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Research Report

# Near optimal encoding of numerosity in typical and dyscalculic development

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ABSTRACT

Dyscalculia is often associated with poor numerosity sensitivity. However, it is not known whether the perceptual systems of dyscalculics have implicit access to the sensory noise of numerosity judgements, and whether their perceptual systems take the noise levels into account in optimizing their perception. We tackled this question by measuring central tendency and serial dependence with a numberline task on dyscalculics and math-typical preadolescents. Numerosity thresholds were also measured with a separate 2AFC discrimination task. Our data confirmed that dyscalculics had poorer numerosity sensitivity and less accurate numberline mapping. Importantly, numberline responses, as well as central tendency and serial dependence strengths, were well predicted by sensory thresholds and could be modelled by a performance-optimizing Bayesian model based on sensory thresholds, suggesting that the functional architecture of systems encoding numerosity in dyscalculia is preserved. We speculate that the numerosity system of dyscalculics has retained those perceptual strategies that are useful to cope with and compensate for low sensory resolution.

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## 1. Introduction

Dyscalculia is a neurodevelopmental disorder compromising acquisition of typical mathematical abilities, affecting 3–7% of school-age population. A growing interest in the disorder arose from evidence implicating impairment of the "number sense": the mechanism mediating the ability to perceive numerosity (Burr & Ross, 2008; Butterworth, 1999; Dehaene, 2011). The causal link between the number sense and mathematical learning is still to be established, but dyscalculic children often suffer severe difficulties with numerosity tasks, showing higher sensory thresholds (lower precision) compared with math-typical age-matched peers (Anobile,

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Cicchini, Gasperini, & Burr, 2018; De Visscher, Noel, Pesenti, & Dormal, 2018; Mazzocco, Feigenson, & Halberda, 2011; Piazza et al., 2010). Why numerosity thresholds are higher in dyscalculia is still debated (for a recent critical review see: Leibovich, Katzin, Harel, & Henik, 2017). One possibility is that they reflect coarser neural tuning in brain areas encoding numerosity. In line with this, the width of numerosity neural tuning in the Intra Parietal Sulcus (IPS)–which may be considered as index of neural sensitivity–correlates with numerosity thresholds measured behaviourally outside the scanner (Kersey & Cantlon, 2017). Similarly, a recent imaging study found that fMRI performance in decoding numerosity from the parietal cortex (an index of discriminability) correlates with behavioural numerosity discrimination thresholds (Lasne, Piazza, Dehaene, Kleinschmidt, & Eger, 2018).

Overall these results suggest that the perceptual system underpinning numerosity encoding may develop in a fundamentally abnormal way in dyscalculics. However, a recent study showed that dyscalculics showed similar numerosity adaptation to that of age-matched math typical controls, despite having abnormally higher sensory thresholds (Anobile et al., 2018). Adaptation-induced aftereffects are thought to reflect the functional organization of encoding mechanisms, advantageous for perception by keeping the systems dynamically calibrated to environmental changes, boosting stimulus discriminability (Clifford et al., 2007; Clifford & Rhodes, 2005; Solomon & Kohn, 2014; Thompson & Burr, 2009; Webster, 2011). That adaptation is intact in dyscalculia suggests that the functional architecture of the number sense may not be qualitatively different in dyscalculia, just more noisy. In the face of poor sensory resolution, the dyscalculic numerosity system may take full advantage of those perceptual principles that allow optimal coping, such as optimizing sensory resolution by adaptation and other noise reduction mechanisms. To implement such strategies, the sensory systems must have access to the characteristics of the system itself, especially its noisiness.

Two robust perceptual effects that minimize response variance are "central tendency" and "serial dependence". Central tendency (or regression to the mean) is a classical psychophysical effect, observed in almost all sensory systems and perceptual attributes (Hollingworth, 1910). Stimuli tend to be misperceived, biased towards the mean of the distribution, resulting in overestimation of small stimuli and underestimation of large ones (Anobile, Cicchini, & Burr, 2012; Cicchini, Arrighi, Cecchetti, Giusti, & Burr, 2012; Jazayeri & Shadlen, 2010). Serial dependence is a more recently discovered perceptual effect, describing the fact that the currently observed stimulus tends to look similar to the previous stimulus (opposite to the effect of adaptation). It is highly pervasive in vision and other senses, seemingly a general principle of information processing. To date is has been observed for stimulus orientation (Fischer & Whitney, 2014; John-Saaltink, Kok, Lau, & de Lange, 2016), motion (Alais, Leung, & Van der Burg, 2017), position (Manassi, Liberman, Kosovicheva, Zhang, & Whitney, 2018), face identity (Liberman, Fischer, & Whitney, 2014), face attractiveness (Xia, Leib, & Whitney, 2016), face gender (Taubert, Alais, & Burr, 2016), body size estimation (Alexi et al., 2018) and even summary statistics of visual images (Manassi et al., 2018).

Central-tendency and serial-dependence have both been reported for numerosity perception (Anobile, Cicchini, et al., 2012; Anobile, Turi, Cicchini, & Burr, 2012; Corbett, Fischer, & Whitney, 2011; Fornaciai & Park, 2018a, 2018b), and have been successfully modelled by Bayesian analysis (Anobile, Cicchini, et al., 2012; Cicchini, Anobile, & Burr, 2014). Like adaptation, central-tendency and serial-dependence both reduce accuracy by biasing perception away from veridical. However, behavioural and computation studies have demonstrated that they both result in increased precision, hence an overall improvement in discrimination, especially with high sensory noise and stimuli uncertainty (Burr & Cicchini, 2014; Cicchini & Burr, 2018; Cicchini et al., 2012, 2014; Cicchini, Mikellidou, & Burr, 2017, 2018; Jazayeri & Shadlen, 2010; Karaminis et al., 2016).

