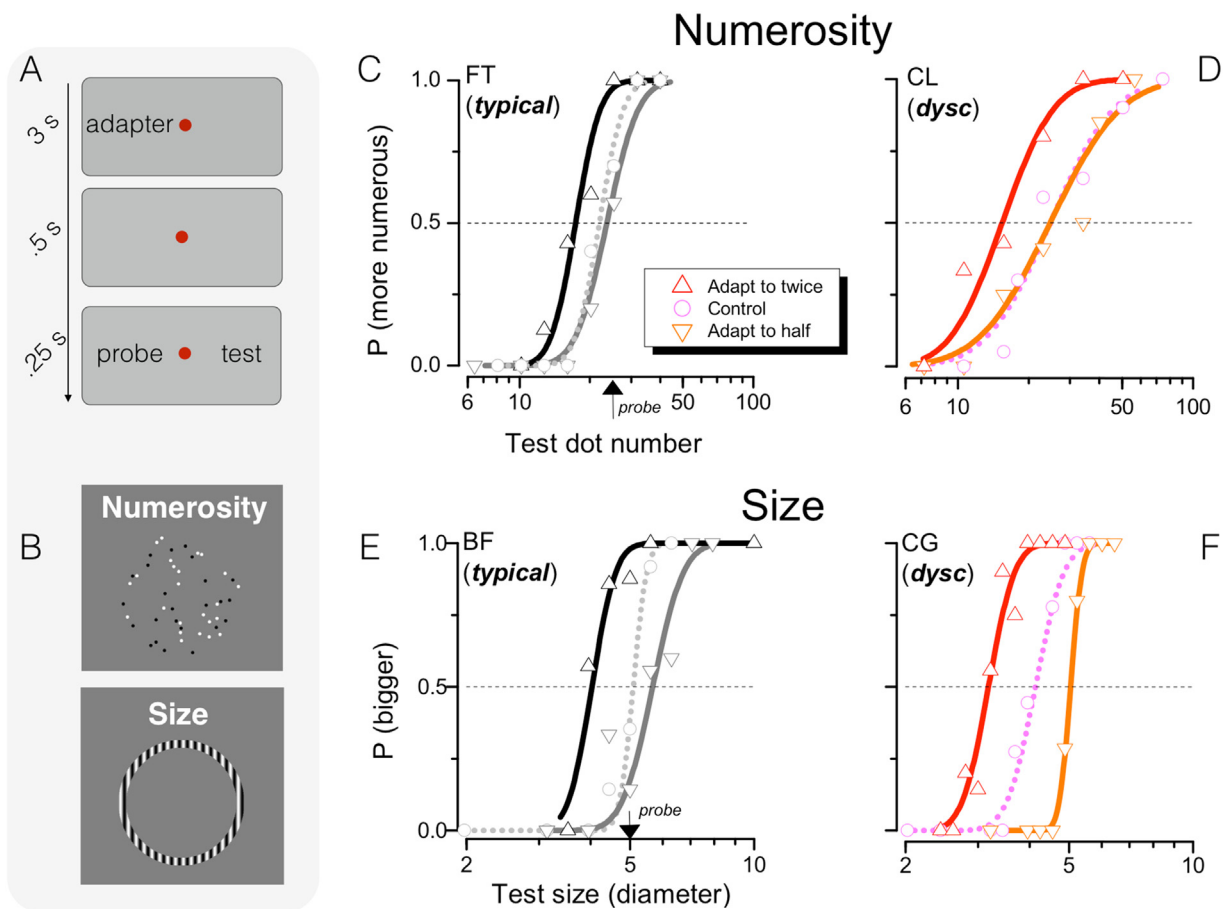For both psychophysical tasks we defined adaptation magnitude as:

Fig. 1. (A) Schematic representation of trial sequences during the adaption conditions. The adapter stimulus was displayed on the left of the screen for 3 s. After this phase a blank pause of 0.5 s precede the test phase in which two stimuli were simultaneously presented for 0.25 s. Participants, in separate sessions, indicate which seemed "more numerous or larger". To sustain attention, during the adaptation phase a colour change-detection task was used: subjects were asked to quickly report any change in colour of the fixation point by pressing the spacebar (1:3 of trials). (B) Sample stimuli used for the numerosity size and tasks. (C–F) Sample psychometric functions for representative participants measured without (circles, dotted lines) and with (triangles, continuous lines) adaptation. Upward and downward triangles report performance after adaptation to high (twice the probe) and low (half the probe) stimuli's magnitude, respectively. Curves plot the proportion of trials where the probe (indicated by the arrow) seemed more numerous/larger than the test, as a function of test magnitude.

$$Adaptation = \frac{PSE_{lowA} - PSE_{highA}}{PSE_{lowA} + PSE_{highA}} \times 100$$

where PSE_{lowA} and PSE_{highA} refer, respectively, to the number of dots or annulus diameter at the PSE after adaptation to lower and higher intensity stimuli (half or twice the numerosity or diameter).

Discrimination thresholds did not follow a normal distribution (Shapiro-Wilk $p < 0.001$) and thus were log transformed (Shapiro-Wilk test $p > 0.05$ after transformation).

Data were analysed by both frequentist and Bayesian statistics (ANOVA, ANCOVA, t-test). For the Bayesian tests we reported Log (BF_{10}) values. Conventionally, log Bayes factors are considered substantial evidence in favor of the null hypothesis when smaller than -0.5, and in favor of the alternative hypothesis when larger than $+0.5$. Factors outside ± 1 are considered strong evidence for one or other hypothesis. Effects sizes were reported ad Cohen-d and η^2. Data were analysed by JASP software (0.8.5).

3. Results

We measured psychophysically perceptual adaptation and discrimination thresholds for numerosity and object size in a group of dyscalculic and typical developing preadolescents. In separate sessions participants judged either which ensemble contained more dots (Numerosity task) or which of two annuli was bigger (Size task) (Fig. 1

A & B). Both tasks were run in a "control" condition, where the stimuli to be judged were the only ones presented, as well as in two "adaptation" conditions, where the probe stimulus was preceded by an "adapter" containing either half or twice the probe magnitude. Fig. 1 (C-F) shows sample psychometric functions for representative typical (C & E) and dyscalculic observers (D & F). These curves yield estimates of both sensory precision (reflected by the steepness of the curve) as well as the strength of adaptation (reflected by the departure between post-adaptation curves).

