

Electrophysiological signatures of visual temporal processing deficits in developmental dyslexia

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Abstract

Developmental dyslexia (DD) is a common neurodevelopmental disorder that affects reading ability despite normal intelligence and education. In search of core deficits, previous evidence has linked DD with impairments in temporal aspects of perceptual processing, which might underlie phonological deficits as well as inefficient graphemic parsing during reading. However, electrophysiological evidence for atypical temporal processing in DD is still scarce in the visual modality. Here, we investigated the efficiency of both temporal segregation and integration of visual information by means of event-related potentials (ERPs). We confirmed previous evidence of a selective segregation deficit in dyslexia for stimuli presented in rapid succession (<80 ms), despite unaffected integration performance. Importantly, we found a reduced N1 amplitude in DD, a component related to the allocation of attentional resources, which was independent of task demands (i.e., evident in both segregation and integration). In addition, the P3 amplitude, linked to working memory and processing load, was modulated by task demands in controls but not in individuals with DD. These results suggest that atypical attentional sampling in dyslexia might weaken the quality of information stored in visual working memory, leading to behavioral and electrophysiological signatures of atypical temporal segregation. These results are consistent with some existing theories of dyslexia, such as the magnocellular theory and the “Sluggish Attentional Shifting” framework, and represent novel evidence for neural correlates of decreased visual temporal resolution in DD.

KEYWORDS

ERPs, methods, reading disorders, temporal attention, temporal integration windows, timing and temporal processing, vision

Laura Franchin and Luca Ronconi shared co-last authorship.

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1 | INTRODUCTION

Developmental dyslexia (DD) is a common neurodevelopmental disorder that manifests with slower reading speed, as well as errors in spelling, letter recognition, and, to a lesser degree, text comprehension (Peterson & Pennington, 2012; Siegel, 2006). Its high prevalence, reported to range between 5 and 20% in the general population (Wagner et al., 2020), as well as the benefits of early intervention, justify the sustained interest in the etiology of the disorder, which remains a matter of debate (Shaywitz et al., 2021). In search of core deficits of dyslexia, different theories have been proposed to explain the variety of its manifestations, ranging from impairments in phonological processing to low-level deficits in sensory and attentive processing. Phonological skills, defined as the ability to manipulate phonemes to process written and oral language, are essential skills in reading development (Melby-Lervåg et al., 2012). Although phonological deficits are most commonly reported, there is evidence that impairments in phonological processing are not necessary or sufficient to account for dyslexia (Pennington, 2006; Snowling et al., 2020). Reading is a complex process that requires not only phonological skills but also precise sequencing of sounds and words, in turn dependent on accurate timing of auditory and visual stimuli, that is, temporal processing (Stein, 2019). Studies have reported atypical temporal processing in dyslexia using auditory (Ben-Yehudah et al., 2004; Cohen-Mimran & Sapir, 2007; Helenius et al., 1999; Hornickel & Kraus, 2013; Murphy & Schochat, 2009) and visual (McLean et al., 2011; Ronconi et al., 2020) tasks (or a combination of the two, see, for example: Casini et al., 2018; Edwards et al., 2004; Gori et al., 2020; Laasonen et al., 2011; Van Ingelghem et al., 2001).

On the theoretical level, temporal processing deficits have been investigated in the auditory domain since the 1980s, with the formulation of the “rapid temporal processing deficit hypothesis” by Tallal (1980). According to the hypothesis, phonological deficits present in DD arise from low-level auditory deficits, where the inability to process the rapid succession of sounds prevents the correct identification of phonemes (Tallal, 1980). In the visual domain, the magnocellular theory has provided a neurobiological basis for temporal processing deficits observed in dyslexia (Stein, 2019; Stein & Talcott, 1999; Stein & Walsh, 1997). The magnocellular pathway, projecting mostly to the dorsal visual stream, has been implicated in the processing of rapidly changing visual stimuli and in oculomotor control, and has been found to be impaired in dyslexia in a number of studies showing increased thresholds in contrast sensitivity and coherent motion (Pammer & Wheatley, 2001), poor

oculomotor adjustments while reading (Jainta & Karpoula, 2011), and reduced activation in area V5/MT for moving stimuli (Eden et al., 1996). Furthermore, dorsal stream sensitivity assessed in preschool years predicts early literacy skills (Kevan & Pammer, 2009). Magnocellular deficits could be responsible for a cascade of effects at different processing levels, affecting both sensory and attentional processing (Hari & Renvall, 2001). Specifically, it has been hypothesized that dorsal magnocellular dysfunction could play a role in temporal and spatial aspects of attention, both necessary for the correct selection and parsing of graphemic units during reading (Krause, 2015). According to the “Sluggish Attentional Shifting” (SAS) framework, a prolonged attentional dwell time is responsible for the slowdown in processing rapidly presented sequences of stimuli (Hari & Renvall, 2001). In other words, when faced with sequences of stimuli, the attentional system of dyslexic individuals fails to efficiently engage and disengage from one item to the next one, which might translate to reduced temporal resolution and temporal segregation deficits. Furthermore, reading requires rapid orienting of spatial attention to the target grapheme among distractors, possibly recruiting visuo-spatial attentional mechanisms deployed in visual search tasks (Franceschini et al., 2012; Krause, 2015; Vidyasagar & Pammer, 2010). Despite its long history, the magnocellular theory of dyslexia has also been controversial (Handler et al., 2011). As magnocellular neurons are thought to be preferentially activated with low spatial and high temporal frequency (Ellemberg et al., 2001; Livingstone & Hubel, 1987), the presence of mixed results using stimuli with these characteristics raises a number of questions (Skottun, 2000). Similarly, the use of higher-level perceptual tasks, such as the coherence motion task, in investigating magnocellular function is not immune to criticism, since it is hard to isolate in these tasks the magnocellular functionality from other critical neural mechanisms, such as temporal integration and perceptual noise exclusion (Goodbourn et al., 2012; Skottun, 2015; Sperling et al., 2006).