Central-tendency and serial-dependence can therefore be considered signatures of optimal encoding. Here we asked whether the perceptual systems of dyscalculics have implicit knowledge of their reduced levels of sensory precision, and whether these reduced levels are taken into account to result in increased levels of central-tendency and serial-dependence. These are important issues as they may reveal subtle but significant clinical signatures. We measured central tendency and serial dependence with a non-symbolic numberline task and sensory thresholds with a separate comparison task. Performance was compared between groups and with those predicted by performance-optimizing Bayesian models designed to predict optimal behaviour from sensory thresholds.

## 2. Materials and methods

### 2.1. *General 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 = 1,920 × 1,080 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. We report how we determined our sample size, all data exclusions, all inclusion/exclusion criteria, whether inclusion/exclusion criteria were established prior to data analysis, all manipulations, and all measures in the study.

### 2.2. *Participants*

We tested 34 children diagnosed with dyscalculia (DD) (aged 8–16 y, mean 11.9 y, SD 1.8) and 35 typically developing (TD) children (aged 11–14 mean 12.1 y, SD .9) matched for age ($t_{(66)} = .68$, $p = .49$). DD met Diagnostic and Statistical Manual of Mental Disorders, Fifth Edition (DSM-V) criteria for dyscalculia. DD performed a full IQ scale (WISC-IV) with total IQ average score 91.5 (SD 9.8, min 75, max 113). 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.

For TD subjects, to reduce testing time and minimise interference with school activities, we employed a simplified test for IQ together with a reduced math-battery and reading measures. Reports from TD parents, teachers as well as the school performance indicate normal general intelligence, like the DD group. TD reasoning abilities were nevertheless estimated by Progressive Raven Matrices (non-verbal IQ) and all subjects met the inclusion criterion of scoring above the 10th percentile (mean 75, SD 19.5, min 15, max 98). Even if non-verbal reasoning abilities were indexed with different tests across groups (Raven for TD and non-verbal reasoning index of the WISC-IV), we performed a comparison on z-scores. Comparison revealed that TD had higher scores compared to DD ($t_{(66)} = 5.04$, $p < .001$, mean difference 1SD). This difference in not surprising as previous studies demonstrated that non-verbal reasoning abilities, as well as working memory, attention and other domain general abilities could be related to math abilities (Anobile, Stievano, & Burr, 2013; Reeve, Reynolds, Paul, & Butterworth, 2018; Rosselli, Matute, Pinto, & Ardila, 2006; Szucs, 2016).

Reading decoding abilities were also assessed. The DD group performed a full battery, which includes word-lists, non-word-lists 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 .14, SD .64 for the DD and TD groups respectively ($t_{(65)=}4.21$, $p < .001$). As often reported in the literature, and well known in clinical practise, most of the dyscalculic patients also met criteria for developmental dyslexia (17 out of 34: 51%). However, reading abilities were found to be uncorrelated with all the perceptual measures (min $p$-value = .18).

Math abilities were assessed by an Italian battery for the diagnosis of dyscalculia (BDE2). The dyscalculia group completed the full version (10 sub-tests), while the matched group performed a shorter version (6 sub-tests). Average math z-scores were: mean −2.16, SD .85, and mean −.06, SD .54 for the DD and TD groups. DD were recruited and tested at the clinical centre IRCCS Stella Maris (Calambrone, Pisa), while TD were tested in a local school. Missing values were left empty and data excluded with pairwise deletion method.

### 2.3. Non-symbolic numberline task

Participants were presented with a cloud of dots and asked to indicate the quantity on a line demarcated by two sample numerosities. Each trial started with participants viewing a 30 cm "numberline" that remained visible throughout the trial with sample dot clouds representing the extremes: one dot on the left of the numberline and 30 on the right. Participants were asked to fixate a red box and when they feel ready make the test dot cloud appear by pressing the space bar. Dot stimuli (half black, half white in order to balance luminance) were presented for 250 msec (in a circular region of 10° diameter). The numerosities were 4, 8, 12, 16, 20, 24, 28. Numerosity levels 12, 16 and 20 had greater probability of occurrence. We focused trials on the central portion of the numberline because, as based on previous studies we know that the serial effect requires many trials to be measured and therefore it was very difficult to measure it accurately over a wide range of, particularly with clinical child participants. Moreover, the central numbers are much less affected by edge effects (numberline boarders), thus leaving participants free to respond over a wide range of possibilities. As the central number (N16) is the only one to have the possibility of being preceded by the same number of predictors with greater and lesser magnitude than itself, we concentrated the analyses at this stimulus level. Subjects responded by adjusting (with left-right mouse movements) a virtual sliding cursor bar and confirmed the response by mouse click. The starting point on the numberline of the sliding cursor was randomized between trials. Even if the tasks did not require speeded responses, reaction time were registered. Subjects performed two separate sessions of 70 trials each. No feedback was provided.

### 2.4. Numerosity discrimination task

Patches of dots were presented simultaneously on either side of a central fixation point for 250 msec. Dots were .25° diameter, half-white and half-black (to balance luminance), 80% contrast on a grey background of 40 cd/m$^2$, 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. Participants indicated by appropriate key-press (left-right keyword arrows) the side of the screen with more dots. All participants performed 1 session of 45 trials. The tasks did not require speeded responses and reaction time were not measured. 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. 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).

