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Impaired Numerical Ability Affects Supra-Second Time Estimation

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Abstract

It has been suggested that the human ability to process number and time both rely on common magnitude mechanisms, yet for time this commonality has mainly been investigated in the sub-second rather than longer time ranges. Here we examined whether number processing is associated with timing in time ranges greater than a second. Specifically, we tested long duration estimation abilities in adults with a developmental impairment in numerical processing (dyscalculia), reasoning that any such timing impairment co-occurring with dyscalculia may be consistent with joint mechanisms for time estimation and number processing. Dyscalculics and age-matched controls were tested on supra-second temporal estimation (12 s), a difficulty-matched non-temporal control task, as well as mathematical abilities. Consistent with our hypothesis, dyscalculics were significantly impaired in supra-second duration estimation but not in the control task. Furthermore, supra-second timing ability positively correlated with mathematical proficiency. All participants reported that they used counting to estimate time, although no specific instructions were given with respect to counting. These results suggest that numerical processing and supra-second temporal estimation share common mechanisms. However, since this conclusion is also based on subjective observations, further work needs to be done to determine whether mathematical impairment co-occurs with supra-second time estimation impairment when counting is not involved in and is objectively controlled for during supra-second timing. We hypothesize that counting, that does not develop normally in dyscalculics, might underlie and adversely affect dyscalculics' supra-second time estimation performance, rather than an impairment of a magnitude mechanism or the internal clock pacemaker.

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Dyscalculia, time estimation, time discrimination, chronometric counting, magnitude

1. Introduction

Although it has been proposed that temporal and numerical processing rely on shared mechanisms (e.g., Cantlon et al., 2009; Cappelletti et al., 2011b; Dehaene & Brannon, 2010; Meck & Church, 1983; Meck et al., 1985; Walsh, 2003; but see Agrillo et al., 2010), most studies investigating these processes focused on very brief temporal durations, usually in the sub-second range (e.g., for reviews see Hayashi et al., 2013a; Walsh, 2003), while investigations in the supra-second time range are very limited (Cappelletti et al., 2009, 2011b; Hayashi et al., 2013b). These studies found that numerical information affects supra-second timing performance. For example, Cappelletti and colleagues found that a numerically-impaired patient performed normally on supra-second time estimations of 15–60 s intervals with neutral stimuli, but was impaired if the (task-irrelevant) stimuli were numbers.

While sub-second timing is considered more automatic, relying on sensory-motor mechanisms, supra-second timing, also termed 'cognitive timing', involves higher-level perceptual and neural mechanisms (Allman et al., 2014; Gilaie-Dotan et al., 2011; Lewis & Miall, 2003; Mauk & Buonomano, 2004; Meck, 1996; Poppel, 1997). In the context of timing and number processing, supra-second timing — but crucially not sub-second timing — often relies on strategies involving numerical processes. For example, counting is a frequently used strategy to estimate supra-second durations (Gilliland & Martin, 1940; sometimes referred to as 'chronometric counting', see Hinton & Rao, 2004; Rakitin et al., 1998; Wearden & McShane, 1988), and other numerical operations such as adding and subtracting are also used, especially for supra-second intervals in the order of minutes or hours. Interestingly, even though counting is a simple numerical skill typically acquired during childhood, people with developmental impairment in numerical processing (developmental dyscalculia — DD) often have difficulty with counting and acquire this skill at later developmental stages (Butterworth, 2003, 2010; Kaufmann, 2008; Rubinsten & Henik, 2009).

Here we focused on the link between numerical processing and *supra-second* temporal processing and took a new perspective by examining whether a developmental impairment in numerical processing may extend to time estimation in the supra-second range. Adults diagnosed with developmental dyscalculia, plus numerically-normal participants performed temporal estimation tasks of supra-second (∼12 s) durations, using an established experimental paradigm (Brown et al., 1995; Gilaie-Dotan et al., 2011). This procedure of supra-second temporal *estimation* (Brown et al., 1995; Gilaie-Dotan et al., 2011) is different from the peak interval (PI) timing paradigm used in humans (Hinton & Rao, 2004; Rakitin et al.,

1998) that assesses supra-second temporal *reproduction* of pre-learned intervals of unknown durations with on-going detailed feedback, and does not allow chronometric counting. In our paradigm we purposely did not instruct participants to use or refrain from using counting, both because we wanted them to perform timing estimation most naturally, and also because we did not want to bias task instructions towards the numerical domain, which is impaired in DDs. To assess whether any possible impairment was specific to time estimation or simply related to sustained attention, participants also performed a non-temporal control task with identical stimuli and matched in difficulty and attentional demands. We also independently assessed participants' temporal discrimination thresholds for twelve-second durations in order to obtain a more sensitive measure of their supra-second time estimation ability. Finally, we examined whether mathematical abilities and supra-second timing estimation were associated. We hypothesised that DDs may be impaired in supra-second timing estimation (but not in the control task) due to their difficulty with numerical processing.

2. Methods

2.1. Participants

All participants were neurologically normal, right-handed adults with normal or corrected to normal vision and who gave written informed consent to participate in the study. The study was approved by the local ethics committee.

2.1.1. Adults with Developmental Dyscalculia

Six participants (six females, mean age 42.7, range 28–72) previously diagnosed with dyscalculia took part in the study. The Dyscalculia Screener (Butterworth, 2003) and additional mathematical tasks were used to diagnose dyscalculia; general intelligence was also assessed.

2.1.2. Control Participants

Nineteen numerically-normal participants who were age-matched to the DDs (11 females, mean age 34.8, range 19–70) participated in all the experiments. Eleven of these participants also completed the IQ and mathematical assessment as detailed in Tables 1 and 2.

