

From numbers to letters: Feedback regularization in visual word recognition

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ABSTRACT

Word reading in alphabetic languages involves letter identification, independently of the format in which these letters are written. This process of letter ‘regularization’ is sensitive to word context, leading to the recognition of a word even when numbers that resemble letters are inserted among other real letters (e.g., M4T3R14L). The present study investigates the electrophysiological correlates of number-to-letter regularization by means of the masked priming paradigm: target words (MATERIAL) were preceded by fully alphabetic primes (MATERIAL), primes with letter-like numbers (M4T3R14L), or primes with unrelated numbers (M7T6R28L). ERPs revealed three subsequent effects. Around 150 ms the unrelated numbers condition elicited a positive effect, compared to the other two conditions, in the occipital electrodes. Then, target words preceded by primes with numbers elicited a more negative N200 in the same electrodes compared to the fully alphabetic condition. Finally, both alphabetic primes and letter-like numbers elicited a posterior positive component peaking around 260 ms compared to unrelated numbers. Source analysis for each electrophysiological effect revealed a similar early increase of activity in the left occipito-temporal pathway for alphabetic primes and primes with letter-like numbers. Around 200 ms, the orthographic interference due to the numerical values correlated with an increase of activity in parietal areas; finally, a recursive effect in the left occipital cortex was found, reflecting abstract letter activation. These results indicate that direct feedback interaction from word units strongly influences the activation of the letter units at a format-independent abstract level.

Keywords: Visual Word-Recognition, Numbers, Letters, ERPs, tPCA, sLORETA

1. INTRODUCTION

In visual word recognition a reader is able to recognize single letters at an abstract level independently of the physical properties of these letters (i.e., *font*, **Size**, **CaSe**; see Jacobs & Grainger, 1991; McCandliss, Cohen & Dehaene, 2003; McClelland & Rumelhart, 1981; Rayner & Pollatsek, 1989). Readers perform fine-grained discrimination processes to correctly differentiate between very similar strings (e.g., *foe* and *toe*), while at the same time they overlook small differences to achieve the corresponding abstract letter representation from different allographs of the same lexical item (e.g., *foot*, **FoOt**, **FOOT**). In other words, readers map heterogeneous low-level featural information onto abstract letter representations which code orthographic information about the presence of a letter identity in a specific location. Thus, these abstract letter representations are activated independently of a letter's case, font or size (Coltheart, 1981; Grainger & Van Heuven, 2003; McClelland, 1976; for reviews, see Bowers, 2000; Thompson, 2009).

Interestingly, readers recognize letters in the context of a word better than when the letter is presented in isolation (Johnston & McClelland, 1973), suggesting that accessing abstract letter representations is sensitive to word context. In this line, some authors (Polk & Farah, 1997; Polk, Lacey, Nelson, Demiralp, Newman et al., 2009) have proposed that the acquisition of abstract letter representations is context-dependent: children learn that *A* and *a* are two variants (allographs) of the same letter by encountering words like *cap* and *CAP* (i.e. words with initial and final letters that do not vary much in their features).

A recent study by Perea, Duñabeitia and Carreiras (2008) used the masked priming paradigm to examine whether briefly-presented words which included some letter-like numbers could effectively activate a normally-written target word. Primes containing letter-

like numbers (e.g., M4T3R14L), facilitated the recognition of a target word (e.g., MATERIAL) as much as an identity priming condition (e.g., MATERIAL). The same effect was obtained when letter-like symbols replaced the critical letters (e.g., MΔTЄR!ΔL for MATERIAL), showing that the cognitive system can activate abstract orthographic representations based on similar perceptual features even when the stimulus is not strictly alphabetical. It should be pointed out that in this study by Perea and colleagues, participants were not aware of the letter-like characters embedded in the strings, since the primes were so briefly presented (i.e., 50 ms) that participants could not consciously process the manipulated strings (see Forster, Mohan, & Hector, 2003), and the effects obtained were taken as evidence of automatic and unconscious regularization of letter-like characters.

In a commentary to the Local Combination Detector model (Dehaene, Cohen, Sigman & Vinckier, 2005), Carreiras, Duñabeitia and Perea (2007) suggested that Perea and colleagues' 2008 findings reflect regularization mechanisms in letter identity assignment, as M4T3R14L, MΔTЄR!ΔL and MATERIAL as primes produce similar facilitation at initial stages of visual word recognition when letter encoding processes are taking place: in a task that requires accessing abstract letter representations (i.e., a reading task), letter-like numbers (e.g., 1 for I, 2 for S, 3 for E, 4 for A) are regularized and perceived as letters. However, this was only the case for targets that were words. Interestingly, there was no facilitation for non-word targets. This led Carreiras and colleagues (2007) to describe the regularization mechanism in terms of feedback activation from the lexical level of word processing: letter-like numbers were processed as letters because of the activation received from word units. For this reason, when the target stimulus is a nonword, no interaction with word-level knowledge and no regularization is expected.

In support of this view, interactive models of visual word recognition (e.g., Grainger & Jacobs, 1994; McClelland & Rumelhart, 1981) assume interactive connections from the word level units, which help to set the orthographic units which constitute the target word. A series of studies (Bowers, 2000; Bowers & Michita, 1998; Bowers, Vigliocco & Haan, 1998) suggest that feature-independent abstract orthographic knowledge is multi-level structured: in other words, there is evidence for both letter and word orthographic codes. As suggested by Bowers and Michita (1998; see also Polk & Farah, 1997), distinct letter-level and word-level abstract orthographic representations would interact in learning and establishing abstract orthographic units. Interestingly, bidirectional connections are assumed to exist between letter and word representations: location-specific letter detectors receive bottom-up activation from featural information of the visual input and send activation to location-invariant abstract letter representations. These representations build the whole-word orthographic code, which in turn can feedback activation to the abstract letter representations that constitute the word (Grainger & Van Heuven, 2003). Through these mechanisms, higher lexical level information contributes to the development of abstract orthographic representations (Bowers & Michita, 1998; Polk & Farah, 1997). This interaction between letter and word codes could be responsible for the number-to-letter regularization process described by Carreiras and colleagues (2007). Specifically, word units similar to the word containing letter-like numbers (MATERIAL-M4T3R14L) would directly interact with the orthographic processing of abstract letter units, leading to the number-to-letter regularization.

On the other hand, a different account has also been offered to explain the results of Perea and colleagues (2008). In a response to Carreiras and colleagues (2007), Dehaene and Cohen (2007) claimed that these effects were due to a certain level of tolerance of abstract letter detector neurons (included in the Local Combination Detector model of Dehaene et al., 2005)

that “*rest on a robust pyramid of lower-level feature detectors with increasingly larger receptive fields and with a considerable redundancy*” (page 456). According to the LCD model groups of neurons would detect letters, with a certain level of tolerance based mainly on bottom-up activation and lateral connections. However, it should be also noted that Dehaene and colleagues also assumed some sort of feedback connections. Unfortunately, the nature of these feedback connections was clearly underspecified within the general architecture of the model. Hence, according to Dehaene and Cohen’s proposal, Perea and colleagues’ results could be interpreted in terms of visual similarity: they argued that a letter like A receives converging input from horizontal and diagonal bars, with some degree of tolerance in placement and orientation. Thus, letter A can be (similarly) activated with the presentation of A and 4. In contrast to Carreiras and colleagues’ (2007) proposal, the activation of abstract letter units would be based only on visual similarity, independently of the whole-word code; in other words, there would be no need for the inclusion of top-down mechanisms that send feedback activation from more abstract word-level representations. In this frame, the letter-by-number conversion would be pursued very early in the word recognition process: visual features that could be common to number and letter would be immediately mapped onto a letter representation at the earliest stages, probably because of the reading task (but see Perea, Duñabeitia, Pollatsek & Carreiras, 2009, for a reply). Admittedly, the mapping of low-level features onto abstract shape-specific letter cells seems to be based on partial information (Grainger, Rey & Dufau, 2008); thus, a noisy processing of the masked primes containing numbers in the Perea and colleagues’ (2008) study could potentially account for their results.

This debate has important theoretical implications for understanding the nature of abstract orthographic codes and the mechanisms through which they can be accessed. Critically, previous findings have shown that abstract letter representations can be accessed through a wide range of case/font-specific stimuli and that the brain can distinguish between different case or fonts at initial stages of processing. Many theoretical proposals suggest that letter recognition involves at least three different stages (Grainger et al., 2008; Jacobs & Grainger, 1991; McClelland & Rumelhart, 1981; Whitney, 2001). In the first stage, the physical features (such as size, orientation and component features) are extracted from the visual input ¹. These features are then integrated, in a second stage, in higher level representations of letter format that are insensitive to size and orientation of the stimulus but sensitive, for example, to case. Finally, in a third stage, the activation related to this representation propagates to a more abstract representation of letter identity, insensitive to the format of the perceived stimulus.