### 2.5. Modelling

#### 2.5.1. Central prior model

We modelled the behaviour of an ideal observer who blends current noisy sensory information with a central prior. Given that the current sensory likelihood is characterized by a certain precision level $\sigma_L$, and that the central prior is also associated with a given uncertainty level $\sigma_P$, it can be demonstrated that the optimal fusion of the two signals is obtained by assigning weight $w_L$ to the sensory evidence and $(1 - w_L)$ to the central prior

$$w_L = \frac{\sigma_P^2}{\sigma_L^2 + \sigma_P^2} \tag{1}$$

Given that $\sigma_L$ depends on numerosity and follows Weber's Law and $\sigma_L = WF \cdot x$ Eq. (1) can be rewritten as

$$w_L = \frac{\sigma_P^2}{x^2 WF^2 + \sigma_P^2} \tag{2}$$

which is dependent on the ratio between the reliability of the two signals $\gamma = \sigma_P / WF$

$$w_L = \frac{\gamma^2}{x^2 + \gamma^2} \tag{3}$$

High values of $\gamma$ suggest broad priors and/or a very high sensory resolution, both of which contribute to assigning little weight to the prior with the whole weight attributed to the current sensory stimulus $w_L \approx 1$.

Overall response of an observer who combines his internal representation of magnitudes ($y = Ax$) with contextual information provided by the prior centred at 15 can be written as:

$$y = 15 + (Ax - 15) w_L \tag{4}$$

$$y = 15 + (Ax - 15) \frac{\gamma^2}{x^2 + \gamma^2} \tag{5}$$

#### 2.5.2. *Lin-log model*

We fitted average responses of observers for each numerosity with a mixed model containing a linear component and a logarithmic component.

$$y = A\left((1-\lambda)x + \lambda \frac{30}{\log_{10} 30} \log_{10} x\right) \tag{6}$$

where $\lambda$ is the logarithmic component and is constrained between 0 (full linear model) and 1 (full logarithmic component) and A is a scaling factor.

#### 2.5.3. *Short-term serial dependence model*

We modelled the behaviour of an ideal observer who used information from the previous trial to minimize error. It can be demonstrated that in this case the optimal blending of the two pieces of information is obtained by giving weight to the previous, i-1-th trial:

$$w_{i-1} = \frac{\sigma_i^2}{\sigma_{i-1}^2 + \sigma_i^2 + \delta^2} \tag{7}$$

where $\sigma_i^2$ and $\sigma_{i-1}^2$ are the reliabilities of the current and previous estimate and $\delta$ is the distance between the two successive numerosities.

#### 2.5.4. *Model comparison*

Typically fits are assessed calculating $R^2$ the ratio between the Explained Sum of Squares and the Residual Sum of Squares (i.e., the sum of squared difference from the mean). However, in a number-to-space mapping task the traditional $R^2$ risks compressing $R^2$ values of models into high values because any model which predicts a monotonic response is going to capture the data much better than the mean (which is in the assumptions of $R^2$). For this reason, we employed a modified version of $R^2$, $R^2_{eq}$ *in which Explained Sum of Squares* is pitted against the *Sum of Squares from the equality*. In this way a model, to be successful (i.e., $R^2$>0) has to provide a better fit than a veridical observer with monotonic performance. When comparing the fits of Bayesian model to actual data, in order to capture better the various models, we binned data of each group in tertiles (see stars in plots).

## 3. Results

We measured central-tendency and serial-dependence in numerosity perception in typical and dyscalculic pre-adolescents, using a numberline task. Participants marked the numerosity of a cloud of dots on a line demarcated by a single dot on the left and a 30-dot pattern on the right. We also measured numerosity thresholds with a separate discrimination task.

### 3.1. *General performance*

Fig. 1A, B shows average response times and precision (standard deviation) of aggregate data, averaged over participants. Dyscalculic participants took more time in mapping number to space than math-typicals ($F_{(1,67)} = 5.733$, $p = .019$, $\eta^2 = .079$), showing that they took the task seriously and tried to do their best: it was not a speeded task, and there were no instructions to complete it quickly. Both groups took more time with the smaller numerosities, but this is hard to interpret as it was not a speeded task. The standard deviations for the responses were also higher for the dyscalculic group ($F_{(1,67)} = 7.971$, $p = .006$, $\eta^2 = .106$). Also in the discrimination task, thresholds were significantly higher in dyscalculics (typical average = .3, SD = .121; dyscalculic average = .612, SD = .379, $t_{(67)} = 4.63$, $p < .001$, Cohen's d = 1.14).

We then looked at biases in number mapping, as previous work suggests that dyscalculic participants show a more logarithmic-like response than controls (Geary, Hoard, Nugent, & Byrd-Craven, 2008). Fig. 2A shows average mapping locations as a function of numerosity for dyscalculics and math-typicals. On inspection, the response pattern of dyscalculics appears more logarithmic. We quantified the logarithm effect by fitting individual and aggregate data with an equation (Eq. (6)) that comprises a logarithmic and linear component, shown by the colour-coded lines of Fig. 2A. The fits describe well the aggregate data ($R^2_{eq} = .86$ and .64; $R^2 = .98$ and .99, for dyscalculics and typicals). Most individual participants were also well fit by this equation (median $R^2_{eq} = .73$ and $R^2 = .95$). In line with previous reports, dyscalculics showed a more logarithmic-like response shape [average $\lambda$ were .4 ± .05 for dyscalculics and .13 ± .04 for controls; t(67) = 4.32, $p < .001$, Cohen's d = 1.04].