2.2. Dyscalculia Diagnosis

The diagnosis of dyscalculia was based on the Dyscalculia Screener and corroborated by additional standardized tests. The Dyscalculia Screener is a standardized software that comprises four computer-controlled, item-timed tasks, divided into two subscales: a 'capacity' and an 'achievement' subscale involving two tasks each (a dot–number matching and a number comparison task for the first subscale, and two math verification tasks for the second subscale; see Butterworth, 2003, 2005). The software diagnoses dyscalculia on the basis of norms that look at performance expressed as an inverse efficiency score (median reaction times over accuracy; see Butterworth, 2003, 2005; Landerl et al., 2004).

Moreover, the following numerical and mathematical tasks were used to corroborate the diagnosis of DD, and specifically: (1) the arithmetic subtest of the Wechsler Adult Intelligence Scale (WAIS-R; Wechsler, 1986), consisting of a series of 20 arithmetical problems embedded in a text and orally presented for an oral answer. Correct answers produced within a maximum time (spanning from 15 to 60 s depending on the problem) were assigned one point; (2) the Graded Difficulty Arithmetic test (GDA; Jackson & Warrington, 1986), a standardised task based on 12 two- to three-digit addition and 12 two- to three-digit subtraction problems of progressive difficulty (e.g., from '13 + 15' to '243 + 149'), orally presented one at a time for an oral answer which scored one point if correctly produced within 10 s; (3) number comparison task, a key test to assess number processing requiring participants to indicate as fast as possible the larger of two Arabic numbers presented to the left and right of a central fixation

Table 1.
DD's performance in IQ subtasks. Percentile and standard deviation (SD) in brackets. Impaired performance (more than two SDs below the mean) is shown in **bold**

Tasks performed	All DD ($N = 6$)	Individual DD					
		1	2	3	4	5	6
IQ[a]	103.5 (5.9)	98	106	103	106	113	94
Verbal scale[a]	98.83	91	95	106	98	112	91
Vocabulary[b]	70.50	**25**	95	63	95	95	50
Similarities[b]	63.33	**37**	84	75	75	84	**25**
Arithmetic[b]	19.83	**9**	**25**	**1**	**25**	**9**	50
Digit span[b]	58.00	**37**	50	**37**	99	50	75
Performance scale[a]	105.17	106	108	99	109	113	96
Block design[b]	69.83	63	84	50	75	63	84
Matrices[b]	74.83	63	75	75	91	95	50

[a] WAIS-3 (Wechsler, 1986). Verbal, Performance, and Full Scale IQ scores are normative (mean of 100, SD of 15). Full Scale IQ calculated disregarding performance in the arithmetical sub-task.
[b] Percentile.

point. Thirty-six pairs of single-digit Arabic numbers (1 to 9) were individually presented. Stimulus pairs were centred along the horizontal line of the computer screen and displayed for 500 ms each to the left or the right of the fixation cross which was presented before each trial for 100 ms; number stimuli were replaced by a black screen for a maximum of 4 s during which participants made an answer. After this, the following trial started immediately. Using a design similar to previous studies (e.g., Cappelletti et al., 2013), the following numerical distances were used: 1 (e.g., 7 vs. 8; eight trials), 2 (e.g., 3 vs. 1; eight trials), 3 (e.g., 5 vs. 2; eight trials), 4 (e.g., 1 vs. 5; eight trials), 5 (e.g., 4 vs. 9; four trials), with an equal number of trials where the smaller digit was on the left or on the right within each numerical distance; and (4) a numerosity discrimination task, which allows obtaining an index of accuracy sensitive to dyscalculia, the Weber fraction (*wf*; Halberda et al., 2008; Mazzocco et al., 2011; Piazza et al., 2010). For this task, the same experimental design, procedure and data analysis of a previous paradigm (Halberda et al., 2008) were used.

General intelligence was assessed with the WAIS-R (Wechsler, 1986).

To be classified as dyscalculic, participants had to demonstrate: (i) a score below 81 on at least one of the two tasks of the capacity subscale of the Dyscalculia Screener (test average of the nationally standardized score = 100, SD = 15); (ii) impaired performance on the two standardized arithmetic tasks relative to norms; (iii) impaired performance on the number comparison task in terms of either low accuracy or abnormally larger or inexistent distance effect (see below) relative to controls; (iv) larger Weber Fraction in the numerosity discrimination tasks relative to controls; and (v) an IQ score within the normal range (full-scale IQ not below 80).

As shown in Tables 1 and 2, all six DD participants showed a score below the cut-off point in the Dyscalculia Screener; they were also significantly impaired in the two standardized calculation tests relative to norms, and relative to the control group [Welch's t-test, WAIS problem: $t(7.81) = -8.55$, $p < 0.0001$; GDA: $t(14.99) = -8.21$, $p < 10^{-5}$], and these results still hold even without any assumptions on sample distribution (Mann–Whitney–Wilcoxon test: $W = 21$, $p < 0.001$ for WAIS problem and for GDA). In the number comparison task, DDs showed an abnormally large distance effect such that the time required to discriminate between stimuli numerically close was significantly longer relative to controls [DD vs. controls: Welch's t-test: $t(5.63) = 3.50$, $p = 0.0174$; Mann–Whitney–Wilcoxon test: $W = 83$, $p < 0.002$], consistent with some previous studies (e.g., Ashkenazi et al., 2009; Holloway & Ansari, 2008; Mussolin et al., 2010). In the numerosity discrimination task, DDs showed an abnormally large Weber Fraction relative to numerically-normal participants [Welch's t-test: $t(5.87) = 3.67$, $p = 0.0145$; or without assumptions on the sample distribution Mann–Whitney–Wilcoxon results: $W = 85$, $p < 0.001$], which typically suggests impaired number processing (Mazzocco et al., 2011; Piazza et al., 2010). DD's IQ was average or high average, indicating preserved intellectual functioning.

Overall these results suggest that the participants' profile was consistent with dyscalculia.