The representative plots of Fig. 1 show how the dyscalculics and typical observers have similar precision in the size judgment (E-F), while they differ greatly in the numerosity judgements (C-D). Group means show that on average the Weber Fraction of dyscalculics in the numerosity judgment is 60% which is nearly twice as much as the typicals (30%) (Fig. 2A). In contrast, Weber Fractions for the size judgment are close to 9% for both groups. To quantify the differences between groups and tasks we ran a repeated measures ANOVA with tasks (numerosity or size judgment) as repeated measures factor and group as between participants factor. The analysis revealed a statistically significant interaction between groups and task confirming that the two groups behave differently depending on the task ($F_{(1,62)} = 9.53$, $p = 0.003$, $\eta^2 = 0.02$, $Log(BF_{10}) = 37$). Post-hoc t-test (independent samples, two-tail) reveals that numerosity but not size discrimination thresholds differ between groups ($t_{(67)} = 5.03$, $p < 0.001$, $d = 1.21$, $Log(BF_{10}) = 8.29$; $t_{(64)} = 1.2$, $p = 0.23$, $d = 0.29$, $Log(BF_{10}) = -0.76$;
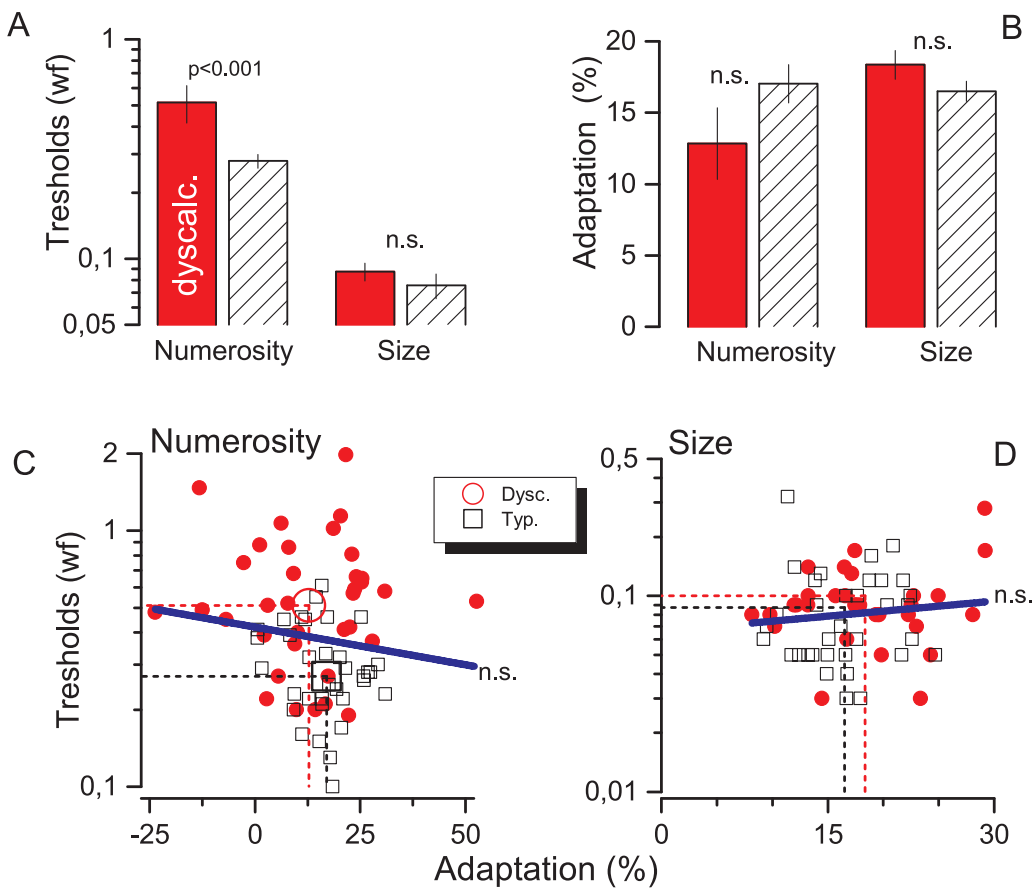
Fig. 2. (A) Geometric mean of discrimination thresholds (dyscalculic, red empty; typically developing, white dashed). (B) Mean perceptual adaptation for the two magnitude tasks (conventions as before). (C & D) Scatterplot of discrimination thresholds in the control condition (Weber fraction) against adaptation magnitude, for all participants (dyscalculic, red circles; typically developing, white squares). Large symbols and drop lines report group averages. Blue lines represent best-fit linear regression lines. n.s.: p > 0.05. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

for numerosity and size respectively). This difference remains significant even after controlling for the effect of non-verbal IQ ($F_{(1,66)} = 10.37$, p = 0.002, $\eta^2 = 0.13$, Log(BF_{10}) = 8.29). To further demonstrate the independence between the two tests we run a grand-correlation (i.e. one group) of Numerosity and Size thresholds. Correlation was very weak (r = 0.25 p = 0.04, Log(BF_{10}) = 0.2) and completely vanished after controlling for non-verbal IQ (r = 0.18, p = 0.15, Log(BF_{10}) = −0.58).