### 3.2. *Central tendency in numberline mapping*

The logarithmic response shape observed in dyscalculics (and other populations) has often been interpreted as reflecting the "native" spatial layout of the so called "mental-number-line" (Dehaene, 2003; Kim & Opfer, 2017; Siegler & Opfer, 2003). However, this idea has been challenged with suggestions that the logarithmic-like non-linearity may reflect contextual effects rather than an intrinsic logarithmic representation (Anobile, Cicchini, et al., 2012; Cicchini et al., 2014). We will refer to this alternative model as "Bayesian central tendency".

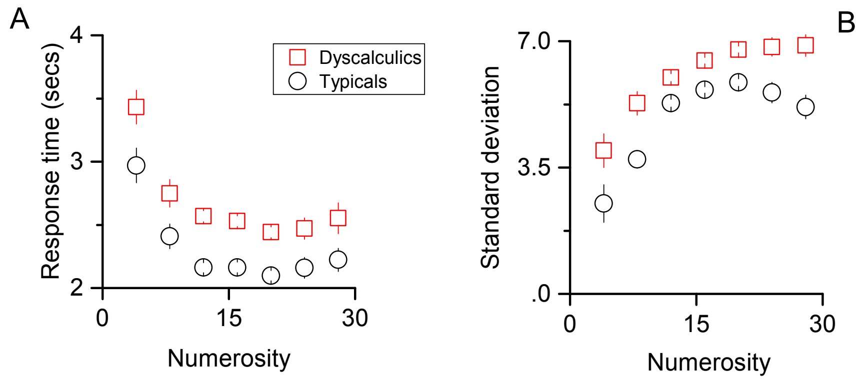


**Fig. 1 – Average (on aggregate data) response time A) and standard deviation B) for the two groups in the numberline task. Error bars indicate bootstrap standard errors.**

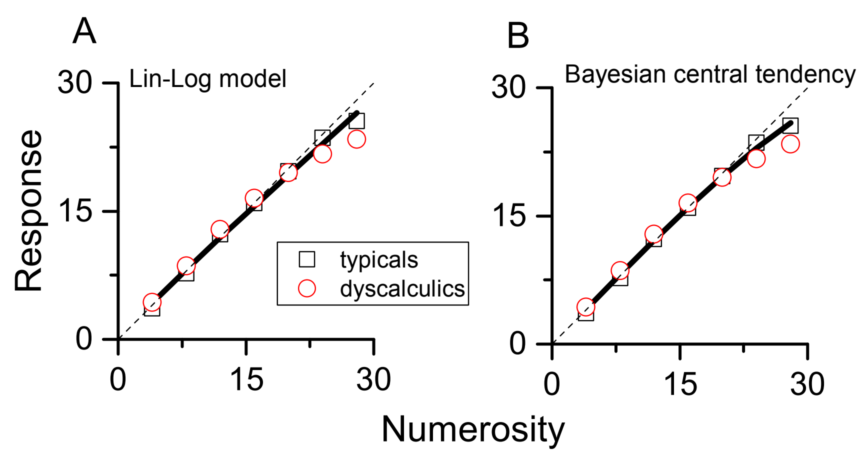


**Fig. 2 – Average response location (aggregate data) against numerosity separated for the two group of participants. Data were fitted with three models, two of which are shown here: A) Log-linear model (Eq. (6)); B) Bayesian central tendency model (Eq. (5)).**

The red and black lines in Fig. 2B show the best fit of the Bayesian central tendency model (Eq. (5)) for dyscalculic and typical participants. This model predicts responses by integrating sensory estimates (*likelihood*) with the a-priori probability that the response is near line centre (the *prior*). As in Anobile, Cicchini, et al. (2012) and Anobile, Turi, et al. (2012), the likelihood is assumed to be a Gaussian distribution centred on the true stimulus value and width determined by precision thresholds. The central tendency prior *p(L)* was also modelled as a Gaussian function, centred in the middle of the range, with variable standard deviation. The extent to which the prior draws the results towards the mean depends on the relative widths of the prior and likelihood (see Eq. (5)). If the prior widths of the two groups are similar, the group with the broader likelihoods (dyscalculics) will show a stronger central tendency.

The model describes well the aggregate data of both dyscalculic and typical participants [$R^2_{eq} = .99$ and .86 ($R^2 > .99$ for both)]. It also fits well the data of single subjects median [$R^2_{eq} = .77$ ($R^2 = .96$)]. The relative width of the prior and likelihood were lower in the dyscalculic group (32 *vs* 67), indicating a stronger attraction towards the prior centre (see Eq. (5)). However, for both groups the estimated prior width was similar, 18 for typicals and 21 for dyscalculics. This suggests that most of the difference in non-linearity results from poorer sensory representation rather than differences in prior.

To obtain individual subject-by-subject measures of central tendency, we fitted individual data (excluding subitizing) with a linear function and extracted a "regression index" as $1-\rho$, reflecting the strength attributed to the prior information (Fig. 3 illustrates this procedure applied on aggregate data). Average regression indexes of individual participants were, as predicted, higher in dyscalculics: .4 ± .04 and .16 ± .04 ($t_{(67)} = 3.78$, $p < .001$, Cohen's d = .91).