Table 2.
DD's performance in the numerical tasks. Stanine, response time, percentile, percent correct or Weber fraction. Mean performance with standard deviation (SD) in brackets. Impaired performance is shown in **bold**; borderline performance in *italics*. DD's group performance was compared to controls in independent (Welch's) *t*-tests. Impaired individual DD's performance was determined according to the Crawford & Howell (1998) *t*-test, unless mentioned otherwise

Tasks performed	Controls	All DD ($N = 6$)	Individual DD					
			1	2	3	4	5	6
DD Screener stanines[a]		**2.54 (1.0)**						
Capacity sub-scale		**2.83 (1.3)**	**2.5**	4.5	**2**	**2**	4.5	**1.5**
Dot–number matching			**3**	**3**	**2**	**2**	**3**	**1**
Number comparison			**2**	6	**2**	**2**	6	**2**
Achievement sub-scale		**2.25 (0.7)**	**1.5**	**3**	**2.5**	**1.5**	**3**	**2**
Addition			**2**	4	**3**	**2**	**3**	**2**
Multiplication			**1**	**2**	**2**	**1**	**3**	**2**
GDA percentile[b]	37–99	**11.5** (11.9)	**1**	**1**	**1**	**25**	**16**	**25**
Numerosity discrimination *wf*[c]	0.27 (0.07)	**0.53** (0.16)	*0.34*	**0.46**	**0.73**	**0.64**	*0.36*	**0.64**
Number comparison								
Accuracy (% correct)	95.3 (3.3)	97.5 (2.7)	92.6	97.05	100	97.05	98.5	100
RTs (ms)	565.1 (97.5)	**1019.1** (311.7)	**1082.5**	**917.9**	**1358.4**	563.6	**1357.9**	**834.5**
de[d] (ms)	98.5 (7.8)	**223.1** (121.0)	**206.5**	**247.0**	**396.4**	22.3	**263.2**	**202.7**

[a] Stanine score ranging from 1 to 9 where $\leqslant 3$ indicates an impairment (see Butterworth, 2003).
[b] Graded Difficulty Arithmetic Test (Jackson & Warrington, 1986) in percentile score. Impaired performance: 2 SD below controls' mean; borderline performance: 1 SD below controls' mean.
[c] Performance expressed as Weber fraction (*wf*; Halberda et al., 2008).
[d] de = distance effect corresponding to the difference in ms in responding to pairs of stimuli numerically close (e.g. 1 vs. 2) relative to far apart (e.g. 1 vs. 9).

2.3. Experiments and Tasks

All participants performed the experiments described below in one testing session. At the end of the session, each participant was debriefed about the experiments: asked whether they used any strategy to perform the tasks, which task was more difficult for them, etc.

2.3.1. Task 1: Temporal Estimation of Supra-second Durations

To examine whether estimation of supra-second duration was preserved in dyscalculic participants, we constructed a temporal discrimination paradigm inspired by Coull and colleagues (Coull et al., 2004), whereby participants had to discriminate between visually presented 12 s and 13.2 s duration intervals in a two alternative forced choice manner. Crucially, the same paradigm also served as a non-temporal control experiment with a simple change of task instructions [see below, Fig. 1, and Gilaie-Dotan et al. (2011) for more details].

In the temporal discrimination task, each trial presented one interval of either 12 s or 13.2 s duration. Participants were instructed to estimate whether the interval duration was 12 s or 13.2 s without using any motor, sensory or verbal aid (i.e., no tapping, speaking etc.). They were not instructed to use any specific method, and were also not instructed to refrain from or use counting, as we did not want to bias the task with numerical-related instructions. No feedback was provided for correct or for incorrect responses as we did not want to influence performance via feedback and learning. Participants were given a few practice trials (see below) to familiarize with the task. Each trial consisted of a small white empty circle (visual angle of 0.286°) appearing at fixation on a black background for 12 s or 13.2 s. Along with the white empty circle, bigger coloured circles (diameter of 7.44° of visual angle) briefly appeared (each for 250 ms), giving the impression of a single flash/flicker with each coloured circle presentation (see Fig. 1A). The colours of the circles were similar to the colour shades reported by Coull et al. (2004) and were red (R, G, B) = (139, 0, 65), pink (139, 7, 108), purple (116, 0, 213), another shade of purple (100, 19, 111), and blue (60, 20, 168). The colours' order and the number of flickering coloured circles in each trial varied across trials (between three and nine circles per trial, average of 6.25). The flickering circles appeared in an asynchronous fashion within each trial (SOA between 400 to 7300 ms, mean 1831 ms), and the onsets of circle appearances varied across trials. Participants were instructed to make unspeeded responses to estimate the duration of the white circle in each trial (while ignoring the bigger coloured circles) by pressing one of two predefined keys for the 12 or 13.2 s responses. Stimuli were presented at 1024 × 768 resolution and a refresh rate of 60 Hz via Cogent MATLAB toolbox (http://www.vislab.ucl.ac.uk/cogent_2000.php) and were viewed from a distance of approximately 50 cm.

Before the main experimental session, participants performed a four-trial practice session to familiarize themselves with the temporal task. Participants then performed 36 trials of the task administered in three blocks (12 trials in each block), half of the trials in each block lasted 12 s, the other half 13.2 s. The order of 12 and 13.2 s trials was counterbalanced within and across blocks. Participants' responses to each block were classified as correct or incorrect. Individual accuracy measures were averaged over all responses from the three blocks.

2.3.2. Task 2: Non-temporal Control

Here we examined whether potential impairments in dyscalculics' performance for supra-second time estimation of durations (12 s) were time-specific or reflected other processes such as sustained attention. Similar to previous studies on numerically-normal adults (Gilaie-Dotan et al., 2011; see also Coull et al., 2004), we used the same supra-second time estimation paradigm but now changed the task instructions to require a discrimination of colour rather than time. On each trial, participants had to attend to the colour of the flickering large circles and judge whether the colour of the last appearing circle was same or different than the colour of its preceding circle. Importantly, as mentioned above, each trial contained a different number of flashing coloured circles presented at an asynchronous rate, so participants could not anticipate the last circle's appearance, and therefore had to remain attentive throughout the whole trial, similar to the time discrimination task.

The order of trials requiring 'same colour' or 'different colour' response was counterbalanced within and across blocks, as well as counterbalanced between trials of 12 and 13.2 s, so that half of the 'same colour' trials lasted 12 s, the other half 13.2 s, and the same for the 'different colour' trials.