One way of investigating information processing with high temporal precision is by means of event-related potentials (ERPs), where deviations from a typical waveform shed light on the nature and temporal locus of divergent processing (Duncan et al., 2009). Previous studies in DD reported atypical electrophysiological signatures in response to basic perceptual processing in the auditory and visual modality (for a review, see Schulte-Körne & Bruder, 2010). Specifically, dyslexic participants present a reduced mismatch negativity (MMN) component, a negative ERP deflection occurring when a train of tone patterns presented rhythmically is interrupted by an infrequent “oddball” tone of

different duration and frequency (Corbera et al., 2006; Kujala et al., 2000; Meng et al., 2005). N1, a prominent component related to auditory processing and attention, is reduced in response to brief stimuli presented at interstimulus intervals (ISIs) of 100–200 ms in poor readers, who perform worse in a temporal ordering task as compared to good readers (Nagarajan et al., 1999). In the visual domain, dyslexic participants show atypical ERP patterns in response to coherently moving dots (Schulte-Körne et al., 2004) as well as flickering checkerboards (Stein, 2021). Using an attentional-shifting task, Wijers et al. (2005) reported that, whereas normal readers presented a positive frontal activity (around 350 ms) lateralized over the right hemisphere, dyslexic participants showed this effect over both hemispheres, suggesting a dysregulation of interhemispheric asymmetry. To our knowledge, only one study investigated electrophysiological correlates of temporal aspects of visual perception in dyslexia. Lallier et al. (2010) used a stream segregation task within an oddball paradigm where an alternating small dot appeared either above or below the central fixation point in rapid succession. By varying the ISI, they could manipulate the predicted percept to be either one or two streams of dots; in the case of longer ISIs (i.e., fast deviant tempo), the two alternating dots would be perceived as belonging to one stream moving up and down, whereas with shorter ISIs (i.e., standard tempo) the two dots would appear as simultaneous, thus belonging to two separate streams. Results showed that participants with DD had higher segregation thresholds as they perceived the two streams as simultaneous at intermediate deviant ISIs, whereas controls did not. Furthermore, the difference in the P3b component elicited in response to intermediate versus fast deviant tempos was smaller in the DD group, suggesting that both the intermediate and the short ISI conditions were salient as they were perceived differently by participants with DD. With an analogous paradigm and results in the auditory modality, the authors suggest that limitations in amodal attentional resources compatible with the SAS framework are responsible for the slowing down of rapid sequential processing.

To further investigate the nature of visual temporal processing deficits in DD, Ronconi et al. (2020) tested an adult population with DD by means of the “SegInt” task, a modified version of the missing element task (Di Lollo, 1980). By keeping constant visual stimulation while changing task instruction, the “SegInt” task allows us to investigate both temporal segregation and integration, the two complementary mechanisms at the basis of temporal processing. More specifically, temporal integration refers to the ability to combine sensory information over time so that it is perceived

as belonging to the same, coherent percept. Temporal segregation, necessary to perceive rapid changes in the environment, refers to the ability to separate sensory information over time, thus providing a more or less fine-grained temporal resolution to the perceptual system. In the “SegInt” task, two displays of stimuli separated by a varying ISI are flashed in rapid succession. Depending on the instruction, participants are asked to either integrate or segregate visual stimuli over time. In the study, the authors found that participants with DD were specifically impaired in the temporal segregation of stimuli presented in rapid succession while performing equally to controls in the integration of visual input.

Taken together, evidence in the literature suggests that, across modalities, dyslexic participants show reduced temporal resolution, as indicated by increased thresholds for the perception of sequential stimuli presented at short ISIs. This result has been interpreted in light of either atypical perceptual or attentional processing, but neuroimaging evidence in support of these theoretical proposals is scarce when considering temporal processing in the visual modality. The aim of the current study is to investigate a specific deficit in visual temporal segregation, as reported by Ronconi et al. (2020), by means of ERPs. In neurotypical populations, studies have shown that successful visual temporal integration acts in early as well as late processing stages, as evidenced by the modulation of N1, N2, and P3 components (Akyürek, Schubö, & Hommel, 2010). Investigating these electrophysiological signatures of temporal processing might shed new light on the underlying mechanisms of impaired segmentation of visual information in DD.

2 | METHOD

2.1 | Participants

A total of 57 participants were recruited for the study (mean age = 22.2 years, age range: 18–30 years), 26 adults with a diagnosis of developmental dyslexia (9 females, 17 males), and 31 normal readers (16 females, 15 males). Participants' level of education ranged between 11 and 21 years, with most of the participants ($n = 54$) being university students. Participants with DD were in possession of an official diagnosis certified by a clinical psychologist (mean age of most recent certification = 17 years, age range: 13–22 years) and were compensated for their participation, whereas control participants could receive university credits, if interested. The research project was approved by the Ethical Committee of the University of Trento, and all participants gave informed consent for participation.

2.2 | Cognitive tests

Participants were administered cognitive tests to assess non-verbal intelligence and reading ability. Non-verbal intelligence was assessed with a shortened version of Raven's Advanced Progressive Matrices (APM; Raven et al., 1998), where participants are requested to make judgments on increasingly complex geometric designs with a missing element. The number of correct responses is taken as a measure of general non-verbal intelligence. Reading ability was assessed by means of two tests. First, a text reading test required participants to read aloud the extract "Funghi in città" (Judica & De Luca, 2005). Second, participants were asked to read lists of words and pseudowords (extracted from Sartori et al., 1995). Reading ability was assessed through three parameters: time, speed, and accuracy (as defined by Stella & Tintoni, 2007). Errors were counted following Cornoldi and Colpo (1981) guidelines.

2.3 | Apparatus and stimuli

Stimuli were presented on a light gray background on a 23.5" EIZO monitor (vertical refresh rate 100 Hz, viewing distance of 57 cm) using the E-prime 3.0 software (Psychology Software Tools, Pittsburgh, PA). Stimuli consisted of two target displays each containing 8 stimuli randomly positioned among 16 possible positions on an invisible 4×4 quadratic grid. The stimuli subtended a 0.5-degree size and a 0.06-degree line width. The size of each location was 1×1 degree, and the invisible grid had a 0.5-degree space between grid locations. Seven random locations were filled with a full black annulus separated by a central gap at different orientations (0°, 45°, 90°, or 135°), whereas one location was filled with an "odd stimulus," a half annulus with mirrored orientation between displays (so that the two halves formed a full annulus if merged across displays). One location was left empty on both displays. The same stimuli were employed in previous studies with the "SegInt" paradigm (Freschl et al., 2019; Ronconi et al., 2018, 2020; Sharp et al., 2018, 2019; Wutz et al., 2016, 2018).