The two models (lin-log and central tendency) both predict that the magnitude of mapping distortions should depend on sensory noise level. The Bayesian model predicts this explicitly (described above). The "native logarithmic theory" (lin-log) embeds this prediction implicitly as it has often been suggested that non-linearity on the numberline task and maturity of perceptual and cognitive numerical abilities proceed in parallel (see discussion for more details). For this reason, we looked at the correlation between model outcome and individual sensory thresholds. Fig. 4A shows the relationship between Central tendency strength and discrimination thresholds. As predicted, subjects with higher discrimination

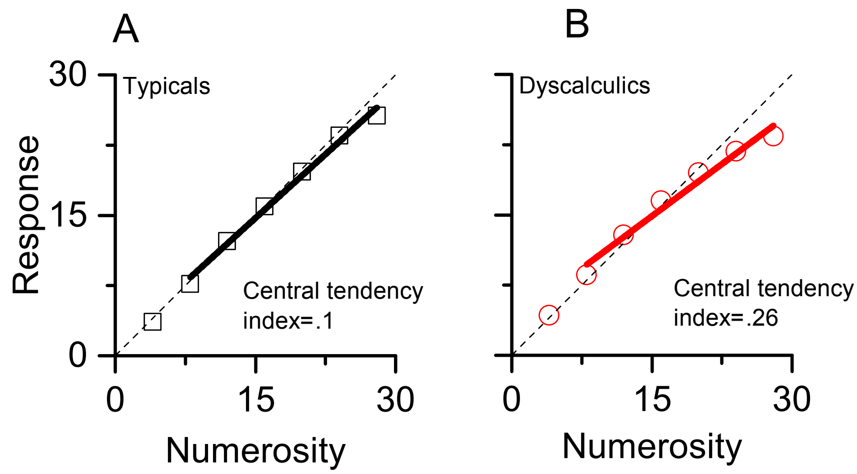


**Fig. 3 – Mean numerosity judgements given to each numerosity, fitted by linear regression to yield an index of central tendency (1-rho). The dotted line shows a veridical, linear response, without regression.**

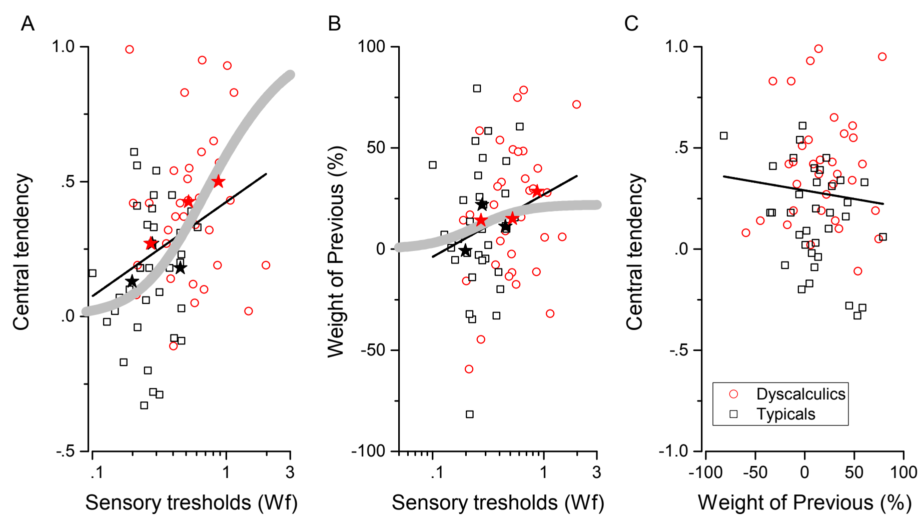


**Fig. 4 – A) Central tendency index plotted against discrimination thresholds. The grey curve shows Bayesian model predictions (see Eq. (5)), the black line shows the best linear fit on log-thresholds. B) Magnitude of serial dependence induced by 1-back stimulus in the numberline task, plotted against discrimination thresholds. The black line shows the best linear fit on log-thresholds, the grey line the predictions from the model of Cicchini, Anobile, et al. (2018) and Cicchini, Mikellidou, et al. (2018) (see Eq. (7)). C) Central tendency plotted against magnitude of serial dependence. Stars in A and B are tertiles calculated separated for each group.**

thresholds also had higher central tendency ($r = .30$, $p = .01$). By contrast the Log component (λ) shows weaker correlation with sensory precision ($r = .18$, $p = .13$). We also show the prediction of an ideal observer model which uses a prior of standard deviation of 15 dots, derived from best fit for the two datasets. The Bayesian model, with only one degree of freedom (width of prior) fits the data well, with $R^2 = .45$ (compared with $R^2 = .59$ for the linear fit, which has two degrees of freedom).

### 3.3. *Serial dependence in numberline mapping*

So far we have examined effects induced by "static" contextual factors: the inert internal logarithmic map ("lin-log" model) and the central prior, which do not require dynamic processes. Serial dependence is a dynamic contextual effect, where both past and current stimuli influence perception, with the relative weights depending dynamically on both. Serial dependence has distinctive psychophysical signatures and quantitative predictions: response errors should vary as a function of the magnitude of the previous stimulus; the effect should decrease for higher magnitude differences between current and past trials ($\delta$ of Eq. (7)); and it should increase with sensory noise ($\sigma$ of Eq. (7)) (Anobile, Cicchini, et al., 2012; Cicchini et al., 2014; Cicchini, Mikellidou, et al., 2018). We tested for these signatures in dyscalculics and math-typicals, concentrating on the numerosity levels that have been tested more extensively (see methods).

