

On the representation of words and nonwords in visual short-term memory: Evidence from human electrophysiology

DAVID PREDOVAN,^{a,b} DAVID PRIME,^{a,b} MARTIN ARGUIN,^{a,b} FRÉDÉRIC GOSSELIN,^{a,b}
ROBERTO DELL'ACQUA,^{c,d} AND PIERRE JOLICŒUR^{a,b}

^aDépartement de Psychologie, Université de Montréal, Montréal, Québec, Canada

^bCentre de Recherche en Neuropsychologie et Cognition, Université de Montréal, Montréal, Québec, Canada

^cDepartment of Developmental Psychology, University of Padova, Padova, Italy

^dCenter for Cognitive Science, University of Padova, Padova, Italy

Abstract

Electrophysiological measures were used to investigate the contribution of lexical status on the maintenance of letter strings in visual short-term memory (VSTM). The sustained posterior contralateral negativity (SPCN), an electrophysiological marker of storage in VSTM, was measured for words and nonwords as well as scrambled letters. A smaller SPCN was found for words than for nonwords (independently of their pronounceability), indicating that lexical status influences storage in VSTM. One possibility is that words produce a smaller SPCN because they can be recoded to a form that does not require a low-level representation in VSTM. For exploratory purpose, a comparison between the nonwords and the scrambled nonwords was also made. Based on previous research, the SPCN component should not be affected by the size of the region enclosing to-be-encoded objects. Surprisingly, significant differences between the SPCN for nonwords and scrambled letters conditions were found, suggesting that special encoding mechanisms may be recruited to encode word-like letter strings.

Descriptors: Sustained posterior contralateral negativity (SPCN), Visual short-term memory (VSTM), Lexical status, Electroencephalography, Event-related potentials (ERPs), Reading

There are reasons to believe that the lexical status of a letter string would interact with the degree to which visual short-term memory (VSTM) may be engaged during the retention of such strings. For example, Cowan (1996) postulated that access to a long-term memory code should facilitate the retention of word stimuli in working memory. We expected that a similar effect might be found when examining the role of VSTM (rather than a more abstract form of memory), but, to our knowledge, no one has used so far a measure of brain activity specifically related to VSTM to examine the influence of lexical status. In the present study we utilized event-related potentials (ERPs) to examine this issue.

Recently, an ERP component, which we refer to as sustained posterior contralateral negativity (SPCN; Jolicœur, Dell'Acqua, Sessa, & Robitaille, 2006b), has been suggested to reflect information storage in VSTM. The SPCN is observed following the visual encoding of a stimulus presented off the vertical midline, either in the left or right visual hemifield. To deconfound memory encoding from low-level stimulus differences, the target stimuli in one visual field are presented with an equivalent set of distractor

stimuli in the other visual hemifield. Klaver, Talsma, Wijers, Heinze, and Mulder (1999) argued that the SPCN (or contralateral negative slow wave) reflects activity related to encoding and retention in VSTM, a view that has recently received empirical support from the work of Vogel and colleagues (Vogel & Machizawa, 2004; McCollough, Machizawa, & Vogel, 2007). In the work of Vogel and colleagues, a centrally displayed arrow stimulus cued participants to encode the stimuli appearing in either the left or right visual hemifield. A target display consisting of simple visual stimuli (e.g., colored squares) was then presented for 100 ms. After a retention interval of 900 ms, another set of stimuli was presented and participants decided whether or not the second set was the same as the first in the encoded hemifield. Starting about 300 ms following the presentation of the target display, the ERP was more negative at posterior electrodes contralateral to the cued visual field (e.g., the voltage was more negative at electrode PO8 than at PO7 for stimuli encoded from the left visual field). This lateralized voltage difference was sustained during the entire retention interval. Importantly, the amplitude of the voltage difference increased as the number of target items increased, reaching a maximum when the number of stimuli to be encoded equaled or exceeded the estimated capacity of VSTM (on a subject-by-subject basis; Vogel & Machizawa, 2004). Furthermore, the voltage difference was smaller on incorrect response trials relative to correct trials, suggesting that

Address reprint requests to: David Predovan, Département de Psychologie, Université de Montréal, C.P. 6128 Succursale Centre-ville, Montréal, QC H3C 3J7, Canada. E-mail: david.predovan@umontreal.ca

this activity contributes to accurate performance (see also Dell'Acqua, Sessa, Jolicœur, & Robitaille, 2006; Jolicœur, Dell'Acqua, Sessa, & Robitaille, 2006a; Jolicœur et al., 2006b; Robitaille, Jolicœur, Dell'Acqua, & Sessa, 2007, for strong associations between behavioral accuracy and the amplitude of the SPCN in the context of the attentional blink paradigm).