2.4 | Procedure

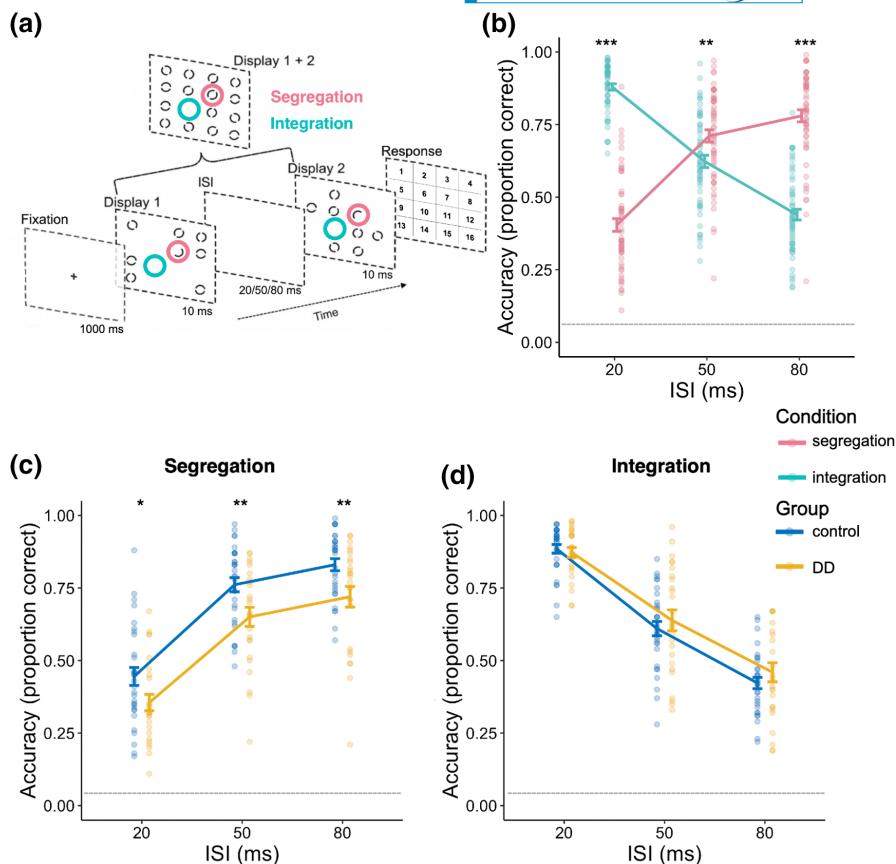
Each trial of the "SegInt" task started with a fixation screen (1000 ms), followed by the presentation of two displays of stimuli presented for a duration of one refresh cycle (10 ms each), separated by a blank interstimulus interval (ISI duration = 20, 50 or 80 ms). During the training phase, participants were instructed to perform the two separate tasks on different blocks. In

segregation blocks, participants were instructed to find the "odd stimulus", and this could be achieved only with correct temporal segregation of the two visual displays. If the two displays were integrated, the two half annuli would be merged in one complete annulus, identical to the others. In integration blocks, participants were instructed to find the empty grid location, which could be achieved only by integrating two sequential displays (see Figure 1a for a schematic representation of the stimuli and task). Changing task instructions prior to each block allowed us to test temporal segregation and integration processes using the same visual stimulation. Once the stimuli disappeared, a response grid was presented, and participants were instructed to respond with a mouse click on the position on the screen corresponding to the target stimulus. Although we specified to participants that only accuracy mattered, we set a temporal constraint of 10 s for providing a response. As the target stimulus appeared randomly among 16 possible locations, chance-level performance was equal to 1/16 (6.25%). The experiment consisted of six blocks in which participants were presented, in alternation, with segregation and integration conditions. Each block lasted 10 minutes, and block order was counterbalanced across participants. Each combination of ISI and condition was presented for 150 trials, for a total of 900 trials.

2.5 | EEG recording and preprocessing

EEG data were recorded using eego™sports (ANT Neuro, Enschede, The Netherlands) from 64 electrode sites (extended international 10–20 system), with AFz electrode as ground electrode and CPz as online reference. Eye blinks were monitored with an electrode placed at the suborbital ridge of the left eye. Raw data were preprocessed using MATLAB R2020a (The MathWorks Inc., 2020) and the EEGLAB toolbox, version 2021.1 (Delorme & Makeig, 2004). Electrode impedance was kept below 20 kΩ. Originally sampled at 500 Hz, offline data were resampled at 250 Hz and re-referenced to an average reference. Afterward, high-pass and low-pass filters (low cutoff 0.5 Hz, high cutoff 80 Hz), as well as a notch filter at 50 Hz, were applied. Epochs of 2000 ms (−1000 ms to 1000 ms relative to the first display onset) were extracted from the continuous data. Spherical interpolation was performed on noisy channels if necessary (average of interpolated channels = 2.5, SD = 2.07). User-based independent component analysis (ICA) was performed to identify and remove artifactual components; we removed components classified by the ICLabel plugin as "eye,"

FIGURE 1 (a) Schematic representation of the stimuli used to evaluate temporal segregation and integration. (b) Accuracy rates for “SegInt” task performance pooled for DD and control participants and plotted as a function of ISI. (c) Accuracy rates for the segregation and (d) integration conditions, plotted as a function of ISI and separated for group. Error bars represent standard error of the mean (SEM), and points represent individual participants' accuracy. The dashed gray line represents chance level (6.25%). * $p < .05$, ** $p < .01$, *** $p < .001$. DD, developmental dyslexia; ISI, interstimulus interval.



“muscle,” “heart,” “line noise,” or “channel noise” with a probability higher than 90% and with zero probability of being categorized as “brain” component. Following ICA-based artifacts correction, visual inspection of the segmented EEG data was used to eliminate epochs where clear artifacts were still present. This procedure led, across participants, to the rejection of 3.6% of artifactual epochs ($SD = 0.04\%$).

