Research Report

Early involvement of dorsal and ventral pathways in visual word recognition: An ERP study

Cristina Rosazza[a,*], Qing Cai[a], Ludovico Minati[b], Yves Paulignan[a], Tatjana A. Nazir[a]

[a]Institut des Sciences Cognitives, 67, Boulevard Pinel, 69675 Bron Cedex, France
[b]Science Direction and Neuroradiology Units, Fondazione Istituto Neurologico "Carlo Besta", Milano, Italy

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ABSTRACT

Visual expertise underlying reading is attributed to processes involving the left ventral visual pathway. However, converging evidence suggests that the dorsal visual pathway is also involved in early levels of visual word processing, especially when words are presented in unfamiliar visual formats. In the present study, event-related potentials (ERPs) were used to investigate the time course of the early engagement of the ventral and dorsal pathways during processing of orthographic stimuli (high and low frequency words, pseudowords and consonant strings) by manipulating visual format (familiar horizontal vs. unfamiliar vertical format). While early ERP components (P1 and N1) already distinguished between formats, the effect of stimulus type emerged at the latency of the N2 component (225–275 ms). The N2 scalp topography and sLORETA source localisation for this differentiation showed an occipito-temporal negativity for the horizontal format and a negativity that extended towards the dorsal regions for the vertical format. In a later time window (350–425 ms) ERPs elicited by vertically displayed stimuli distinguished words from pseudowords in the ventral area, as confirmed by source localisation. The sustained contribution of occipito-temporal processes for vertical stimuli suggests that the ventral pathway is essential for lexical access. Parietal regions appear to be involved when a serial mechanism of visual attention is required to shift attention from one letter to another. The two pathways cooperate during visual word recognition and processing in these pathways should not be considered as alternative but as complementary elements of reading.

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1. Introduction

Skilled readers can process written words at a remarkable speed. Despite this apparent ease, reading comprises several functional components (Marshall and Newcombe, 1973) which range from visual/orthographic processing at early stages, to phonological and semantic processing at later stages and takes many years to learn (Aghababian and Nazir, 2000). At early visual/orthographic levels of coding, words are thought to pass through a series of hierarchically organised processing steps that start with the elaboration of simple visual features, followed by increasingly larger visual units from single letters up to whole words (Dehaene et al., 2004; Vinckier et al. 2007). Some important characteristics of skilled reading are parallel letter processing (e.g. Weekes, 1997, Lavidor and Ellis, 2002) and perceptual invariance, that is, the ability to identifying

words irrespective of location, font and size (Dehaene et al., 2005).

Research into the neural bases of early processing levels in reading has indicated that the visual skill underlying reading is based on the expertise of occipito-temporal region in the left hemisphere, in particular of the "Visual Word Form Area" (VWFA; Cohen and Dehaene, 2004). A number of functional imaging and event-related potential (ERP) studies have revealed that this region is more responsive to orthographic stimuli than to non-orthographic symbols (Cohen et al., 2003; Maurer et al., 2005), even though the hypothesis of a functional specialization of this region for words has been challenged by contrasting results (e.g., Cai et al. 2008; Hillis et al. 2005; Price and Devlin, 2004; Price et al., 2006). Studies with neurological patients have also shown that damage to areas that include the VWFA can cause pure alexia or "letter-by-letter reading", an acquired reading deficit that typically spares other language functions (Dejerine, 1982; Montant et al. 1998; Rosazza et al., 2007; Warrington and Shallice, 1980). Response properties of the VWFA, such as invariance to spatial location (i.e., the VWFA is activated independently of where in the visual field a word is displayed, Cohen et al., 2000; Cai et al., 2008) and invariance to letter case (i.e., the VWFA is sensitive to word repetition across letter case, Dehaene et al., 2001) have led to the hypothesis that this region serves the extraction of abstract information about the structure of visual words, making rapid word recognition possible (Dehaene et al., 2005).

It is important to note, though, that word recognition in skilled readers can be significantly disrupted simply by displaying words in unusual visual formats (Nazir, 2000). When words are presented vertically, for instance, reading time can double from 13 ms to 25 ms per letter (Bub and Lewine, 1988) and beyond orientation angles of 60° reading time increases with word length, indicating a switch from a parallel to a serial letter-processing mode, that is usually only observed in beginning readers (Aghababian and Nazir, 2000; Bub and Lewine, 1988; Koriat and Norman, 1985; Lavidor et al., 2001). Similarly, words that are most frequently perceived with initial letter capitalization like proper names or nouns in German are less well perceived when the first letter is *not* capitalized (Peressotti et al., 2003; Jacobs et al., 2008), suggesting that case-specific information is used for word recognition. The ability of skilled readers to rapidly recognize a word is thus dependent on familiarity with visual aspects of the word and does not solely rely on the elaboration of abstract representation.

When orthographic stimuli are visually unfamiliar, either because of non-standard visual formats or because the stimulus is itself novel (e.g. nonwords or new words), parietal regions have been reported to be additionally recruited, presumably because alternative reading strategies are engaged. According to Pugh and colleagues, left temporo-parietal (i.e., dorsal) regions, including the angular gyrus and the supramarginal gyrus, are strongly involved in the assembly of orthographic and phonological information, in particular with unfamiliar words (Pugh et al., 2001; Katz et al., 2005). According to other studies (Mayall et al., 2001; Vidyasagar, 2005; Pammer et al., 2006), right parietal regions are more engaged: in a PET-study by Mayall et al. (2001), stronger right-hemisphere activity in the posterior parietal

cortex (PPC) was observed when words were presented in mixed case, compared to the familiar case configuration. Similarly, in a MEG study, Pammer et al. (2006) have shown that right PPC activity, which is observed very early (100–300 ms) following stimulus onset, increases when words are presented in unfamiliar formats. Since right parietal lobe activity is associated with visual attention (e.g. Corbetta and Shulman, 1998), increased PPC activity has been interpreted as indicating higher attentional demands. A recent fMRI study by Cohen et al. (2008) further confirmed the intervention of (bilateral) dorsal posterior parietal cortex in reading words with different modes of degradation, such as rotation, letter spacing and displacement to visual periphery. Furthermore, increased activation of the occipito-parietal dorsal regions was also observed in presence of a strong behavioural length effects, that is, when comparing long with short pseudoword processing (Valdois et al., 2006).

