The impact of string length on neural categorization processes for letters and digits

Abstract

Letters and Arabic digits are the building blocks of words and numbers. In the visual cortex, these culturally acquired characters are characterized by a differential involvement of the left and right hemispheres. Letters, as language-related symbols, predominantly involve left-hemispheric structures in the occipito-temporal cortex, while digits, as quantity-related symbols, elicit right-hemispheric or bilateral visual recognition processes. However, it remains unclear whether the human brain processes single elements and strings of characters differently depending on their category. This question is important because in the Latin alphabet, letters are usually combined in strings to form words and do not stand alone, while digits have meaning in both cases. Using Fast Periodic Visual Stimulation (frequency-tagging) during EEG recordings, we investigated how adults (N=18) discriminate letters and digits from each other, as a function of their string length (i.e. 1 vs. 5 characters). One category of stimuli (e.g., single letters) was periodically inserted (1/5) in a stream of stimuli of the other category (e.g., single digits) displayed at 10Hz. Results showed clear discrimination responses at 2Hz (i.e., 10Hz/5) with occipito-temporal topography, stronger for strings than for single elements. Digits gave rise to right-lateralized responses whatever the length. Letters displayed a left-lateralized topography only when strings were presented, while single letters were right-lateralized. A second experiment (N=20) replicated these novel and unexpected findings. The results are discussed as potentially indicating that expert readers perceive single letters as visual objects of expertise, whereas letter strings engage linguistic (orthographic, phonological) processes that rely on the left hemisphere.

Keywords:

Letters, digits, FPVS-EEG, brain lateralization, visual cortex specialization, string length

1. Introduction

Written words and numbers are cultural inventions that structure much of our daily life, from following instructions to managing quantities. Good readers effortlessly translate print into speech and meaning, and because they have decoded countless words from an early age, this process has become highly automatized (Logan, 1997; Norton & Wolf, 2012). Correspondingly, neural changes in connectivity, lateralization and functional specialization are observed during literacy and numeracy acquisition (Chyl et al., 2021; Dehaene-Lambertz et al., 2018; Emerson & Cantlon, 2012; Siemann & Petermann, 2018; Simon et al., 2013; Wandell et al., 2012). Both words and numbers are constituted of smaller "building blocks": letters (for alphabetic words) and digits (for Arabic numbers), which are both arbitrary shapes that are culturally assigned to different categories. In young children, the ability to process these units crucially predicts later reading (Caravolas et al., 2013; Leppänen et al., 2008) and arithmetic (Göbel et al., 2014; Schneider et al., 2017) skills.

Despite their apparent similarity, words and numbers are read through different processing steps. Reading words is frequently conceived as involving a dual-route process (Coltheart et al., 2001; Friedmann & Coltheart, 2018; Zorzi, 2010). Word reading starts with visual analysis of the single letters' identity and position. After initial morphological decomposition (Beyersmann et al., 2011; McCormick et al., 2008), reading follows either the direct lexical route, matching the word to its orthographic entry linked to phonological and semantic information, or the indirect non-lexical route, converting letters to phonological information. Familiar words are typically processed with the lexical route given that they are stored in memory, while pseudowords and unknown words trigger slow and effortful letter-by-letter processes along the non-lexical route (Coltheart et al., 2001; Share, 1995). Reading numbers is usually referred to as "transcoding" as it necessitates to go from one code (the Arabic base-10 system) to another one (the verbal number system). Although certain highly familiar numbers can be processed through a stored-knowledge system (Cipolotti, 1995; Cohen et al., 1994; Lochy & Schiltz, 2022), most numbers are transcoded according to a complex set of rules in order to be read aloud. This mechanism is best understood with Dotan & Friedmann's model of reading multidigit numbers (Dotan & Friedmann, 2018, 2019). Single digits are processed based on their identity and order, while the decimal structure is extracted based on string length, triplet parsing, and the position of 0's. These two sub-processes generate a number word frame. Then, number words are produced by filling the frame with each digit in the correct order,

following language-specific rules (e.g., 5050 in English is read as "{5;ones}[thousands][and]{5;tens}; thus "five thousand and fifty").

Does the brain process letters and digits differently when presented as single elements versus strings? Although string processing lies at the heart of literacy and numeracy acquisition this fundamental question remains underexplored. Reading words and multidigit numbers requires not only recognizing individual symbols but also integrating them into structured representations governed by orthographic or numerical rules. If the brain treats strings of letters differently from single letters but does not apply the same principle to digits, this would entail domain-specific constraints on how visual expertise develops in cultural symbol systems.

Previous studies have partly addressed this issue: single letters vs. letter strings (Dehaene et al., 2005; Flowers et al., 2004; Grainger, 2008), single letters vs. single digits (Lochy & Schiltz, 2019; Price & Ansari, 2011; Yeo et al., 2020), or strings of letters vs. strings of digits (Baker et al., 2007; Carreiras, et al., 2015a; McCloskey & Schubert, 2014; Park et al., 2011, 2014, 2017; Schubert, 2017). However, very few studies (Aurtenetxe et al., 2020; James et al., 2005; Park et al., 2014) have directly combined both factors—symbol type and string length—within the same design. In the fMRI study of James et al. (2005), certain areas (in the left fusiform gyrus) showed similar activation for pseudowords, single characters (Roman letters, Arabic digits, or Chinese characters), or random strings of characters in a 1-back task, but other brain regions were specialized for either single letters (anterior left fusiform) or strings of letters (left fusiform region posterior to the VWFA). ERP and MEG studies have shown higher N1 amplitudes for letters than digits in left occipital sites, while the opposite was observed in right homologous sites for digits (Park et al., 2014), although bilateral responses to digits was also reported (Aurtenetxe et al., 2020). Later components also showed left lateralization of electrophysiological processes for letters over digits. Interestingly, higher P2 amplitudes for letters in the left hemisphere were observed only for strings of letters and not for digits or single letters. Such a greater activity for strings of letters only is striking, as any type of characters' string can be thought as more demanding, increasing attentional processes dedicated to multi-element array perception, and complexifying the uptake of information as suggested by cognitive models of reading (e.g., Coltheart et al., 2001) or transcoding (Dotan & Friedmann, 2018) and recent eye-tracking data (de Chambrier et al., 2023). The specificity of this "string" effect for letters may thus reflect a processing step unique to letters, possibly of orthographic nature, required before they can be read as words (Dehaene et al., 2005). In contrast, digits always refer to a quantity, whether presented in isolation or within a random string. The lateralization of responses to the two categories of elements fits well with the idea

that even at the earliest visual recognition level, VOTC specialization reflects the co-activated specific brain networks (e.g., biased connectivity hypothesis, see Hannagan et al., 2015), with the language-related regions of the left hemisphere for letters and the magnitude-related intraparietal brain areas of the right hemisphere for numbers.

These studies suggest category-specific lateralization patterns (letters–left hemisphere; digits–right/bilateral) and greater left-lateralized responses for letter strings compared to single letters, pointing toward specialized orthographic processing. But the evidence remains limited and fragmented since to the best of our knowledge no study to date systematically compared letters and digits both presented as single elements and presented as strings. Moreover, all studies used a task actively requiring the processing of the visual symbols, for example to compare each character(-string) with the previously presented one, or to detect a certain character identity. As these tasks require a top-down activation and explicit processing of the characters, it remains to be determined whether and how differential processing can also be observed in a passive viewing context. This would allow to understand the bottom-up visual processing involved in the different character types and formats. In addition, it would set the stage for future studies comparing letters and digits processing at different developmental stages. Here, we address this gap using fast periodic visual stimulation EEG (FPVS-EEG), a method particularly sensitive to implicit visual discrimination (Heinrich et al., 2009; Norcia et al., 2015). This frequency-tagging paradigm measures neural responses synchronizing to visual stimulus frequency. “Deviant” stimuli (e.g., strings of letters; Figure 1 and Figure 2) are periodically inserted (1 out of 5, thus at 2 Hz) into a stream of “base” stimuli (e.g., strings of digits at 10 Hz), similar to an oddball paradigm (see Figure 2). If deviant stimuli are discriminated from base stimuli, then a differential brain activity is observed at the frequency of deviant stimuli (2 Hz) and its harmonics (e.g., 4, 6, 8 Hz). The paradigm thus highlights the processes specific to the deviant category, over and above those common to both categories of stimuli. Contrasting single letters vs. digits in 6-year-old children, it highlighted greater right-hemispheric (RH) responses to digits than letters and a trend for left-lateralization (LH) for letters, with an occipito-temporal topography (Lochy & Schiltz, 2019).

Here, by contrasting single versus strings of letters and digits in adults, we aim to test whether string processing amplifies category-specific responses—particularly, whether letters uniquely recruit orthographic processes in the left hemisphere while digits engage magnitude-related networks. Clarifying this interaction between symbol type and string length will not only refine models of visual word and number recognition but also illuminate how cultural inventions shape hemispheric specialization.

2. Material and methods

2.1. Participants

Eighteen right-handed young adults, with normal/corrected-to-normal vision and no reading difficulty nor diagnosed dyslexia (9 males; between 18-35 years old) volunteered to participate in this study. This sample size was determined a priori, based on a recent study using a similar design although in young children (Crollen et al., 2025). That exploratory study (N=12 per group) provided, in the supplementary material, the statistics for the sample size required to reach a power between .70 and .80 given their observed effect sizes. Specifically, the crucial interaction in those data had an effect size $f = 0.41$ (η^2_p=0.149) and an achieved power of 0.48. The required sample size to achieve a power of 0.70 was thus n=20 per group (power= 0.716). Given that the present study test adults, in whom effect sizes are presumably higher, and that studies using the same approach typically included samples of 10 to 20 participants (Liu-Shuang et al., 2014; Lochy et al., 2015, 2024; Stothart et al., 2017), we decided to recruit 18 participants for this experiment.