2.6 | ERP analysis

To extract ERP data, MATLAB toolbox ERPLAB version 8.30 was used (Lopez-Calderon & Luck, 2014). The ERP components selection was performed using a two-step method. First, potential components of interests and their latencies were identified from prior literature employing similar tasks (namely P1, N1, P2, and P3 components; identified based on Akyürek, Schubö, & Hommel, 2010, which used a missing element task; Ronconi, Pincham, et al., 2016, which used an attentional blink task; and Ronconi et al., 2017, which used a two-flash fusion task). Afterward, ERP components were identified in the present data set using the collapsed localizer method (Kappenman & Luck, 2016), where data from all participants, conditions, and ISIs were averaged into a single grand-grand-average

waveform (Figure S1). This method allows to determine time windows for ERP components while being blind to between-condition or between-group differences that could bias selection (Kappenman & Luck, 2016). The following components and time windows were selected: P1 (110–140 ms), N1 (180–220 ms), N2 (260–300 ms), and P3 (350–500 ms). These components emerged and were analyzed over three posterior clusters: posterior left (P7, P5, P3, PO7, and PO5), posterior midline (P1, Pz, P2, PO3, POz, PO4, O1, Oz, and O2), and posterior right (P4, P6, P8, PO6, and PO8) clusters. A repeated-measures analysis of variance (RM-ANOVA) was performed on mean amplitude values of correct trials for each identified component using JASP (version 0.16.1; JASP Team, 2022).

3 | RESULTS

3.1 | Reading and non-verbal IQ scores

As revealed by independent samples t tests, DD and control participants had a comparable non-verbal IQ score, $t_{(55)} = 1.215$, $p = 0.23$, while they differed significantly in all reading measures (all $ps < .05$), indicating that DD diagnoses reflected slower and less accurate reading performance (Table 1).

TABLE 1 Results from reading and non-verbal IQ tests in participants with developmental dyslexia and controls.

	Controls (<i>n</i> = 31) mean (<i>SD</i>)	DD (<i>n</i> = 26) mean (<i>SD</i>)	T-test type	<i>t</i> value	<i>df</i>	<i>p</i>
Raven's AMP matrices	7.968 (2.168)	7.192 (2.654)	Student	1.215	55.000	.230
Text reading speed	0.042 (0.770)	-3.419 (3.895)	Welch	4.459	26.642	<.001
Text reading accuracy	0.777 (0.585)	-0.916 (1.609)	Welch	5.089	30.535	<.001
Words reading speed	0.764 (1.121)	-1.080 (1.046)	Student	6.376	55.000	<.001
Words reading accuracy	0.083 (0.630)	-0.722 (1.604)	Welch	2.406	31.446	.022
Pseudowords reading speed	0.863 (1.414)	-1.237 (0.937)	Student	6.469	55.000	<.001
Pseudowords reading accuracy	0.626 (0.548)	-0.328 (1.414)	Welch	3.242	31.280	.003

Note: All reading measures are reported in *z* scores. Welch's *t* tests were applied when Levene's test of significance suggested a violation of the equal variance assumption.

Abbreviations: APM, advanced progressive matrices; DD, developmental dyslexia.

3.2 | Accuracy in the “SegInt” task

Segregation and integration performance were investigated by means of repeated-measures ANOVA with condition (segregation vs. integration) and ISI (20, 50 vs. 80) as repeated-measures factors and group (DD vs. controls) as a between-subject factor (Table S1). Greenhouse–Geisser correction was applied when the assumption of sphericity was violated. A main effect of ISI ($F_{(1.373,75.538)} = 17.432$, $p < .001$, $\eta_p^2 = 0.241$) and an interaction between ISI and condition ($F_{(1.729,95.087)} = 1125.431$, $p < .001$, $\eta_p^2 = 0.953$) indicated that task accuracy depended on ISI and condition. As shown in Figure 1b, the direction of the interaction was in accordance with previous results reporting an increase in segregation performance for longer ISIs and an increase in integration performance for shorter ISIs, showing that the ISI manipulation proved successful (as in Ronconi et al., 2020). Importantly, an interaction between condition and group ($F_{(1,55)} = 5.072$, $p < .05$, $\eta_p^2 = 0.084$) emerged, with planned contrasts showing a significantly reduced accuracy in the DD group only in the segregation condition ($t_{(106,147)} = 2.969$, $p < .01$; Figure 1c,d, Table S2). A series of independent *t* tests (planned contrasts) were conducted to further analyze this effect, revealing that the two groups differed in the segregation condition at ISI 20 ms ($t_{(146,749)} = 2.369$, $p < .05$), ISI 50 ms ($t_{(146,749)} = 2.914$, $p < .01$), and ISI 80 ms ($t_{(146,749)} = 2.898$, $p < .01$).

3.3 | ERP results

To unveil the temporal dynamics of the segregation deficit in DD, we tested possible between-group differences in the mean amplitude of early and late ERP components by means of RM-ANOVAs, with condition (segregation vs. integration), channels cluster (left, midline

vs. right posterior cluster), and ISI (20, 50 vs. 80 ms) as within-subject factors, and group (controls vs. DD) as a between-subject factor. Greenhouse–Geisser correction was applied when the assumption of sphericity was violated. See Table 2 for ERP mean amplitude values. Figures 2a-c and 3 show, respectively, ERP waveforms and topographic maps averaged over ISI levels (see Figure S2 for waveforms separated for ISI level). Concerning P1 mean amplitude, the ANOVA showed only a main effect of channel cluster ($F_{(1.715,94.331)} = 18.287$, $p < .001$, $\eta_p^2 = 0.25$). No interactions were found (all $ps > .056$; see Table S3). Investigating N1 mean amplitude, main effects of ISI ($F_{(1.747,96.091)} = 11.069$, $p < .001$, $\eta_p^2 = 0.168$), channels cluster ($F_{(1.4,76.994)} = 21.398$, $p < .001$, $\eta_p^2 = 0.28$), and group ($F_{(1,55)} = 4.095$, $p < .05$, $\eta_p^2 = 0.069$) emerged, with the DD group having a reduced N1 mean amplitude as compared to controls (Figure 2b). An interaction between ISI and channel cluster emerged ($F_{(1.788,98.336)} = 3.589$, $p < .05$, $\eta_p^2 = 0.061$; see Table S4). When considering N2 mean amplitude, main effects of ISI ($F_{(1.562,85.888)} = 12.647$, $p < .001$, $\eta_p^2 = 0.187$), channel cluster ($F_{(1.447,79.589)} = 7.211$, $p < .01$, $\eta_p^2 = 0.116$), and condition ($F_{(1,55)} = 4.097$, $p < .05$, $\eta_p^2 = 0.069$) were found, with the integration condition being linked to a reduced N2 mean amplitude as compared to the segregation condition. Furthermore, an interaction between channel cluster and condition emerged ($F_{(1.278,70.294)} = 18.949$, $p < .001$, $\eta_p^2 = 0.256$; see Table S5). Regarding P3 mean amplitude, main effects of ISI ($F_{(1.541,84.732)} = 6.591$, $p < .01$, $\eta_p^2 = 0.107$), channel cluster ($F_{(1.583,87.073)} = 16.013$, $p < .001$, $\eta_p^2 = 0.225$), and condition ($F_{(1,55)} = 37.556$, $p < .001$, $\eta_p^2 = 0.406$) were present, with lower amplitude for the integration condition. Interactions among condition, ISI, and channel cluster ($F_{(3.06,168.323)} = 3.979$, $p < .01$, $\eta_p^2 = 0.067$) and, importantly to our hypothesis, among condition, group, and channel cluster ($F_{(1.353,74.394)} = 4.208$, $p < .05$, $\eta_p^2 = 0.071$) were present (see Table S6). To analyze this effect, an