The hypothesis of an involvement of the parietal lobe in reading novel letter-strings and words presented in unfamiliar formats is also supported by the deficits seen in patients with parietal lesions. For example, Hall et al. (2001) studied the patient GK who showed symptoms of Balint's syndrome (optic ataxia and simultanagnosia) and of attentional dyslexia, caused by bilateral parietal damage. GK was able to read words displayed in familiar visual formats, while reading nonwords was impaired. GK was also poor at naming words presented in alternate case and when one or two extra spaces were inserted between letters. Analogously, Vinckier et al. (2006; see also Nazir et al., 2004) reported on a patient with bilateral lesions in the occipito-parietal region who showed left neglect, Gertmann's syndrome and simultanagnosia. The patient was able to read words correctly but had serious problems with pseudowords. Reading words was also found to be disrupted when letters were separated by double spaces and when words with upright letters were presented with an orientation angle greater than 50°. Parietal lesions can thus prevent patients from processing visually novel configurations of letters while sparing processing of visually familiar words. For the latter stimuli, processes in occipito-temporal regions seem to be fully sufficient.

According to Vidyasagar (1999, 2005), attentional feedback from PPC to early sensory areas allows identifying letter order and shifting processing from one letter to another. This hypothesis of a parietal influence on the activity of temporal regions to enable focused spatial attention is supported by recent studies with macaques involving simultaneous recording of neurons in PPC and in medial temporal areas during a selective visual attention task: results revealed that activity in the two regions becomes synchronized, with the PPC leading medial temporal activity by about 10–15 ms. This phase delay is indicative of top-down influences from PPC to medial temporal cortex and has been taken as an evidence that parietal neurons increase activity in earlier sensory areas to enable focused spatial attention (Saalmann et al., 2007).

Processing in ventral and dorsal visual pathways should thus not be considered as alternative but as complementary elements of reading. Since PPC feedback appears to be more important during processing of unfamiliar than familiar visual configurations (Mayall et al., 2001; Pammer et al., 2006), it is likely that this feedback also serves the development of visual
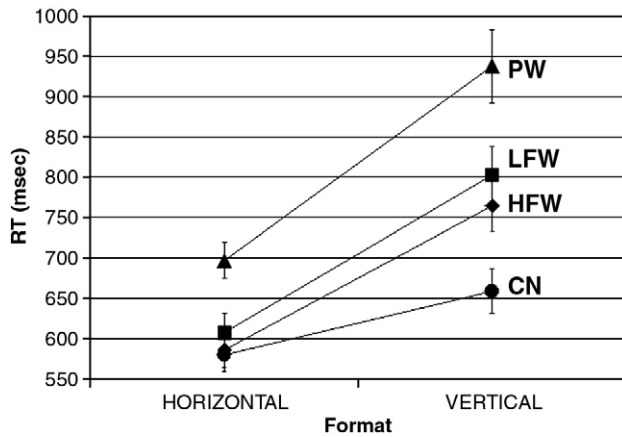
Fig. 1 – Behavioural results. Response times (ms) for the different types of letter-strings as a function of visual format. PW, LFW, HFW and CN refer to pseudowords, low frequency words, high frequency words and consonant strings, respectively. Error bars depict standard errors.

expertise in occipito-temporal regions (see Gilbert et al., 2001 for similar arguments). Understanding the interaction between occipito-parietal and occipito-temporal pathways in visual word recognition may help uncovering the properties of skilled reading.

The aim of the present study is to investigate with ERPs the early temporal dynamics of visual word recognition in terms of engagement of the ventral occipito-temporal and dorsal occipito-parietal pathways. We examined the effect of format variations on early stages of word processing using a lexical decision task where format familiarity (horizontal vs. vertical presentation) and stimulus type (words, pseudowords and consonant strings) were manipulated. Hence, a total of 280 letter-strings comprising high frequency words (HFW), low frequency words (LFW), pseudowords (PW) and consonant strings (CN) were presented once horizontally and once vertically (in random order) to healthy readers of French. With horizontal presentation, we expected to observe typical modulations of early ERP components (N1 and N2) over occipito-temporal sites as a function of orthographic famil-iarity (Bentin et al., 1999; Cohen et al., 2000; Hauk et al., 2006; Maurer et al., 2005; Proverbio et al., 2008). With vertical presentation, however, distinguishing words from nonwords should take longer and a stronger involvement of parietal
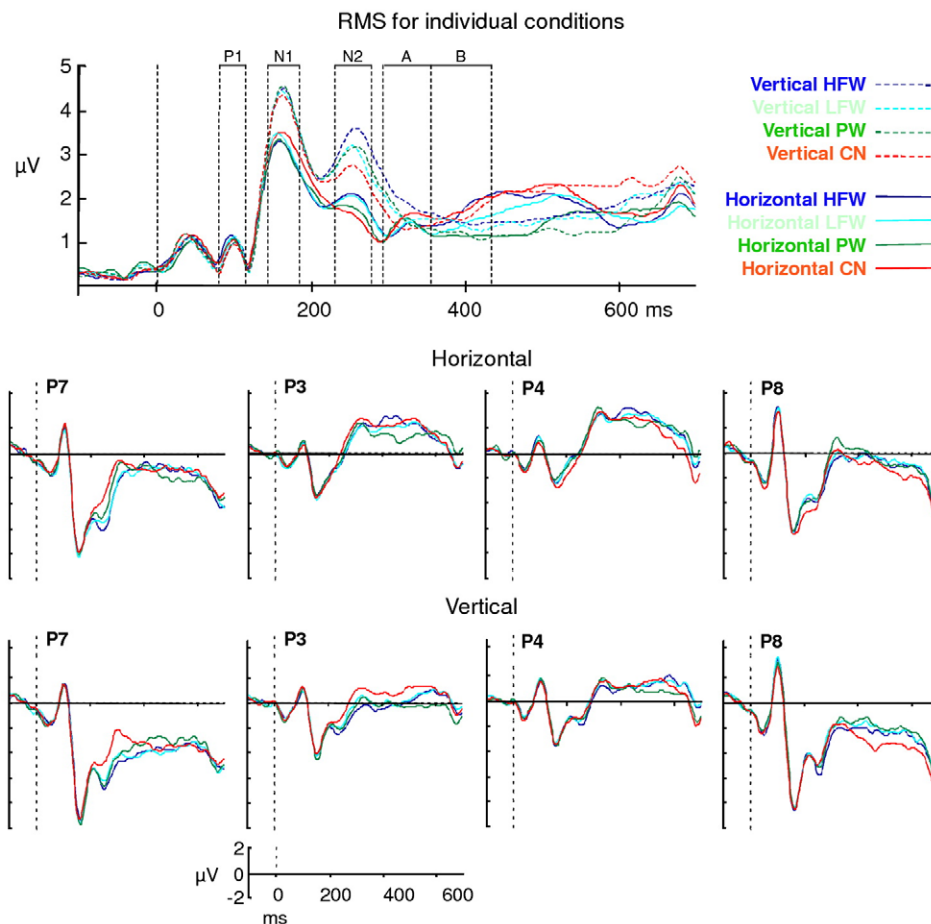

Fig. 2 – Time course of ERP data. Root-mean-square (RMS) curves for each condition. Time windows selected for analysis (P1: 85–115 ms, N1: 140–180 ms, N2: 225–275 ms, A: 285–385 ms, B: 350–425 ms) are marked on the RMS curve. Grand-average ERP waveforms recorded at left and right temporal (P7 and P8) and parietal (P3 and P4) electrodes for the horizontal and vertical formats.

regions should become evident early in processing. In addition to classical ERP analyses, source localisation (sLORETA) was performed in order to confirm the differential involvement of the dorsal and ventral visual pathways.