Previous studies that have investigated the relationship between VSTM and the SPCN have used very simple stimuli, such as colored squares and oriented bars. Here, we study how VSTM involvement might vary for stimuli such as words, for which we have preexisting long-term memory (LTM) representations, compared to groups of random letters (forming nonwords). Our approach is to measure the SPCN component elicited when subjects encode and remember letter strings that form either a word or a nonword. We hypothesize that lexical status of the words should reduce the load in VSTM in comparison to the nonword condition, because of the availability of a supplementary form of representation (in LTM), and that this reduction will be reflected in a significant attenuation of the SPCN component in the word condition. Perhaps such stimuli can be encoded directly from a form of iconic memory to a very abstract level that may not require the protracted storage of words in VSTM or may require it to a reduced extent compared to different visual stimulation (e.g., via immediate phonological recoding [Holcomb & Grainger, 2006, 2007] or recoding to an abstract representation in semantic memory; see the Discussion for alternative hypotheses concerning this issue). There is good evidence that representations in LTM interact with processing at earlier levels (letters, features) to produce effects such as the word superiority effect (Cattell, 1886; McClelland & Rumelhart, 1981) or the letter superiority effect (Reingold & Jolicœur, 1993).

Our expectation that lexical status of stimuli may affect early visual representations in VSTM is predicated on a subfield of the neurophysiological literature, mainly based on electroencephalographic (EEG) and magnetoencephalographic (MEG) recordings, showing that lexical access, under particular conditions, may be extremely rapid. For example, Sereno, Rayner, and Posner (1998) presented participants with high-frequency or low-frequency regular and irregular English words. ERPs time-locked to these words during performance in a lexical decision task differed as a function of condition with effects of word frequency that started as early as 132 ms post-target and continued into the N1 time range (~ 170 ms). These effects suggest that lexical access took place within this time range on a significant number of trials. Pulvermüller, Assadollahi, and Elbert (2001) recorded MEG activity while participants performed a lexical decision task on distinct sets of words that varied in strength of semantic association. Differences in the event-related magnetic fields across the different sets of words were apparent as early as 150 ms following word onset, with the magnetic field responses being particularly pronounced for words characterized by strong semantic association. These findings also suggest fast semantic access, consistent with Sereno et al.'s findings (see also Hauk, Davis, Ford, Pulvermüller, & Marslen-Wilson, 2006; Pulvermüller, 2001, for similar conclusions). Note that semantic effects on event-related magnetic fields in the Pulvermüller studies were strongest at sensors over left infero-temporal brain regions (see also Pulvermüller, Shtyrov, & Ilmoniemi, 2005).

It should be mentioned that this prediction may appear not entirely congruent with the different view that one reliable indicator of lexical/semantic processing of words would be reflected in the centro-parietal N400 component, that usually begins at

about 350 ms poststimulus, and it is not, contrary to the SPCN, characterized by a scalp distribution contralateral to the eliciting stimuli (e.g., Heil, Rolke, & Pecchinenda, 2004; Rolke, Heil, Streb, & Hennighausen, 2001; Vogel, Luck, & Shapiro, 1998). However, as noted by Dell'Acqua, Pesciarelli, Jolicœur, Eimer, and Peressotti (2007), Holcomb (1993), and Pesciarelli et al. (2007), it is likely that N400 activity may reflect semantic integration of sequential verbal stimuli rather than semantic/lexical access per se. N400 activity modulations are normally found when the eliciting stimulus is semantically evaluated following the prior activation of a context, either via the presentation of a prime stimulus (e.g., Holcomb & Grainger, 2006) or via the inclusion of the word stimulus in a sentence, as done originally in seminal work on the N400 (e.g., Kutas & Hillyard, 1980).