TABLE 2 Mean amplitude values (μV) for P1 (110–140 ms), N1 (180–220 ms), N2 (260–300 ms), and P3 (350–500) components.

Group	Segregation			Integration		
	20 mean (SD)	50 mean (SD)	80 mean (SD)	20 mean (SD)	50 mean (SD)	80 mean (SD)
Controls						
P1	1.344 (1.723)	1.315 (1.545)	1.455 (1.777)	1.741 (1.704)	1.460 (1.553)	1.410 (1.635)
N1	-5.448 (-3.922)	-5.183 (3.480)	-4.951 (3.612)	-5.308 (3.813)	-5.263 (3.569)	-5.001 (3.684)
N2	-2.278 (3.943)	-2.022 (3.956)	-1.639 (3.724)	-2.788 (3.918)	-2.256 (3.729)	-2.053 (3.898)
P3	1.682 (2.967)	2.150 (3.634)	2.014 (3.632)	1.270 (3.009)	1.025 (3.149)	0.646 (3.555)
DD						
P1	1.399 (1.454)	1.318 (1.256)	1.246 (1)	1.354 (1.115)	1.206 (1.078)	1.301 (0.898)
N1	-3.801 (2.344)	-3.418 (2.265)	-3.281 (2.219)	-3.729 (2.125)	-3.443 (2.156)	-3.484 (2.297)
N2	-2.327 (2.837)	-2.156 (2.542)	-2.042 (2.472)	-2.520 (2.632)	-2.325 (2.455)	-2.015 (2.501)
P3	1.198 (1.943)	1.585 (2.226)	1.161 (2.130)	0.770 (1.746)	0.769 (1.893)	0.383 (1.850)

Abbreviations: DD, developmental dyslexia; ISI, interstimulus interval.

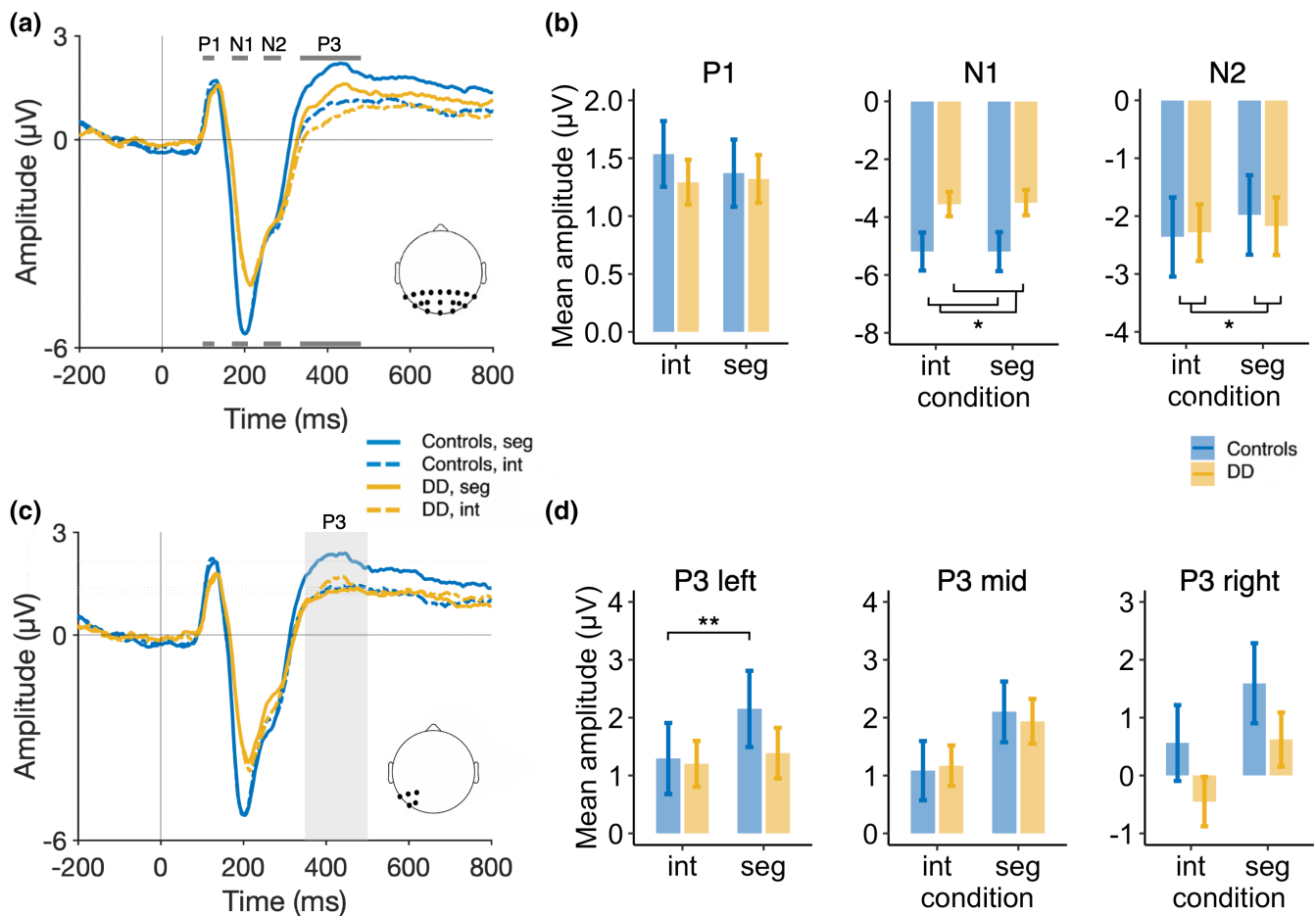


FIGURE 2 (a) ERP waveforms for group and condition averaged for ISI level and over three posterior channel clusters. (b) Mean amplitude (μV) averaged over ISI levels for P1 (110–140 ms), N1 (180–220 ms), and N2 (260–300 ms) components. Main results from RM-ANOVA are reported as follows: A main effect of group in N1 mean amplitude and a main effect of condition in N2 mean amplitude. (c-d) P3 (350–500 ms) mean amplitude was significantly different between conditions in the control, but not in the DD group. The effect was only found over left posterior channels. Error bars represent SEM, * $p < .05$, ** $p < .01$. DD, developmental dyslexia; int, integration condition; ISI, interstimulus interval; seg, segregation condition.