Next we measured adaptation strength in the two populations. Continuous lines in Fig. 1C–F show psychometric curves after adaptation for the numerosity and size tasks. After adaptation to high or low intensity adapters, the probe is matched by a test of lower or higher intensity, indicating that repulsive adaptation is taking place. To quantify adaptation strength, we calculated the distance between the PSEs after the two adaptation conditions (low and high), normalized by their sum (eq. 1). This shows that the two groups have very similar adaptation effects for both numerosity (13% vs 17% for dyscalculics and typicals respectively) and size task (18% vs 16% for dyscalculics and typicals respectively). Repeated measures ANOVA (within factor, task, between factor group) revealed only a marginally significant interaction between groups ($F_{(1,64)} = 3.92$, p = 0.052, $\eta^2 = 0.05$, Log(BF_{10}) = −1.14). This arose from the fact that the dyscalculic group showed a slightly weaker adaptation on the numerosity task while slightly stronger adaptation in the size task. However, post-hoc analyses reveals that both adaptation measures did not differ between groups ($t_{(69)} = 1.5$, p = 0.138, d = 0.35, Log(BF_{10}) = −0.44; $t_{(64)} = 1.55$, p = 0.125, d = 0.38, Log(BF_{10}) = −0.35; for numerosity and size respectively) (Fig. 2B).

Also for this measure we checked for independence between the two tasks. We correlated the strength of adaptation in the numerosity paradigm and in the size paradigm. This analysis again revealed a very weak correlation between the adaptation measures indicating that the adaptabiliy of both size and numerosity mechanism are largely independent, and presumably impinge on different neurobiological substrates (r = 0.2, p = 0.1, Log(BF_{10}) = −0.58)

We next examined the correlation between adaptation strength and sensory thresholds. That numerosity thresholds but not adaptation is impaired in dyscalculics suggests that these two parameters are measuring different sensory attributes. This was confirmed by null correlations both when keeping dyscalculic and typicals as separate samples, and when pooling all participants together (Fig. 2C, blue lines r = −0.13, p = 0.26, Log(BF_{10}) = −1.28). Similar results were obtained for the size task (Fig. 2D), with the strongest correlation being far from significance (Fig. 2 D, blue lines r = 0.11, p = 0.35, Log(BF_{10}) = −1.44).

To better understand if the null correlation in the numerosity task reflects a genuine independence or rather lack of statistical power, we retrieved all the data collected by our laboratory on children measuring numerosity thresholds and numerosity adaptation. This procedure resulted in a cohort of 221 participants aged between 6 and 16 (average = 10.3, SD = 1.8). The sample comprised 171 typical children, 15 with autism spectrum disorder (Turi et al., 2015) and 35 with developmental dyscalculia. Since these data were collected with slightly different paradigms we recomputed thresholds and adaptation strength as z-scores from the averages and SDs of each paradigm. As many previous studies showed that numerosity thresholds refine with age (Halberda et al., 2012), as a sanity-check we first correlated thresholds with chronological age. As expected, we found a highly significant negative correlation (r = −0.28, p < 0.001, Log(BF_{10}) = 6.68). Interestingly, adaptation also decreased with age, although less steeply (r = −0.16, p = 0.01, Log(BF_{10}) = 0.47). More importantly, even with this large and heterogeneous sample size, numerosity thresholds and adaptation strength were clearly uncorrelated (r = 0.05, p = 0.42, Log(BF_{10}) = −2.15) (Fig. 3). Importantly this
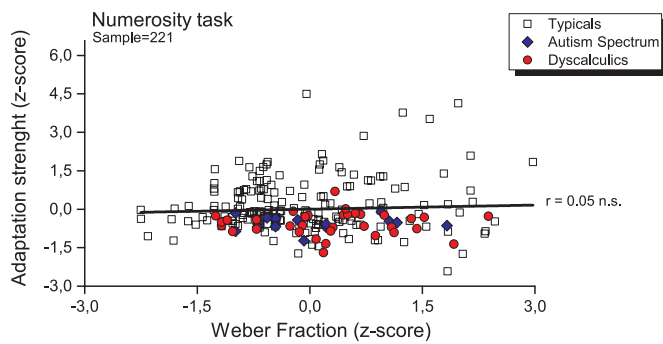
Fig. 3. Individual differences in amount of numerosity sadaptation as a function of individual numerosity discrimination thresholds. Different symbol represent data collected with different cohorts of participants by our lab over the last years (171 typical developing, 35 dyscalculics and 15 with autism disorder; age range 6–16 [M = 10.3, SD = 1.8]). The line represents the best linear regression fit with associated Pearson's r value.