Participants were neither aware of the goal of the experiment, nor that a change of stimulus type occurred at a periodic rate during stimulation. They were tested after having signed an informed consent form approved by the local Ethical Committee at the University of Luxembourg as conform to the Declaration of Helsinki.

2.2. Stimuli

For the single character condition, the stimuli were identical to those used in Lochy & Schiltz (2019). The nine digits from 1 to 9 and nine letters (matched in overall shape and number of strokes, Figure 1A) were presented in 5 different fonts (arial, agency fb, comics sans MS, Lucida sans typewriter, OCR A extended), yielding a total of 45 images per category (see Figure 1). Letters were presented in upper-case and were chosen to match digits in overall visual shape (number of strokes, closed shapes, etc.).

For the strings condition, single elements were combined in strings of 5 characters (all from the same font), respecting the frequency of occurrence of each character over the total set of stimuli. Nine different stimuli were presented in each of the 5 fonts, for a total of 45 images per category. Non-words letter-strings were built by positioning letters at the same position as the digits they

were matched to. Out of 45 letter-strings, 7 did not contain any vowels and were constituted of consonants only (see Figure 1).

Single characters were centered on images measuring 236 x 236 pixels, whereas strings were displayed on images with a height of 236 pixels and a width ranging from 472 to 709 pixels, depending on the font and characters' size.

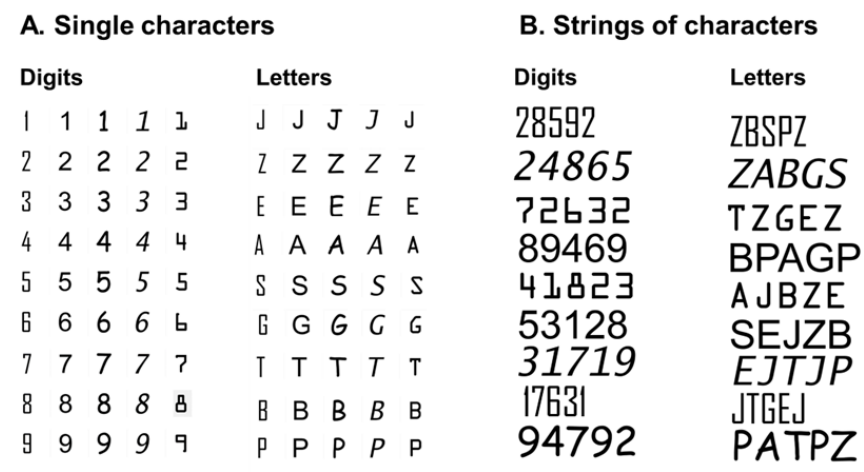

Figure 1. Stimuli used in the experiment. A. Complete set of single element stimuli. All the digits from 1 to 9 were presented in 5 different fonts for a total of 45 stimuli per condition. **B.** Examples of 5-characters strings. Strings were built by controlling the frequency of occurrence of each digit/letter in each position and using 5 different fonts. Letter stimuli were matched to digit stimuli by using the corresponding letter in the corresponding position and using the same font as digit stimuli.

2.3. Procedure

The procedure was very similar to previous research using the FPVS-oddball approach to assess word-selective responses (Lochy et al., 2015, 2024, 2025; Lutz et al., 2024; Marchive et al., 2025) or the categorization of letters/digits as reported here (Crollen et al., 2025; Lochy & Schiltz, 2019).

Four conditions were presented, in a 2x2 design crossing oddball stimulus type (letters/digits) and string length (1 character vs 5 characters).

Each stimulation sequence started with a fixation cross for 2 – 5 seconds, 2 seconds of gradual stimulation fade-in, 60 seconds of stimulation, and 2 seconds of gradual fade out (see Figure 2). As in previous studies (e.g., Lochy et al., 2015), stimuli were presented by means of sinusoidal contrast modulation at a base frequency rate of 10Hz (i.e., one item every 100 ms) (Figure 2). Stimuli were presented with Java SE Version 8. Every sequence had the same

structure: stimuli of the base category were presented at 10Hz, and every fifth item was a stimulus of the deviant category (frequency of 2Hz, thus every 500 ms). In the letters-digits conditions (lett-DIG), letters constituted the base stimuli and digits the oddball category, such as: L L L L D L L L L D L… In the digits-letters (dig-LETT) condition, it was the reverse (D D D D L D D D D L…).

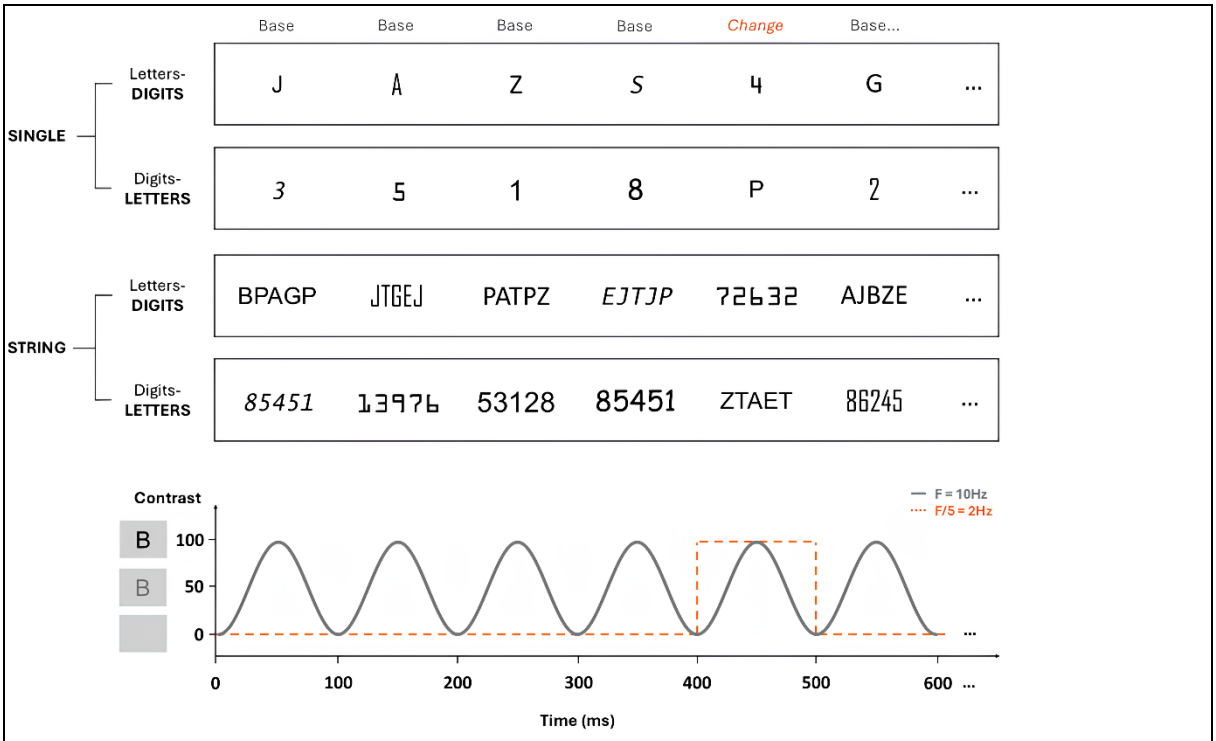

Figure 2. Experimental design. In the single character conditions, base stimuli were constituted of letters and deviant stimuli of digits (letters-DIGITS) or the reverse (digit-LETTERS). The same two categories were used for the strings condition, displaying images of 5 characters. Stimuli were presented with a sinusoidal contrast modulation at 10Hz (10 images per second), with deviant stimuli (digits or letters) presented every 5 items thus at 10Hz/5, 2Hz.

Participants had to perform an orthogonal task on the fixation cross during stimulation, chosen to ensure that participants kept a similar level of attention across sequences and to reduce eye-movements. They were required to monitor and to press the space bar when they detected color changes of the fixation cross (from blue to red, 200ms), that occurred randomly 8 times during each 60-second sequence.

The four conditions (2 oddball stimulus types x 2 string length) were part of a larger project presenting altogether 8 conditions. Each sequence lasted 60 seconds and was repeated 3 times.

A pause was taken between each of the sequences, which were initiated manually to ensure low-artefact EEG signals.

2.4. EEG acquisition and data processing

Participants were seated comfortably at 1 m from the computer screen in a quiet room of the laboratory. EEG was acquired at 512Hz using a 64-channel Biosemi Active II system (Biosemi, Amsterdam, Netherlands), with standard 10-20 system locations (http://www.biosemi.com) plus a row of posterior electrodes including PO9, I1, I2, PO10. The magnitude of the offset of all electrodes, referenced to the common mode sense (CMS), was held below 50 mV. EEG analyses were carried out using Letswave 6 (https://github.com/NOCIONS/letswave6), and Matlab 2012 (The Mathworks). After FFT band-pass filtering between 0.1 and 100Hz, EEG data were segmented to include 2 seconds before and after each sequence, resulting in 64-second segments (-2 – 62 s). Data files were then resampled to 256Hz to reduce file size and data processing time. Artefact-ridden or noisy channels were replaced using linear interpolation (on average, 2.42% of channels). All channels were re-referenced to the common average. EEG recordings were then segmented again from stimulation onset until 59.998 seconds, corresponding to the largest number of complete cycles of 500 ms (120 cycles) at the 2 Hz frequency within the 60 seconds of stimulation period.