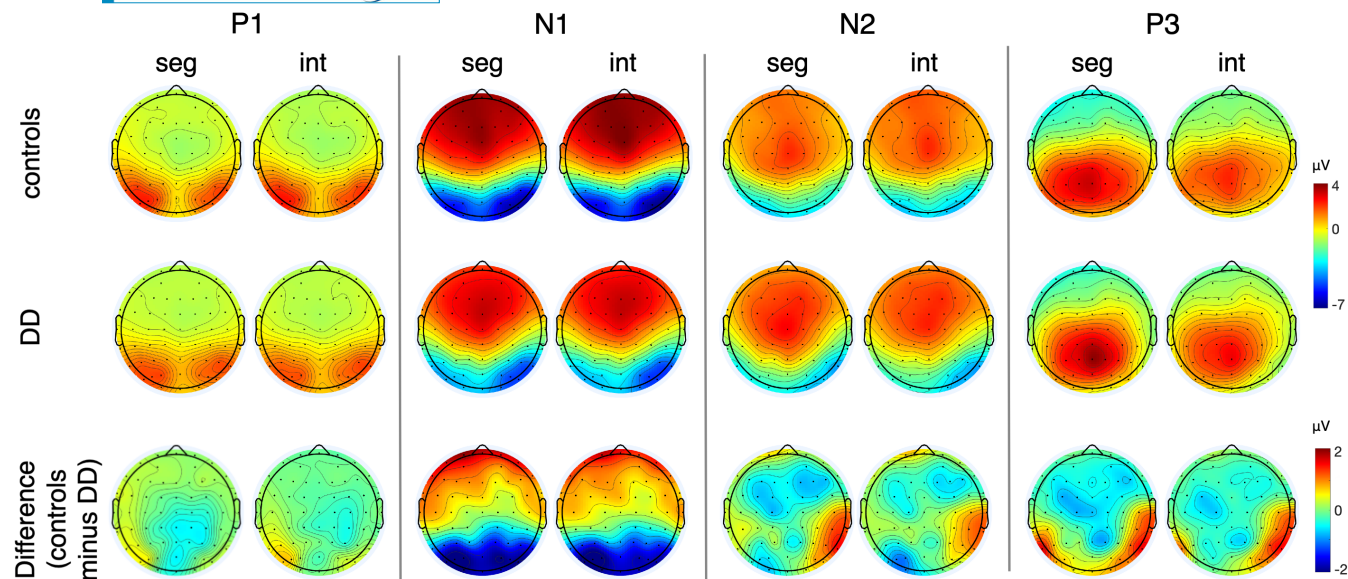


FIGURE 3 Topographic maps of ERPs, averaged over ISI level and divided for segregation and integration conditions. DD, developmental dyslexia; int, integration; ISI, interstimulus interval; Seg, segregation.

RM-ANOVA was conducted separately on each posterior cluster, revealing an interaction between group and condition in the posterior left cluster ($F_{(1,55)}=4.170$, $p < .05$, $\eta_p^2=0.07$), but not in the midline ($F_{(1,55)}=1.083$, $p = .303$) or right ($F_{(1,55)}=0.013$, $p = .909$) clusters (Figure 2d). Holm–Bonferroni corrected post hoc comparisons revealed that neurotypical participants presented higher P3 in the segregation condition as opposed to the integration condition in the posterior left cluster ($t_{(57)}=3.858$, $p_{Holm} < .01$, $d=0.283$). Importantly, this effect was absent in the DD group ($t_{(57)}=0.764$, $p_{Holm}=1$) as shown in Figure 2d. Post hoc comparisons did not reveal significant differences between controls and DD groups neither in the segregation ($t_{(57)}=-0.962$, $p_{Holm}=1$) nor in the integration ($t_{(57)}=-0.116$, $p_{Holm}=1$) conditions.

4 | DISCUSSION

The current findings replicate a specific deficit in temporal segregation abilities in adults with DD, as previously reported by Ronconi et al. (2020), suggesting that dyslexic individuals have a reduced temporal resolution of the visual system. We extend this previous evidence by showing that impaired visual temporal segregation in the DD group was accompanied by different stimulus-evoked electrophysiological signatures. Investigating the post-stimulus period by means of ERPs, we found no difference between dyslexic and neurotypical individuals in the P1 component (110–140 ms after the appearance of the first stimulus) but a reduction in N1 mean amplitude (180–220 ms) in the DD group for both integration and

segregation conditions. Furthermore, we found a task-specific modulation of P3 mean amplitude (350–500 ms) which was present in neurotypical participants but absent in the DD group.

The first positive deflection of the ERP waveform, the P1 component, is modulated by stimulus parameters and selective attention and reflects early cortical activation (Luck, 2005). Interestingly, P1 has been linked to magnocellular function, as it is primarily activated by stimulus manipulation eliciting magnocellular neurons (Elleberg et al., 2001), and its generators have been found along the dorsal visual stream (Di Russo et al., 2002). Reduced P1 amplitudes have been reported in the literature in populations presenting putative magnocellular deficits, such as schizophrenia (Doniger et al., 2002; Foxe et al., 2001; Schechter et al., 2005), although criticisms regarding interpretation and methodology remain (see, for example, Skottun & Skoyles, 2007). In a previous study using forward masking, the evoked MEG response was found to differ between masked and detected stimuli already in this early component (Wutz et al., 2014). A MEG study comparing integration and segregation, however, did not find any task-related difference (reduced evoked response for integration trials) until a period of around 160–290 ms after display 2 onset (Wutz et al., 2016).