independence was found whether we regressed out the effect of age or not, indicating a genuine independence in the sources of variance.

We then went on to test whether the perceptual measures correlate with math and reading abilities in our sample (Table 1). For simplicity we summarized mathematical and reading skills in an aggregate index calculated as the average of the z-scores obtained in the math and reading sub-tests. Pooling all participants together in a single group, numerosity thresholds correlate negatively with math (r = −0.44, p < 0.001; Fig. 4 A), as expected from the literature (Halberda, Mazzocco, and Feigenson, 2008). Even after controlling for the effect of non-verbal IQ the correlation remains significant (r = −0.29, p = 0.029). Interestingly the link seems to be specific, as numerosity thresholds do not correlate with word reading abilities (r = −0.15, p = 0.2). This suggests that numerosity is not a general predictor of learning. This specificity is also maintained across perceptual tasks as thresholds for size discrimination correlate neither with mathematics nor with reading abilities (both p > 0.05). Running correlations within the two groups separately (Table 1: dyscalculics only and typicals only in), none of the perceptual variables correlates with math or reading skills (all p > 0.05). This suggests that perceptual measures do not explain much of the severity of dyscalculia symptomatology. Regarding adaptation strengths, none of the perceptual variables correlate with math and reading skills, either by considering participants as a single group (Fig. 4 B) or by splitting the samples (all p > 0.05) (see Table 1 for full correlation matrix).

4. Discussion

In this study we measured discrimination thresholds and adaptation strength for numerosity and size perception in a cohort of dyscalculics

and age-matched controls. Our research confirmed much previous literature showing that dyscalculics have reduced sensitivity for numerosity discrimination. Interestingly, the difficulty in numerosity discrimination, that correlated clearly with math abilities, did not correlate with size discrimination thresholds nor with reading abilities, making it unlikely to result from a generalized sensory or attentional deficit (Braddick et al., 2016, 2003). Also, size discrimination thresholds did not correlate with math abilities, reinforcing the idea of a domain-specific impairment affecting the "number sense" in dyscalculia (Butterworth et al., 2011; Piazza et al., 2010).

In contrast to the clear alteration in numerosity discrimination, children with dyscalculia adapted to visual numerosity, in a similar way to non-dyscalculic peers. Aftereffects induced by adaptation are assumed to result from changes in the response functions of the neurons sensitive to the features of the adapted stimulus resulting from their sustained activation (Barlow and Hill, 1963; Clifford and Rhodes, 2005; Clifford et al., 2007; Kohn, 2007; Webster, 2011). Numerosity adaptation unbalances the activity of IPS, a key area for numerosity perception and math reasoning (Castaldi et al., 2016), while size adaptation changes brain activity of earlier visual area (V1) (Pooresmaeili et al., 2013). Adaptation is a form short-term plasticity which, although not entirely understood, is thought to reflect an adaptive phenomenon useful to dynamically re-calibrate perception to environmental changes (Barlow, 1990a, 1990b; Barlow and Hill, 1963; Solomon and Kohn, 2014; Thompson and Burr, 2009; Webster, 2011). The current results suggest that the system encoding numerosity in dyscalculia is not less adaptable, or less plastic than the typical system. Moreover, the system encoding object size is completely spared.