Based on evidence suggesting a rapid access of lexical information from words (and also from pictures; see Thorpe, Fize, & Marlot, 1996) presented in isolation, we used electrophysiological recordings to study potential interactions between lexical access mechanisms and mechanisms responsible for the encoding and maintenance of representations in VSTM. In addition to a comparison of strings of three letters that formed a word or a nonword, we also presented nonwords in which letters were misaligned horizontally (scrambled letters condition) to determine if the spatial layout of letter stimuli can have consequences for the SPCN. McCollough et al. (2007) showed that the SPCN for colored squares is unaffected by the size of the region in which the squares were presented, suggesting that the spatial layout of simple stimuli does not influence the SPCN. We thought it was important to verify this supposition for letters, however, because of our extensive reading experience that may have produced specialized mechanisms for dealing with compact horizontal letter strings. Operations such as chunking of groups of letters, leading to representations of pairs or triads of letters (e.g., "the") could reduce the need for the retention of the visual features of the stimuli themselves. In short, specialized encoding mechanisms built up over many years of practice may affect the nature of subsequent representations in VSTM.

Method

Participants

Sixty two native French speakers (ages 18–29 years, mean = 22.5 and $SD = 3$) participated in this experiment. All participants were naïve volunteers and were paid 20 Canadian dollars. All participants reported normal or corrected-to-normal vision and no history of neurological problems. Thirty individuals participated in the pronounceable nonword condition and 32 individuals participated in the nonpronounceable nonword condition. Seven participants from the pronounceable nonword condition and 8 participants from the nonpronounceable nonword condition were excluded from data analysis because an excessive number of trials were rejected mainly due to a tendency to shift their gaze toward the attended hemifield but also due to EEG artifacts. On average, subjects who were retained for detailed analyses moved their eyes less than 0.15° of visual angle in the direction of the target.

Task and Design

The experimental task required participants to encode and retain the identity of three visually presented letters. The target letters

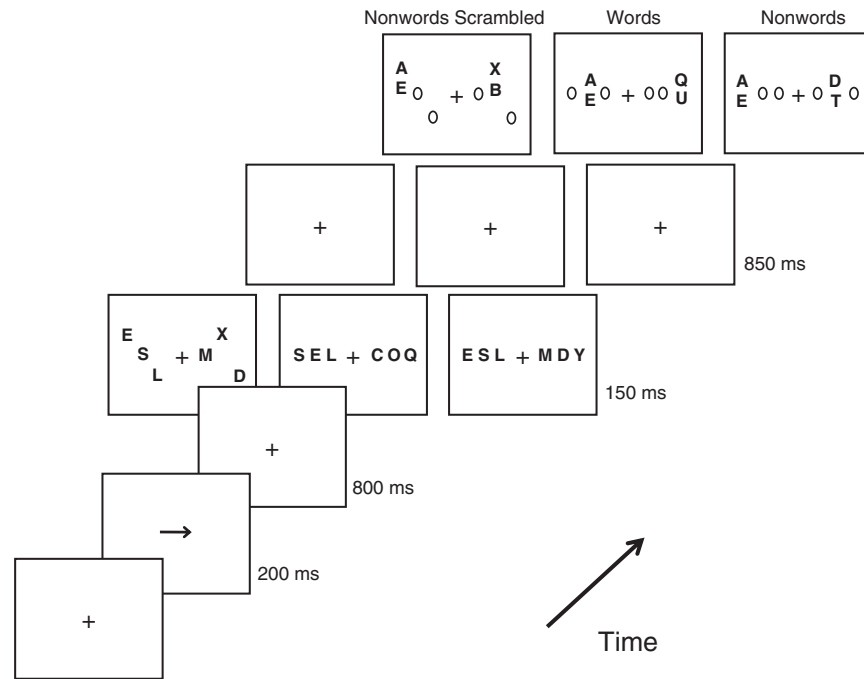


Figure 1. Sequence of events in each trial for the word, nonword, and nonword scrambled conditions.

were equally likely to be presented in the left or right visual field. A retention period of 850 ms ensured that the task could not easily be carried out on the basis of a very low-level form of memory such as visible persistence (Coltheart, 1980). After the retention interval the participants performed a two-alternative forced-choice identification test on the identity of one of the letters. A 2×3 between-within design was employed. The within-participant manipulation varied the lexical status of the target letters. In the *word* condition the three target letters were grouped into a horizontal string that formed a French word. In the *nonword* condition the target letters were grouped into a horizontal string that did not form a valid word. In the *scrambled letters* condition the letters were not aligned horizontally and did not form a word. The between-participants manipulation varied the *pronounceability* of the letters in the nonword condition. In the pronounceable condition, to which about half the participants were submitted, the nonwords had a pronounceable sequence of consonants and vowels that closely matched the proportions of strings with particular sequence structure in the word condition (i.e., CVC, VCC, CCV, etc.). In the *unpronounceable* condition the nonwords were random consonant strings.