Regarding dyslexia, evidence reporting P1 modulations is mixed (Kubová et al., 2015; Meng et al., 2022; Sayeur et al., 2013). As the current study does not test magnocellular function directly, the absence of a P1 reduction cannot be used as evidence against a magnocellular deficit in dyslexia. However, it suggests that the observed segregation deficit is not related to early visual

processing and that this processing stage seems unimpaired in dyslexia.

Differently from P1, the between-group differences in N1 could possibly relate to segregation deficits. As the N1 component has been linked to the deployment of attentional resources (Luck et al., 1994; Ozernov-Palchik & Gaab, 2016; Vogel & Luck, 2000), its reduced activation in DD might reflect a deficit in the correct allocation of attentional resources to task-relevant stimulus information. This hypothesis falls within the SAS framework, according to which DD deficits arise from the inability to shift temporal attention from one item to the next one rapidly enough (Hari & Renvall, 2001). In support of this hypothesis, previous studies investigating dyslexic children reported inadequate engagement and disengagement of temporal attention in the attentional blink task (Facoetti et al., 2008; Visser et al., 2004), as well as impairments in a temporal attention task that requires the identification of forward and backward masked objects (Ruffino et al., 2014). As temporal shifts of attention are necessary to disengage processing resources from the current object onto the next one, deficits in temporal attention might translate into an impaired temporal segregation performance, where rapidly succeeding stimuli have to be distinguished, but not necessarily impact temporal integration processes, where a fast attentional disengagement from the first appearing stimulus is not required to complete the task. This possible scenario might explain why, in the present study, we observe a specific behavioral deficit in the segregation condition but a suppression of the N1 component regardless of task instruction in the DD group.

We found a task/condition difference in evoked responses in the P3 component (350–500 ms), consistent with previous findings of a difference in evoked responses for integration and segregation (with MEG) in the 300–450 ms period (Wutz et al., 2016), but this was only present for the neurotypical group. Following the facilitation of target processing by attentional resources, task-relevant information is transferred into visual working memory, where it is maintained for further processing (Awh et al., 2006). The functional role of P3 has been linked to stimulus updating (Donchin & Coles, 1988; Duncan-Johnson, 1981; Kok, 2001) and/or maintenance in working memory, with P3 amplitude reflecting working memory load (Akyürek, Leszczyński, & Schubö, 2010; Brouwer et al., 2012; Korpela & Huotilainen, 2011). Studies employing the attentional blink task found a reduced P3 amplitude when the second target in a rapid serial visual presentation stream is missed, thus advancing P3 amplitude to be an index of successful transmission of stimulus information and allocation in working memory (Kranzioch et al., 2003; Sergent et al., 2005; Ronconi, Pincham, et al., 2016; for a review, see Zivony & Lamy, 2022). Using a visual temporal

segregation task similar to the one used in the present study, Akyürek et al. (2017) found that the P3 component was modulated as a function of the perceptual outcome, with higher P3 amplitudes for temporally segregated stimuli, and lower amplitudes for two integrated stimuli (see also Wutz et al., 2016, for a similar finding). In the present study, we report the same pattern of results in neurotypical individuals, who presented higher P3 amplitudes in segregation trials, where visual information within the two displays should be kept separate to perceive the “odd element,” as opposed to integration trials, where visual information is expected to be combined between the two displays to find the empty location. Taken together, these results suggest that a greater P3 amplitude reflects the processing effort necessary to maintain more information units, since temporal integration allows the stimuli to be condensed into fewer units of information. We suggest that in DD participants, possibly due to an excessive attentional engagement to the first display, information from the first display was still available when the second display appeared, resulting in involuntary integration. As a result, incoming stimuli for working memory maintenance and processing would mostly be one information unit regardless of task instruction. In this scenario, the absence of a P3 increase for segregation trials might be interpreted as a consequence of inefficient attentional allocation in time, rather than inefficient working memory processing itself.

Another possible explanation for the lack of P3 modulation in dyslexic participants could be inefficient stimulus updating in working memory, as described by a large number of studies investigating working memory capacity in DD. Previous research has reported reduced P3 amplitude and behavioral accuracy in DD populations in response to visual working memory tasks (Lofti et al., 2022). Furthermore, training in working memory tasks resulted in improvements in working memory capacity and reading ability in DD participants, reflected by increased P3 amplitude (Shiran & Breznitz, 2011). However, we should stress that we did not find significant differences in P3 amplitudes between dyslexic and control participants, but a significant difference among conditions in the control group, which was absent in the DD group. Given the absence of a generally reduced P3 amplitude in participants with DD, we interpret the result as an index of the impoverished processing load on working memory rather than a consequence of inefficient working memory processing in dyslexia. Furthermore, P3 modulation was only significant over posterior left scalp channels, possibly indicating the involvement of left-lateralized ventral stream areas that are specialized for processing letter stimuli (Dehaene et al., 2005; Ronconi, Bertoni, & Bellacosa Marotti, 2016; Vinckier et al., 2007), and thus could be similarly specialized

to process letter-like stimuli such as the half annuli of the “SegInt” task. Finally, we would like to pinpoint that while we labeled this late positive inflection in the ERP waveform as P3, there might be a certain overlap with the late positive component (LPC), a component thought to be mostly related to memory maintenance and memory trace strength in visual recognition paradigms (Finnigan et al., 2002; Yang et al., 2019). Similar to the modulation of the P3 component in missing element and attentional blink tasks (Akyürek, Leszczyński, & Schubö, 2010; Akyürek, Schubö, & Hommel, 2010; Sergent et al., 2005), the LPC appears to be modulated by the amount of information retrieved (Vilberg et al., 2006). Interestingly, previous accounts found that the effect of the LPC is also left lateralized (Finnigan et al., 2002). These common aspects between the P3 and LPC modulation based on memory maintenance suggest that these two components might partially reflect similar processes.