Petit, Midgley, Holcomb and Grainger (2006) described specific electrophysiological correlates - Event-Related Potentials (ERPs) - for each of these three stages. In their study, participants were required to identify letters that were briefly preceded by a letter prime. Visual similarity between primes and targets modulated the N/P150, a negative deflection around 150 ms associated with visual processing of the target stimulus (see Chauncey, Holcomb & Grainger, 2008, for converging ERP evidence in a masked priming experiment testing words with different sizes or fonts). Specifically, this was occipitally more positive for dissimilar target letters following their same-name primes (such as D-d or d-D) compared with very similar target letters following their primes (as S-s or s-S) ². In the same study, letter case manipulations affected the P200 component at occipital sites. The P200 component was more positive-going for targets preceded by the same letter with a different case (as a-A)

compared to the same case (as A–A). This was interpreted as reflecting the second stage of case letter recognition. Interestingly, orthographic overlap in a prime-target word pair (e.g., the pseudoword *trock* preceding the word *truck*) has been reported to affect either the N200 (Grossi & Coch, 2005) or the early phase of the N250 (i.e. between 150 and 200 ms, Grainger, Kiyonaga & Holcomb, 2006; see also Carreiras, Duñabeitia & Molinaro, in press). It thus seems that this time window around 200 ms is sensitive to the processing of sub-lexical information, such as fine-grain orthographic properties of the target word (see however, Duñabeitia, Molinaro, Laka, Estévez & Carreiras, 2009a).

In these two early stages, the brain thus seems to extract all the critical feature information to reliably activate the relative abstract letter units. Grainger and Holcomb (2009a, pages 156-157) propose that ERPs in the time window between 90 and 200 ms (the first two time windows discussed by Petit et al., 2006) are “*modulated by the level of feature overlap between prime and target stimuli and, in the case of printed words, likely reflect the mapping of visual features onto location-specific letter representations*”. Another study (Rey, Dufau, Massol & Grainger, 2009) recorded ERPs elicited by letters and pseudoletters, revealing a transition from feature analysis to letter identification in the 100–200-ms time window. Measures indexing this transition were then computed at the level of individual letters: some information about individual letter identities was already available in the waveform before the peak of the P200 (but see Finkbeiner & Coltheart, 2009, for a discussion of these findings).

After the two earliest stages, Petit and colleagues (2006) referred to the P260 component as being representative of the stage at which abstract letter representations are accessed. This positive deflection in the posterior electrodes just before 300 ms was in fact sensitive to case-

independent letter identity manipulations. It was always more negative to the target preceded by a different letter as a prime (as A-B or a-B) compared to the same letter (as A-A, a-A).

These findings are in line with the LCD model proposed by Dehaene and colleagues (2005): a hierarchy of local combination detectors selectively responds to the increasingly complex properties of a printed word. According to this model, low-level features are mapped onto detectors that respond selectively to case-specific letter shapes before activating banks of abstract letter detectors.

In sum, several stages have been identified during visual word recognition. However, the issue that has not been settled yet is whether these stages follow a feed-forward architecture, or whether feedback mechanisms are at work. We aim to address this question in the present study by combining the use of non-alphabetic stimuli embedded in words that are perceptually similar to letters, while measuring ERPs to evaluate the role of the word context in letter recognition.

1.1. The present study

Event-related potentials are here employed to analyze the time course of the number-to-letter regularization and investigate the mechanisms through which letter-like numbers activate perceptually similar letter units, and consequently the corresponding abstract letter representations. Determining the processing stage at which a letter-like number is processed as a letter is critical to evaluate the role of the word context in the activation of abstract letter units, and to discriminate the interaction between bottom-up and feedback mechanisms (see Dehaene & Cohen, 2007, vs. Carreiras et al., 2007). ERPs were here recorded while 26 Spanish speakers were engaged in a reading task, with targets (*MATERIAL*) that could be preceded by an identical prime (*MATERIAL*), by the same word with some letter-like numbers

replacing the corresponding letters (M4T3R14L), or by a word with unrelated numbers in the same positions (M6T2R76L). Note that in the three cases, there was a noticeable perceptual change in font between primes and targets as a consequence of the different font size. However, differently from the Perea and colleagues (2008), we employed a semantic categorization task for two reasons: (i) there was no need to use nonword stimuli (note that non-words did not show any regularization effects in Perea et al., 2008) but in addition, (ii) this task requires focussing attention on the word meaning more than the word form. Thus, if regularization is still found with this task, this will be a clearer demonstration that this process is present under normal situations of reading for comprehension.

As stated above, two contrasting hypotheses have been posited: while Carreiras and colleagues (2007) discuss Perea and colleagues' findings as evidence of a feedback regularization mechanism due to the word context, Dehaene and Cohen (2007) propose that the effect is mainly due to visual similarity, i.e. noisy processing of the masked primes based on the detection of critical features (for a discussion of low-level features see Grainger et al., 2008). These two proposals would predict differences in the ERPs in the three conditions in three successive time windows (as also reported by Petit et al., 2006) corresponding to the following components: N/P150, N200 (or N250) and P260³.

The N/P150. A similar N/P150 for MATERIAL and M4T3R14L (as primes for MATERIAL) is predicted by both Carreiras and colleagues (2007) and Dehaene and Cohen (2007) since only the perceptual similarity between letters and letter-like numbers is initially evaluated. This component reflects the initial retinotopic mapping of visual features, to activate location-specific letter detectors. Holcomb and Grainger (2006) reported for example that 1-letter different primes did not differ significantly from complete repetition in this time-window,

probably because a higher number of visual features have to differ between prime and target to modulate the N/P150. At this stage of processing, the lexicality of the string of letters does not influence ERPs: both primes *table* (word) and *teble* (nonword) elicited the same N/P150 amplitude time-locked to the target word *TABLE* (Holcomb & Grainger, 2006).

Dehaene and Cohen (2007) critically predict that no further distinction would be made between a letter and a letter-like number.

The N200. At a later orthographic stage (i.e. around 200 ms), retinotopic features are integrated to distinguish case (Petit et al., 2006) and orthographic dissimilarities (Carreiras et al., in press; Duñabeitia et al., 2009a; Grainger et al., 2006; Grossi & Coch, 2005; Holcomb & Grainger, 2006). Low-level orthographic manipulations, very similar to our manipulation, were shown to affect ERPs around 200 ms (Grossi & Coch, 2005; Petit et al., 2006; for item-level manipulations see Rey et al., 2009). Petit et al. (2006) showed that visual similarity between upper and lower cases of the same letter affected ERPs around 200 ms, probably because of case-specific letter-shape detectors (see also Dehaene et al., 2005): *e* and *E* elicited distinct ERP effects in this time window, so that, predictably, *E* and *3* will differentially modulate ERPs around 200 ms.

In line with the findings of Petit and colleagues (2006), Carreiras and colleagues' (2007) proposal predicts that words containing numbers and alphabetic words should produce distinguishable ERP effects: in other words, the two number conditions would elicit similar ERP effects, and these should differ from the alphabetic condition. In this frame, perceptual similarity does not matter at this stage of processing for two main reasons. Firstly, the information concerning the whole word context is still not available at this stage, so that no number-to-letter regularization could take place. Grainger and Holcomb (2009a) propose that

this time window represents the processing of abstract orthographic representations (letters and letter clusters) that will be mapped onto higher-level lexical representations. *Only* at a later stage, around 300 ms (Holcomb & Grainger, 2006), would the whole word orthographic code be available for further computation. Secondly, while low-level letter features with different formats could converge on case-specific letter representations (remember the fine-grain sensitivity that permits distinguishing between *foe* and *toe*), low-level number features should activate qualitatively distinct numerical representations independently from their similarity with letters.

In contrast, according to Dehaene and Cohen (2007) visual similarity should exert an influence from the earliest stage of processing onwards. Based on the relative tolerance of the letter recognition system, a letter and a perceptually similar number (A and 4) should be processed similarly while the same letter and a control number (A and 7) should elicit larger ERP differences. In other words, the effect discussed by Perea et al. (2008) would be mainly due to basic perceptual similarity, and no (or less) orthographic interference would be caused by letter-like numbers since they were interpreted as letters at an initial perceptual stage of processing. In this frame, around 200 ms, both identity primes (MATERIAL) and primes containing letter-like numbers (M4T3R14L) should differ from a control condition (M6T2R76L).