2.3.3. Task 3: Temporal Sensitivity to Supra-second Durations

In this experiment we measured individual temporal sensitivity to intervals of the order of 12 s, i.e., the duration difference at which a participant was able to discriminate 12 s from longer intervals. To yield this finer psychometric measure, we varied the duration length in each of the trials longer than 12 s (as described earlier in Gilaie-Dotan et al., 2011). We used a Bayesian adaptive procedure that efficiently estimated the individual duration difference at which a participant performed at a desired level of 75% accuracy (QUEST; Watson & Pelli, 1983) in discriminating between intervals of 12 s and longer intervals, using the mean of the posterior probability density function.

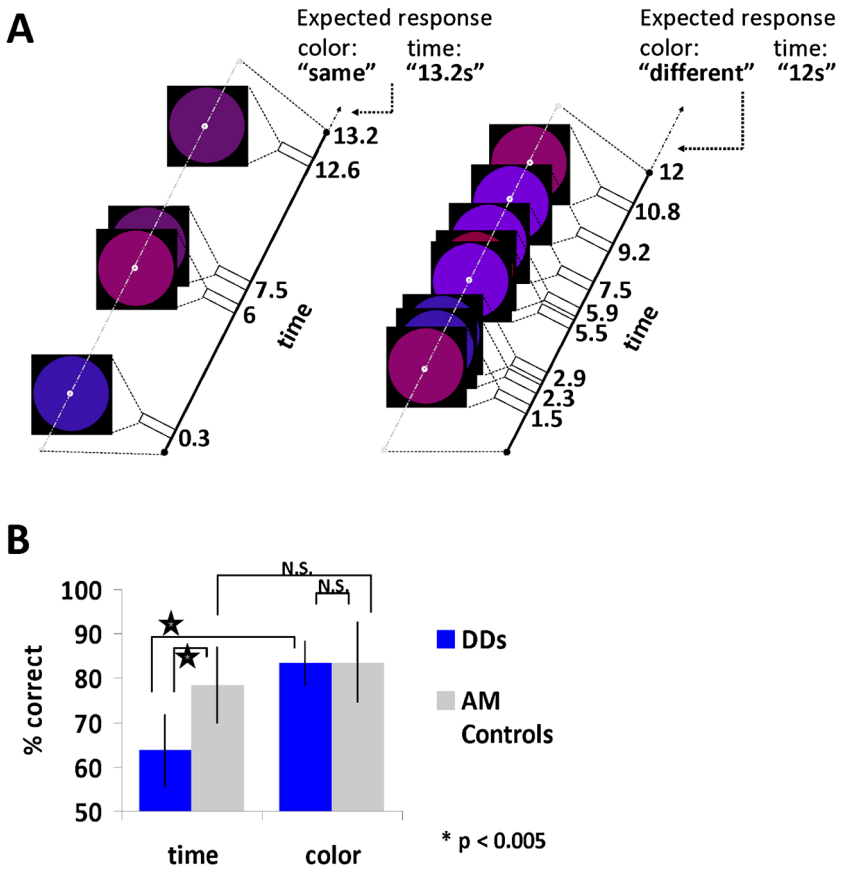

Figure 1. Experimental paradigm and results of supra-second timing (Task 1) and non-temporal control (Task 2). (A) Timeline and stimuli from two experimental trials. The same paradigm was used for the supra-second timing and the colour discrimination control tasks (Tasks 1 and 2 respectively, see Methods). The temporal task (Task 1) required discriminating between 12 s and 13.2 s durations while ignoring the coloured circles; the colour task (Task 2) required discriminating between the colours of the last presented circle in a trial and the one preceding it ('same' or 'different'). Expected correct responses according to the task are indicated on the top right corner. Both colour and time tasks required sustained attention throughout the trials since the number of flashing circles and their appearances were unexpected (number of circles per trial varied across trials and stimulus appearances were asynchronous, i.e., different SOA). A small white empty circle appeared at the beginning of each trial until the end of the trial. Participants responded after the white small circle disappeared. (B) Accuracy in the supra-second temporal discrimination (left) and non-temporal colour tasks (right) for dyscalculics (in darker shade) and numerically-normal controls (AM Controls, in lighter shade). Dyscalculics were significantly impaired in supra-second duration estimation compared to controls and compared to their performance in the colour task, but no significant differences were found between dyscalculics and controls in the control non-temporal colour task, or between the controls' performance on the time and colour tasks. Asterisks indicate significant differences, N.S. non-significant (see Results for further details). Error bars represent standard deviations (SD). This figure is published in colour in the online version.

Each trial consisted of centrally presented blue rectangle with purplish borders (14.14° × 6.61°, width × height), lasting exactly 12 s or a variable longer duration. The durations of the intervals longer than 12 s were determined adaptively during the experiment by the QUEST algorithm according to the participant's sensitivity (example duration ranges: high supra-second temporal sensitivity participant with 12 952–13 125 ms; low sensitivity participant with 13 199–20 112 ms). There were six trials of 12 s interspersed randomly among fourteen trials of longer duration. Participants were instructed to judge whether each trial lasted 12 s or longer. The temporal perceptual threshold was defined as the estimated duration (Δ) that allowed each participant to discriminate 12 s and 12 + Δ s at the predetermined accuracy level, as described above.

3. Results

We first examined whether DDs were impaired in supra-second timing (Task 1), and whether any such impairment was time-specific or instead due to non-temporal factors (Task 2).