Taken together, the present results provide further evidence for domain-general temporal processing anomalies in DD that are not limited to linguistic or auditory stimuli (Facoetti et al., 2008, 2010; McLean et al., 2011; Stanley & Hall, 1973). A reduced temporal resolution in response to rapid sequences of stimuli, as indicated by an impaired temporal segregation performance, might be explained by attentional mechanisms responsible for the sampling or parsing of visual information. On this account, temporal resolution deficits fit both with the magnocellular theory of dyslexia as well as with the SAS framework. As magnocellular neurons are hypothesized to be primarily activated in response to fast (in the time range of 100 ms) and transient stimuli given their rapid conduction rates (Derrington & Lennie, 1984; Legge, 1978; Maunsell et al., 1999), previous accounts have linked temporal parsing deficits to magnocellular dorsal impairments (see, e.g., evidence in relation to coherence motion and attentional blink tasks; Hari et al., 1999; Pammer & Wheatley, 2001; Schulte-Körne et al., 2004). According to this framework, weaker magnocellular responses could be responsible for reduced visual sampling rates, while at the same time representing the neural basis of higher-level deficits, such as an inefficient engagement and disengagement of visual attention (Steinman et al., 1997). In line with the current finding, this scenario would translate to a temporal segregation deficit across all ISI levels where segmentation of visual input is required on a rapid timeframe (< 80 ms). Contrarily, temporal integration performance would remain unaffected, or might even benefit, from a more sluggish activation of the magnocellular dorsal system. These impaired mechanisms could contribute to inefficiency

in reading, which is essentially a demanding temporal and spatial order acquisition task where graphemes are sequentially processed between one fixation and the other (Laycock & Crewther, 2008). The influential dual-route model of reading predicts that reading acquisition, in particular, requires fine graphemic parsing, as the correct identification of individual sub-lexical units precedes learning to map grapheme onto corresponding phonemes (Coltheart, 1978; Coltheart et al., 2001; Ruffino et al., 2014; Vidyasagar & Pammer, 2010). Moreover, an important aspect of reading is the ability to shift attention to the upcoming (parafoveal) word (for a review, see Schotter et al., 2012; Huber-Huber et al., 2021). Slow or inefficient shifts in attention and in updating in working memory could result in reduced parafoveal preview benefits and slower reading times.

Despite some effort in bridging magnocellular function and higher-level temporal processing tasks (Nieuwenhuis et al., 2008; Omtzigt & Hendriks, 2004), conclusions regarding the involvement of magnocellular mechanisms should be drawn with caution. As the task used here employs supra-threshold, letter-like stimuli in the temporal-processing domain, it might also relate to higher-level processing impairments (see Skottun, 2015, 2016, for critical reviews). A potential role of the magnocellular stream in rapid temporal segregation in the current study is also called into question by the lack of between-group differences in the P1 component, previously linked to magnocellular response (Di Russo et al., 2002; Elleberg et al., 2001). Designing a task that requires high temporal resolution while at the same time employing stimuli that selectively stimulate the magnocellular stream would help disambiguate this critical aspect. In this direction, a study by Peters et al. (2020) manipulated temporal frequency in a flicker fusion task to selectively assess magnocellular function, finding that only a subgroup of DD participants presented impaired magnocellular-temporal processing thresholds. They also reported that reading abilities and flicker fusion thresholds correlated differently in the two DD subgroups.

Moreover, the link among graphemic parsing, attention, and magnocellular function has been supported by results from Omtzigt and Hendriks (2004; see also Omtzigt et al., 2002), who presented normal readers with single (e.g., a) or flanked (e.g., xax) letters. By changing physical attributes of the stimuli, letters could either selectively target magnocellular or parvocellular function. Those authors reported that, when attentional processing was loaded with flanked stimuli, only the perception of magnocellular-activating letters would be impaired. Furthermore, this effect was absent when attention was cued to the target location, thus implicating that the role of the magnocellular system in identifying flanked letters is in

the spatial allocation of attention for target letters. Future contributions should aim at designing tasks that sensibly disambiguate between magno- and parvo-cellular contributions to improve the characterization of DD in subgroups and to help reconcile inconsistencies reported in the literature.

In conclusion, the present study provided further evidence for a deficit in rapid segmentation of visual information in DD, as well as atypical electrophysiological signatures of temporal processing. Specifically, a suppression of the N1 component in dyslexic participants regardless of task instruction (i.e., segregation and integration) is compatible with a general impairment of attentional sampling that might translate into temporal segregation deficits, as temporal segregation relies heavily on the fast deployment of attentional resources. Furthermore, the absence of P3 modulation for temporal segregation in dyslexic participants would reflect weakened stimulus representations in visual working memory. These findings provide new evidence of electrophysiological correlates of visual temporal processing deficits in DD while providing support to theories of dyslexia focusing on perceptual and attentional processing, such as the magnocellular theory of dyslexia as well as the “Sluggish Attentional Shifting” framework.

AUTHOR CONTRIBUTIONS

Alessia Santoni: Data curation; formal analysis; investigation; visualization; writing – original draft; writing – review and editing. **David Melcher:** Conceptualization; methodology; writing – review and editing. **Laura Franchin:** Conceptualization; investigation; resources; writing – review and editing. **Luca Ronconi:** Conceptualization; formal analysis; methodology; supervision; writing – original draft; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors have no relevant financial or non-financial interests to declare.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available upon request to the corresponding authors.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1 Results from repeated-measures ANOVA results for task accuracy. Greenhouse-Geisser correction was applied when the assumption of sphericity was violated (Mauchly's test of sphericity).

Table S2 Planned comparisons for group*condition interaction. Results are averaged over the levels of ISI.

Figure S1 ERP waveform collapsed for group, ISI, condition and cluster.

Figure S2 ERP waveforms for group and condition for the three ISI levels. Waveforms are averaged over three posterior channel clusters. DD, developmental dyslexia; int, integration; seg, segregation.

Table S3 Results from repeated-measures ANOVA for P1 component mean amplitude (110–140 ms from first stimulus onset). Greenhouse-Geisser correction was applied when the assumption of sphericity was violated (Mauchly's test of sphericity).

Table S4 Results from repeated-measures ANOVA for N1 component mean amplitude (180–220 ms from first stimulus onset). Greenhouse-Geisser correction was applied when the assumption of sphericity was violated (Mauchly's test of sphericity).

Table S5 Results from repeated-measures ANOVA for N2 component mean amplitude (260–300 ms from first stimulus onset). Greenhouse-Geisser correction was applied when the assumption of sphericity was violated (Mauchly's test of sphericity).

Table S6 Results from repeated-measures ANOVA for P3 component mean amplitude (350–500 ms from first stimulus onset). Greenhouse-Geisser correction was applied when the assumption of sphericity was violated (Mauchly's test of sphericity).

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