The P260. Holcomb and Grainger (2006) have suggested that the earliest ERP evidence of whole word activation is around 300 ms (the P325) before lexical processing, represented by the early stage of the N400 in their model (see also Grainger & Holcomb, 2009a). This ERP component is suggested to reflect word-level processing at the interface between sub-lexical and lexical processing. This time window could thus be the candidate for representing the interaction between letter-level and word-level abstract orthographic representations.

According to Carreiras and colleagues' (2007) proposal, if letter-level and word-level abstract orthographic representations directly interact at this stage of processing (Bowers et al., 1998; Bowers & Michita, 1998), feedback mechanisms should lead to the identification of letter-like numbers as letters, so that the same abstract letter representations are activated before lexical access when the stimuli contain either letters or letter-like numbers. This should be reflected in a more positive component around 300 ms for targets preceded by words (MATERIAL) and words containing letter-like numbers (M4T3R14L) compared to a control condition (M6T8R76L). In parallel with Petit and colleagues' (2006) findings, the activation of similar abstract letter representation should modulate the P260. The same P260 pattern is predicted also by Dehaene and Cohen (2007) hypothesis: noisy perceptual processing of letter-like numbers should converge activation on the same banks of abstract letter detectors.

sLORETA. We will also perform a source analysis (through *sLORETA*) to provide information about the possible cortical generators of the electrophysiological modulations recorded at the scalp. *sLORETA* has the lowest localization error possible at present (see Fuchs, Kastner, Wagner, Hawes & Ebersule, 2002; Jurcak, Tsuzuki & Dan, 2007; Pascual-Marqui, 2002). The source analysis will help us in constraining the stream of processing elicited by our stimuli containing numbers and letters.

Across the three processing stages discussed above, the proposals of Dehaene and Cohen (2007) and Carreiras et al. (2007) predict increases of activation in different brain regions. On the one hand, Dehaene and Cohen (2007) would predict an increase of activation only in the brain areas involved in visual word processing, according to their LCD model (Dehaene et al., 2005). This model proposes a ventral occipito-temporal pathway for the processing of visually presented words. A hierarchy of brain regions irradiating from occipital to temporal

areas should show increases of activation for targets preceded by identity primes and primes containing letter-like numbers compared to the control across time (150 ms, 200 ms and 260 ms). The left fusiform gyrus, and some temporal areas should be involved in the processing of orthographic units.

On the other hand, Carreiras et al.'s (2007) proposal predicts similar results around 150 ms. However, the orthographic interference elicited by numbers around 200 ms should correlate with a qualitatively different increase of activation for letter-like numbers and controls compared to the identity condition. If there is an increase of activation due to numerical processing, the orthographic interference exerted by number could be evident in the parietal areas that have been suggested to be involved in numerical processing (Dehaene, Piazza, Pinel & Cohen, 2003). Finally, if the same abstract letter representations are activated by letters and letter-like numbers these two conditions should show increases of activation compared to the control. According to the LCD model, banks of abstract letter detectors are bilaterally located in the occipital areas, so that we could predict the same occipital increase of activity for letters and letters-like numbers due to recursive feedback connections to these posterior regions.

2. METHOD

2.1. Participants

Twenty-six undergraduate students (17 women, 9 men) from the University of La Laguna participated in the experiment for course credit. All of them were native Spanish speakers, with no history of neurological or psychiatric impairment, and with normal or corrected-to-normal vision. Average age of the participants was 19.8 (SD: 5.5). Handedness was assessed through a Spanish version of the Edinburgh Handedness Inventory (Oldfield, 1971), in which

a score higher than 6 reflected right-handedness. Participants ranged from 8 to 12 (mean: 10.32; SD: 1.28). Each participant gave informed consent before running the experiment.

2.2. Materials

A total of 210 words were selected from the Spanish LEXESP database (Sebastián-Gallés, Martí, Carreiras & Cuetos, 2000). The mean frequency of these words was 20.57 appearances per million (range: 10.18-47.14), the mean length was 9.2 letters (range: 7-11), and the mean number of orthographic neighbors was 0.6 (range: 0-3). These words were used as targets (e.g., PRIMAVERA, the Spanish word for ‘spring’), and could be preceded by 1) the same word (Identity condition; e.g., PRIMAVERA), 2) the same word including letter-like numbers (Numbers condition; e.g., PR1M4V3R4), or 3) the same word including unrelated numbers in the critical positions (Control; e.g., PR2M8V6R8). As a Control condition, we selected prime strings containing no letter-like numbers, instead of primes with deleted letters (M-T-R--L, as proposed by Dehaene and Cohen (2007). The control conditions in Perea et al (2008) were adequate, since they could hardly imply any sort of facilitation on the target (acting as pure controls). However, Peressotti and Grainger (1999) showed that when complex symbols were inserted between the shared letters (e.g., M%T%R%%L-MATERIAL), the magnitude of the priming effect was much lower than in the case of simple symbols (e.g., M-T-R-L). They attributed this difference to the visual complexity of symbols as compared to hyphens. Therefore, our materials included unrelated letters/numbers with higher visual complexity than a hyphen (e.g., 4 vs. -), to achieve a better control condition than that proposed by Dehaene and Cohen (2007). The letter-like numbers that were used for the number condition were 1, 3, 4, 5 and 7 (I, E, A, S and T, respectively). The mean number of letter-like numbers in the words was 48.15%, and in all cases, numbers replaced at least 40% of the

letters, in the two critical conditions (Numbers and Control conditions). Since there is evidence indicating that the first letter of the string is the anchoring letter for orthographic encoding, none of the words included a manipulation on the initial character. The present study naturally follows from the findings of Perea and colleagues (2008). They showed how target words primed by the same word containing either some letter-like numbers or some letter-like symbols showed similar effects to a regular repetition priming. In the present paper we focused on the number-to-letter regularization ⁴. Three lists of materials were created, so that each target appeared once in each, but each time in a different priming condition. Different participants were assigned to each of the lists.

Participants were required to recognize the target words that referred to animals. In order to make this semantic categorization possible, 30 animal names were presented as primes and followed by 30 unrelated animal target words. All of the experimental targets were non-animal words. A prime visibility test was also included in order to check for conscious identification of the masked primes.

2.3. Experimental procedure

Participants were individually tested in a well-lit soundproof room. The presentation of the stimuli and recording of the responses was carried out using Presentation software on a PC compatible computer associated to a CRT monitor. All stimuli were presented on a high-resolution monitor that was positioned at eye level 80-90 cm in front of the participant. Each trial consisted in the presentation of a forward mask created by hash mark symbols for 500 ms, followed by the display of the prime for 50 ms, and immediately followed by the presentation of the target. Primes were presented in 10 pt. Courier New font and targets in 12 pt. Courier New font; this procedure was the same used in the Perea and colleagues' (2008)

experiment, where in order to minimize physical overlap a different font size was implemented between prime and target. The font size difference is a common way to solve the physical overlap problem without the need of a backward mask (Bowers et al., 1998; Bowers & Michita, 1998; Grainger, Granier, Farioli, Van Assche & Van Heuven, 2006). Target items remained on the screen for 500 ms; the largest word covered a visual angle of 3.37 degrees. The inter-trial interval varied randomly between 700 and 900 ms. Participants reported no awareness of the primes when asked after the experiment. All items were presented in a different random order for each participant. Participants were instructed to press the spacebar on the keyboard to indicate whether the letter string displayed referred to an animal name. Twenty warm-up trials, containing different stimuli from those used in the experimental trials, were provided at the beginning of the session. Participants were asked to avoid eye movements and blinks during the interval when the row of hash marks was not present. Each session lasted approximately one hour and fifteen minutes.

2.4. EEG recording and analyses

Scalp voltages were recorded using a BrainAmp recording system from 60 Ag/AgCl electrodes mounted in an elastic cap (ElectroCap International, Eaton, USA, 10-10 system). The average activity of the two mastoids was used as reference during acquisition and for following analyses. Eye movements and blinks were monitored with four further electrodes providing bipolar recordings of the horizontal (Heog-, Heog+) and left and right vertical (Veog-, Veog+) electro-oculogram. EEG was filtered with an analogue band-pass filter of 0.01-100 Hz and a digital 30 Hz low-pass filter was applied before analysis. The signals were sampled continuously throughout the experiment with a sampling rate of 512 Hz.