Stimuli

The visual field cue was a centrally presented 0.2° gray arrow pointing toward the left or right. Target displays consisted of three letters presented on each side of the vertical meridian (six letters total). The letter stimuli were 0.7° -tall capital letters (A–Z) presented in gray on a black background. In the word and nonword conditions the letter strings were centered 2.4° to the left and right of fixation on the horizontal meridian. The horizontal center-to-center distance between each letter was 1.3° . In the scrambled condition the letters had the same horizontal arrangement as in the other two conditions but each letter was randomly displaced, upward or downward, by 0.95° or 1.90° . The test displays had the same spatial arrangements as the target displays, except that one letter in each visual field was probed by two test

letters positioned directly above and below its former location (Figure 1). The horizontal position of the test letters was always different in the left and right visual fields. The other letters were replaced by gray oval outlines. One of the two test letters matched the identity of the letter at the probed position in the target display. In the word condition both test letters formed valid words in conjunction with the other letters in the target display. For example, in English, if the target letters had been SUN, the identity of the first letter could be tested with the letters S and F, each of which forms a word. Furthermore, the distractor letter string in the opposite hemifield was always of the same type as the string in the attended hemifield (i.e., word, nonword, or scrambled letters).

Experimental Procedure

The trial sequence is illustrated in Figure 1. Participants viewed the experimental stimuli displayed on a computer monitor from a distance of 57 cm and a chin rest was used to stabilize the head. Each trial began with the presentation of a central fixation cross that remained on the screen throughout the trial. Participants were instructed to maintain their gaze at fixation during a trial, and to blink only between trials. An arrow cue indicating the visual field of the to-be-remembered letters replaced the fixation cross for 200 ms. After a further 800-ms delay, the target display was presented for 150 ms, followed by a blank screen with the fixation cross. One second after the onset of the target display, the test display was presented. Participants were required to indicate which of the two test letters in the to-be-remembered visual field matched the letter in the target display. To select the letter, participants had to respond by pushing predetermined keys on the keyboard (standard Qwerty natural keyboard). Half of the subjects responded with the right hand (key “j” to select top letter and “n” to select bottom letter) and the other half responded with the left hand (keys “g” and “b”). Accuracy feedback was provided immediately after the response in the form of a plus sign

for correct responses or a minus sign for errors. Participants initiated the next trial by pressing the space bar.

The experimental session consisted of 18 practice trials and 720 experimental trials (240 trials per condition) divided into two blocks of 360 trials. Participants were required to rest between blocks and could rest at any time during the experiment. The experimental session lasted approximately 1.5 h.

Electrophysiological Recording and Analysis

The electroencephalogram (EEG) was recorded with active Ag/AgCl electrodes (Biosemi Active Two) mounted on an elastic cap at standard 10–10 scalp sites (Fp1, Fpz, Fp2, AF7, AF3, AFz, AF4, AF8, F7, F5, F3, F1, Fz, F2, F4, F6, F8, FT7, FC5, FC3, FC1, FCz, FC2, FC4, FC6, FT8, T7, C5, C3, C1, Cz, C2, C4, C6, T8, TP7, CP5, CP3, CP1, CPz, CP2, CP4, CP6, TP8, P9, P7, P5, P3, P1, Pz, P2, P4, P6, P8, P10, PO7, PO3, POz, PO4, PO8, O1, OZ, O2, Iz, M1, and M2). Eye position was monitored by both the horizontal and vertical electro-oculogram (EOG). The vertical EOG was recorded as the voltage between Fp1 and an electrode placed below the left eye. The horizontal EOG was recorded as the voltage between electrodes placed lateral to the external canthi. Amplified EEG and EOG channels were low-pass filtered at 67 Hz and digitized at 256 Hz. After acquisition the EEG channels were referenced to the average of the left and right mastoids and high-pass filtered at 0.01 Hz (half power cutoff).