We performed a 2 × 2 analysis of variance (ANOVA) on accuracy with group (DDs vs. controls) and task (time estimation vs. colour) as factors. We found a significant main effect of group [$F(1, 46) = 7.13$, $p < 0.02$] and task [$F(1, 46) = 19.8$, $p < 0.0001$], and a significant interaction between group and task [$F(1, 46) = 6.86$, $p < 0.02$]. Post-hoc between-group analysis revealed that DD participants were significantly impaired relative to controls in supra-second (12 s) temporal estimation [DDs: 63.9% ± 8.1%, controls: 78.5% ± 8.6%; Welch's t-test: $t(8.9) = -3.81$, $p < 0.01$, see Fig. 1B, left panel]. These results still hold even without any assumptions on sample distribution [Mann–Whitney–Wilcoxon test: $W = 33$, $p < 0.005$]. In contrast to the temporal task (Task 1), on the colour judgement task (Task 2), DDs were as accurate as controls [DD: 83.4% ± 5.9%, controls: 83.6 ± 8.9%, $t(15.48) = -0.05$, $p > 0.95$; or without assumptions on sample distribution Mann–Whitney–Wilcoxon test: $W = 69$, $p > 0.58$, see Fig. 1B right panel]. Furthermore, within-group comparisons revealed that DDs' performance was significantly reduced in the time task compared to the colour task [two-tailed paired t-test, $t(5) = 5.00$, $p < 0.005$], while in the controls there was no significant performance difference between the two tasks [$t(18) = 1.7$, $p > 0.1$].

The difference between the groups in temporal estimation was also significant when we examined the temporal sensitivities of both groups obtained from Task 3 (see Fig. 2). Specifically, relative to controls DDs needed more time to discriminate successfully 12 s interval from a longer interval: DDs' thresholds were 3.6 ± 0.21 corresponding to duration Δ of 4342 ± 1991 ms, while thresholds for controls were 3.3 ± 0.3, corresponding to a duration Δ of 2551 ± 1652 ms [Welch's t-test for DDs vs. controls on thresholds: $t(11.84) = 2.52$, $p < 0.03$; nonparametric tests also confirm these results for the thresholds or for their converted duration Δ: Mann–Whitney–Wilcoxon test: W's = 111, p's < 0.04].

These results suggest that DDs were impaired in estimating supra-second temporal durations and that this impairment was not due to attentional factors, as the DDs were not impaired in the non-temporal control task (Task 2) that had similar attentional demands as the temporal task (Task 1). This conclusion was further

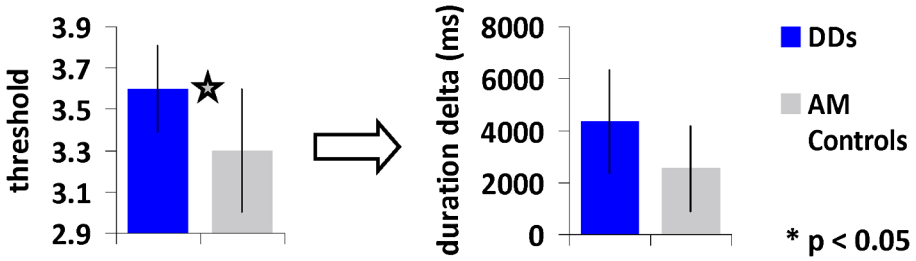

Figure 2. Supra-second perceptual thresholds (Task 3). This task measured the duration difference in milliseconds (ms) needed to discriminate 12 s from longer intervals (see Methods, DDs in darker shade, controls in lighter shade). Perceptual thresholds are presented on the left and converted to their corresponding durations (ms) that are presented on the right. DDs needed significantly longer durations than controls to discriminate correctly 12 s from longer intervals (due to data dependency, only thresholds (left) were statistically compared). This figure is published in colour in the online version.

supported by the absence of any correlation between performance on the time and the colour tasks in both groups [DDs: $R^2 = 0.0001$, p(non-directional) > 0.98, $t(4) = -0.024$, age-matched controls: $R^2 = 0.008$, p(non-directional) > 0.71, $t(17) = -0.37$]. Next, we validated that our supra-second temporal discrimination measure was not too coarse by comparing the accuracy levels in the temporal task (Task 1) to the finer temporal sensitivity thresholds measured in our second time discrimination task (Task 3). These independent temporal measures were highly correlated [correlations between time accuracy and measured threshold: DDs: $R^2 = 0.56$, p(non-directional) $= 0.089$, $t(4) = -2.239$, age-matched controls: $R^2 = 0.27$, p(non-directional) $= 0.022$, $t(17) = -2.52$, all: $R^2 = 0.42$, p(non-directional) $= 0.0005$, $t(23) = -4.08$, see Fig. 3 for the estimated thresholds converted to ms]. Thus, accuracy levels in our temporal task (Task 1) reliably predicted individual's supra-second timing sensitivity threshold (Task 3).

We also examined whether DDs' reduced accuracies for supra-second durations (Task 1) might reflect perceptual shortening or lengthening of supra-second intervals. Perceiving 12 s intervals as lasting 13.2 s corresponds to subjective slowing down of the time ('speeding up of the pacemaker', see Treisman, 1963; Treisman et al., 1990), or to overestimation of supra-second durations, while perceiving 13.2 s as lasting 12 s corresponds to subjective speeding up of the subjective time ('slowing down of the pacemaker'), or underestimation of supra-second durations. Four of the six DDs responded to most trials (individual percentages of 75, 62.5, 63.9, 75) as lasting 13.2 s (overestimation) while the other two DDs responded to the majority of the trials (individual percentages of 88.9, 58.3) as lasting 12 s (underestimation). Therefore our data did not support a consistent bias of subjective shortening or lengthening of supra-second intervals in DDs, but rather reduced accuracy levels.