2. Results

2.1. Behavioural data

Incorrect responses occurred for 6% of stimuli and reaction times (RTs) more than 2.5 standard deviations away from the mean occurred for 2% of stimuli. Average RTs and corresponding standard errors of the mean are plotted in Fig. 1.

Analysis of the RTs revealed a strong effect of format, with longer RTs for the vertical format ($F(1,14)=99.8$, $p<.0001$, $\eta_P^2=.88$), and an effect of stimulus type ($F(3,42)=121.2$, $p<.0001$, Greenhouse–Geisser $\varepsilon=1.87$, $\eta_P^2=.90$) with shorter RTs for HFW than LFW ($p<.05$), for LFW than PW ($p<.0005$) and for CN than PW ($p<.0005$); as indicated by the format×stimulus type interaction ($F(3,42)=49.6$, $p<.0001$, $\eta_P^2=.78$, Greenhouse–Geisser $\varepsilon=1.96$), these differences were stronger for the vertical than the horizontal format ($p<.0005$). Accuracy was higher for the horizontal ($97\pm3\%$) than for the vertical format ($88\pm7\%$), as

Table 1 – Summary of main effects, interactions, and post-hoc tests.					
	P1 (85–115 ms)	N1 (140–180 ms)	N2 (225–275 ms)	285–350 ms	350–425 ms
Temporal sites (P7 and P8)					
Main effects:					
Format	$p<.05$	$p<.005$	$p<.05$	$p<.0001$	$p<.0001$
Stimulus type			$p<.0001$	$p<.0001$	
Laterality	$p<.005$			$p<.05$	
Interactions:					
F×ST					
L×F×ST			$p<.01$	$p=.057$	$p<.05$
Post-hoc tests:					
Left, horizontal			HFW vs. PW, LFW vs. PW, HFW vs. LFW, CN vs. all	HFW vs. PW, LFW vs. PW, CN vs. all	
Right, horizontal					HFW vs. PW, LFW vs. PW, PW vs. CN
Left, vertical			HFW vs. LFW, CN vs. all	HFW vs. PW, HFW vs. LFW, CN vs. all	HFW vs. PW, LFW vs. PW, HFW vs. CN, LFW vs. CN
Right, vertical					HFW vs. PW, LFW vs. CN, PW vs. CN
Parietal sites (P3 and P4)					
Main effects:					
Format		$p<.05$	$p<.0001$	$p<.0001$	$p<.0001$
Stimulus type	$p=.053$		$p<.001$	$p<.01$	
Laterality					
Interactions:					
F×ST			$p<.05$	$p=.06$	
L×F×ST					$p<.05$
Post-hoc tests:					
Left, horizontal					HFW vs. PW, HFW vs. LFW, LFW vs. CN, PW vs. CN
Right, horizontal					
Left, vertical			HF vs. LF HF vs. PW CN vs. all	HF vs. LF HF vs. PW	HFW vs. PW, HFW vs. LFW, CN vs. all
Right, vertical					

For the interactions, F×ST=format×stimulus type; L×F×ST=laterality×format×stimulus type; for the post-hoc tests, HFW=high frequency words; LFW=low frequency words; PW=pseudowords and CN=consonant strings.

indicated by a significant main effect of format ($F(1,14)=145.8$, $p<.0001$, $\eta_p^2=.91$).

2.2. Event-related potentials

Fig. 2 shows the RMS ERP traces for the 8 conditions (Horizontal/Vertical, HFW/LFW/PW/CN) and the ERP traces for temporal and parietal electrodes. The main effects, interactions, and post-hoc tests for the five windows are summarised in Table 1.

2.3. P1 component

Kolmogorov–Smirnov tests revealed no significant deviation from normality in any design cell.

As shown in Fig. 3, the effect of format was strongest over the parietal–central scalp, where the amplitude was significantly more positive for the vertical than for the horizontal condition.

At the temporal electrodes, there was a main effect of laterality, with larger amplitude over the right than over the left hemisphere ($F(1,14)=11.5$, $p<.005$, $\eta_p^2=.45$) and an effect of format, with larger amplitude for the horizontal than for the vertical format ($F(1,14)=5.38$, $p<.05$, $\eta_p^2=.28$). At the parietal electrodes the effect of format approached statistical significance ($F(1,14)=4.45$, $p=.053$, $\eta_p^2=.24$): here, the effect was opposite to that observed at the temporal electrodes, with larger amplitude for the vertical format.

Source localisation with sLORETA for the effect of format revealed differences in activity bilaterally mainly in occipital regions.

2.4. N1 component

Kolmogorov–Smirnov tests revealed no significant deviation from normality in any design cell.

As shown in Fig. 3, the effect of format was more diffuse than observed for the P1 component and associated with an anterior–posterior gradient: the vertical minus horizontal subtraction was characterised by negative polarity at posterior electrodes and positive polarity at frontal and central electrodes.

At the temporal electrodes there was a main effect of format ($F(1,14)=18.64$, $p<.005$, $\eta_p^2=.57$), with larger amplitude for the vertical format. An analogous effect of format was found at the parietal electrodes ($F(1,14)=17.4$, $p<.001$, $\eta_p^2=.55$).

Source localisation with sLORETA for the effect of format revealed differences in activity bilaterally in occipital and occipito-temporal regions.

2.5. N2 component

Kolmogorov–Smirnov tests revealed no significant deviation from normality in any design cell.

As shown in Fig. 3, the effect of format was associated with a pattern essentially similar to that observed for the N1 component, but with stronger positive polarity at the frontal electrodes and stronger negative polarity at the posterior electrodes, including the occipital and parietal sites. Source localisation with sLORETA for the effect of format identified differences in activity in the mesial frontal and temporal regions.

Visual inspection of the grand average ERPs, shown in Fig. 2, revealed that for the horizontal format the N2 was clearly absent on the P3 left parietal electrode and absent or very weak on the P4 right parietal electrode. Conversely, for the vertical format the N2 was found at both parietal electrodes.