Trials containing blinks, eye movements, and EEG artifacts were removed prior to ERP averaging by applying automated artifact detection routines. Participants who had less than 60% of trials remaining in one or more conditions after artifact rejection were excluded from further analysis. Separate ERP averages were calculated from EEG epochs time-locked to the presentation of the target display for each experimental condition and visual field of the target items. The resulting ERP averages were low-pass filtered at 6 Hz and baseline corrected relative to mean voltage of the 200-ms prestimulus interval. To isolate the SPCN activity, ERP waveforms from electrodes ipsilateral to the target items were subtracted from those from contralateral electrodes and the resulting difference waves for each visual field were averaged. For purposes of statistical analysis, pooled SPCN waves were formed in order to improve the signal-to-noise ratio of the data. The pooled SPCN waves were derived from electrode pairs PO7/PO8, O1/O2, and P7/P8. These electrode locations were chosen because they correspond to the location of the maxima of the SPCN topography (Figure 4b, below). The SPCN amplitude for each condition was quantified as the mean voltage of the pooled SPCN wave in the 400–1000-ms latency range.

Results and Discussion

Behavior

Mean percent correct and mean SPCN amplitude measures were submitted to separate 2×3 between-within analyses of variance (ANOVAs) with factors of Group (pronounceable nonword, unpronounceable nonword) and Lexical Status (word, nonword, scrambled). The Geisser–Greenhouse correction procedure was used for repeated-measures involving more than one degree of freedom.

Mean accuracy rates for the word, nonword, and scrambled conditions were, respectively, 95%, 94%, and 89% for the pronounceable nonword group and 94%, 88%, and 83% for the unpronounceable nonword group. The ANOVA of accuracy

rates revealed a significant main effect of Lexical Status, $F(2,90) = 78.6$, $p < .001$, $\epsilon = .67$, $\eta_p^2 = .64$. In addition, both the main effect of Group (mean accuracy of 93% for the pronounceable group vs. 88% for the unpronounceable group), $F(1,45) = 6.8$, $p < .02$, $\eta_p^2 = .13$, and the interaction effect, $F(2,90) = 5.9$, $p < .02$, $\epsilon = .67$, $\eta_p^2 = .12$, were significant.

ERP

Figure 2 shows grand average waveforms, collapsed across both groups, separately for stimuli encoded from the left and right visual fields at all electrode sites. The word condition is shown in Panel a, the nonword condition in Panel b, and the nonword scrambled condition in Panel c. The SPCN can be seen as a relative negative shift in the ERP wave at electrode sites contralateral to the visual field of the target. As expected, the SPCN difference is largest at lateral occipital sites (see also the topographic maps in Figure 4b). Furthermore, the SPCN difference can be seen in all three conditions for stimuli encoded from both visual fields.

Figure 3 shows the pooled response at three posterior electrode sites for stimuli encoded from the left visual field or right visual field for left-sided and right-sided electrodes, for each stimulus type (words, nonwords, and scrambled letters). As is evident in the figure, there was no evidence of left–right asymmetries in the SPCN waveforms for any of the stimulus types.

Figure 4a shows the SPCN subtraction waves (contralateral–ipsilateral) pooled over electrode pairs PO7/PO8, O1/O2, and P7/P8 for each group and condition. Figure 4b shows the scalp distributions of the SPCN for each type of letter string, averaging over the two groups. These scalp distributions are based on the SPCN subtraction waves at each lateralized electrode pair (zero voltage assumed at midline electrodes) and they exhibit the same relatively focused voltage peak at posterior electrodes (e.g., Brisson & Jolicœur, 2007). The distributions were quite similar in general topography, suggesting that the same component was elicited in the three string type conditions, but with different amplitudes.

The SPCN amplitudes were subjected to an ANOVA of the same type as used for the accuracy results. SPCN amplitude was highest for the scrambled condition, intermediate for the nonword condition, and smallest for the word condition, producing a significant main effect of Lexical Status, $F(2,90) = 33.9$, $p < .001$, $\epsilon = .80$, $\eta_p^2 = .19$. In contrast to the accuracy results, neither the main effect of Group, $F(1,45) = 0.84$, $p > .36$, $\eta_p^2 = .02$, nor the interaction effect, $F(2,90) = 1.0$, $p > .35$, $\epsilon = .80$, $\eta_p^2 = .02$, approached significance. The lack of any Group effects indicates that the pronounceability of the nonwords did not affect the amplitude of the SPCN.