As in prior research with the masked priming technique (Holcomb & Grainger, 2006), the focus was on target words. Only trials which were free of ocular artifacts (blinks and eye movements) and muscular artifacts were averaged and analyzed. This resulted in 9% of rejections overall, with no significant differences in the number of rejection across condition. Epochs of the EEG up to 600 ms after the onset of the target word (i.e. 100 ms after the target word disappeared from the monitor) were the primary data. The baseline correction was performed using the average EEG activity in the 100 ms preceding the onset of the target as a reference signal value. Since the earliest ERP effects for word identification have been reported after 100 ms (Hauk et al., 2006; Sereno et al., 1998; for a discussion see Luck, 2005), we did not expect the ERPs elicited by the prime word to affect the ERPs time locked to the target word at least until 50 ms after target word onset. For this reason we included the prime presentation period in the baseline. However, we visually compared the grand-average with 100 ms pre-prime stimulus with our analysis. There were no reliable differences apparent.

Separate ERPs were obtained through epoch averaging for each of the experimental conditions, each of the subjects, and each of the electrode sites. Mean amplitudes were obtained for different time windows.

We expected ERP effects in subsequent time windows referring to the following components: the N/P150, the N200 (or P200), the P260 and possibly the N400. The exact time windows of interest were selected based on a temporal PCA (henceforth tPCA). Through this analysis it is possible to isolate the time windows which have differential variability across the epoch. More specifically, we down-sampled our data to 256 Hz and we considered the time points as variables. We then performed a Varimax rotation of the matrix made by 4680 rows (26 subjects x 60 scalp electrodes x 3 conditions) and 175 columns (each

containing 1 time point each 4 ms in the [-100 to 600] ms epoch). The limit of 90% of the variance was calculated to determine the temporal factors of interest.

We planned two types of analyses of the ERP: a *distributed* analysis for evaluating effects widely distributed over the scalp and a *localized* analysis for evaluating local effects that could be evident at the occipital electrodes for early perceptual ERP effects.

As shown in recent studies (Grossi & Coch, 2005; Holcomb & Grainger, 2006) masked priming studies show the earliest effects around 150 ms in the occipital electrodes. We evaluated these effects through a ‘localized’ analysis considering only the occipital (O1, O2), temporal-occipital (PO7/PO8) and posterior temporal electrodes (T5, T6). For each time window of interest we ran a three-way ANOVA with Electrode (Occipital, Temporal-Occipital, Posterior Temporal), Hemisphere (Left, Right) and Condition (Identity, Numbers, Control) as factors. Post-hoc comparisons were run for each electrode (considering also the midline occipital electrode Oz) contrasting the conditions in a pairwise manner for each time window of interest.

The ‘distributed’ analysis was performed with separate ANOVAs on four groups of electrodes homogeneously distributed over the scalp (see also Holcomb & Grainger, 2006, for similar analysis patterns). In the Midline we ran a two-way analysis of variance considering the Electrode factor (4 levels: Fz, Cz, Pz, Oz) and the Condition (Identity, Numbers, Control). The effects on the electrodes belonging to the Column 1 group (C1) were initially evaluated with a four-way ANOVA crossing the Condition factor with the Electrode factor (three levels: FC1/FC2, C3/C4, CP1/CP2) and with the Hemisphere (2 levels: Left, Right). The Column 2 electrodes (C2) were analyzed crossing the same Condition and Hemisphere factors with a four levels Electrode factor (F3/F4, FC5/FC6, CP5/CP6, P3/P4). Finally, the Column 3 electrodes (C3) were analyzed crossing Condition and Hemisphere with a six-level Electrode

factor (AF3/AF4, F7/F8, C5/C6, T5/T6, PO7/PO8, O1/O2). The contrasts between conditions were evaluated by means of pairwise comparisons for each group of electrodes with ANOVAs entailing the same spatial factors (Electrode and Hemisphere) with a two-level Condition factor (Identity vs. Numbers, Identity vs. Control, Numbers vs. Control).

Where appropriate, critical values were adjusted using the Greenhouse-Geisser (1959) correction for violation of the assumption of sphericity.

2.5. sLORETA analysis

We analyzed the possible cortical generators of the EEG activity recorded at the scalp using the standardized low-resolution electromagnetic tomography (sLORETA). This procedure extracts the more plausible neural generator of an electric field recorded on the scalp surface. The high number of electrodes (60 channels) and the high sampling rate (512 Hz) used in the present experiment makes the source localization plausible with a spatial resolution on the order of approximately 1 cm (Cuffin, Schomer, Ives & Blume, 2001). We extracted the sLORETA solution for each single-subject average separately for each condition for the whole epoch. Then, for each time window of interest (as indicated by both the tPCA and the ERP effects) we determined the statistical differences between conditions: differences in regional neural activity were evaluated using the statistical nonparametric mapping procedure implemented in the sLORETA software package. Conditions were compared in a pairwise manner using a paired t-test procedure based on each voxel value for each participant. We operated a subject-wise normalization for each condition without any data transformation and we ran one single test for average in each specific interval. Before running each test we set a variance smoothing parameter of 0.2 (correction for multiple testing, Nichols & Holmes, 2002) and a pre-test SnPM randomization (N=5000; Manly, 2007).

This type of procedure shows which cortical areas have an increased activity for the first condition (indicated by positive t-values) and which ones show increased activity for the second condition (indicated by negative t-values). For each specific time window of interest we report the regions in which there is the peak of differential activity (expressed in MNI coordinates), indicated by the larger t-values above the critical threshold ($p < 0.05$, one-tailed).

We should point out that the LORETA procedure works better in determining the cortical generators for localized effect over the scalp than distributed effects. As a consequence, we expect the possible early activations, with a more localized topography, to identify cortical generators that are more reliable, compared to later effects that are usually more distributed.

3. RESULTS

3.1. Behavioral measures

Participants correctly categorized 98.3% (SD=0.8) of the animal names when these words were presented as targets. None of the participants responded with more than 6% of errors in the categorization task.

When the animal names were presented as masked primes, participants only identified them in 0.7% (SD=0.8) of the trials. In fact, none of the participants identified the masked animal names in more than 3% of cases. This result confirms that participants were mostly unaware of the existence of the masked primes, and in the case of perceiving something, they were not able to consciously recognize the briefly-presented word.

3.2. Electrophysiological measures

The tPCA analysis revealed 4 principal Temporal Factors (henceforth TF) that explained 90% of the variance. The relative loadings (i.e. the time course of each TF) are reported in Figure 1.

<Please insert Figure 1 about here>

No TF showed high loading after 300 ms. TF 1 (that explained 67.9% of the total variance) shows the first peak around 150 ms and a following slow increasing trend. This type of slowly increasing loading without a clear peak is commonly found in tPCA analysis: it is probably a result of the auto-correlated nature of ERP data, reflecting the increasing variance in time after the critical event (Wastell, 1981). TF 2 (12.2% of the total variance) shows its highest loading at 260 ms. It probably reflects the P260 component previously discussed by Petit et al. (2006). TF 3 (8% of the total variance) has its peak at 150 ms. We assume that it reflects the N/P150 component, i.e. the earliest ERP component associated with pure perceptual processing of the target word. Finally, TF 4 (2.5% of the total variance) shows the highest loading between 180 and 220 ms. This last TF probably reflects the effect at 200 ms that we have suggested reflects the orthographic processing of the stimulus.

Visual inspection of the grand-average (Figure 2) in the time windows indicated by the tPCA, reveal the effect around 150 ms to be occipitally distributed (specifically between 140 and 170 ms): in this time window Numbers and Identity conditions are more negative compared to the Control. Around 200 ms (between 180 and 220 ms) in the same electrodes, a positive deflection is visible for the Identity condition that is not evident for the other two conditions. Finally, there is a more positive deflection for the Numbers and Identity condition compared to the Control right after 250 ms. This deflection lasts until 300 ms in the more

posterior electrodes and seems to last even longer in the more central electrodes. Since this effect is more consistent between 250 and 300 ms we selected this time window for statistical analysis.