At the temporal electrodes, main effects of format ($F(1,14)=7.85$, $p<.05$, $\eta_p^2=.36$) and stimulus type ($F(3,42)=15.6$, $p<.0001$, $\eta_p^2=.53$) on the N2 amplitude were found. The laterality×format×stimulus type interaction was significant ($F(3,42)=6.06$, $p<.01$, $\eta_p^2=.30$, Greenhouse–Geisser $\varepsilon=1.92$). Post-hoc analyses revealed that, in the left hemisphere only, for the horizontal format the N2 amplitude was significantly larger for HFW than PW ($p<.0005$), for HFW than LFW ($p<.05$) and for LFW than PW ($p<.01$). For the vertical format the N2 was significantly stronger for HFW than LFW ($p<.05$). For both formats, CN were associated with a smaller amplitude than all other letter-strings ($p<.001$).
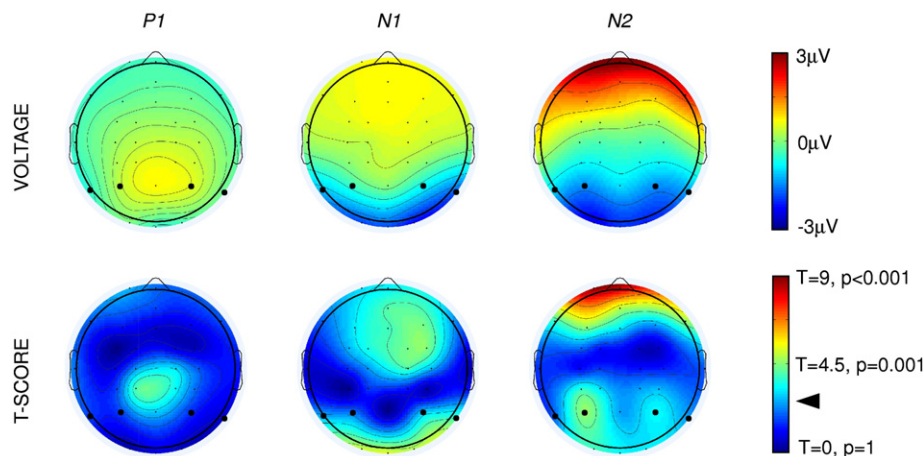

Fig. 3 – Topographic maps for the effect of format on the P1, N1 and N2 components: vertical minus horizontal voltage maps (upper row) and t-score maps (bottom row) for all stimulus types. The filled circles represent the positions of the P7, P3, P4 and P8 electrodes.
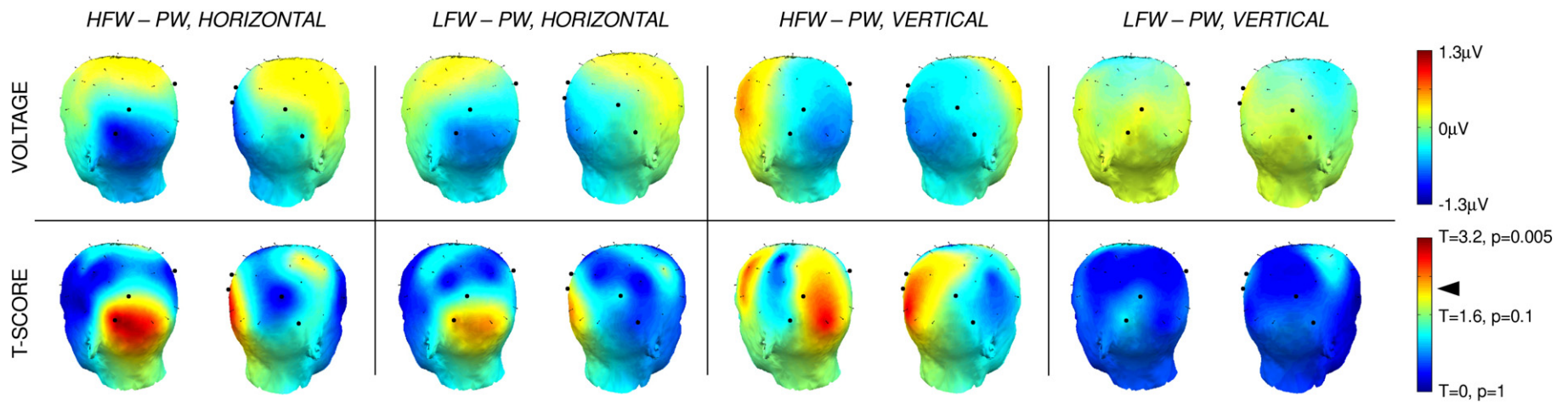
Fig. 4 – Scalp maps for the effect of lexicality (type) as a function of orientation (format) on the amplitude of the N2 component (225–275 ms). Voltage maps (upper row) and corresponding t-score maps (bottom row) for the comparison between high and low frequency words and pseudowords (HFW vs. PW and LFW vs. PW). The filled circles represent the positions of the P7, P3, P4 and P8 electrodes.

At the parietal electrodes, main effects of format ($F(1,14) = 22.64$, $p < .0001$, $\eta_P^2 = .62$) and stimulus type ($F(3,42) = .85$, $p < .001$, $\eta_P^2 = .32$) on the N2 amplitude were found. The format × stimulus type interaction was significant ($F(3,42) = 3.78$, $p < .05$, $\eta_P^2 = .13$). Post-hoc analyses revealed that, for the horizontal format, the N2 did not distinguish the stimulus types. Conversely, for the vertical format, the N2 negativity was stronger for HFW than LFW, for HFW than PW and for CN than for all other letter-strings ($p < .05$).

As shown in Fig. 4, with the horizontal presentation, the negativity associated with the HFW minus PW subtraction was strongest at the P7 left temporal electrode and extended towards the O1 left occipital electrode and, less markedly, towards the P3 left parietal electrode. The LFW minus PW subtraction was characterised by a similar but weaker pattern. For both comparisons, the area of strongest significance was clearly localised in the left temporal–occipital region. With vertical presentation, the HFW minus PW subtraction was associated with a negativity which, when compared to that observed with horizontal presentation, was shifted away from the P7 electrode towards the medial occipital–parietal region. Here, the area of maximum significance was less clearly left-lateralized. This pattern was not seen in the LFW minus PW subtraction, for which no statistically significant differences were found.

The HFW minus PW contrast was also analysed for both horizontal and vertical orientations, by means source locali-sation with sLORETA. As shown in Fig. 5, for horizontal format, current density was higher for HFW than PW in left temporo-occipital regions ($t(14) = 2.3$, $p < .04$). Conversely, for vertical format, current density appeared higher for HFW than PW in parieto-occipital dorsal regions bilaterally and in left temporal regions; however, the effect did not reach statistical signifi-cance ($t(14) = 1.9$, $p = .075$).