To explore further the effect of Lexical Status on the amplitude of the SPCN, 2×2 between-within ANOVAs were performed for each pairing of the Lexical Status variable. Analysis of the difference between the word and nonword conditions revealed that the words elicited a significantly smaller SPCN than nonwords, $F(1,45) = 9.8$, $p < .01$, $\eta_p^2 = .18$. Neither the main effect of Group nor the interaction effect approached significance, both $ps > .62$, indicating that the pronounceability of the nonwords had no effect on the difference in SPCN amplitude between words and nonwords.

Analyses of the difference in SPCN amplitude between the scrambled and the other two conditions revealed that the scrambled condition elicited a significantly larger SPCN than either the word condition, $F(1,45) = 48.2$, $p < .001$, $\eta_p^2 = .52$, or the

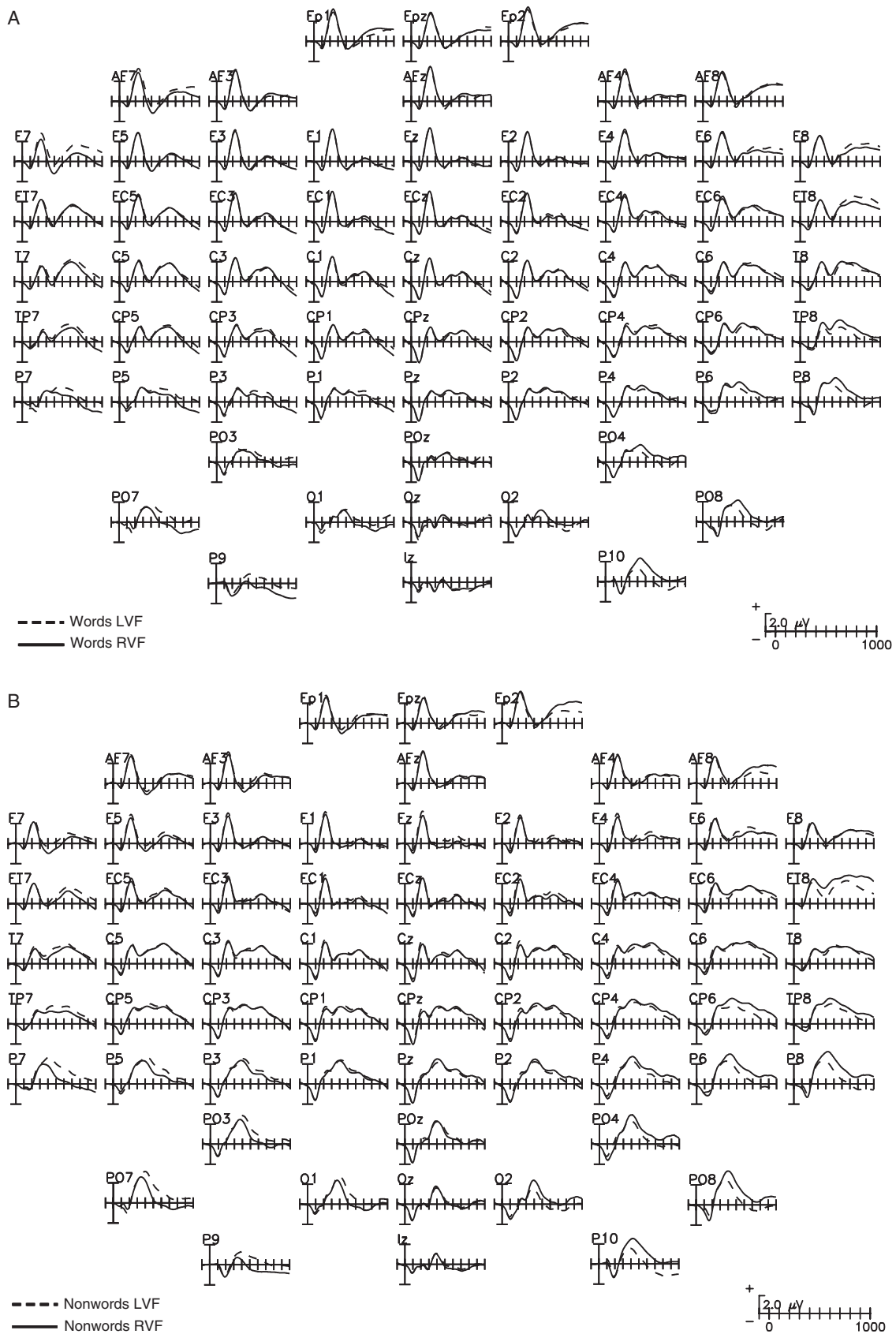


Figure 2. A: Grand averaged waveforms, collapsed across groups, at all electrode sites for the word condition. Separate waveforms are shown for stimuli encoded from the left and right visual fields. B: Grand averaged waveforms, collapsed across groups, at all electrode sites for the nonword condition. Separate waveforms are shown for stimuli encoded from the left and right visual fields. C: Grand averaged waveforms, collapsed across groups, at all electrode sites from the nonword scrambled condition. Separate waveforms are shown for stimuli encoded from the left and right visual fields.