The data were analysed following the same procedure as in previous studies with similar paradigms (e.g., Liu-Shuang et al., 2014; Lochy et al., 2015, 2016, 2024; Retter et al., 2021; Retter & Rossion, 2016; Rossion et al., 2012) but is nevertheless detailed here.

2.5. Frequency domain analysis

Per condition, the three stimulation sequences were averaged in the time domain for each participant, to increase SNR. A Fast Fourier Transform (FFT) was applied to the averaged time-window, and normalized amplitude spectra were extracted for all channels. This yielded EEG spectra with a high frequency resolution (1/59.998 s = 0.016Hz), increasing SNR and allowing unambiguous identification of the response at the exact frequencies of interest (i.e., 10Hz for the base stimulation rate and 2Hz and harmonics for the other category stimulation). Given that our response of interest falls into a strictly defined frequency bin (related to stimulation frequency), we considered surrounding bins as noise, or baseline. The latter is defined as the 20 surrounding bins of each target bin, excluding the immediately adjacent and the extreme (min and max) bins (Liu-Shuang et al., 2014; Rossion et al., 2012; Srinivasan et al., 1999). We then

computed three indices. First, the signal-to-noise ratio (SNR) was estimated across the EEG spectrum, by dividing the amplitude at each frequency bin by the average amplitude of 20 surrounding bins (10 on each side; Liu-Shuang et al., 2014). Second, to quantify the responses of interest in microvolts, the average voltage amplitude of the 20 surrounding bins (i.e., the noise) was subtracted out (Retter & Rossion, 2016). This is done because the amplitude at any given frequency is considered as a combination of signal and noise (Heinrich et al., 2009). Finally, Z-scores were computed based on the grand-averaged amplitude spectrum for each condition, to assess the significance of the response at each stimulation frequency (base-10Hz, categorical change-2Hz) and harmonics (Liu-Shuang et al., 2014; Lochy et al., 2015). Z-scores (*Z(x)= x-mean(noise)/SD (noise*) were considered significant if larger than 2.48 ($p < 0.01$, one-tailed, signal > noise).

In order to quantify the periodic response distributed across several harmonics, the baseline subtracted amplitudes of significant harmonics (excluding the base stimulation frequency) were summed for each participant, task, and condition (Retter et al., 2021; Retter & Rossion, 2016).

The study procedures and analysis plans were not preregistered. All study data and analysis code are available on the Open Science Framework platform (https://osf.io/jxezd/?view_only=37447ca8ccf94699be50cd4374bae749).. The complete list of stimuli is provided in Supp. Mat.

3. Results

3.1. Categorization of letters among digits and vice-versa

Oddball responses were visible at 2Hz and harmonics on SNR response spectra (Fig 3C) and on 3D maps with lateralized occipito-temporal topographies (Fig 3A). Across oddball stimulus type and string length, Z-scores were significant ($p<.01$) on consecutive harmonics up to the 6th harmonic (12Hz) on a group of posterior electrodes. When examining Z-scores per length and condition, we observed stronger responses for strings than single characters, and topographical changes according to oddball type: in the lett-DIG condition, significant responses were mostly right-lateralized (P08, PO4, P10), while for dig-LETT they were mainly left-lateralized (P5, P7, P9, PO7) and significant up to 4 harmonics (8Hz).

To take an equivalent number of harmonics in each condition and length, we selected the highest number of significant harmonics across all conditions and lengths, thus 6 harmonics

from 2Hz to 12Hz (excluding the base rate 10Hz). We then summed the amplitude values of these 6 harmonics and ranked the electrodes (Retter et al., 2021). Over all lengths and conditions, the best 5 electrodes were: PO8, PO7, P9, P10 and O2. Taking left and right homologs, we averaged PO7, P9 and O1 over a left ROI, and PO8, P10 and O2 over a right ROI. Before doing so, and because of the different topographies observed in each condition, we had verified that those ROI encompassed correctly the strongest responses in each condition (in the lett-DIG condition, the 6 electrodes with the strongest responses were: PO8, O2, P10, P8, P9, PO7, and in the dig-LETT, it was: PO7, P9, P7, PO8, P10, O2).

The sum of baseline corrected amplitudes over 6 harmonics (Figure 3) was analyzed using unilateral t-tests on one mean (H_0 being that $\mu <= 0$). Results showed that every condition (single or string; dig-LETT or lett-DIG) was associated with EEG activity above zero (all $p<.05$), except for single dig-LETT in the left hemisphere (*IC95%* = [-.05µV; .259µV], $t_{17}=1.429$, $p=.086$).

Data were analyzed using a 2x2x2 repeated-measures ANOVA with *Hemispheres* (LH, RH), *Condition* (dig-LETT, lett-DIG), and *Length* (single, string) as within-subject factors. (see Fig3).

There was a main effect of *Length*, F (1,17) =9.019; p <.008; $\eta^2_p=.347$, responses being two times stronger for strings (M=.41µV; SE=.06) than for single elements (M=.20µV; SE=.05). The difference between *Conditions* (lett-DIG: M=.38µV; SE=.07; dig-LETT: M=.24µV; SE=.05) was marginally significant, F (1,17) =3.817; p<.067; $\eta^2_p=.183$, and there was no main effect of *Hemisphere* (LH: M=.29µV; SE= .04; RH: M=.32µV; SE=.06), F <1. The interaction between *Conditions* and *Hemisphere* was significant, F (1,17) = 5.838; p<.027; $\eta^2_p=.256$; as well as the triple interaction between all these factors, F (1,17)= 17.779; p<.001; $\eta^2_p=.511$. A sensitivity analysis (N = 18, $\alpha = .05$) for the triple interaction (length × condition × hemisphere) indicated that the design has ~80% power to detect effects of $f \approx 0.70$ ($\eta^2p \approx .33$) and ~90% power for $f \approx 0.81$ ($\eta^2p \approx .40$) (see Figure 4 for the full sensitivity curve).

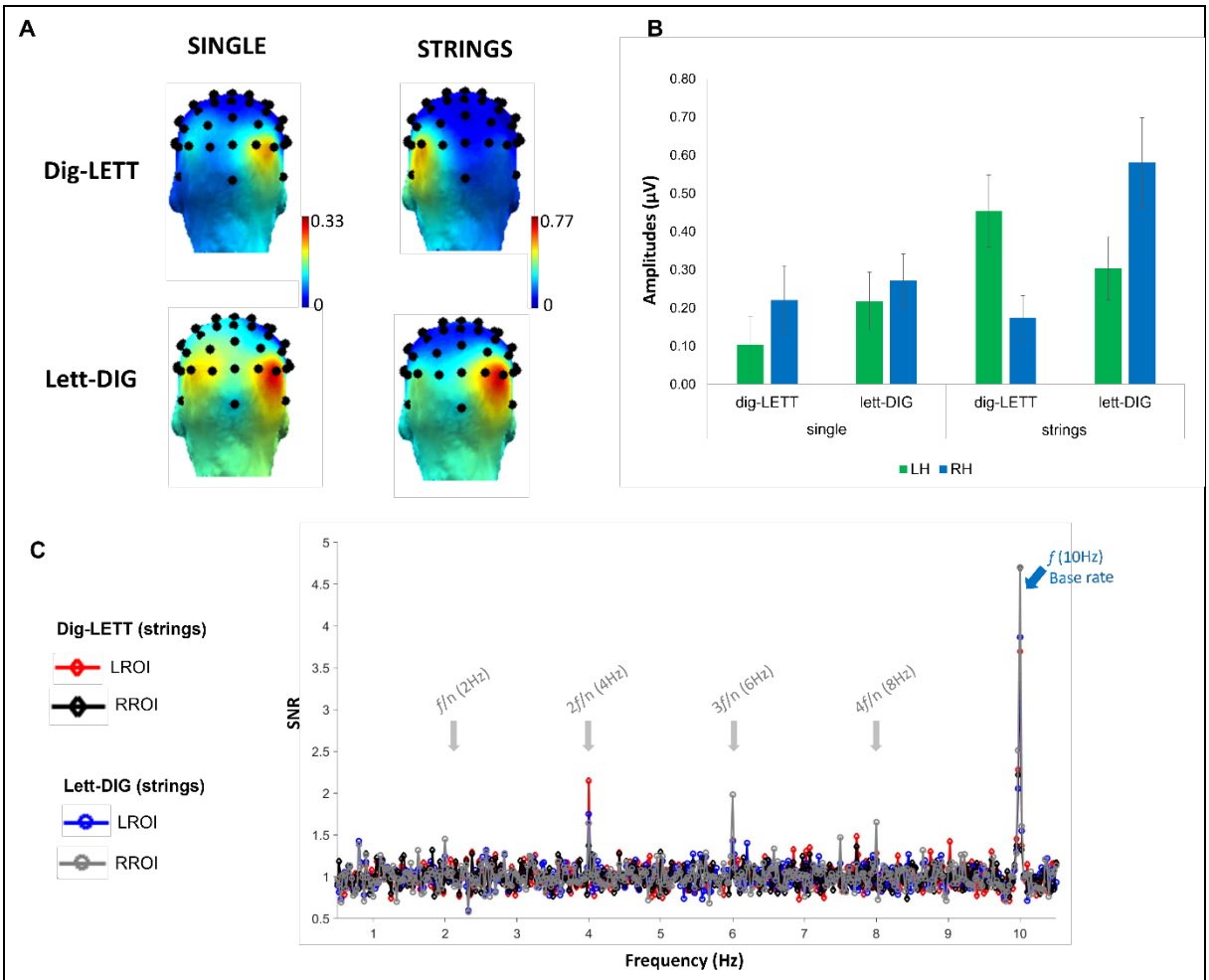

Figure 3. categorical responses to letters among digits (dig-LETT) and vice versa (lett-DIG). A. topographies of response amplitudes for dig-LETT and lett-DIG, when presented as single elements (left column) or strings of elements (right column). **B.** Histogram of response amplitudes: means and SD for the sum of baseline corrected amplitudes for 6 harmonics, from 2Hz to 12Hz (excluding the base rate 10Hz), for each condition and string length. **C.** example of response spectra for strings of characters, for each condition (dig-LETT and lett-DIG) in left and right ROI (LROI, RROI).