Up to the latency of this component, both hEOG and vEOG were analysed for the vertical letter-strings (0–300 ms). Visual inspection of the grand average EOGs showed that the time–amplitude characteristics of the EOGs traces elicited by vertical HFW, LFW and PW were very different from those observed at the P3 and P4 electrodes. Peaks seen in the EOGs between 220 and 250 ms did not find correspondence in the P3 and P4 electrodes. Moreover, no significant differences were found between HFW-PW and LFW-PW in the hEOG and vEOG responses (paired t-test, $p > .05$, corrected for Bonferroni).

2.6.   285–350 ms window

Kolmogorov–Smirnov tests revealed no significant deviation from normality in any design cell.

At the temporal electrodes, main effects of format ($F(1,14) = 27.59$, $p < .0001$, $\eta_P^2 = .66$) stimulus type ($F(1,14) = 7.39$, $p < .0001$, $\eta_P^2 = .35$) and laterality ($F(1,14) = 6.26$, $p < .05$, $\eta_P^2 = .31$) were found. A trend towards a laterality × format × stimulus type interac-tion ($F(3,42) = 2.71$, $p = .057$, $\eta_P^2 = .16$) was found. Post-hoc tests revealed that in the left hemisphere the amplitude was significantly larger for HFW than PW for both the horizontal and vertical formats ($p < .01$) and larger for LFW than PW ($p < .01$) for the horizontal format only.
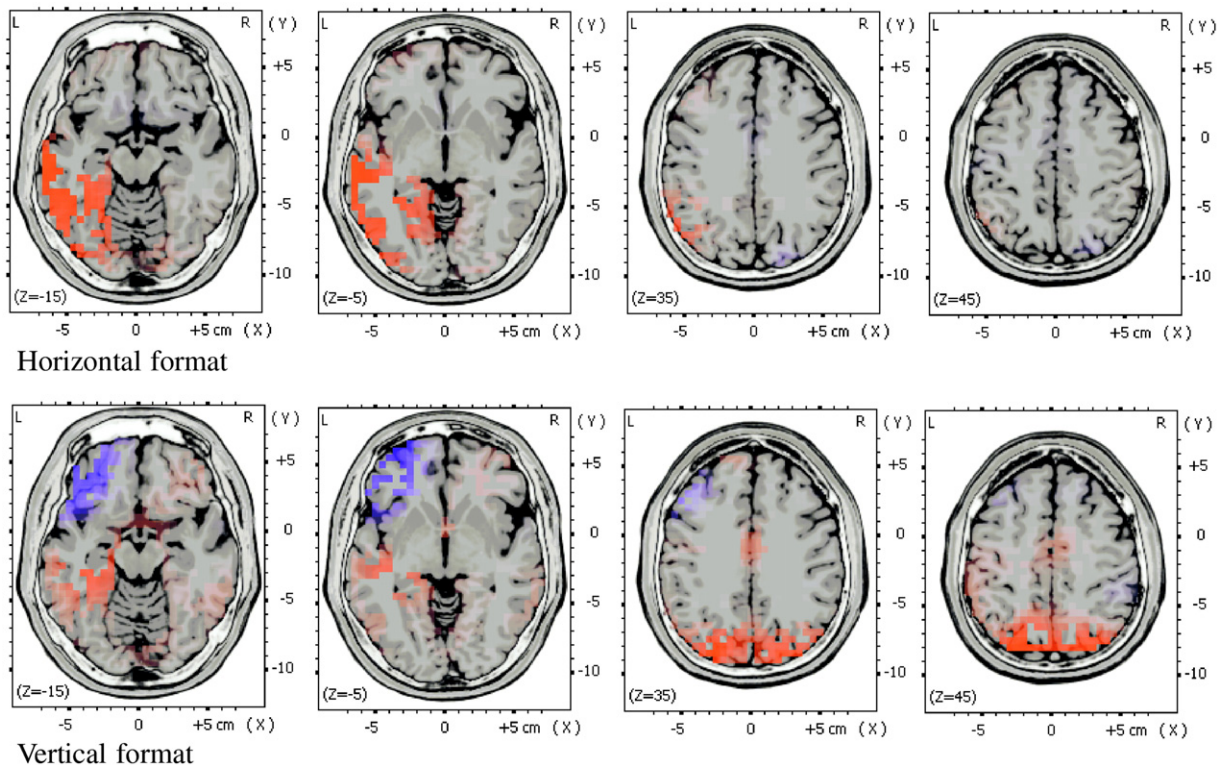

Fig. 5 – sLORETA maps for the N2 component (225–275 ms) for the contrast between high frequency words and pseudowords (red: HFW>PW, blue: PW>HFW), for the horizontal (upper row) and the vertical format (bottom row).
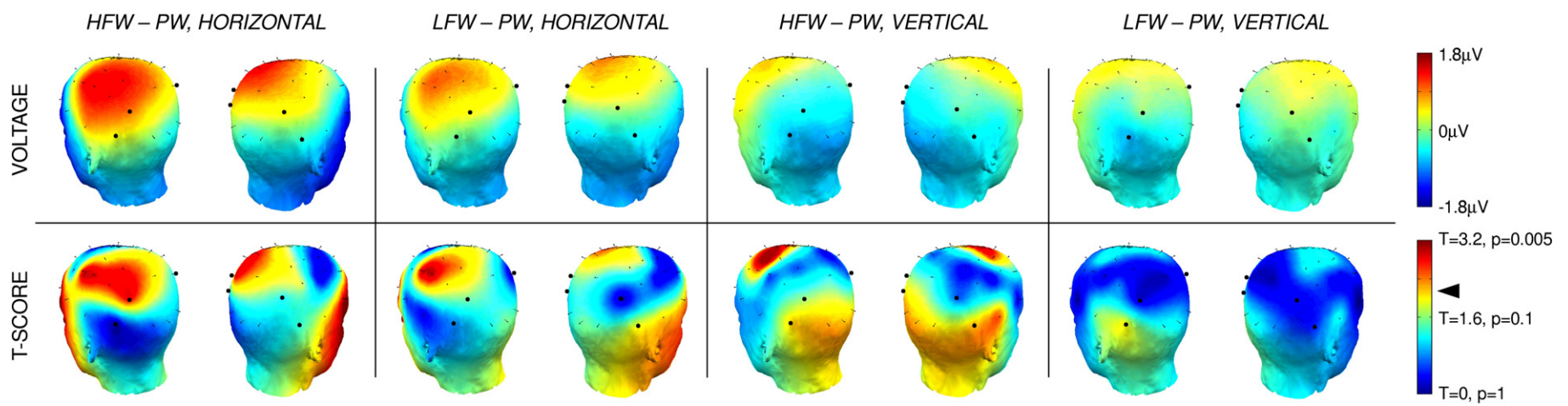
Fig. 6 – Scalp maps for the effect of lexicality (type) as a function of orientation (format) on the amplitude in the 350–425 ms window. Voltage maps (upper row) and corresponding t-score maps (bottom row) for the comparison between high and low frequency words and pseudowords (HFW vs. PW and LFW vs. PW). The filled circles represent the positions of the P7, P3, P4 and P8 electrodes.