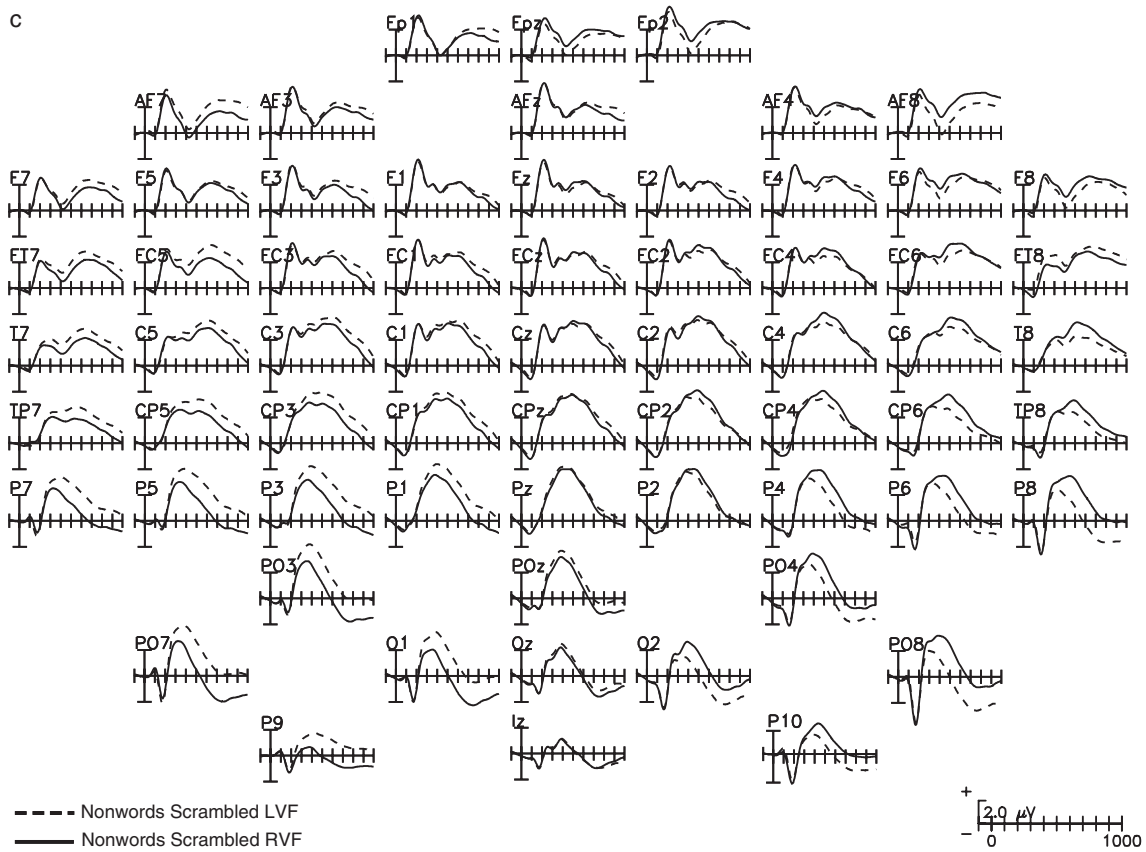


Figure 2. Continued

nonword condition, $F(1,45) = 28.1, p < .001, \eta_p^2 = .38$. Neither the main effect of Group nor the interaction effect approached significance in either ANOVA, all $ps > .25$.