We then decomposed the triple interaction by length. For single elements, there was a main effect of *Hemisphere*, $F(1,17) = 7.013$; $p < .017$; $\eta^2_p = .292$, with stronger RH responses (.25µV) than LH responses (.16µV). No effect of *Conditions*, $F(1,17) = .907$, $p = .354$; $\eta^2_p = .051$; and no interaction between *Conditions* and *Hemispheres* emerged, $F(1,17) = .715$; $p = .409$; $\eta^2_p = .040$; the RH leading stronger responses in both conditions (lett-DIG, RH: $M = .27$µV; $SE = .07$ vs LH: $M = 22$µV; $SE = .07$; dig-LETT, RH: $M = 22$µV; $SE = .09$ vs. LH: $M = .10$µV; $SE = .07$).

For 5-characters strings, responses were stronger for lett-DIG (*M*=.51µV; *SE*=.09) than for dig-LETT (*M*=.31µV, *SE*=.06) as revealed by the significant main effect of *Conditions, F*(1,17) = 4.961; *p* <.040; η^2_p=.226. Hemispheres did not differ overall (F<1), but there was a significant interaction between *Conditions* and *Hemispheres*, *F*(1,17) = 12.383; *p* <.003; η^2_p=.421. For letters (dig-LETT), responses were stronger in the LH (*M*=.45µV; *SE*=.09 vs RH: *M*=.17µV, *SE*=.06), t(17)=3.241; p <.002, while for digits (lett-DIG), responses were stronger in the RH (*M*=.63µV; *SE*=.12 vs LH: *M*=.39µV; *SE*=.09), t(17)=-1.792; p <.045. Response amplitudes did not differ between *Conditions* in the LH (p=.256) but were significantly stronger for digits than letters in the RH (p<.001).

Given that topographies might have been slightly different according to conditions, we ran the same analysis including 6 electrodes in each ROI to encompass P7/P8, PO3/PO4 and P5/P6 that also emerged when inspecting Z-score values. The results were the same.

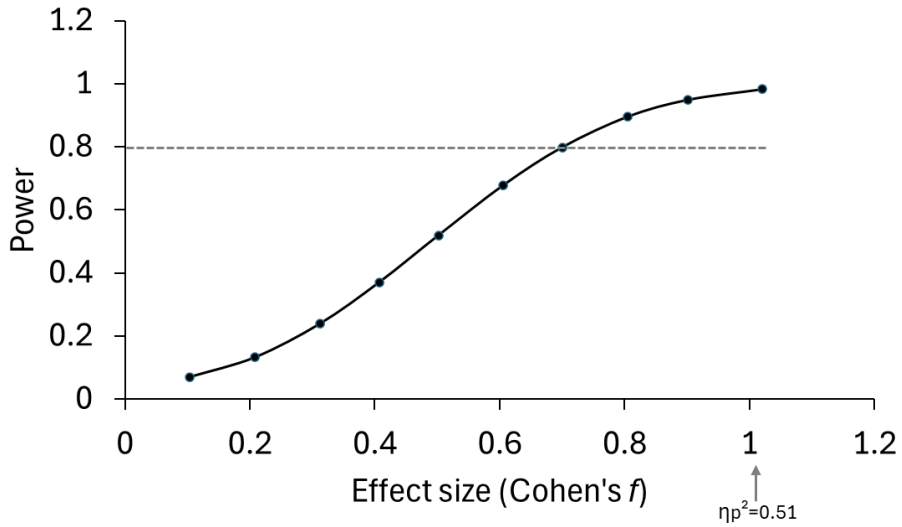

Figure 4. Sensitivity analysis given a sample size of N=18, displaying the effect size obtained in Experiment 1 for the triple interaction Length x Condition x Hemisphere (ηp^2=0.51, *f*=1.02)

3.2. General visual responses

Over all conditions and lengths, base rate responses were significant on 2 consecutive harmonics, i.e., 10Hz and 20Hz, on a series of posterior-medial electrodes but also slightly right-lateralized (see fig 5). When ranking the electrodes after summing the two significant harmonics, O2 (0.89µV), PO8 (0.81µV) and Oz (0.86µV) emerged as the first three strongest channels. They were followed by O1, Iz and PO4 (amplitude values 0.62µV to 0.64µV). We decided to group those 6 electrodes in a medial-occipital ROI, as in previous studies (Lochy et al., 2015; van de Walle de Ghelcke et al., 2021) for further analysis.

The 2x2 repeated-measures ANOVA with *Length* (single, string) and *Condition* (dig-LETT/ lett-DIG) showed a main effect of length F(1,17)=5.736; p<.028; η^2_p=252, with stronger responses for strings (*M*=.85µV; *SE*=.12) than for single elements (*M*=.64µV; *SE*=.08). There was no significant effect of *Condition* F<1 (dig-LETT: *M*= .737µV; *SE*=.09; lett-DIG: *M*=.756 µV; *SE*=.10) and the interaction between the 2 factors was not significant F(1,17)=1.988; p<.177; η^2_p=.105.

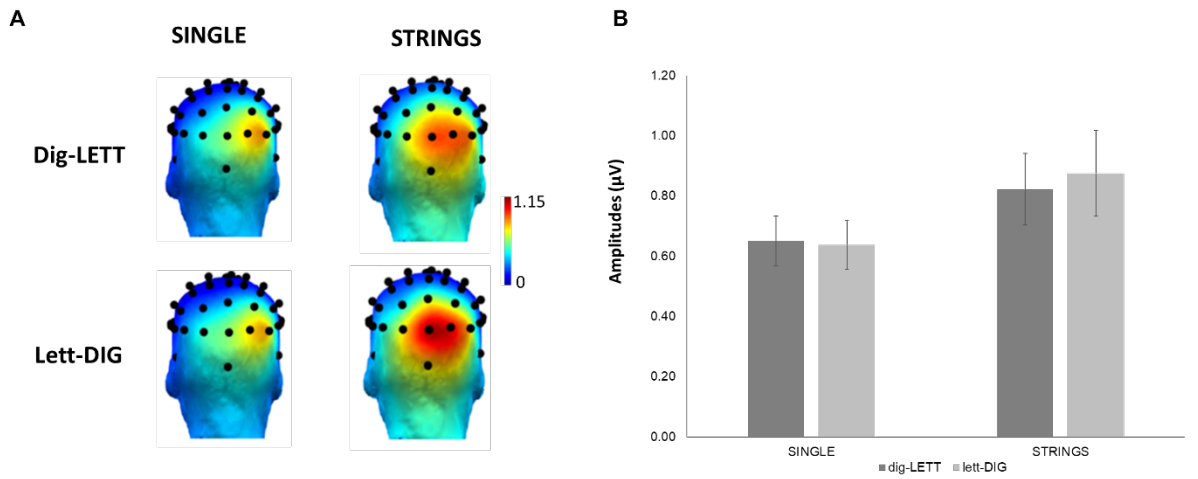

Figure 5. General visual (base rate) responses. A. Topographies of summed baseline corrected amplitudes of the 2 significant harmonics of the base rate (10Hz, 20Hz), displaying stronger responses for strings than single characters and no overall differences between letters as oddballs (Dig-LETT) or digits as oddballs (Lett-DIG). **B.** Histogram of response amplitudes over the medial-occipital ROI encompassing 6 electrodes (bars represent SD of the mean).

3.3. Control experiment on single characters

The results of our experiment revealed right-lateralization of the responses to single letters, which was unexpected. Therefore, we wanted to ensure the replicability of this surprising finding and benefitted of another on-going project to add a few sequences to the testing and ran again the dig-LETT and lett-DIG conditions on single elements on a new group of 20 participants (9 males, mean age = 39.8 years; min=20; max=57).

All materials were the same as the ones described here above. The stimulation frequency was however slower (see Figure 6C), as the overall general visual stimulation was set at 6Hz (instead of 10Hz) and the deviant stimulation at 6Hz/5, 1.2Hz (instead of 2Hz).

Results confirmed the right-lateralization of responses in both conditions, dig-LETT and lett-DIG (see Figure 6A, B). An ANOVA with 2 *Hemispheres* (LH, RH) x 2 *Conditions* (dig-LETT, lett-DIG), was performed on the sum of baseline amplitudes for 6 harmonics (excluding the base rate 6Hz) in the same left and right ROIs as defined in the main experiment. There was a significant main effect of *Hemisphere*, $F(1,19)=33.024$; $p<.001$; $\eta^2_p=.63$, with stronger responses in the RH (M= .34µV, SE = .05 µV) than in the LH (M=.15 µV; SE = .04 µV); and a main effect of *Condition*, $F(1,19)=7.922$; $p=.011$; $\eta^2_p=.29$, with stronger responses for digits (M=.33 µV, SE=.05 µV) than for letters (M=.16 µV; SE = .04 µV). The interaction was not significant, $F(1,19)=2.594$; $p=.124$; $\eta^2_p=.12$.