Fig. 5A shows that responses to trials preceded by a less numerous stimulus (negative values on the abscissa) were on average lower than those to trials preceded by a more numerous stimulus, the first psychophysical signature. This was particularly true for small separations of numerosity ($\delta = \pm 4$ dots), the second signature of serial effects. This was true both for average data (blue curve) and when considering dyscalculics and typicals (black and red curves) separately. We quantified the tuning of the effect by comparing the serial weights for stimuli preceded by similar numerosities ($\delta = \pm 4$ dots) to those preceded by larger numerosities ($\delta = \pm 8$ dots). Only the more similar numerosities produced effects statistically different from zero across both groups. For $\delta = \pm 4$, bootstrap average effects were 18% ($p < .001$, sign-test, one-tailed) and 12% ($p = .008$, sign-test, one-tailed) for dyscalculics and typicals. For $\delta = \pm 8$, serial effects were 1.7% ($p = .315$, sign-test, one-tailed) and 7.6% ($p = .02$, sign-test, one-tailed) for dyscalculics and typicals. The two groups did not differ significantly at either numerosity separation ($p > .05$, sign-test, one-tailed). Overall, these analyses show that estimation errors suggest a qualitatively similar pattern of serial dependence for numerosity for dyscalculics and math-typicals.

Fig. 5C shows the average serial dependence weights for the aggregate data as a function of trial history, considering only trails where $\delta = \pm 4$ dots (giving the strongest and most reliable effects). The effect is significant for stimuli one trial back ($p = .005$, $p < .001$, one-tailed sign-test for typicals and dyscalculics), but becomes insignificant for stimuli two trials back ($p > .05$ for all the other levels; Bonferroni corrected $\alpha = .0125$). The weights are larger for the dyscalculic than control group, but the difference was not statistically different. Importantly, there were no significant dependence on future trials ($p > .05$), a strong control against statistical artefacts.

As serial dependence is stronger in conditions of high sensory noise (Cicchini, Mikellidou, et al., 2018) or deprived attentional resources (Anobile, Cicchini, et al., 2012), we predicted higher serial dependence for participants with higher sensory thresholds. Fig. 4B plots serial dependence measured at numerosity 16 and $\delta = \pm 4$ (the peak of the effects for both typical and dyscalculics) against sensory thresholds measured by the comparison task. The linear correlation (against log-thresholds) was significant ($r = .25$, $p = .04$). We also modelled the results quantitatively with the Bayesian model of Eq. (7), which predicts higher serial effects for higher Weber Fractions. The model (grey line of Fig. 4B), which has only one degree of freedom (a gain factor), clearly captures the relationship between serial effects and Weber Fraction, with a

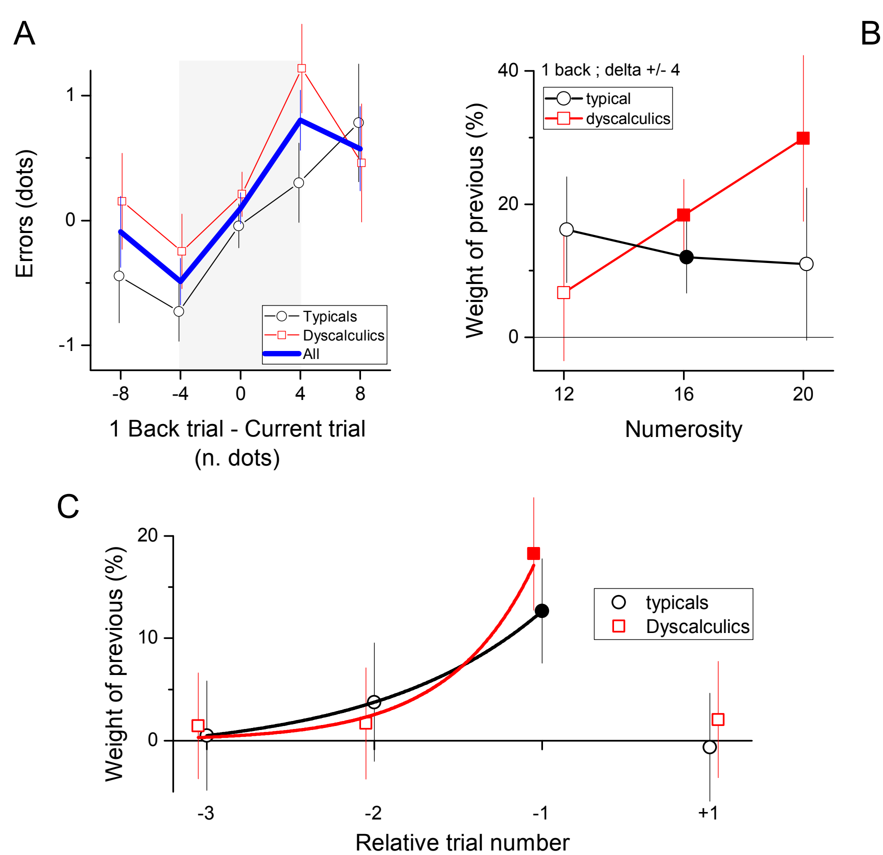


**Fig. 5 – Serial dependence. A) Estimation errors from pooling data for numerosities 12, 16 and 20, as a function of the numerical difference with preceding stimulus (1-back). B) Serial dependence effects shown separately for numerosities 12, 16 and 20, induced by the previous stimuli ($\delta = \pm 4$ dots). C) Average serial dependence by pooling numerosities 12, 16 and 20 induced by deltas equal to $\pm 4$ dots as a function of trials presented 1, 2 or 3 in the past, or the immediate future (shown as +1). The black and red curves show exponential fits. Graphs report results on aggregate data. Bars are bootstrap standard errors, with filled symbols reporting data statistically different from zero (sign-test).**

good coefficient of determination ($R^2 = .42$). The gain factor to yield best fits was $k = .47$, suggesting that for both groups the serial effect predicted by the model is about twice that measured, similar for typicals and dyscalculics (42% and 52% respectively). Many factors could explain the under-scaling of serial dependence, including decay and corruption of the trace of the previous stimulus, which would predict a higher variance associated with previous representation and hence less serial effect.