<Please insert Figure 2 about here>

The first peak around 150 ms is more negative for the Numbers and Identity compared to the Control condition mainly in the left electrodes. This trend is confirmed by the three-way ANOVA described in the ‘localized’ analysis. We considered the mean amplitude values in the 140-170 ms time window. A significant interaction between Hemisphere and Condition emerged from this analysis [$F(2,50)=4.253$, $p<0.05$]. Post-hoc comparisons were run for each electrode (T5, T6, PO7, PO8, O1, Oz and O2) contrasting the three conditions in a pairwise manner. Results are reported in Table 1 in the 140-170 ms line: F-values for each contrast are reported corrected for sphericity through the Greenhouse-Geisser procedure. This post-hoc analysis confirms that the interaction that emerged in the overall ANOVA is due to a statistical difference between the Control and the other two conditions mainly in the left occipito-temporal electrodes, as is evident in the grand-average. Given the polarity (the Control is more positive) and the topography (occipital) of the effect, we identify this component as the N/P150 described by Holcomb and Grainger (2006), which would tap into early perceptual processes.

In the occipital electrodes (Figure 2), this early component was followed by a slight positive deflection more pronounced for the Identity condition compared to both the Control and Numbers conditions. We quantified this latter deflection as the mean amplitude in the 180-220 ms time window. The same ‘localized’ ANOVA performed in the previous time

window was carried out here. A significant effect of Condition emerged from this analysis [$F(2,50)=3.23, p<0.05$]. The post-hoc analyses reported in Table 1 (180-220 ms line) confirm the effects evident in the grand-average. The main difference in the grand-average between the Numbers and Identity conditions is evident in the left posterior temporal electrodes (PO7, see Figure 1). On the other hand, the main difference between the Identity and Control conditions emerges over the more occipital areas bilaterally: this second component, more negative for the Control and Number conditions as compared to the identity condition is similar to the N200 reported by Grossi and Coch, (2005) as reflecting orthographic processes.

<Please insert Table 1 about here>

Later in time, the grand-average shows a more distributed positive deflection just before 300 ms, more evident at posterior areas of the scalp (Figure 2), but, compared to the two previous effects, it is more distributed even on the central electrodes. We therefore ran the ANOVA described in the ‘distributed’ analysis in the 250-300 ms time window. The overall ANOVA contrasting the three conditions revealed a main effect of Condition [midline: $F(2,50)=3.206, p<0.05$; C3: $F(2,50)=6.709, p<0.01$] and the interaction between Electrode and Condition [midline: $F(6,150)=2.888, p<0.05$; C2: $F(6,150)=3.177, p<0.05$; C3: $F(8,200)=4.814, p<0.01$]. Further post-hoc analyses contrasting the Identity and Control conditions, using the same scheme of analysis as for the overall ANOVA, showed a main effect of Condition (midline: $F(1,25)=4.446, p<0.05$; C3: $F(1,25)=10.224, p<0.01$) and the interaction between Electrode and Condition (midline: $F(3,75)=4.113, p<0.05$; C3: $F(4,100)=6.405, p<0.05$). Similar results emerged from the contrast between the Numbers and the Control condition: there was in fact a main effect of Condition (midline: $F(1,25)=4.498, p<0.05$; C3: F

(1,25)=6.499, $p<0.05$) and an interaction between Electrode and Condition (C1: $F(2,50)=4.171$, $p<0.05$; C2: $F(3,75)=5.313$, $p<0.05$; C3: $F(4,100)=5.959$, $p<0.01$). The interactions between Electrode and Condition found for both the previous two comparisons (mainly on the midline and at the Column 3 electrodes) confirm the positive component that is evident in the grand-average mainly in the central-posterior areas of the scalp. No difference was found between the Identity and Numbers conditions in this time window as evident in the post-hoc analyses presented for the occipital electrodes in Table 1 (250-300 ms). Given the polarity and distribution of this effect, we consider it as reflecting a P260 component (see Grainger & Holcomb, 2009a) that is larger for Identity and Numbers than for the Control condition.

The next component evident in the grand-average is the N400. This component did not differ across conditions, as indicated by the statistical analysis in the 350-450 ms time window and by the tPCA that did not show any specific variance in this time window.

3.3. Source analyses

We separately focus on the cortical generators of each ERP effect in the three time windows described above. For each of them we compared the three conditions (Identity, Number and Control) in a pairwise manner, reporting only the significant differences as indicated by the voxel-by-voxel t-test for that time window. For each time window, the sign of the t-value for the significant voxels indicates which one of the two compared conditions shows activity increases in specific regions.

3.3.1. The N/P150 time window (140-170 ms)

In this time window the comparison between Identity and Control revealed a distributed differential activity, with the Identity showing increased activity (Figure 3a, left panel). This

early increase of activity shows its maximum in the Superior Parietal Lobule in the right hemisphere (SPL, BA 7: $x=20, y=-65, z=65; t=4.54, p<0.01$), even if the homologous area in the left hemisphere was also involved (SPL, BA 7: $x=-10, y=-70, z=55; t=4.31, p<0.01$) and, bilaterally, the Precuneus (larger on the right hemisphere; BA 7: $x=15, y=-65, z=55; t=4.33, p<0.01$). In addition, in Occipital and posterior Temporal areas of the left hemisphere we found increase of activity for the Identity condition: the Middle Temporal Gyrus (MTG, BA 37: $x=-50, y=-60, z=0; t=4.11, p<0.01$), the Inferior Temporal Gyrus (ITG, BA 19: $x=-50, y=-65, z=-5; t=4.09, p<0.01$), the Middle Occipital Gyrus (MOG, BA 19: $x=-50, y=-70, z=-15; t=4.01, p<0.05$), and the Fusiform Gyrus (FG, BA 19: $x=-50, y=-70, z=-20; t=3.99, p<0.01$).

<Please insert Figure 3 about here>

While the comparison between Identity and Numbers did not show any significant differences, the comparison between Numbers and Control revealed a pattern of differential activity similar to the Identity-Control comparison. More specifically, we found bilateral increase of activity for the Numbers condition (Figure 3a, right panel) in the SPL (BA 7; left hemisphere: $x=-20, y=-55, z=65; t=3.62, p<0.05$; right hemisphere: $x=20, y=-65, z=55; t=3.56, p<0.05$). Moreover, also in the left occipito-temporal areas the Numbers condition determined increase of activity, including the MTG (BA 39: $x=-55, y=-75, z=10; t=3.2, p<0.05$), the MOG (BA 19: $x=-55, y=-75, z=5; t=3.12, p<0.05$) and the ITG (BA 19: $x=-50, y=-75, z=-5; t=2.99, p<0.05$).

3.3.2. *The N200 time window (180-220 ms)*

In this time window the comparison between Identity and Control showed a peak of differential occipital activity bilaterally (increase for the Control condition; Figure 3b, left panel) in the Cuneus and in the MOG (BA 19; left hemisphere: $x=-15, y=-95, z=30; t=-4.83, p<0.01$; right hemisphere: $x=45, y=-85, z=15; t=-4.24, p<0.01$). This activity extends bilaterally at the Precuneus in the parietal lobe (BA 7; left hemisphere: $x=-5, y=-80, z=40; t=-4.18, p<0.01$; right hemisphere: $x=5, y=-85, z=40; t=-3.91, p<0.01$). Finally, involvement of posterior portion of the right temporal lobe was found, i.e. the MTG (BA 19: $x=40, y=-85, z=20; t=-4.21, p<0.01$) and the ITG (BA 19: $x=50, y=-75, z=-5; t=-3.81, p<0.05$).

The Identity-Numbers comparison (Figure 3b, right panel) revealed that the Numbers condition determined an increase of activity in the left parietal (SPL, BA 7: $x=-20, y=-55, z=65; t=-3.81, p<0.05$) and occipital lobe (Cuneus, BA 19: $x=-20, y=-95, z=20; t=-3.52, p<0.05$). As in the Identity-Control comparison, the involvement of the posterior portion of the right temporal lobe was evident, i.e. the MTG (BA 39: $x=55, y=-70, z=10; t=-3.58, p<0.05$) and the ITG (BA 19: $x=50, y=-80, z=-5; t=-3.43, p<0.05$). In this time window, the Numbers and the Control conditions did not reveal any significant differential effect.

3.3.2. The P260 time window (250-300 ms)

In the last time window, the distributed effect we recorded with ERPs (i.e. the P260) for Identity and Numbers compared to Control corresponds to a localized cortical generator (Figure 3c).

In fact, both the Identity-Control (Figure 3c, left panel; Cuneus, BA 18: $x=-5, y=-100, z=15; t=3.42, p<0.05$) and the Numbers-Control comparison (Figure 3c, right panel; Cuneus, BA 18: $x=-10, y=-85, z=25; t=3.5, p<0.05$) showed differential activity in the left occipital areas. In these areas the Identity and Numbers conditions compared to the Control condition

determined an increase of activity. The Identity-Numbers comparison did not show any significant effects.