It is interesting to compare these data with those of autistic children, where exactly the opposite effect occurs: reduced adaptation to numerosity (compared with TD), but unchanged discrimination thresholds (Turi et al., 2015). Adaptation to faces is similarly weaker among autistic children, again with unchanged discrimination thresholds (Pellicano et al., 2007). Weaker adaptation has been interpreted as implying dysfunction in adaptive mechanisms that help perceive environment changes, a deficit in dynamically "tuning the mind to the world" (Pellicano and Burr, 2012). Interestingly, all this evidence clearly shows that adaptation is independent from sensory thresholds. Indeed, even within the typical group there was no correlation. To ensure that this null link was not due to the sample size or specific sample characteristics, we combined the data with those collected by several past experiments performed by our laboratory, reaching a very heterogeneous sample of 221 participants. Even in this case there was no link between these two perceptual parameters, and Bayesian analysis suggested that the lack of correlation was real. This dissociation is important as it demonstrates that people with dyscalculia are still selectively tuned to numerosity (even if the tuning may be less precise), and the tuning adapts.

The fact that adaptation is not affected by dyscalculia is also consistent with a recent study investigating spontaneous numerosity
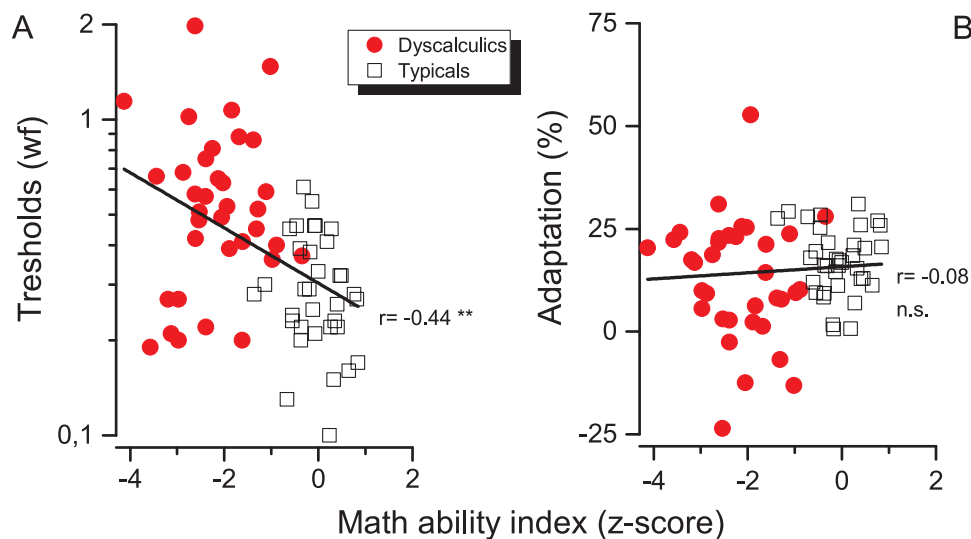
Table 1
Correlation matrix.

Tasks	Participants		
	Whole group	**Dyscalculics only**	**Typicals only**
Thresholds	**M: r = −0.44 (< 0.001) [5.1]** [*]	M: r = 0.1 (0.56) [−1.39]	M: r = −0.20 (0.25) [−0.93]
Numerosity	R: r = −0.15 (0.2) [−1]	R: r = 0.09 (0.61) [−1.4]	R: r = 0.05 (0.76) [−1.5]
Thresholds	M: r = −0.21 (0.08) [−0.38]	M: r = −0.16 (0.38) [−1.14]	M: r = −0.19 (0.25) [−0.92]
Size	R: r = −0.11 (0.36) [−1.44]	R: r = −0.15 (0.41) [−1.16]	R: r = 0.09 (0.6) [−1.41]
Adaptation	M: r = 0.08 (0.5) [−1.68]	M: r = −0.14 (0.39) [−1.2]	M: r = −0.08 (0.64) [−1.46]
Numerosity	R: r = −0.04 (0.69) [−1.8]	R: r = −0.20 (0.25) [−0.9]	R: r = 0.19 (0.26) [−0.97]
Adaptation	M: r = −0.11 (0.37) [−1.4]	M: r = 0.12 (0.49) [−1.29]	M: r = 0.03 (0.85) [−1.52]
Size	R: r = −0.12 (0.34) [−1.4]	R: r = −. 12(0.52) [−1.28]	R: r = 0.24 (0.17) [−0.63]