At the parietal electrodes, main effects of format ($F(1,14) =$ 55, $p < .0001$, $\eta_p^2 = .8$) and stimulus type ($F(1,14) = 5.96$, $p < .01$, $\eta_p^2 = .3$) were found, as well as a trend towards a format × stimulus type interaction ($F(3,42) = 2.26$, $p = .06$, $\eta_p^2 = .16$). Post-hoc tests showed that for the vertical format the amplitude remained significantly larger for HFW than LFW and for HFW than PW ($p < .01$).

2.7.   350–425 ms window

Kolmogorov–Smirnov tests revealed no significant deviation from normality in any design cell.

At the temporal electrodes a main effect of format ($F(1,14) = 27.13$, $p < .0001$, $\eta_p^2 = .66$) and a laterality × format × stimulus type interaction ($F(1,14) = 4.01$, $p < .05$, $\eta_p^2 = .22$) were found. Post-hoc tests indicated a negativity larger for HFW than PW bilaterally and for LFW than PW in the left hemisphere ($p < .01$), for the vertical format only.

At the parietal electrodes a main effect of format ($F(1,14) = 63.57$, $p < .0001$, $\eta_p^2 = .82$) and a laterality × format × stimulus type interaction ($F(1,14) = 3.82$, $p < .05$, $\eta_p^2 = .21$) were found. Post-hoc tests revealed that for the vertical format the amplitude remained significantly larger for HFW than PW ($p < .05$) and for HFW than LFW ($p < .05$) in the left hemisphere only. Moreover, the amplitude was significantly larger for HFW than PW and for HFW than LFW, for the horizontal format ($p < .001$) in the left hemisphere only.

As shown in Fig. 6, with horizontal presentation the positivity associated with the HFW minus PW subtraction was strongest in left central–parietal regions; the area over which the difference was significant included left central electrodes and the P3 parietal electrode. For the LFW minus PW subtraction, the positivity was weaker and less extensive, and the area of significant difference did not include the P3 left parietal electrode. With vertical presentation, the HFW minus PW subtraction was associated with a positivity at the frontal electrodes and a negativity at the occipital and temporal electrodes; the difference was significant in both regions. For the LFW minus PW subtraction, the gradient was only slightly weaker; however, according to the t-score maps, the difference approached statistical significance only around the P7 electrode site.

For vertical orientation, the HFW minus PW contrast was also analysed by means of source localisation with sLORETA (Fig. 7), which revealed that current density was higher for HFW than PW in left occipito-temporal regions ($t(14) = 2.4$, $p < .03$).

3.   Discussion

In this study the time course of the ventral occipito-temporal and dorsal occipito-parietal pathways during the early stages of word recognition was investigated by contrasting ERPs elicited by letter-strings presented in familiar (horizontal) and unfamiliar (vertical) visual formats. To this end, a lexical decision task was employed, in which format familiarity and stimulus type were manipulated.

As expected, behavioural data showed a strong effect of format on response time (i.e., responses were faster to horizontal than vertical letters-strings) and a format × stimulus type interaction (i.e., the difference between words and pseudowords was more marked in the vertical than in the horizontal format). These findings are consistent with previously reported effects of format distortions on word recognition (Young and Ellis, 1985; Koriat and Norman, 1985; Bub and Lewine, 1988; Lavidor et al., 2001; Mayall and Humphreys, 1996; Jordan et al., 2003).

While the full statistical analysis of ERPs was conducted for the temporal (P7 and P8) and parietal (P3 and P4) electrodes, the topographic maps for voltage and t-scores clearly confirmed that, for the time windows of interest, the effect size was indeed largest in these regions (see Figs. 3 and 4). Analyses of ERPs revealed a strong effect of format for all time windows considered, which spanned from 85 ms to 425 ms. Topographic maps of voltage and t-scores revealed that the P1 amplitude was significantly larger for vertical than horizontal presentation, especially at medial parietal and central electrodes (see Fig. 3). For the N1 component, vertical presentation elicited a stronger negativity than horizontal presentation at occipital, temporal and parietal electrodes. The topography of the N1 component was characterised by a typical bilateral posterior negativity, likely originating from bilateral occipito-temporal regions (Proverbio et al., 2007; Rossion et al., 2003;
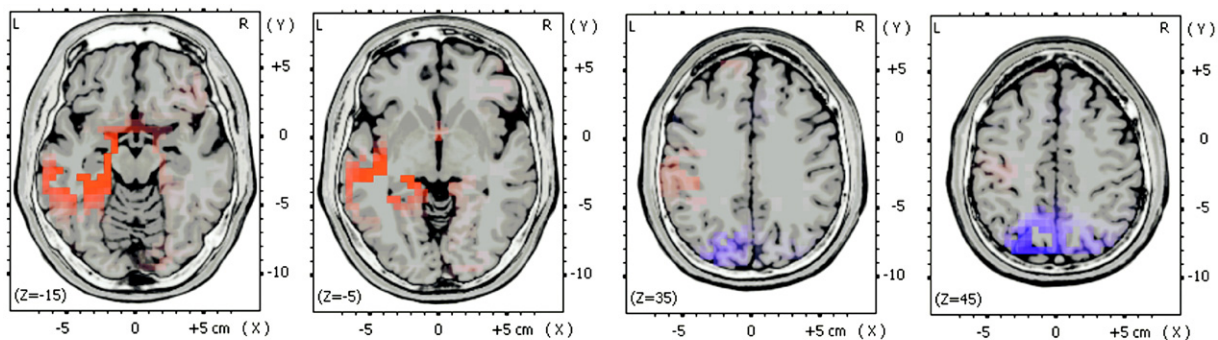
Vertical format

Fig. 7 – sLORETA maps for the 350–425 ms window for the contrast between high frequency words and pseudowords (red: HFW>PW, blue: PW>HFW), for the vertical format.

Maurer et al., 2005). The effect of format on the N2 component was similar, but associated with a stronger antero-posterior gradient.