4. DISCUSSION

The present study focuses on the findings of Perea and colleagues (2008), who showed that target word processing was facilitated to the same extent by both an identical prime and a prime with embedded numbers that are perceptually similar to the substituted letters. This is a constraining phenomenon for models of letter perception (Dehaene et al., 2005; Grainger et al., 2008), since the same abstract letter units (Coltheart, 1981; McClelland, 1976) are apparently accessed by both a letter and a perceptually similar stimulus (when unconsciously presented; see Duñabeitia, Perea & Carreiras, 2009b).

Based on the fact that the effect emerged only for word primes, Carreiras and colleagues (2007) suggested that the word context influences the interpretation of perceptually similar numbers as letters. This proposal suggests that the activation of abstract letter units is sensitive to the word context: whole word abstract units would directly interact with abstract letter units because of feedback activation from higher lexical representations. Support for this derives from studies that posit a bidirectional interaction between letter-level and word-level units in the acquisition of abstract orthographic knowledge at multiple levels (Bowers & Michita, 1998; Polk & Farah, 1997).

Differently from Carreiras and colleagues (2007), Dehaene and Cohen (2007) discussed that the effect reported by Perea and colleagues (2008) was a consequence of the relative tolerance of the features needed to activate the abstract letter detectors. According to this last proposal (based on the LCD model, Dehaene et al., 2005), letter processing should be completed before further pre-lexical operations could start (e.g., the computation of the open

bigrams). Even if these last authors recognize the possibility that feedback and lateral connections contribute in letter recognition within the visual system, these mechanism were underspecified in their LCD model.

These two antithetical hypotheses were tested in the present study using the ERP technique. In line with previous findings, visual similarity between prime and target affected ERPs around 150 ms: the conditions with an identity prime (Identity condition: MATERIAL) and a prime containing letter-like numbers (Numbers condition: M4T3R14L) did not differ and were both more negative than the control (Control condition: M6T8R76L). Sensitivity to visual-orthographic overlap increases with time, around 200 ms post-target onset because of the shift to orthographic rather than purely visual effects: at this stage of processing, the two conditions with numbers showed the same amplitude, both more negative than the identity condition. Then, this sensitivity decreases around 300 ms post-target onset, possibly because of lexical feedback effects kicking in at that point in time (see Holcomb & Grainger, 2006).

In the following discussion we will separately focus on each subsequent phase of processing in line with the findings in the temporal/spatial components. sLORETA findings are integrated in this discussion, but they should be considered with caution, since source localization is prone to error when more than one source contributes to determining an ERP effect recorded at the scalp. In addition, sLORETA has a lower spatial resolution than other neuroimaging techniques (such as fMRI). Nevertheless, we believe that these findings could stimulate further research on the topic and could be compared with MEG studies that use similar source localization strategies to identify the source of an electromagnetic component.

4.1. Initial perceptual analysis

The earliest ERP dissociation between Identity and Control conditions emerged between 140 and 170 ms at the left temporal-occipital electrodes: the Control condition was more positive-going as compared to the Identity condition. The more positive effect elicited by the visually more dissimilar prime (Control) has been previously described by Holcomb and Grainger (2006) as an N/P150 component. The distributional and temporal similarity of this effect across several studies using words (Holcomb & Grainger, 2006), single letters (Petit et al., 2006) and pictures of objects (Eddy, Schmid & Holcomb, 2006) suggests that it reflects an early perceptual process, possibly involved in mapping visual features onto higher level representations.

The Numbers condition did not differ from the Identity condition in this early time window. Thus, it seems that at very early moments the cognitive system does not distinguish between numbers and letters, but evaluates only the elementary visual match between prime and target, based on basic low-level feature information.

Interesting evidence derives from the sLORETA solutions computed in this early time window (140-170 ms). In fact, we found an increase of activity in a similar network of brain areas for the Identity and the Numbers condition compared to the Control. The peak of the activity involves bilaterally the Superior Parietal Lobe that is considered a critical associative area responsible for the integration of the perceptual information based on attentional priorities (Molenberghs, Mesulam, Peeters & Vandenberghe, 2007): this effect could be considered as task related (Molholm, Sehatpour, Mehta, Shpaner, Gomez-Ramirez et al., 2006).

More critical for our discussion, an early (140-170 ms) increase of activity in the left occipito-temporal pathway was also found for the Identity and the Numbers condition compared to the Control. Based on our previous discussion, visual similarity seems to lead to

an increase of activation in the areas supposedly involved in word recognition (Dehaene et al., 2005; Glezer, Jiang & Reisenhuber, 2009; Reinke et al., 2008).

The left occipito-temporal involvement for both the Identity and Numbers condition suggests that the expectations induced by the reading task could lead to the fast activation of a brain network associated to word recognition when the visual properties of the stimulus are similar to a string of letters. Based on the visual similarity, both primes used in the Identity and the Numbers condition pre-activate word units stored in the left posterior ventral network, as suggested by Dehaene and Cohen (2007): they proposed a relative tolerance, given the high redundancy in the brain architecture and the existence of abundant lateral connections for mapping visual features onto more specific letter detectors, i.e. specific neurons that respond to each letter. These detectors then would activate larger word units in the left fusiform gyrus (see also Glezer et al., 2009). However, in our opinion, this phase only corresponds to an initial rough perceptual analysis of the visually presented string (Grainger & Holcomb, 2009a). In other words, low-level feature analysis of a word does not imply its full recognition as a lexical pattern stored in memory; probably at this stage, excitatory connections send initial activation to sets of open bigrams (as suggested by Dehaene et al., 2005). This early pre-activation should, however, be supported by further fine-grain orthographic processing.

4.2. Fine-grained orthographic analysis

A clear-cut qualitative distinction between numbers and letters emerged in the following time window (180-220 ms). Many studies have shown that around 200 ms the cognitive system operates an orthographic analysis of the target item (Carreiras et al, 2009a, 2009b, in press; Grainger et al., 2006; Grossi & Coch, 2005). At this stage, the physical properties of the

visual stimulus converge in activating a representation of the single letters that maintain purely orthographic distinctions, such as font or case (Petit et al., 2006). Our results in this time window showed that the (alphabetic) Identity condition has more positive amplitude compared to both the Control and the Numbers conditions. This effect is similar both to the N200 effect described by Grossi and Coch (2005) and to the ‘early’ N250 effect reported by Grainger et al. (2006; see also Carreiras et al., 2009a, 2009b, in press), who described a more negative effect for targets preceded by orthographically inconsistent primes. Since the Numbers condition (M4T3R14L) shows the same amplitude as the Control condition (M6T8R76L), we infer that numbers within a word context exert similar orthographic interference (represented by a larger N200) on the following target word, independently of the visual similarity between numbers and letters.

This pattern of effects around 200 ms was predicted by the Carreiras and colleagues (2007) proposal: at this stage of processing, word level information is still not processed, but the brain is sensitive to the orthographic properties of the single letters (font or case). It thus makes sense to assume that numerical information within the word context converges in a qualitatively distinct type of representation (digits). Some models assume that case-specific detectors would be active at this stage (Grainger et al., 2008; Grainger & Van Heuven, 2003).

In contrast, the *tolerance* hypothesis of Dehaene and Cohen (2007) predicted (at least) differences between the Number and the Control conditions also at this stage of processing: if the cognitive system ‘confounds’ a letter and a number because it treats them as perceptually similar (see N/P150 data), they should activate similar orthographic representations, while a perceptually dissimilar condition (i.e., the control condition) should create stronger interference. In other words, the level of tolerance of abstract letter detector neurons should treat the stimuli (MATERIAL-M4T3R14L) as similar. However, this was not the case in the

present study. Thus, the present set of data supports the proposal that fine-grain orthographic discriminations are computed before accessing larger word units in contrast with the perceptual tolerance hypothesis proposed by Dehaene and Cohen (2007).

The sLORETA analysis revealed that Number and Control conditions differed in the cortical generators of the N200 effects. We found for the two conditions a similar right temporal increase of activation that has been associated with numerical processing in adults, as reported by Izart, Dehaene-Lambertz and Dehaene (2008). However, while the Identity and Control comparison showed increase of activity for the latter condition in the occipito-parietal areas bilaterally, the Identity and Numbers comparison showed increase of activity for the Numbers condition mainly in the left occipito-parietal areas (Figure 3b). The fact that the processing of the Numbers and Control (which also contain numbers embedded in letter strings) involves (partially) distinct neural networks could be critical.