Correlations between perceptual measures and math as well as reading skills.
Boferroni corrected alpha 0.004 M = math; R = reading; r = Pearson's r; (p-value); [Log(BF$_{10}$)].

Fig. 4. Correlations between math abilities and numerosity discrimination thresholds (A) or adaptation strength (B). Lines represent best-fit linear regressions along with the corresponding Pearson's r value.

encoding in preadolescent with and without dyscalculia (Cicchini et al., Under review.). In that study, participants were asked to reproduce dot arrays varying in area, numerosity and density, without any explicit instructions of what to match. Although dyscalculics had longer reaction times than typicals and a tendency to rely also on area as well as numerosity, they did spontaneously reproduce numerosity. This indicates that even for dyscalculics, numerosity is a salient environmental feature, spontaneously picked up and used to modulate behaviour. Taken together these studies suggest that not all the functional mechanisms underlying numerosity encoding are impaired in dyscalculia, and that the mechanisms for perceiving number are not dramatically different for dyscalculic children, implying the existence of a similar "number sense" – albeit with poorer numerosity discrimination thresholds.

Why the thresholds are higher is still unclear. One possibility is that they reflect coarser neural tuning in IPS. This is in line with a recent imaging study showing that children numerosity discrimination thresholds (WF) measured behaviourally outside the scanner are comparable and correlated with the numerosity IPS neural tuning widths (Kersey and Cantlon, 2017). A second option, not mutually exclusive with the previous, is that the higher thresholds arise from additional noise from post sensory stages. Two meta-analysis show that numerosity thresholds usually explain a significant, but only marginal, portion of math skills variance, about 5% (Chen and Li, 2014; Schneider et al., 2017). In this study, the relationship with numerosity thresholds explains 19% of the variance.

The portion of unexplained variance is high and might be accounted by other more domain-general factors. This is in line with studies showing that dyscalculia is characterized by impairments in working memory, inhibitory control, visuospatial processing (Szucs et al., 2013), as well as with those documenting correlations between attention and executive controls with both numerosity thresholds and math skills (Anobile et al., 2013; Gilmore et al., 2013; but see also, Tinelli et al., 2015). The possible involvement of visuospatial skills also fits with a recent study showing that in typical children, spatial (dot arrays) but not temporal (sequences of sounds and flashes) numerosity thresholds correlates math skills (Anobile et al., 2018). With the current data we cannot completely rule out any of these hypotheses. However, dyscalculics perform very similarly to typicals in the size judgments, suggesting that generic post-sensory factors alone cannot account for the impairment in numerosity judgments. The actual results also challenge a recent model suggesting that numerosity perception is part of a generalized magnitude system also encoding physical size (Henik et al.,

2017; Leibovich et al., 2017), as we found a severe impairment of numerosity thresholds but not of size thresholds.

To summarize, we found that the numerosity but not size perception is impaired in dyscalculia. Despite the higher thresholds, the dyscalculic numerosity system is still able to recalibrate its activity according to what it has experienced in the recent past, as shown by unimpaired numerosity perceptual adaptation. Future work might explore whether other "short-term plasticity" phenomena – such as serial dependence for number judgements (Cicchini et al., 2014) and perceptual learning (Dewind and Brannon, 2012) – are also spared in dyscalculia.

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