Neither the P1 nor the N1 component was affected by stimulus type. Conversely, in the latency range of the N2 component (225–275 ms), differential involvement of the ventral and dorsal pathways for stimulus type started to emerge, as a function of format and laterality for the temporal electrodes, and as a function of format only for the parietal electrodes. At the left temporal electrodes, ERPs elicited by horizontal strings clearly differed as a function of stimulus type, with the strongest negativity being observed for high frequency words (HFW), followed by low frequency words (LFW), pseudowords (PW) and consonant strings (CN), as shown in Fig. 2. ERPs elicited by vertical letter-strings also discriminated HFW from LFW and singled out CN. At the parietal electrodes, while ERPs elicited by horizontal strings were insensitive to stimulus type, those elicited by vertical strings distinguished HFW from LFW and HFW from PW, and singled out CN.

As shown in Fig. 4, for horizontal stimuli, in the N2 time window the difference between HFW and PW and between LFW and PW was localised in the left occipito-temporal region. Conversely, for vertical stimuli the difference between HFW and PW emerged as an occipito-parietal negativity that extended towards dorsal areas. As shown in Fig. 5, source localisation with sLORETA performed for the HFW minus PW contrast confirmed a clear left-lateralized activation in the ventral region for the horizontal format, and for the vertical format a bilateral activation in the occipito-parietal dorsal regions, with involvement also of the ventral region.

The subsequent time window (285–350 ms) appeared to reflect a transition, during which the difference between vertical HFW and PW becomes evident also at the left temporal electrode. However, at these latencies there was still no difference between LFW and PW in the unfamiliar orientation (see Proverbio et al., 2004 for similar findings).

At longer latencies (350–425 ms), different patterns appeared for both formats (see Fig. 6). For horizontal stimuli, the effect of stimulus type (HFW vs. PW and LFW vs. PW) was characterised by a centro-parietal positivity, which has been consistently found in lexical decision tasks, putatively reflecting access to meaning (Carreiras et al., 2005; Hauk et al., 2006). For vertical stimuli, conversely, strong differences among stimulus types became evident in ventral and frontal areas. In particular, the ventral pathway appeared to discriminate HFW from PW and LFW from PW; the source underlying this effect was located in the temporal cortex.

Our data show that ventral occipito-temporal processes operate faster when letter-strings are displayed in the familiar horizontal format: with horizontal presentation, clear differentiation among stimulus types can be observed at 225–275 ms after stimulus onset. With vertical presentation, differentiation between stimulus types starts in the N2 time window, but a clear discrimination among all types of letter-string becomes visible only 350–425 ms after stimulus onset. Moreover, while stimuli presented in horizontal format engage the ventral region only, stimuli presented in vertical format engage mainly parietal regions, in addition to the ventral region. The influence of parietal regions appears

essentially limited to the N2 time window. Differentiation among stimulus types begins to appear in the same latency range irrespective of format, but is sustained over a longer period and requires the contribution of parietal regions when the visual format is unfamiliar. Evidence of sustained contribution of occipito-temporal processes in distinguishing vertical words from pseudowords lends support to the hypothesis that the ventral pathway is essential for accessing lexical representations (Hillis et al., 2005).

Engagement of the occipito-parietal dorsal regions for unfamiliar visual format in the N2 time window (see Fig. 5 vertical format) is in line with previous studies showing that these regions are involved in visuo-spatial and visual attentional processing (Gottlieb, 2007; Saalmann et al., 2007; Kanwisher and Wojciulik, 2000) and in reading visually unfamiliar letter-strings (Borowsky et al., 2006; Cohen et al., 2008; Pammer et al., 2006; Pugh et al., 2001). In particular, the involvement in reading could be subserving a serial mechanism of visual attention that is required to shift attention from one letter to another (Valdois et al., 2006; Vidyasagar, 1999, 2005). A similar interaction between stimulus type (words vs. nonwords) and case (mixed vs. same) was found in the right parietal cortex by Mayall et al. (2001, see Fig. 2), in which the difference between words and nonwords became evident for mixed-case stimuli. Evidence of early effects of stimulus type in the vertical format in both ventral and dorsal pathways seems to suggest that these pathways do not support alternative reading processes but work together with partially different contributions depending on format familiarity.

It is important to note that the latency at which ERPs start to distinguish the two conditions does not necessarily correlate with variations in behavioural RTs (see, for instance, Braun et al., 2006). In the present study the effect of stimulus type began to appear in the N2 time window for both formats, but a complete lexicality effect was observed at a later latency (350–425 ms) for the unfamiliar vertical format, paralleling the difference in RTs between vertical and horizontal stimuli. Models of word recognition have proposed a variable threshold in the decision process to account for such variations (see Grainger and Jacobs, 1996, Braun et al., 2006). Furthermore, it has been shown that in lexical decision tasks, nonwords with a large number of word neighbors result in slower reaction times, possibly because they activate word neighbor representations, thus prolonging the variable threshold of the yes/no decision process (Braun et al., 2006).

One may argue that the parietal activity observed in the N2 time window could be related to eye movements, which are likely to be more frequent for the unfamiliar than the familiar format. However, three facts seem to exclude this possibility. First and most importantly, in the present study lexical effects were not observed prior to the N2 time window: as a consequence, eye movements triggered during the N2 time window should not depend on the lexical status of the stimulus. Distinguishing the stimulus type and programming eye movements that are specific to stimulus type cannot happen at the very same moment. In addition, an EOG analysis was done for the sole purpose of verifying that the pattern of activity observed for the vertical letter-strings at the parietal electrodes in the first 300 ms was not related to EOG

responses. Results showed that the peaks of electrical activity of EOGs were not reflected in the parietal electrodes; third, no significant differences were found between HFW-PW and LFW-PW for hEOG and vEOG responses. As a result, no effect of lexicality was present in the EOGs elicited by vertical pronounceable letter-strings. To sum up, the effect of stimulus type observed for the unfamiliar format in the N2 time window seems to reflect attentional processes related to lexical access.

An alternative interpretation in terms of mental rotation appears also unlikely: in fact, behavioural studies of word recognition have shown that for words with orientation angles greater than 60°, reading involves a serial process, rather than a holistic process of mental rotation (Koriat and Norman, 1985; Bub and Lewine, 1988; Lavidor et al., 2001). These findings and the type of vertical stimuli used here, i.e. letter-strings with upright letters, exclude the hypothesis that the involvement of the parietal regions is related to mental rotation. The hypothesis that this effect is related to attentional processing seems thus the most likely.

Our findings are in line with the hypotheses put forward by Vinckier et al. (2006), according to which parietal involvement is mandatory whenever words are displayed in unfamiliar format because the ventral pathway is tuned to represent words in their familiar format only. The current work corroborates existing fMRI and lesion studies, additionally revealing the temporal dynamics of visual word recognition. The present results suggest that the two pathways cooperate during the early stages of visual word recognition and should therefore not be considered as supporting alternative reading strategies. It appears that the ventral stream can process words in familiar formats without (or with little) feedback from the parietal cortex. One possibility is that the visual expertise of the ventral pathway consists of better feature binding for frequently seen visual configurations (Gilbert et al., 2001), which prevents frequent letter combinations from being processed in a letter-by-letter fashion (Nazir et al., 2004). A more holistic processing of letters in words would require less attentional resources as there is no need to identify letter order and to shift processing from one letter to another.