Therefore, this control experiment replicated the right-lateralization of neural discrimination responses for single characters, both letters and digits, as well as the stronger responses for digits than letters, as in the main experiment.

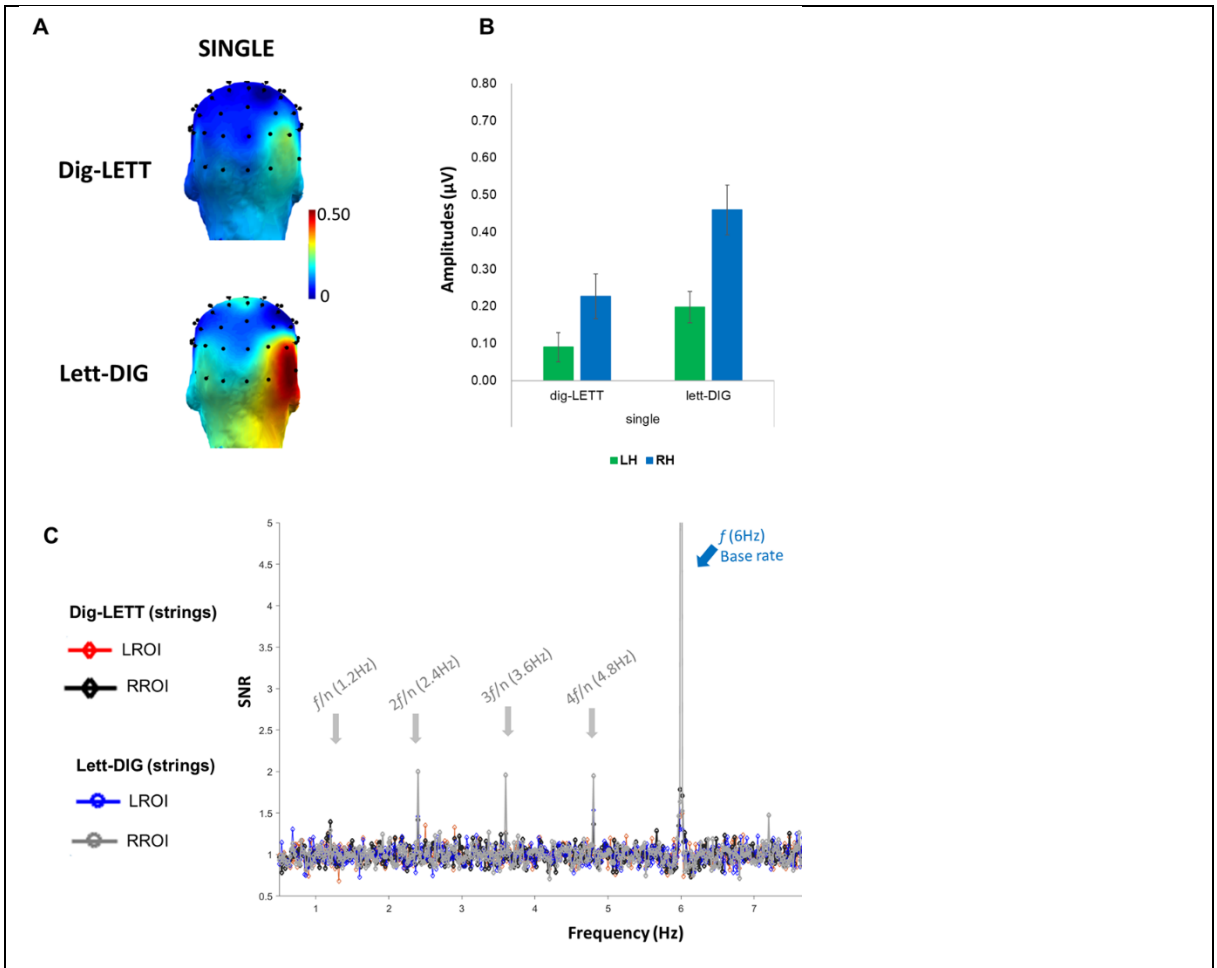

Figure 6. Control experiment with single characters. A. Topographies for responses at the deviant frequency (here, 1.2Hz and harmonics) for the two conditions lett-DIG and dig-

LETT. **B.** Histograms of amplitude values in the left and right ROIs. **C.** SNR response spectrum displaying deviant responses at 1.2Hz and harmonics, and base response at 6Hz.

4. Discussion

In the current study, we explored neural discrimination responses to letters among digits and vice versa, as a function of stimulus length (single characters vs strings), using a Fast Periodic Visual Stimulation paradigm with EEG recordings.

For strings of five characters, we found as expected a left-lateralized response for letters and a right-lateralized response for digits, along with an overall stronger response compared to single characters. The left- and right-lateralized response for letters and digits replicates previous findings (Baker et al., 2007; Dehaene et al., 2005; James et al., 2005; Park et al., 2011, 2014, 2018; Polk et al., 2002; Thesen et al., 2012; Yeo et al., 2020; but see Tagamets et al., 2000) and is in line with the automatic activation of lateralized visual recognition processes, related to the category of characters. Although the finding of a left hemisphere preference for letter strings, presumably in relation to language regions (e.g., "biased connectivity hypothesis", Abboud et al., 2015; Hannagan et al., 2015; Polk & Farah, 1998; Stevens et al., 2017) is overwhelmingly admitted in the literature, the case of digits has given rise to equivocal findings, with reported bilateral (Aurtenetxe et al., 2020; Eger et al., 2003; Grotheer et al., 2016) or right hemispheric preference for numbers (Carreiras, Monahan, et al., 2015b; Crollen et al., 2025; Lochy & Schiltz, 2019; Park et al., 2014). The finding of an overall stronger response for strings than single characters also replicates the results of the MEG-MVPA study by Nara et al. (2023), where strings of letters and digits were better differentiated by a classifier than when they were presented in isolation.

Surprisingly, for single characters, both deviant letters and digits elicited stronger responses in the right than in the left hemisphere. For letters, the visual discrimination response was not even significantly above zero in the left hemisphere (*IC95%*= [-.05µV; .259µV]) in the main experiment. To confirm these unexpected results, we ran a control experiment with another group of participants, and another stimulation frequency using the slower 6Hz presentation rate. Its results confirmed the right-lateralization for single letters and digits, as well as overall stronger responses to digits than letters – this latter finding being in agreement with the idea of a greater sensitivity to numerals (Lochy & Schiltz, 2019; Yeo et al., 2020). In two previous EEG-FPVS studies with children using single elements (6 years old in Lochy &

Schiltz 2019; 8-12 years old in Crollen et al., 2025), right-lateralized responses were found for digits and trends for left lateralization for letters (although statistically the two hemispheres did not differ). In contrast, an exploratory study on children who are deaf (Crollen et al., 2025) observed right-lateralized responses for single letters. This finding was interpreted as reflecting either the brain reliance on adaptive processes given the lack of phonological representations in deaf children, or as a delay in developing representations for letters. Indeed, initial right-lateralized N170 responses for letters in young hearing children (Maurer et al., 2005) have been assumed to reveal a first stage of visual familiarity with letters. The relative left-lateralization was proposed to emerge later due to automatic relation between orthography and phonology (Maurer & McCandliss, 2008). In studies with adults, responses to single letters have been reported to be mostly left-lateralized when compared to non-familiar symbols (shapes, scrambled letters) (Dehaene et al., 2005; Flowers et al., 2004; James et al., 2005; Tarkiainen et al., 1999; Yeo et al., 2020), or when directly comparing ERP waveforms between letters and digits (Park et al., 2014), although others found no greater activation to single letters by comparison to digits (Price & Ansari, 2011) or even by comparison to various control stimuli (Joseph et al., 2016). To understand the discrepancy between our current findings and previous ones, one must recall some specificities of our paradigm. First, it does not perform a "cognitive subtraction" between conditions (e.g., response to letters minus response to digits) but rather stimulates the visual system using one category (e.g., digits) and measures a direct differential neuronal processing between categories if they are discriminated from each other. The topography of the response has been interpreted in the past as in line with neural structures known to be involved in the processing of those categories (e.g., left occipito-temporal responses to letters and words, right-lateralized responses to face identity discrimination, Lochy et al., 2015; Rossion et al., 2020). A second major difference with several previous studies lies in the use of passive viewing of letters and digits here, while others used explicit tasks (one-back task, specific stimulus detection).

Although we replicate the unexpected finding of right-lateralized response for single letters in a second Experiment, we acknowledge several limitations in our study. First, our sample sizes (N=18 and N=20) are small. A post-hoc sensitivity analysis (see Figure 4) reveals that such sample sizes might be insufficient for moderate or small effect sizes. Second, while our results clearly reveal different neural mechanisms for single and strings of letters, we only contrasted 1 and 5 characters, lacking a more parametric manipulation of length. Third, given that letters were chosen here mainly to constitute a visual control for digits, different factors in

the letter-strings themselves were not controlled (character repetition, consonant/vowel structure, phonology, morphology, or even lexicality and semantics). These limitations actually open new avenues for research aiming at understanding which key aspects of letters, when combined in strings, contribute to triggering left hemispheric processes.

Nevertheless, our results raise questions about how adults perceive single letters, by opposition to letter-strings, once they have become skilled readers and are not explicitly instructed to attend the stimuli. Here below we speculate about potential factors that may play a role in our findings and are worth being tested in future research.