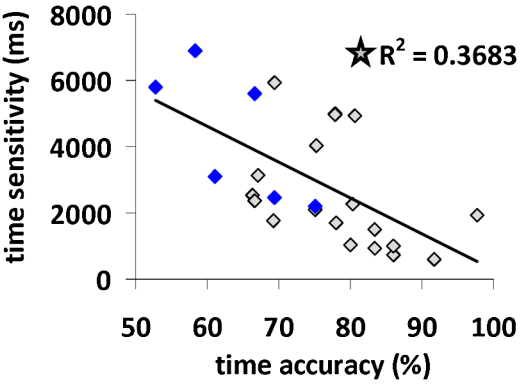

Figure 3. Supra-second temporal performance: accuracy vs. perceptual threshold. Temporal estimation accuracy measured in Task 1 (x-axis), and temporal discrimination perceptual threshold for supra-second durations (12 s) measured in Task 3 (the duration difference in milliseconds (ms) needed to discriminate 12 s durations at a fixed accuracy level of 75%) for supra-second durations by an adaptive method (y-axis). Each point in the scatter plot represents data from one participant (DDs in darker shade, controls in lighter shade). The significant correlation found between these two measurements indicates on the reliability of the main experimental task for assessing individual supra-second temporal discriminations ability. This figure is published in colour in the online version.

Since we found that a developmental numerical impairment affects supra-second time estimation, we directly examined whether numerical/arithmetical abilities correlated with the ability to estimate long durations. We found that supra-second temporal estimation significantly correlated with mathematical proficiency [supra-second timing accuracy vs. WAIS percentile: $R^2 = 0.46$, $t(15) = 3.59$, $p = 0.003$ (Fig. 4A); vs. GDA percentile: $R^2 = 0.45$, $t(15) = 3.51$, $p = 0.003$ (Fig. 4B); vs. Weber fraction: $R^2 = 0.23$, $t(15) = -2.11$, $p = 0.052$ (Fig. 4C); vs. number comparison mean RTs: $R^2 = 0.17$, $t(15) = -1.75$, $p = 0.099$, see Fig. 4D]. To examine whether these results are driven by a main effect of group, we explored whether they hold in each group separately. However, given the low number of DDs for a correlation analysis, we assessed the correlation between supra-second temporal estimation and mathematical proficiency in the controls only ($N = 11$ that had the mathematical measurements). The correlation in the controls was not significant but indicated a possible tendency [supra-second timing accuracy vs. WAIS percentile: $R^2 = 0.23$, $t(9) = 1.65$, $p = 0.13$; vs. GDA percentile: $R^2 = 0.18$, $t(9) = 1.42$, $p = 0.19$ (Fig. 4B)]. Although we cannot rule out that these results are driven by a main effect of group, they provide an additional illustration of the DDs' impairment in supra-second timing. We further examined whether the correlation between supra-second temporal ability and numerical skills was number–specific. To that end we examined whether supra-second temporal estimation correlated with verbal IQ, but found that they were not significantly correlated [$R^2 = 0.001$, $t(11) = -0.107$, $p = 0.91$].

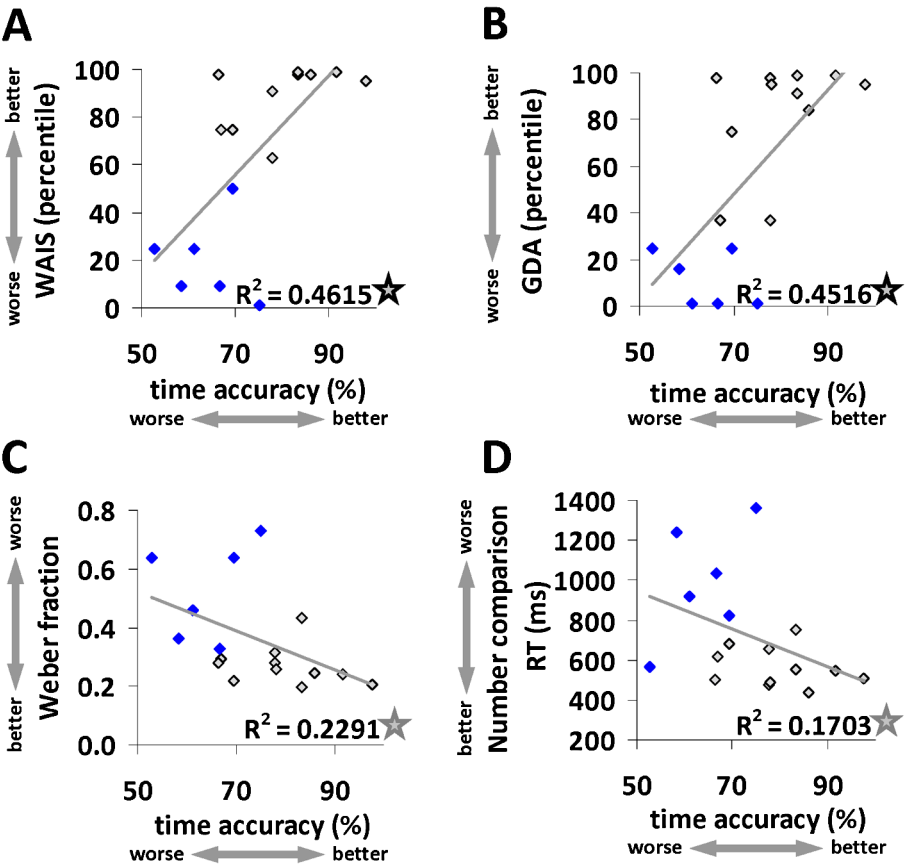

Figure 4. Correlations between supra-second temporal discrimination and mathematical performance. Performance for each participant is indicated by a point in each panel (dyscalculics in darker shade, controls in lighter shade). For all plots timing accuracy (Task 1) is plotted on the x-axes and mathematical performance on the y-axes: (A) WAIS, (B) GDA, (C) Weber fraction scores, and (D) number comparison response times (see Methods for more details). Pearson R^2 values are reported on each plot, with dark asterisks indicating correlation significance at $p < 0.05$, and light asterisks at $p < 0.1$. This figure is published in colour in the online version.

Finally we wanted to assess whether DD's impairment in supra-second temporal estimation might result from a difference in the strategies used to perform the task. Since counting is a commonly used strategy to estimate supra-second intervals (e.g., Brown et al., 1995; Gilliland & Martin, 1940), which might be defective in DDs (Butterworth, 2003, 2010; Kaufmann, 2008; Rubinsten & Henik, 2009), we reasoned that they might rely on different strategies to estimate supra-second durations. However, in the post-experimental debriefing all DDs as well as their controls reported that they relied on counting to estimate the supra-second intervals despite not being instructed to do so, and despite possible difficulties that

DDs might have with counting. Although this does not rule out the possibility that counting in DDs was different than counting in the controls, it suggests that DD and controls relied on a similar strategy to estimate supra-second durations.