### 3.4. *Central tendency versus serial dependence*

A recent study using a similar paradigm found that indexes of Central tendency and serial dependence did not correlate with each other, suggesting two separate processes (Alexi et al., 2018). Fig. 4C plots the indexes of central tendency against those of serial dependence for the current study. Although both correlate with sensory thresholds (Fig. 4 A&B), they do not correlate with each other (Fig. 4C, $r = -.09$, $p = .44$), reinforcing the idea they are independent, parallel processes.

## 4. Discussion

This study investigates encoding strategies of numerosity in dyscalculics and math-typical preadolescents by measuring central-tendency and serial-dependence effects in a numerosity-to-space mapping task (numberline). We also measured numerosity sensitivity directly with a separate 2AFC comparison task. We replicated studies showing poorer numerosity sensitivity and less accurate number-mapping in dyscalculia. However, we showed that dyscalculics do show both central-tendency and serial-dependence effects. Importantly, the Mapping biases, central tendency and strength of serial dependence were all well explained by performance-optimizing Bayesian models that use the independently measured numerosity thresholds as estimates of sensory noise. In other words, all the differences in numberline-mapping and serial dependence are fully explained by the reduced numerosity sensitivity of dyscalculics, without implicating any other deficits in these processes. These results suggest that both math-typical and dyscalculic participants had implicit access to their own sensory resolution, and automatically adjusted number-mapping to maximize performance.

Many previous studies have suggested that dyscalculic individuals have a poor "number sense", as they show higher thresholds in numerosity judgements (Anobile et al., 2018; De Visscher et al., 2018; Mazzocco et al., 2011; Piazza et al., 2010). The increased noisiness of these judgements may arise from dysfunctional development of sensory systems encoding numerosity. Early deficits in development of the number sense may negatively impact on the later learning of language based math abilities (Butterworth, 1999; Butterworth, Varma, & Laurillard, 2011; Halberda, Mazzocco, & Feigenson, 2008; Mazzocco et al., 2011; Piazza, 2010). Similarly, other domain-general functions, such as non-verbal reasoning, attention and working memory skills correlate with math skills (Anobile et al., 2013; Reeve et al., 2018; Rosselli et al., 2006; Szucs, 2016). Although they were measured with different scales, our DD sample also had lower non-verbal reasoning scores compared with controls. Due to time limitation and ethical reasons we could not take many measures in typical children, leaving open the question on the role of general intelligence and domain-general functions in modulating perceptual context effects like serial dependence and central tendency. Future studies are needed to address this issue.

Not all aspects of numerosity perception seem to be atypical in dyscalculia. For example, numerosity adaptation, a signature of efficient coding, is not impaired in dyscalculia (Anobile et al., 2018). Similarly, when asked to reproduce the characteristics of briefly presented clouds of dots, dyscalculics spontaneously reproduce its numerosity (rather than other visual features), albeit with more errors than math-typical controls (Cicchini, Anobile, & Burr, 2018). These results suggest that dyscalculics are not "numerical-blind", but that they are well equipped for extracting numerosity from the environment. Here we report another aspect related to number perception where dyscalculics perform normally, given their reduced precision in numerosity perception. Importantly, their perceptual systems seem to have access to this reduced precision, and take this information into account to minimize errors. Other studies have shown that dyscalculics can use contextual information about numerosity, such as priming of reaction times for similar numerosities (Defever, Gobel, Ghesquiere, & Reynvoet, 2014).

While this is the first study to measure serial dependence in a clinical population, forms of "sensory meta-cognition" have been reported in other specific populations, and by experimentally manipulating signal to noise ratio of the sensory input. For example, expert drummers, who show better than average precision in discriminating interval duration, showed reduced central tendency effects in a time reproduction task (Cicchini et al., 2012). Young children, who have lower duration sensory precision compared to older individuals, show higher central tendency (Karaminis et al., 2016; Sciutti, Burr, Saracco, Sandini, & Gori, 2014). Similarly, central tendency assessed by numberline tasks in neurologically typical adults can be enhanced by depriving attentional resources (Anobile, Cicchini, et al., 2012; Anobile, Turi, et al., 2012). Other studies have found higher serial dependence for noisy stimuli in numerosity mapping, orientation reproduction and duration reproduction (Anobile, Cicchini, et al., 2012; Anobile, Turi, et al., 2012; Cicchini, Mikellidou, et al., 2018; Jazayeri & Shadlen, 2010).

However, not all clinical groups use perceptual strategies optimally. For example, autistic children have lower levels of central tendency in temporal reproduction than predicted by temporal thresholds (Karaminis et al., 2016). Similarly, autistic children also show less perceptual adaptation to many attributes (Pellicano, Jeffery, Burr, & Rhodes, 2007), including numerosity (Turi et al., 2015), another sign of poor use of prior information (Pellicano & Burr, 2012). These results with autism show that optimal encoding is not guaranteed.