First, we found a stronger contrast between strings (of letters and digits) than single elements. This could be due to the fact that strings entail differences between character types in terms of position coding (i.e., coarse- or fine-grained, Carreiras et al., 2015; Grainger et al., 2016), structural properties processing (i.e., decimal structure versus morphological structure; Dotan & Friedmann, 2018, 2019) and top-down influences (or lack of them for digits; Grainger & Hannagan, 2014). Here, as letter stimuli were chosen primarily to match digits visually in our design, not all of these factors might come to play. For instance, the morphological structure partially differs from that of most previous studies (as some letter strings did not contain any syllabic structure or vowels). Some letters (and digits) were repeated in a string, and some strings were not even pronounceable. Thus, in the future, it would be interesting to investigate the impact of syllabic and morphological structure, phonology, and even lexicality, together with varying the number of characters, to understand which letter-related factors and how many characters are necessary and sufficient to produce the observed shift in brain lateralization. Nevertheless, given that neural responses are also stronger at the base rate for strings than single characters sequences, stronger responses for strings might also simply reflect that a greater portion of the visual field is stimulated by the larger stimuli.

Second, we found right-lateralization for single letters, rather than left-lateralization. Actually, a previous study on single-letter processing found that letters induced a bilateral N170, but a greater left-lateralization was observed in (adult) individuals who were more sensitive to rhymes between consecutive letters (e.g., e-b vs e-h) (Stevens et al., 2013), suggesting the role of the spontaneous activation of phonology when viewing letters. For young children learning to read, emphasis is first placed on learning each single letter of the alphabet in association to its name or sound, so that letters (orthography) can later be bound to speech (phonology). Thus, although children might first develop pure visual expertise to print (Bentin et al., 1999; Brem et al., 2013; Maurer et al., 2005), with increased reading skills and

phonological mapping, this component becomes more clearly left-lateralized (Maurer & McCandliss, 2008). Contrary to children learning to read, adults may not all activate phonological/ orthographic representations when viewing individual letters (Stevens et al., 2013). Our findings could be interpreted within a "visual expertise" hypothesis put forward by James et al. (2005, p454), but not confirmed in their findings, stating that "*isolated letters may themselves be objects of expertise that do not elicit complex linguistic processing, and in that sense could be processed in similar regions as other objects of expertise.*" Indeed, expertise for various visual objects has been repeatedly reported to rely on brain structures of the right hemisphere (Tanaka & Curran, 2001) and some authors have suggested that elements of orthographic processing involve the right hemisphere visual object system for processing perceptual features of words rather than their specific orthographic characteristics (Deason & Marsolek, 2005; Marsolek et al., 1992; Rossion et al., 2003; Tagamets et al., 2000). However, such a visual expertise account would especially be relevant if contrasting letters against non-familiar shapes like pseudoletters, here it was not the case as letters were presented in a stream of digits, which are also familiar characters. Other authors have proposed that letters and digits follow different processing routes only when they are part of a string of characters but not in isolation (Grainger & Hannagan, 2014). In a string context, stimuli are perceived as features of a higher-order object (a word or a number), diverging in position coding precision: for instance, approximate position coding is enough to identify a familiar word (Grainger & Ziegler, 2011; Schoonbaert & Grainger, 2004), but not for retrieving magnitude information from a number. The difference in lateralization for strings of letters (left hemisphere) and digits (right hemisphere) fits well with this perspective, but we note that the very discrimination of single elements reveals that they are processed differently by the brain.

Beyond their theoretical relevance, our findings raise broader questions about literacy acquisition. In early reading instruction, children first learn to associate isolated letters with their names or sounds, but it may be the repeated exposure to strings of letters that truly recruits the left-hemispheric structures dedicated to orthography. In that case, pedagogical approaches emphasizing string-level processing may be particularly important to foster automatic orthographic–phonological mapping (Bentin et al., 1999; Maurer & McCandliss, 2008).

Finally, our findings also highlight the methodological contribution of FPVS-EEG. Because this approach captures implicit discrimination responses without requiring explicit categorization, it may reveal early, automatic processing stages that are not accessible when participants perform demanding tasks such as one-back or target detection relying on character

identity processing (Norcia et al., 2015; Hauk et al., 2021). This is particularly relevant for studies with children or clinical populations, where task demands may bias results. By combining FPVS with developmental and cross-population designs (e.g., in dyslexia, dyscalculia, or sensory-deprived groups), future work could help disentangle whether right-lateralized responses to single letters reflect developmental stages, compensatory mechanisms, or stable features of visual expertise.

Conclusion

Our findings show that string length critically shapes the neural categorization of letters vs. digits. Digits consistently elicited right-lateralized responses, whereas letters engaged left-hemispheric processes only when presented as strings. We speculate that these findings suggest that in skilled readers, single letters appear to be processed as visual objects of expertise rather than linguistic symbols, while orthographic processing emerges specifically in multi-letter contexts. These results refine models of visual specialization for cultural symbols and underscore the distinct neural constraints underlying literacy and numeracy acquisition.

References

Abboud, S., Maidenbaum, S., Dehaene, S., & Amedi, A. (2015). A number-form area in the blind. *Nature Communications*, *6*, 1–9. https://doi.org/10.1038/ncomms7026

Aurtenetxe, S., Molinaro, N., Davidson, D., & Carreiras, M. (2020). Early dissociation of numbers and letters in the human brain. *Cortex*, *130*, 192–202. https://doi.org/10.1016/j.cortex.2020.03.030

Baker, C. I., Liu, J., Wald, L. L., Kwong, K. K., Benner, T., & Kanwisher, N. (2007). Visual word processing and experiential origins of functional selectivity in human extrastriate cortex. *Proceedings of the National Academy of Sciences*, *104*(21), 9087–9092. https://doi.org/10.1073/PNAS.0703300104

Bentin, S., Mouchetant-Rostaing, Y., Giard, M. H., Echallier, J. F., & Pernier, J. (1999). ERP manifestations of processing printed words at different psycholinguistic levels: time course and scalp distribution. *Journal of Cognitive Neuroscience*, *11*(3), 235–260. http://www.ncbi.nlm.nih.gov/pubmed/10402254

Beyersmann, E., Castles, A., & Coltheart, M. (2011). Early morphological decomposition during visual word recognition: Evidence from masked transposed-letter priming. *Psychonomic Bulletin and Review*, *18*(5), 937–942. https://doi.org/10.3758/S13423-011-0120-Y/TABLES/2

Brem, S., Bach, S., Kujala, J. V., Maurer, U., Lyytinen, H., Richardson, U., & Brandeis, D. (2013). An electrophysiological study of print processing in kindergarten: The contribution of the visual N1 as a predictor of reading outcome. *Developmental Neuropsychology*, *38*(8), 567–594. https://doi.org/10.1080/87565641.2013.828729

Caravolas, M., Lervåg, A., Defior, S., Seidlová Málková, G., & Hulme, C. (2013). Different patterns, but equivalent predictors, of growth in reading in consistent and inconsistent orthographies. *Psychological Science*, *24*(8), 1398–1407. https://doi.org/10.1177/0956797612473122

Carreiras, M., Monahan, P. J., Lizarazu, M., Duñabeitia, J. A., & Molinaro, N. (2015a). Numbers are not like words: Different pathways for literacy and numeracy. *NeuroImage*, *118*, 79–89. https://doi.org/10.1016/j.neuroimage.2015.06.021

Carreiras, M., Monahan, P. J., Lizarazu, M., Duñabeitia, J. A., & Molinaro, N. (2015b). Numbers are not like words: Different pathways for literacy and numeracy. *NeuroImage*, *118*, 79–89. https://doi.org/10.1016/j.neuroimage.2015.06.021

Carreiras, M., Quiñones, I., Hernández-Cabrera, J. A., & Duñabeitia, J. A. (2015). Orthographic coding: Brain activation for letters, symbols, and digits. *Cerebral Cortex*, *25*(12), 4748–4760. https://doi.org/10.1093/cercor/bhu163

Chyl, K., Fraga-González, G., Brem, S., & Jednoróg, K. (2021). Brain dynamics of (a)typical reading development—a review of longitudinal studies. *Npj Science of Learning*, *6*(1), 1–9. https://doi.org/10.1038/s41539-020-00081-5

Cipolotti, L. (1995). Multiple routes for reading words, why not numbers? evidence from a case of arabic numeral dyslexia. *Cognitive Neuropsychology*, *12*(3), 313–342. https://doi.org/10.1080/02643299508252001

Cohen, L., Dehaene, S., & Verstichel, P. (1994). Number words and number non-words: A case of deep dyslexia extending to arabic numerals. *Brain*, *117*(2), 267–279. https://doi.org/10.1093/brain/117.2.267

Coltheart, M., Rastle, K., Perry, C., Langdon, R., & Ziegler, J. (2001). DRC: a dual route cascaded model of visual word recognition and reading aloud. *Psychological Review*, *108*(1), 204–256. http://www.ncbi.nlm.nih.gov/pubmed/11212628

Crollen, V., Buyle, M., Schiltz, C., & Lochy, A. (2025). Impact of Deafness on the Lateralized Brain Responses to Letters and Digits: A Fast Periodic Visual Stimulation Exploratory Study in Deaf and Hearing Children. *Developmental Science*, *28*(3). https://doi.org/10.1111/desc.70001

de Chambrier, A. F., Pedrotti, M., Ruggeri, P., Dewi, J., Atzemian, M., Thevenot, C., Martinet, C., & Terrier, P. (2023). Reading numbers is harder than reading words: An eye-tracking study. *Acta Psychologica*, *237*(November 2022), 103942. https://doi.org/10.1016/j.actpsy.2023.103942

Deason, R. G., & Marsolek, C. J. (2005). A critical boundary to the left-hemisphere advantage in visual-word processing. *Brain and Language*, *92*(3), 251–261. https://doi.org/10.1016/J.BANDL.2004.06.105

Dehaene, S. (1992). Varieties of numerical abilities. *Cognition*, *44*, 1–42.