In conclusion, word recognition involves a dynamic interplay between the dorsal and ventral visual pathways. The two streams have different roles in reading depending on whether the letter-string is visually familiar or not. The occipito-temporal ventral area displays expertise for printed words displayed in familiar visual formats. The dorsal pathway comes into play when the visual format is unfamiliar and its engagement is seen for a limited period, during which the ventral pathway appears less involved.

4. Experimental procedures

4.1. Participants

Fifteen right-handed native French speakers (7 female, 8 male) with no history of neurological or psychiatric disorders participated in the study. The age of participants ranged between 18 and 35 years (mean 26.2 years) and all of them had normal or corrected-to-normal vision. Informed consent was obtained according to institutional procedures prior to participation in the experiment.

4.2. Stimuli

Four types of letter-strings were used for this experiment: high frequency words (HFW), low frequency words (LFW), pseudo-words (PW) and consonant strings (CN). All letter-strings were 5 letters long and 70 stimuli per type were selected, for a total of 280 stimuli. HFW (Frant frequency average = 122.23, range 25.4–696.4) and LFW (Frant frequency average = 10.48, range .7–24.5) were selected from the French lexical database "Lexique" of text-based frequencies per million (New et al., 2001). The group of PW was created by changing at least 2 letters from existing words in French, while preserving the orthographic and phonological rules of French. The three HFW, LFW and PW groups were matched for bigram frequency ($F(2,138) = .17$, $p = .82$). Finally the CN set, matched for word shape (e.g. "vnbfc" = "sable"), was created. Stimuli were presented in "Courier New" font, size 28 points, in lowercase. Letters appeared white on a black background. All 280 stimuli, with upright letters, were presented once in horizontal format and once in vertical format, for a total of 560 stimuli. The distance between two letters was the same in both display conditions (2 mm). Stimuli were presented at the centre of the screen.

4.3. Procedure

Stimuli were presented on a high-resolution monitor positioned at eye-level at a distance of about 80 cm. Participants performed a standard yes/no lexical decision task: they were instructed to press one of two mouse buttons to indicate whether the letter-string was a French word or not. For half of participants, the right button was used to signal the "yes" response and the left button to signal the "no" response; for the other half, response assignment was reversed. Subjects were instructed to fixate a small fixation cross at the centre of the screen and to avoid blinking. After 400 ms the fixation cross disappeared and 120 ms later the orthographic stimulus was displayed. The stimulus remained on the screen for 500 ms and was followed by a 1400 ms interval during which blinking was encouraged. Horizontal and vertical items were presented in random order in 3 blocks containing approximately the same number of stimuli of each type and format; breaks of about 5 min occurred between blocks. Block order was counterbalanced across participants. A short practice session preceded the experiment.

4.4. Data recording

EEG was recorded continuously from 30 Ag/AgCl scalp electrodes mounted on an elastic cap (Electro-Cap International, Inc., USA) and arranged according to the international 10–20 system. Data were acquired with a sampling rate of 500 Hz. Cz was used as recording reference. Eye-movements and blinks were monitored with an electrooculogram (EOG) through bipolar electrodes placed on the right outer canthus (hEOG) and below the right eye (vEOG). Impedances were kept below 5 kΩ. Signals were amplified with a band-pass filter set to .1–30 Hz and transformed to average reference. Data were

epoched from 100 ms prior to stimulus onset to 700 ms post onset. Epochs with incorrect responses or with peak-to-peak potential differences larger than 100 μV in one EEG or EOG channel were rejected. The remaining trials were baseline corrected over a 100 ms interval prior to stimulus onset and were averaged for each condition and participant.

4.5. Statistical analyses

For the behavioural analyses, reaction times (RTs) were recorded starting from stimulus onset. Responses with RTs above or below 2.5 standard deviations of individual means were considered as incorrect. RTs were analysed with repeated-measures analysis of variance (ANOVA); factors were stimulus type (HFW/LFW/PW/CN) and format (Horizontal/Vertical). Greenhouse–Geisser correction of the degrees of freedom was applied where appropriate.

The time windows for ERP analysis were chosen on the basis of the main components identified on the root-mean-square (RMS) of all 32 electrodes, as shown in Fig. 2 (Picton et al., 2000). The P1 and N1 components, which peaked in the RMS traces at about 100 ms and 160 ms, were measured between 85 and 115 ms and 140 and 180 ms, respectively. The N2 component, which peaked in the RMS at about 250 ms, was measured between 225 and 275 ms. Two further time windows, 285–350 ms and 350–425 ms (labelled as "A" and "B" in Fig. 2), were also analysed. Mean window amplitudes were analysed for the P7, P8 (temporal), P3 and P4 (parietal) electrodes, at which the peak amplitude was maximal for the N1, N2 and in the 285–350 ms window (Bentin et al., 1999; Proverbio et al., 2007). ERP amplitudes were analysed with repeated-measures ANOVA with the factors stimulus type (HFW/LFW/PW/CN), format (Horizontal/Vertical) and laterality (Left/Right hemisphere). Normality was verified by means of Kolmogorov–Smirnov tests. ANOVAs were conducted using Greenhouse–Geisser adjusted degrees of freedom and they were followed by post-hoc Newman Keuls tests. In order to verify that the pattern of activity observed at the parietal electrodes was not related to EOG responses, hEOG and vEOG elicited by the vertical letter-stings were analysed for the first 300 ms on the basis of averaged consecutive 20-ms blocks of the sample points. Paired t-test corrected for multiple comparisons (Bonferroni) were then performed between HFW-PW and LFW-PW.

Topographical voltage maps were generated by interpolation between electrodes; corresponding t-score maps were obtained by means of paired-sampled t-tests.

In order to confirm differential involvement of the dorsal and ventral pathways, source localisation was performed by means of sLORETA (standard Low Resolution Elecromagnetic Tomography), which provides unbiased localisation by computing the smoothest cortical current density distribution (Pascual-Marqui, 2002). The inverse solution was computed separately for each subject and condition. Paired comparisons were performed for each voxel using the non-parametric method implemented in the sLORETA software, performing randomization and correcting for multiple comparisons (Pascual-Marqui, 2002). Rather than reporting the peak voxel significance value as such, t-tests were performed over the current density values of voxels that were found significantly active according to the sLORETA voxel-based test. The corresponding t-scores and p-values were reported.

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