4. Discussion

Our study examined the link between different dimensions of magnitude processing, and specifically time and number processing. We investigated whether a developmental impairment in numerical processing (developmental dyscalculia) generalized to another magnitude dimension, time perception. We reasoned that if numerical impairment co-occurred with time perception impairment, then some of the mechanisms supporting number and time processing might be shared. Anecdotally DD often report difficulties with daily life timings, for instance in calculating how much time there is between appointments, in estimating what time they need to leave home to be on time for an event, or sometimes not being able to estimate the duration of events, for example how long a traffic light stays red, how long a movie lasts, or even estimating how long it takes to travel to familiar destinations. Our dyscalculic participants also reported recurrent time estimation difficulties that emerge during mundane activities. This of course could be a result of numerical calculations often involved in temporal estimation, for instance calculating how much time is left until a deadline involves subtracting current time from the target time. In this study we focused on supra-second time ranges since timing in this time range (and not sub-second timing) commonly involves numerical processes such as counting (for time estimation), subtracting (to estimate an event's duration from start to end) and adding (how long consecutive events will last), and we used a temporal estimation task that did not require direct numerical calculations. We found that dyscalculia co-occurred with significant impairment in estimating supra-second temporal durations ($\sim$12–13 s). This was not due to sustained attention being impaired, as dyscalculics were not impaired in a non-temporal control task with similar sustained attentional demands. Moreover, the ability to estimate supra-second durations significantly correlated with proficiency in mathematical tasks. Thus our results are suggestive of a shared mechanism involved in both supra-second timing estimation and at least some numerical abilities.

Why would supra-second time estimation and numerical ability rely on joint mechanisms? One possibility might be that dyscalculics are globally impaired on many tasks, which could explain their time estimation impairment. However, our DDs showed average or high average IQ (see Table 1), and they were not impaired in the non-temporal colour control task, ruling out such an explanation. A second possibility is that impaired attention in DD might affect both their numerical ability and their supra-second time estimation. However, this possibility is also unlikely given the results of the control task, where DDs showed no sustained atten-

tion deficit in a non-temporal control task (see above). It may also be possible that both supra-second time estimation and numerical ability rely on counting, which some consider critical to the development of higher mathematical skills (for the relationship between counting and higher mathematical skills see Butterworth, 1999, 2010). Even though counting is a basic and almost effortless skill, for individuals with numerical impairments as DDs, counting may not be straightforward, and even when it is fully developed in adulthood, its acquisition might not have followed the normal developmental trajectory (Geary et al., 1992, 2000; Landerl et al., 2004). Furthermore, even when fully developed, counting in DDs may elicit an abnormal emotional response such as stress (Rubinsten & Tannock, 2010). When typical numerically developed individuals need to perform supra-second timing estimation, they often rely on counting strategies (Brown et al., 1995; Gilaie-Dotan, Kanai & Rees, unpublished observations; Gilliland & Martin, 1940) that allow them to estimate slightly better supra-second intervals (Grondin et al., 1999, 2004; Rakitin et al., 1998; but see Hinton & Rao, 2004). Studies investigating the effectiveness of counting found that counting is advantageous for estimating intervals longer than 1.18 s but not for sub-second intervals (Grondin et al., 1999, 2004) and that musicians with extensive musical training reproduce supra-second intervals more accurately than non-musicians, whether relying on counting or singing (Grondin & Killeen, 2009). Due to this common tendency to use counting for estimating supra-second intervals, studies examining supra-second timing mechanisms often use a dual task to interfere or prevent counting (see Hinton & Rao, 2004; Rakitin et al., 1998), or specifically instruct participants not to count when timing (Hinton & Rao, 2004; Rakitin et al., 1998; Treisman, 1984). Therefore, we suggest that while counting does not adversely affect supra-second time estimation in typical numerically-developed individuals, for DDs, due to their possible difficulties with counting, their reliance on counting to perform supra-second timing estimation may have adversely affected performance and lowered accuracy rates.

The timing performance we measured here may rely on a counting strategy, giving the impression that timing and number sense are associated because of the counting strategy. However, this is not necessarily the case as timing with and without counting has yielded similar although not identical performances (Brown et al., 1995; Gilliland & Martin, 1940), with counting reducing the variance in performance (Grondin et al., 1999, 2004; Hinton et al., 2004). Future studies need to determine whether DD's would also be impaired in supra-second timing when not relying on counting, as for example in the 'peak interval' paradigm, whereby one learns through feedback to reproduce a supra-second interval (see Hinton & Rao, 2004; Rakitin et al., 1998, and below).

The internal clock model proposes that timing behaviour is based on the interaction of an internal clock, memory storage of a reference duration, and comparison processes (e.g., Allman et al., 2014; Treisman, 1963; Treisman et al., 1990; for review see Wearden, 2005). Briefly, depending on a sensory arousal centre,