Dehaene, S., Cohen, L., Sigman, M., & Vinckier, F. (2005). The neural code for written words: a proposal. *Trends in Cognitive Sciences*, *9*(7), 335–341. https://doi.org/10.1016/j.tics.2005.05.004

Dehaene-lambertz, G., Monzalvo, K., & Dehaene, S. (2018). *The emergence of the visual word form : Longitudinal evolution of category-specific ventral visual areas during reading acquisition*.

Dotan, D., & Friedmann, N. (2018). A cognitive model for multidigit number reading: Inferences from individuals with selective impairments. *Cortex*, *101*, 249–281. https://doi.org/10.1016/j.cortex.2017.10.025

Dotan, D., & Friedmann, N. (2019). Separate mechanisms for number reading and word reading: Evidence from selective impairments. *Cortex*, *114*, 176–192. https://doi.org/10.1016/j.cortex.2018.05.010

Eger, E., Sterzer, P., Russ, M. O., Giraud, A. L., & Kleinschmidt, A. (2003). A supramodal number representation in human intraparietal cortex. *Neuron*, *37*(4), 719–726. https://doi.org/10.1016/S0896-6273(03)00036-9

Emerson, R. W., & Cantlon, J. F. (2012). Early math achievement and functional connectivity in the fronto-parietal network. *Developmental Cognitive Neuroscience*, *2*(SUPPL. 1), S139–S151. https://doi.org/10.1016/J.DCN.2011.11.003

Flowers, D. L., Jones, K., Noble, K., VanMeter, J., Zeffiro, T. A., Wood, F. B., & Eden, G. F. (2004). Attention to single letters activates left extrastriate cortex. *NeuroImage*, *21*(3), 829–839. https://doi.org/10.1016/j.neuroimage.2003.10.002

Friedmann, N., & Coltheart, M. (2018). Types of developmental dyslexia. *Handbook of Communication Disorders: Theoretical, Empirical, and Applied Linguistic Perspectives*, 721–751. https://doi.org/10.1515/9781614514909-036/PDF/FIRSTPAGE

Göbel, S. M., Watson, S. E., Lervåg, A., & Hulme, C. (2014). Children's arithmetic development: it is number knowledge, not the approximate number sense, that counts. *Psychological Science*, *25*(3), 789–798. https://doi.org/10.1177/0956797613516471

Grainger, J. (2008). Cracking the orthographic code: An introduction. *Language and Cognitive Processes*, *23*(1), 1–35. https://doi.org/10.1080/01690960701578013

Grainger, J., Dufau, S., & Ziegler, J. C. (2016). A Vision of Reading. In *Trends in Cognitive Sciences* (Vol. 20, Issue 3, pp. 171–179). Elsevier Ltd. https://doi.org/10.1016/j.tics.2015.12.008

Grainger, J., & Hannagan, T. (2014). What is special about orthographic processing? *Written Language & Literacy*, *17*(2), 225–252. https://doi.org/10.1075/wll.17.2.03gra

Grainger, J., & Ziegler, J. C. (2011). A dual-route approach to orthographic processing. *Frontiers in Psychology*, *2*(APR), 1–13. https://doi.org/10.3389/fpsyg.2011.00054

Grotheer, M., Herrmann, K.-H., & Kovacs, G. (2016). Neuroimaging Evidence of a Bilateral Representation for Visually Presented Numbers. *Journal of Neuroscience*. https://doi.org/10.1523/JNEUROSCI.2129-15.2016

Hannagan, T., Amedi, A., Cohen, L., Dehaene-lambertz, G., & Dehaene, S. (2015). Origins of the specialization for letters and numbers in ventral occipitotemporal cortex. *Trends in Cognitive Sciences*, *19*(7), 374–382. https://doi.org/10.1016/j.tics.2015.05.006

Heinrich, S. P., Mell, D., & Bach, M. (2009). Frequency-domain analysis of fast oddball responses to visual stimuli: a feasibility study. *International Journal of Psychophysiology : Official Journal of the International Organization of Psychophysiology*, *73*(3), 287–293. https://doi.org/10.1016/j.ijpsycho.2009.04.011

James, K. H., James, T. W., Jobard, G., Wong, A. C. N., & Gauthier, I. (2005). Letter processing in the visual system: different activation patterns for single letters and strings. *Cognitive, Affective & Behavioral Neuroscience*, *5*(4), 452–466. http://www.ncbi.nlm.nih.gov/pubmed/16541814

Joseph, J. E., Cerullo, M. A., Farley, A. B., Steinmetz, N. A., & Mier, C. R. (2016). fMRI correlates of cortical specialization and generalization for letter processing. *NeuroImage*, *32*(2), 806–820. https://doi.org/10.1016/J.NEUROIMAGE.2006.04.175

Leppänen, U., Aunola, K., Niemi, P., & Nurmi, J. E. (2008). Letter knowledge predicts Grade 4 reading fluency and reading comprehension. *Learning and Instruction*, *18*(6), 548–564. https://doi.org/10.1016/J.LEARNINSTRUC.2007.11.004

Liu-Shuang, J., Norcia, A. M., & Rossion, B. (2014). An objective index of individual face discrimination in the right occipito-temporal cortex by means of fast periodic oddball stimulation. *Neuropsychologia*, *52*, 57–72. https://doi.org/10.1016/j.neuropsychologia.2013.10.022

Lochy, A., Collette, E., Rossion, B., & Schiltz, C. (2025). Impaired neural discrimination of regular words from pseudowords in dyslexic adults as revealed by fast periodic visual stimulation. *Neuropsychologia*, *212*. https://doi.org/10.1016/j.neuropsychologia.2025.109137

Lochy, A., Rossion, B., Ralph, M. L., Volfart, A., Hauk, O., & Schiltz, C. (2024). Linguistic and attentional factors e Not statistical regularities e Contribute to word-selective neural responses with FPVS-oddball paradigms. *Cortex*, *173*, 339–354. https://doi.org/10.1016/j.cortex.2024.01.007

Lochy, A., & Schiltz, C. (2019). Lateralized Neural Responses to Letters and Digits in First Graders. *Child Development*, *90*(6), 1866–1874. https://doi.org/10.1111/cdev.13337

Lochy, A., & Schiltz, C. (2022). An Input Lexicon for Familiar Numbers. *Journal of Numerical Cognition*, *8*(2), 244–258. https://doi.org/10.5964/jnc.7385

Lochy, A., Van Belle, G., & Rossion, B. (2015). A robust index of lexical representation in the left occipito-temporal cortex as evidenced by EEG responses to fast periodic visual stimulation. *Neuropsychologia*, *66*, 18–31. https://doi.org/10.1016/j.neuropsychologia.2014.11.007

Lochy, A., Van Reybroeck, M., & Rossion, B. (2016). Left cortical specialization for visual letter strings predicts rudimentary knowledge of letter-sound association in preschoolers. *Proceedings of the National Academy of Sciences of the United States of America*, *113*(30), 8544–8549. https://doi.org/10.1073/pnas.1520366113

Logan, G. D. (1997). *Reading & Writing Quarterly: Overcoming Learning Difficulties AUTOMATICITY AND READING: PERSPECTIVES FROM THE INSTANCE THEORY OF AUTOMATIZATION*. https://doi.org/10.1080/1057356970130203

Lutz, C. G., Coraj, S., Fraga-González, G., & Brem, S. (2024). The odd one out – Orthographic oddball processing in children with poor versus typical reading skills in a fast periodic visual stimulation EEG paradigm. *Cortex*, *172*, 185–203. https://doi.org/10.1016/j.cortex.2023.12.010

Marchive, M., Rossion, B., & Lochy, A. (2025). Optimal Word Reading Rate as Evidenced by Frequency-tagging Electrophysiology. *Journal of Cognitive Neuroscience*, *37*(5), 988–1008. https://doi.org/10.1162/jocn_a_02286

Marsolek, C. J., Kosslyn, S. M., & Squire, L. R. (1992). Form-specific visual priming in the right cerebral hemisphere. *Journal of Experimental Psychology. Learning, Memory, and Cognition*, *18*(3), 492–508. https://doi.org/10.1037//0278-7393.18.3.492

Maurer, U., Brem, S., Bucher, K., & Brandeis, D. (2005). Emerging Neurophysiological Specialization for Letter Strings. *Journal of Cognitive Neuroscience*, *17*(10), 1532–1552.

Maurer, U., & McCandliss, B. D. (2008). The development of visual expertise for words: the contribution of electrophysiology. *Single Word Reading: Behavioral and Biological Perspectives*, *4*.