One feasible explanatory hypothesis is that the visual similarity between numbers and letters influences the orthographic evaluation of the target word activating a neural population more related to the processing of the whole word features (i.e. in the left hemisphere). On the other hand, the bilateral occipito-parietal effect emerging from the comparison between the Control and Identity conditions would reflect the more extended occipito-parietal network related to number processing compared to letter processing (Halpern, Glosser, Clark, Gee, Moore et al., 2004; Pesenti et al., 2000). However, critical for our discussion, the source localization analysis suggests an involvement of areas related to numerical processing that were not predicted by Dehaene and Cohen (2007) and could be explained within the Carreiras and colleagues' (2007) proposal.

4.3. Recursive abstract letter activation

Despite this orthographic interference caused by numbers inserted within words, in the next time window (250-300 ms) the Identity and Numbers conditions elicited a more positive component peaking at 260 ms compared to the Control condition. This neurophysiological effect shows the same trend and distribution as the P260 reported by Petit and colleagues (2006). They proposed that this component reflects the activation of the abstract representation of the target letters, independently of the specific orthographic properties of the item which build the whole-word orthographic code.

The time window around 300 ms has also been associated to the initial processing of whole word properties (Grainger & Holcomb, 2009a). Therefore, one possible explanation is that, at the interface between sub-lexical and lexical processing, word level pre-activated units feedback their activation to abstract letter units, influencing the identification of the single letters constituting the target word (as suggested by interactive models; see Grainger & Jacobs, 1994; McClelland & Rumelhart, 1981). This mechanism could explain the similar P260 component for the Identity and Numbers condition and the behavioral data reported by Perea and colleagues (2008) for lexical units.

In the present experiment participants performed a reading task, and consequently, it makes sense to think of a regularization process which is aimed at identifying letters. As the reader is expecting letters in the string, the cognitive system converts to a letter whatever looks like one, in order to be able to read and perform the required task (see Jordan, Thomas & Scott-Brown, 1999, for an illusory letter phenomenon).

Similar increased activity at this later stage for letters and letter-like numbers is supported also by the sLORETA source analysis: the cortical generator of the posteriorly distributed P260 effect was found in the left occipital cortex for both the Identity and the Numbers condition. Similar occipital increase of activation for Identity and Numbers suggests the

existence of feedback connections directed toward more occipital areas after an initial partial analysis of the visual stimulus. It is possible that these recursive connections represent the late establishment of the whole-word orthographic code, based on the abstract representation of the single letters. The left occipital cortical generators are slightly different between the two conditions, but we should note that sLORETA solutions tend to be less accurate in localizing the source of distributed ERP effects such as the P260.

4.4. Interaction between number and letter processing

The overall pattern of the ERP effects thus provides clear insights into the plasticity of the word recognition system, extending the findings of Perea and colleagues (2008). Carreiras and colleagues (2007) discussed a regularization mechanism in letter identity assignment, explaining why a reader confounds M4T3R14L and MATERIAL at initial (and unconscious) stages of letter encoding. Carreiras and colleagues indicated that these results could pose some problems for the Local Combination Detectors (LCD) model (Dehaene et al., 2005), since it assumes the existence of case-specific letter detectors activated to access abstract letter units. Dehaene and Cohen (2007) responded to this argument explaining that the LCD model includes letter detector neurons that “*rest on a robust pyramid of lower-level feature detectors with increasingly larger receptive fields and with a considerable redundancy*” (page 456). They argued that a letter like A receives converging input from horizontal and diagonal bars, with some degree of tolerance in placement and orientation. Thus, letter A can be (similarly) activated with the presentation of A, and 4. These authors recognized the possible existence of feedback and lateral connection that “*contribute to shaping the neurons’ receptive field*”, however, these mechanism were not made explicit in their LCD model. In addition,

these authors claimed that “*there is nothing in Carreiras et al.’s experimental design that forces [their] interpretation - visual similarity alone can explain the results*”.

The present electrophysiological findings suggest that, despite the visual similarity detected between A and 4 (evidenced by the left occipito-temporal activation around 150 ms) the brain finely distinguishes between letter strings and strings of mixed letters and numbers (as shown by the N200 effect originating in the occipito-parietal network) at a level of processing where the whole word code is still not active. Only when the abstract representations of the letters have to be activated is there a direct interaction with the whole word pre-activated units. This leads to the identification of abstract letter units activated by both the letter and letter-like numbers (as indicated by the left occipital increase of activity after 250 ms).

The present results strengthen the idea that a direct interaction between letter-level and word-level abstract orthographic codes could be critical for letter identification mechanisms (as in Jordan et al., 1999). This finding is supported by the proposal that abstract letter units are acquired by children through a mechanism sensitive to the word context, and specifically initial and final letters (Bowers & Michita, 1998; Polk & Farah, 1997). Also, Duñabeitia and colleagues (2009b) recorded participants’ eye movements while they were presented with words containing letter-like characters (e.g., YESTERDAY I SAW THE SECRE74RY WORKING VERY HARD). In their study, manipulations of the initial letter of a word produced a greater reading cost than manipulations of internal letters. This finding is consistent with the view that beginning letters are critical for word recognition, whereas the processing of internal letters may be shallower and influenced by regularization.

In light of the present data, it seems that both Dehaene and Cohen (2007) and Carreiras and colleagues (2007) were correct to some extent. Dehaene and Cohen (2007) proposed a

hierarchy of detectors according to which letters are uniquely identified at a very early stage of word processing. The present findings support the claim that before 200 ms the single letter codes are finely extracted from the visual information (as suggested also by Grainger & Holcomb, 2009a): despite the high redundancy and the relative tolerance of the letter detectors, the brain can distinguish between a number and a letter that are perceptually similar. However, at a more abstract level, the direct interaction with word level processing should be assumed to obtain the whole word orthographic code (as suggested by Carreiras et al., 2007).

Also, this interaction between word-level and letter-level information should be accounted for by models of visual letter recognition (Dehaene et al., 2005; Grainger et al., 2008; Grainger & Van Heuven, 2003), that propose only a single-direction way of accessing abstract letter representations, through shape-specific letter cells. The overall data on number-to-letter regularization in fact suggests that word context (and mainly initial and final letters, Duñabeitia et al., 2009; in line with Bowers & Michita, 1998; Polk & Farah, 1997; Thompson, 2009) critically influences the recognition of letters at an abstract level.

4.5. Conclusions

The present study, which tests the sensitivity of the cognitive system to non-alphabetic stimuli embedded in a word context, strengthens the idea that letter identification could be achieved in three distinct stages. Critically, the last stage in which orthographic specificity is mapped onto abstract letter units is shown to be sensitive to the interaction with word level information, as suggested by a consistent body of behavioral research. The present study goes beyond previous ERP studies that discussed letter recognition and used either single letters (Petit et al., 2006; Rey et al., 2009) or fully alphabetic stimuli (Chauncey et al., 2008). Our

proposal suggests that due to the influence of feedback from higher (lexical) levels of processing, low-level feature-based processes (such as letter identity assignment) are modulated such that the most parsimonious or plausible letter identity for the given lexical context is chosen.

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Footnotes:

1. Feature extraction from the visual input could be further divided into distinct sub-levels (see Grainger, Rey & Dufau, 2008 for a discussion).
2. Evidence for sensitivity to visual form in letter perception has been also found in experiments using the alphabetic decision task. Bowers and colleagues (1998, see also Jacobs & Grainger, 1991), for example, reported a masked priming study in which participants had to perform an alphabetic decision task: stronger priming was found across lower- and uppercase versions of the same letter when they are visually similar (c–C) than when they are visually dissimilar (a–A). Sensitivity to perceptual similarity, however, disappeared when dissimilar letters were embedded in a word context. The same facilitation was found for similar and dissimilar across-case manipulations in a lexical decision task.
3. In the following section we refer to the ERP literature on masked primed word processing (see Grainger & Holcomb, 2009a). However, it should be stated that ERP studies on isolated word processing reported contrasting data on the timing of pre-lexical and lexical ERP effects (see Hauk, Patterson, Woollams, Watling, Pulvermuller & Rogers, 2006; Sereno, Rayner & Posner, 1998, but also Pylkkanen & Maranz, 2003).
4. We did not consider the symbols because they are visually too similar to the letters. On the other hand, the lower visual similarity between numbers and letters should activate to a greater extent the regularization process described by Carreiras et al. (2007) and so produce clearer ERP effects. In a questionnaire we asked 28 participants to evaluate on a 7-point scale (1: very dissimilar; 7 very similar) the visual similarity between full alphabetic words and both words containing letter-like numbers and words containing letter-like symbols. Words with symbols were significantly ($t(27)=4.563$, $p<0.01$) more similar to letters (average value: 5.66; SD: 0.08) than the numbers-letter comparison (4.77; SD: 0.52).