the pacemaker usually produces ticks/pulses at a constant basic characteristic rate/frequency (Treisman et al., 1990, 1994) and sends them to a counter (i.e., the accumulator). Comparing the values in the counter with the reference duration stored in memory, determines the behavioural response. More sophisticated variations of this model accommodating for the complexity of biological systems have been suggested by Treisman and colleagues (see Treisman et al., 1990, 1994). For example, different arousal or emotional states, or sensory inputs may affect the pacemaker function by perturbing its characteristic output frequency which in turn might slow or speed up the internal clock function and cause over- or under-estimation of time (see Treisman et al., 1990, 1994). We hypothesize that in DD the pacemaker may commonly tick normally. However, when DDs performed time estimations that involve counting, which might have developed abnormally in DDs, the counting process itself might have led to perturbations (delivered as sensory inputs) in their pacemaker outputs, or to a noisier function of their internal clock counter (i.e., the accumulator), thereby lowering their accuracy rates. Counting may also lead to storing numerical values in the internal clock memory storage rather than reference durations, thereby modifying the temporal magnitude comparisons (counter vs. memory) to numerical magnitude comparisons (Grondin et al., 2004), which DDs might be impaired in. Therefore, we suggest that DDs might perform normally on supra-second timing tasks that do not involve counting (e.g., judging which of two clip or two song excerpts is longer, and in paradigms as the peak interval procedure (see above; Hinton & Rao, 2004; Rakitin et al., 1998). In such tasks numerical processing might not interfere with the characteristic rhythmic activity of the pacemaker. Support for the interference of numbers with timing processes in DD comes from a recent study showing that DDs were not impaired in sub-second duration tasks, but when task-irrelevant number stimuli were introduced, DDs' sub-second timing performance dropped significantly (Cappelletti et al., 2011a). Thus, despite normal sub-sec timing in DD, even irrelevant numerical involvement can disrupt it. So it remains possible that counting could create interference in supra-second time estimation, and that the degree of interference could be related to numerical competence. Whether supra-second timing is impaired in DDs when counting is not involved (see above) remains to be tested in future research.

An alternative hypothesis to explain the supra-second time estimation impairment in DDs that we observed may be that sub- and supra-second distinctions in the time domain parallel small (up to 3–4) and bigger numerosity (bigger than 4) processing in the numerical domain (Agrillo et al., 2012; Buhusi & Cordes, 2011; Butterworth, 2010; Trick & Pylyshyn, 1993). This suggestion is based on the proposal that smaller numbers rely on similar mechanisms as sub-sec time perception, while bigger numbers rely on joint mechanisms as supra-second time estimation (Buhusi & Cordes, 2011). This idea is consistent with the proposition that dyscalculics would be more impaired when bigger numbers are involved (but see But-

terworth, 2010), and also with the fact that DDs are not significantly impaired in sub-sec timings (Cappelletti et al., 2011a). Furthermore, the transition between sub-second ('automatic' or 'sensory-motor' timing, Bueti et al., 2012; Buhusi & Meck, 2005; Buonomano, 2007; Lewis & Miall, 2003; Macar et al., 2006; Naatanen et al., 2004; Wiener et al., 2010) and supra-second ('cognitive') timing mechanisms occurs at around 3 s (Gilaie-Dotan et al., 2011; Poppel, 1997), which might parallel the transition between mechanisms supporting small and larger numerosities (Agrillo et al., 2012; Buhusi & Cordes, 2011; Cordes & Brannon, 2009), although there is no consensus about this idea (see Buhusi & Cordes, 2011 for review). While a distinction between 'small' and 'large' numerosities can be dichotomised, one might also consider it on a magnitude continuum. Taking that view, DDs might be impaired in accumulating continuous information, as evident in bigger numerosities or supra-second durations, and even in counting. We note however, that our control task did not involve a continuous accumulation process, so it is not possible to fully test the accumulation hypothesis. Here we focused on supra-second durations of the order of 12 s that are well within the supra-second domain to ensure that we were not tapping into short sub-second temporal mechanisms (Hayashi et al., 2013a; Poppel, 1997), and are also in the big numerosities range (Agrillo et al., 2012; Butterworth, 2010).

Finally, time and number sense (for review see Allman et al., 2011) might have developed together, as supported by similar developmental trajectories (Brannon et al., 2007; Cordes & Brannon, 2008; Roitman et al., 2007; but see Yates, 2012), by behavioural evidence of magnitude/processing interference between temporal and numerical dimensions (Javadi & Aichelburg, 2012; Tokita & Ishiguchi, 2011), and by the anatomical proximity of the brain regions involved in time and number processing. For example the parietal cortex is activated by both sub-second temporal information and by numeric information (Castelli et al., 2006; Hayashi et al., 2013a), and lesion studies in parietal cortex indicate its involvement in processing both dimensions (Cappelletti et al., 2011b; see also Bueti & Walsh, 2009).

It has been proposed that magnitude dimensions such as space, time and number share common mechanisms (e.g., Aagten-Murphy et al., 2014; Bueti & Walsh, 2009; Cantlon et al., 2009; Lustig, 2011; Walsh, 2003; but see Agrillo et al., 2010; Dehaene & Brannon, 2010; Murphy, 1997; Yates et al., 2012), but it is not clear whether this applies to bigger values/quantities within each magnitude dimension. The parietal cortex has been suggested to be the underlying common magnitude processing region (Cohen Kadosh et al., 2012; Walsh, 2003), especially for smaller quantities, in activation studies (Castelli et al., 2006; Hayashi et al., 2013a), lesion studies (Cappelletti et al., 2011b), and TMS (e.g., Hayashi et al., 2013a), but whether such a 'hub' exists for bigger quantities is still unclear. Furthermore, while bigger numerosities (bigger than 4, see above) might parallel supra-second time range, it is not clear what would be the spatial parallel. In the time domain there are many indications that time perception in different temporal scales (from milliseconds

to years), are probably supported by distinct perceptual and neural mechanisms (Buhusi & Meck, 2005; Cappelletti et al., 2009; Gilaie-Dotan et al., 2011; Lewis & Miall, 2003; Merchant et al., 2013; Poppel, 1997). We suggest that timing mechanisms for time ranges longer than supra-second may be supported by mechanisms that may not be serving numerical or spatial processing. These could rely on rhythmic bodily oscillatory mechanisms, circadian cycles, and even memory-related networks for longer-term timings, and will have to be tested in future studies.

In conclusion, we found a specific impairment in supra-second time estimation in developmental dyscalculia that was not due to attentional factors, and that correlated with mathematical ability. We hypothesize that the abnormal development of counting in developmental dyscalculia might underlie the supra-second timing estimation impairment, rather than a general magnitude mechanism impairment. Such atypical counting, when involved in timing operations, may adversely affect the function of internal clock components.

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