Our results speak to the debate about what causes biases in numberline mapping. Dyscalculics, young children, unschooled adults or typical adults tested under attentional load, all show characteristic biases, mapping of number onto space in a logarithmic-like manner. This result has been interpreted as evidence that humans start numerical development with a logarithmic numerical response that becomes linearized by education (Dehaene, 2003; Dehaene, Izard, Spelke, & Pica, 2008; Kim & Opfer, 2018; Siegler & Opfer, 2003). Our data confirm the logarithmic-like distortion of the numberline in dyscalculia, but suggest that it may derive from noise-reducing contextual effects, as previously suggested (Anobile, Cicchini, et al., 2012; Anobile, Turi, et al., 2012; Cicchini et al., 2014). The tendency to compress the responses towards the centre of the numberline generates overestimation of the numbers below the average of the range and underestimation of the higher ones. This, together with the fact that the small numbers are less influenced by context effects, creates the logarithmic-like distortion. Here we demonstrate quantitatively that, in line with many previous studies, central tendency depends on noisiness, reinforcing the notion that it is a perceptual strategy increasing efficiency (Burr & Cicchini, 2014; Cicchini et al., 2017; Cicchini, Mikellidou, et al., 2018). That the logarithmic-like numberline shape may derive from central tendency, induced by noise, also fits well with existing data showing that a more logarithmic numberline often goes hand in hand with higher sensory noise. This is the case for young children (Piazza, 2010), dyscalculics (Anobile et al., 2018; Piazza et al., 2010), unschooled adults (Piazza, Pica, Izard, Spelke, & Dehaene, 2013), and typical adults under attentional load (Anobile, Cicchini, et al., 2012; Burr, Anobile, & Turi, 2011). All have strong numberline biases together with higher numerosity thresholds.

Other interpretations for non-linear numberline mapping have been advanced. Some proposed that non-linearities are generated from proportion judgements relative to the ends and centre of the numberline (Barth & Paladino, 2011), from the bounded nature of numberline tasks (Cohen & Quinlan, 2018), or from cognitive strategies induced by the confidence with numbers (Chesney & Matthews, 2013). Some authors even suggested that there is no "inherent left-right mental number line" (Aiello et al., 2012). Our data overall agree with those suggesting caution in interpreting the numberline response shape as reflecting the native spatial layout of the mental number line: a good logarithmic fit may be an excellent mathematical description of the data, but with limited implications for the underlying cognitive processes (Cohen & Quinlan, 2018). We would like to point out that our intention here is not to question the importance of numberline tasks and related training procedures. Performance on number-to-space tasks is a good predictor of math abilities and is therefore of particular interest.

Individual differences in serial dependence and central tendency did not correlate with each other, replicating a recent study on perception of body-size using a "body-line" mapping task, similar to the numberline (Alexi et al., 2018). That serial dependence and central tendency occur in both studies, but did not correlate with each other, suggests that they represent at least partially distinct but parallel processes. For tasks requiring mapping of stimuli on a defined range (bounded size-line or number-line), central tendency may not require any dynamic learning. Indeed, a simple fixed prior centred on the midline was well able to describe performance. On the other hand, serial dependence requires – by definition – dynamic integration between previous stimuli and current perception. This "static" versus "dynamic" nature of the effects maybe the feature constrains their correlation. Although there is evidence that the intraparietal cortex is a key area for numerosity perception (Kersey & Cantlon, 2017; Lasne et al., 2018; Piazza & Eger, 2016), little is known about the neural underpinnings of context effects in numerosity, other than that adaptation seems to operate at the level of the intraparietal cortex (Castaldi, Aagten-Murphy, Tosetti, Burr, & Morrone, 2016). Investigating the neural basis of numerosity context effects is clearly an important direction for future research.

## 5. Conclusions

In conclusion, we found that dyscalculic and math-typical preadolescents show statistically near-optimal encoding of numerosity. Central-tendency and serial-dependence strengths were well predicted by sensory thresholds and by performance-optimizing Bayesian models incorporating sensory resolution to stimuli context. These results imply that the perceptual systems of dyscalculics have implicit access to their own sensory uncertainty and unconsciously adjust performance in order to minimize errors. Together with previous research demonstrating spared numerosity perceptual adaptation in developmental dyscalculia, the current study suggests that while dyscalculics have reduced sensory resolution of numerosities, other perceptual strategies, including those that help compensate for this reduced resolution, seem to be unaffected. Future studies should attempt to uncover the neural substrate of these processes.

## CRediT authorship contribution statement

**Giovanni Anobile:** Conceptualization, Investigation, Writing - original draft, Visualization, Project administration, Funding acquisition. **David C. Burr:** Conceptualization, Methodology, Writing - review & editing, Supervision, Project administration, Funding acquisition. **Filippo Gasperini:** Investigation. **Guido Marco Cicchini:** Conceptualization, Methodology, Data curation, Writing - original draft, Visualization, Writing - review & editing.

## Open practices

Ethical restrictions prevent us from publicly archiving the anonymised data from this study. Thus access to the datasets used and analysed during the present study will be available from the corresponding author who will request the ethics committee of the Azienda Ospedaliero-Universitaria Meyer to lift the ban and allow the data to be provided. There are no conditions on data release imposed by the authors.

The study in this article earned Open Materials badge for transparent practices. Materials and data for the study are available at https://osf.io/2hm6p/.

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