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Table 1: t-values derived from pairwise comparisons (pairwise t-tests, d.f.=25) of the three critical conditions for each posterior electrode in each time window of interest. Probability values are separately corrected across electrodes according to the False Discovery Rate procedure (Benjamini & Hochberg, 1995). Values written in bold letters indicate significant differences.

Time window	Comparison	T5	PO7	O1	Oz	O2	PO8	T6
140-170 ms	Identity vs. Numbers	<i>0.88091</i>	<i>0.99398</i>	<i>0.10954</i>	<i>0.47434</i>	<i>0.65955</i>	<i>0.22136</i>	<i>0.04472</i>
	Identity vs. Control	2.54696*	<i>2.12673</i>	<i>1.63829</i>	<i>0.92520</i>	<i>0.56569</i>	<i>1.06677</i>	<i>0.43704</i>
	Numbers vs. Control	<i>2.13729</i>	2.25344*	<i>1.11803</i>	<i>1.20748</i>	<i>0.90885</i>	<i>0.88600</i>	<i>0.74699</i>
180-220 ms	Identity vs. Numbers	<i>2.17141</i>	2.20409*	<i>1.95857</i>	<i>1.74557</i>	<i>1.51294</i>	<i>1.38672</i>	<i>0.51088</i>
	Identity vs. Control	<i>1.55692</i>	<i>2.07220</i>	<i>1.79360</i>	<i>1.74728</i>	<i>2.07413</i>	2.26186*	<i>1.85661</i>
	Numbers vs. Control	<i>0.61074</i>	<i>0.19494</i>	<i>0.04472</i>	<i>0.28983</i>	<i>0.62530</i>	<i>1.00598</i>	<i>0.67082</i>
250-300 ms	Identity vs. Numbers	<i>0.96281</i>	<i>1.13534</i>	<i>1.11355</i>	<i>1.14630</i>	<i>1.41386</i>	<i>1.29769</i>	<i>1.02470</i>
	Identity vs. Control	<i>2.33281</i>	3.11881*	3.35693**	3.14944*	3.30802**	3.03529*	<i>2.56593</i>
	Numbers vs. Control	<i>1.83712</i>	<i>2.55265</i>	2.88201*	2.86636*	2.89983**	2.89137*	<i>2.19636</i>

* ($p < 0.05$); ** ($p < 0.01$)

Figure captions

Figure 1: Loading of each Temporal Factors (TF) extracted by the temporal PCA. While TF1 shows an increasing trend, TF2, TF3 and TF4 show independent peaks of interest respectively around 260 ms, around 150 ms and around 200 ms.

Figure 2: ERPs elicited by the target word in the three conditions (Identity, Numbers and Control) in the all the electrodes. Negative values are plotted up. Blow-up focuses on the main ERP effects at PO7.

Figure 3: sLORETA solutions for the 140-170 ms (3a), the 180-220 ms (3b) and the 250-300 ms time window (3c). Brain 3D Colin model is here presented from a posterior point of view. Increases of activity are mainly evident in the posterior regions of the cortex. In Figure 3a we present the Identity-Control comparison on the left and the Numbers-Control comparison on the right. In Figure 3b we present the Identity-Control comparison on the left and the Identity-Numbers comparison on the right. In Figure 3c we present the Identity-Control comparison on the left and the Numbers-Control comparison on the right. t-values were corrected through the Nichols & Holmes (2002) procedure.

Figure 1

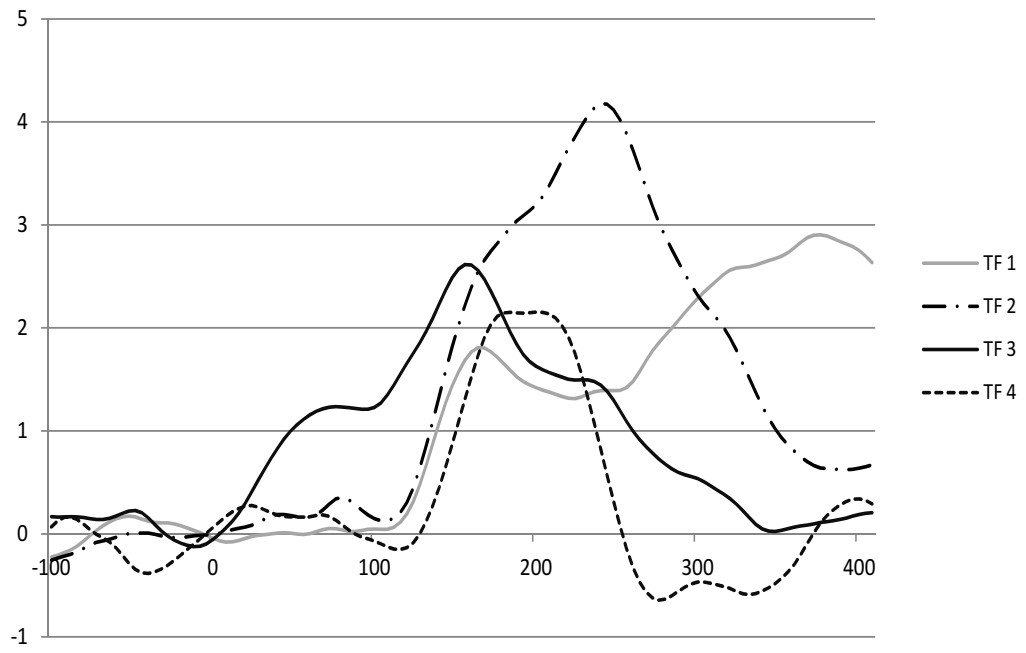


Figure 2

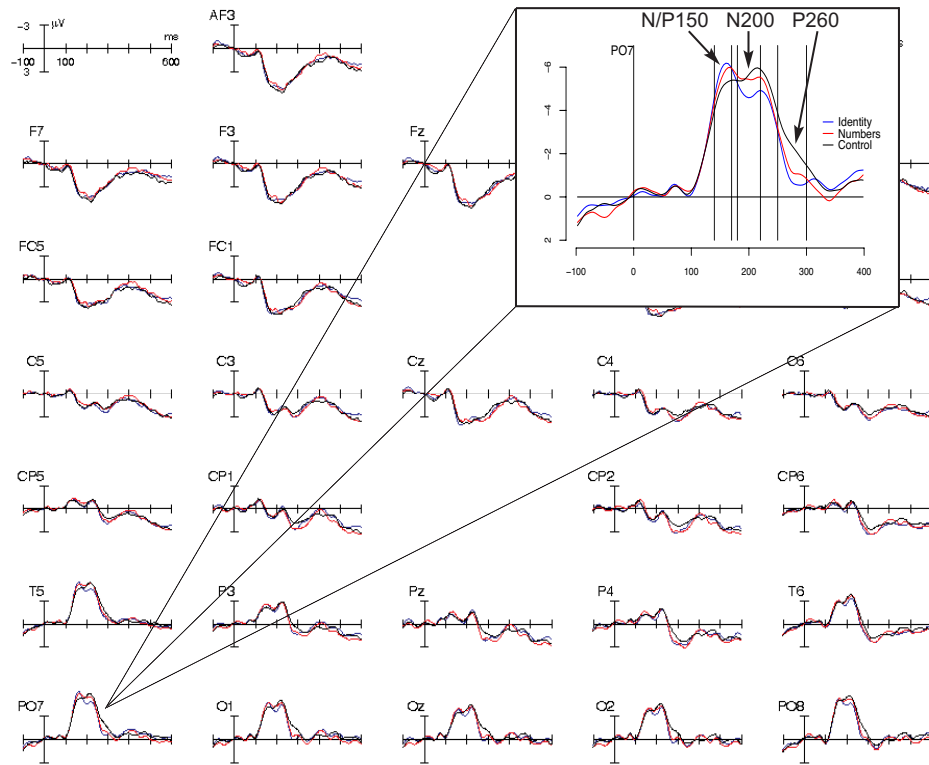


Figure 3