McCloskey, M., & Schubert, T. (2014). Shared versus separate processes for letter and digit identification. *Cognitive Neuropsychology*, *31*(5–6), 437–460. https://doi.org/10.1080/02643294.2013.869202

McCormick, S. F., Rastle, K., & Davis, M. H. (2008). Is there a 'fete' in 'fetish'? Effects of orthographic opacity on morpho-orthographic segmentation in visual word recognition. *Journal of Memory and Language*, *58*(2), 307–326. https://doi.org/10.1016/J.JML.2007.05.006

Nara, S., Raza, H., Carreiras, M., & Molinaro, N. (2023). Decoding numeracy and literacy in the human brain: insights from MEG and MVPA. *Scientific Reports*, *13*(1), 1–9. https://doi.org/10.1038/s41598-023-37113-0

Norcia, A. M., Appelbaum, L. G., Ales, J. M., Cottereau, B. R., & Rossion, B. (2015). The steady-state visual evoked potential in vision research : A review. *Journal of Vision*, *15*(6), 1–46. https://doi.org/10.1167/15.6.4.doi

Norton, E. S., & Wolf, M. (2012). Rapid automatized naming (RAN) and reading fluency: Implications for understanding and treatment of reading disabilities. *Annual Review of Psychology*, *63*(Volume 63, 2012), 427–452. https://doi.org/10.1146/ANNUREV-PSYCH-120710-100431/CITE/REFWORKS

Park, J., Berg, B. Van Den, Chiang, C., Woldorff, M. G., & Brannon, E. M. (2017). Developmental trajectory of neural specialization for letter and number visual processing. *Developmental Science*, *January 2016*, 1–14. https://doi.org/10.1111/desc.12578

Park, J., Chiang, C., Brannon, E. M., & Woldorff, M. G. (2014). Experience-dependent Hemispheric Specialization of Letters and Numbers Is Revealed in Early Visual Processing. *Journal of Cognitive Neuroscience*, *26*(10), 2239–2249. https://doi.org/10.1162/jocn

Park, J., Hebrank, A., Polk, T. A., & Park, D. C. (2011). Neural Dissociation of Number from Letter Recognition and Its Relationship to Parietal Numerical Processing. *Journal of Cognitive Neuroscience*, *24*(1), 39–50.

Park, J., van den Berg, B., Chiang, C., Woldorff, M. G., & Brannon, E. M. (2018). Developmental trajectory of neural specialization for letter and number visual processing. *Developmental Science*, *21*(3). https://doi.org/10.1111/desc.12578

Polk, T. A., & Farah, M. J. (1998). The neural development and organization of letter recognition: Evidence from functional neuroimaging, computational modeling, and behavioral studies. *Proceedings of the National Academy of Sciences*. https://doi.org/10.1073/pnas.95.3.847

Polk, T. A., Stallcup, M., Aguirre, G. K., Alsop, D. C., D'Esposito, M., Detre, J. A., & Farah, M. J. (2002). Neural specialization for letter recognition. *Journal of Cognitive Neuroscience*, *14*(2), 145–159. https://doi.org/10.1162/089892902317236803

Price, G. R., & Ansari, D. (2011). Symbol processing in the left angular gyrus: Evidence from passive perception of digits. *NeuroImage*. https://doi.org/10.1016/j.neuroimage.2011.05.035

Retter, T. L., & Rossion, B. (2016). Uncovering the neural magnitude and spatio-temporal dynamics of natural image categorization in a fast visual stream. *Neuropsychologia*, *91*, 9–28. https://doi.org/10.1016/j.neuropsychologia.2016.07.028

Retter, T. L., Rossion, B., & Schiltz, C. (2021). Harmonic amplitude summation for frequency-tagging analysis. *Journal of Cognitive Neuroscience*, *33*(11), 2372–2393. https://doi.org/10.1162/jocn_a_01763

Rossion, B., Joyce, C. A., Cottrell, G. W., & Tarr, M. J. (2003). Early lateralization and orientation tuning for face, word, and object processing in the visual cortex. *NeuroImage*, *20*(3), 1609–1624. https://doi.org/10.1016/j.neuroimage.2003.07.010

Rossion, B., Prieto, E. A., Boremanse, A., Kuefner, D., & Van Belle, G. (2012). A steady-state visual evoked potential approach to individual face perception: effect of inversion, contrast-reversal and temporal dynamics. *NeuroImage*, *63*(3), 1585–1600. https://doi.org/10.1016/j.neuroimage.2012.08.033

Rossion, B., Retter, T. L., & Liu-Shuang, J. (2020). Understanding human individuation of unfamiliar faces with oddball fast periodic visual stimulation and electroencephalography. *European Journal of Neuroscience*, *52*(10), 4283–4344. https://doi.org/10.1111/ejn.14865

Schneider, M., Beeres, K., Coban, L., Merz, S., Susan Schmidt, S., Stricker, J., & De Smedt, B. (2017). Associations of non-symbolic and symbolic numerical magnitude processing with mathematical competence: a meta-analysis. *Developmental Science*, *20*(3), e12372. https://doi.org/10.1111/DESC.12372

Schoonbaert, S., & Grainger, J. (2004). Letter position coding in printed word perception: Effects of repeated and transposed letters. *Language and Cognitive Processes*. https://doi.org/10.1080/01690960344000198

Schubert, T. M. (2017). Why are digits easier to identify than letters? *Neuropsychologia*, *95*(November 2016), 136–155. https://doi.org/10.1016/j.neuropsychologia.2016.12.016

Share, D. L. (1995). Phonological recoding and self-teaching: sine qua non of reading acquisition. *Cognition*, *55*(2), 151–218. https://doi.org/10.1016/0010-0277(94)00645-2

Siemann, J., & Petermann, F. (2018). Evaluation of the Triple Code Model of numerical processing—Reviewing past neuroimaging and clinical findings. *Research in Developmental Disabilities*, *72*, 106–117. https://doi.org/10.1016/J.RIDD.2017.11.001

Simon, G., Lanoë, C., Poirel, N., Rossi, S., Lubin, A., Pineau, A., & Houde, O. (2013). Dynamics of the Anatomical Changes That Occur in the Brains of Schoolchildren as They Learn to Read. *PloS One*, *8*(12). https://doi.org/10.1371/journal.pone.0081789

Srinivasan, R., Russell, D. P., Edelman, G. M., & Tononi, G. (1999). Increased synchronization of neuromagnetic responses during conscious perception. *Journal of Neuroscience*, *19*(13), 5435–5448. http://www.scopus.com/inward/record.url?eid=2-s2.0-0033169051&partnerID=tZOtx3y1

Stevens, C., McIlraith, A., Rusk, N., Niermeyer, M., & Waller, H. (2013). Relative laterality of the N170 to single letter stimuli is predicted by a concurrent neural index of implicit processing of letter names. *Neuropsychologia*, *51*(4), 667–674. https://doi.org/10.1016/j.neuropsychologia.2012.12.009

Stevens, W. D., Kravitz, D. J., Peng, C. S., Tessler, M. H., & Martin, A. (2017). Privileged Functional Connectivity between the Visual Word Form Area and the Language System. *The Journal of Neuroscience*, *37*(21), 5288–5297. https://doi.org/10.1523/JNEUROSCI.0138-17.2017

Stothart, G., Quadflieg, S., & Milton, A. (2017). A fast and implicit measure of semantic categorisation using steady state visual evoked potentials. *Neuropsychologia*, *102*(December 2016), 11–18. https://doi.org/10.1016/j.neuropsychologia.2017.05.025

Tagamets, M. A., Novick, J. M., Chalmers, M. L., & Friedman, R. B. (2000). A parametric approach to orthographic processing in the brain: An fMRI study. *Journal of Cognitive Neuroscience*, *12*(2), 281–297. https://doi.org/10.1162/089892900562101

Tanaka, J. W., & Curran, T. (2001). A neural basis for expert object recognition. *Psychological Science*, *12*(1), 43–47.

Tarkiainen, a, Helenius, P., Hansen, P. C., Cornelissen, P. L., & Salmelin, R. (1999). Dynamics of letter string perception in the human occipitotemporal cortex. *Brain : A Journal of Neurology*, *122 (Pt 1*, 2119–2132. http://www.ncbi.nlm.nih.gov/pubmed/10545397

Thesen, T., McDonald, C. R., Carlson, C., Doyle, W., Cash, S., Sherfey, J., Felsovalyi, O., Girard, H., Barr, W., Devinsky, O., Kuzniecky, R., & Halgren, E. (2012). Sequential then interactive processing of letters and words in the left fusiform gyrus. *Nature Communications*, *3*, 1284. https://doi.org/10.1038/ncomms2220

van de Walle de Ghelcke, A., Rossion, B., Schiltz, C., & Lochy, A. (2021). Developmental changes in neural letter-selectivity: A 1-year follow-up of beginning readers. *Developmental Science*, *24*(1), 1–17. https://doi.org/10.1111/desc.12999

Wandell, B. a, Rauschecker, A. M., & Yeatman, J. D. (2012). Learning to see words. *Annual Review of Psychology*, *63*, 31–53. https://doi.org/10.1146/annurev-psych-120710-100434

Yeo, D. J., Pollack, C., Merkley, R., Ansari, D., & Price, G. R. (2020). The “Inferior Temporal Numeral Area” distinguishes numerals from other character categories during passive viewing: A representational similarity analysis. *NeuroImage*, *214*(February), 116716. https://doi.org/10.1016/j.neuroimage.2020.116716

Ziegler, J. C., & Goswami, U. (2005). Reading acquisition, developmental dyslexia, and skilled reading across languages: a psycholinguistic grain size theory. *Psychological Bulletin*, *131*(1), 3–29. https://doi.org/10.1037/0033-2909.131.1.3

Zorzi, M. (2010). The connectionist dual process (CDP) approach to modelling reading aloud. *European Journal of Cognitive Psychology*, *22*(5), 836–860. https://doi.org/10.1080/09541440903435621