An inspection of Figure 4a reveals that the SPCN appears to begin at a shorter latency in the scrambled condition than in the

other to two conditions. To analyze this effect, SPCN onset was measured using a fractional area latency measure (Kiesel, Miller, Jolicœur, & Brisson, 2008) on jackknife-subsample average waveforms (Ulrich & Miller, 2001). The SPCN onset for each condition was defined as the point in time at which the area under

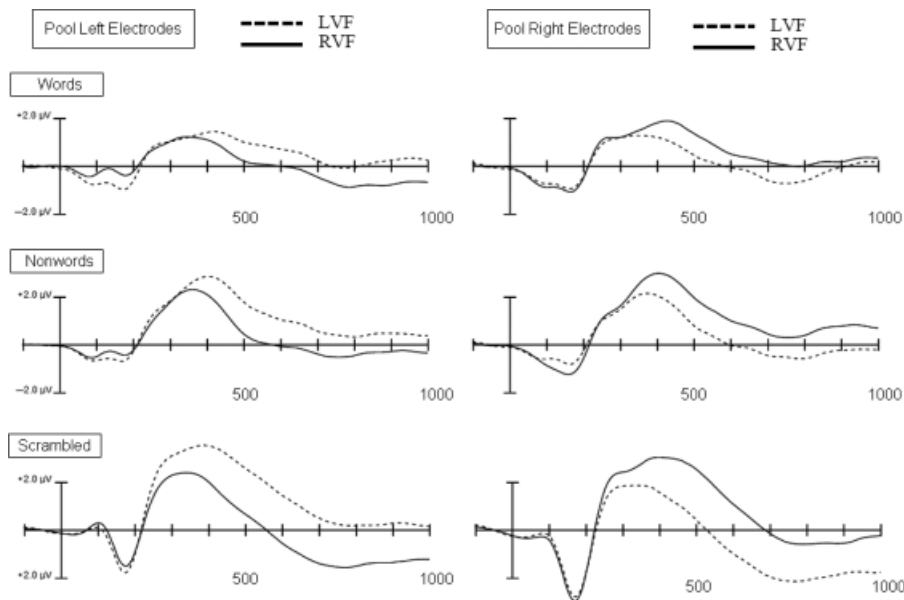


Figure 3. Pooled response at left-sided and right-sided posterior electrode sites for stimuli encoded from left visual field or right visual field, for each stimulus type (words, nonwords, and scrambled letters).

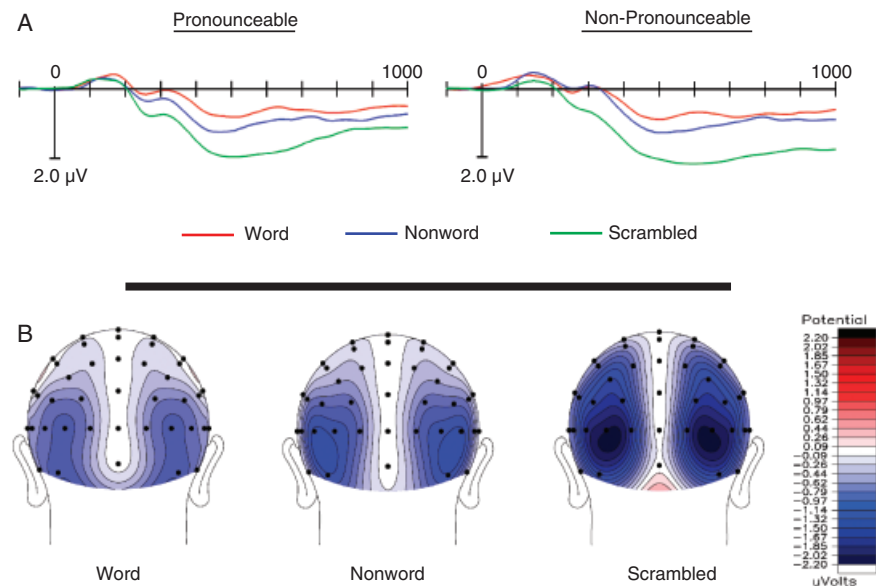


Figure 4. A: Contralateral minus ipsilateral waveforms showing the SPCN for the pooled response at three posterior electrode sites for each type of stimulus (words, nonwords, and scrambled letters) for each group. B: Scalp distributions of the SPCN for each stimulus type (mean activity from 400–1000 ms after memory stimulus onset).

the SPCN wave reached 20% of the total area in the interval between the start of the negative portion of the curve and 500 ms (this interval corresponds to the growing portion of the SPCN wave). Analysis of the onset latencies revealed a significant main effect of Lexical Status, $F(2,90) = 5.5$, $p < .01$. Neither the main effect of Group, $F(1,45) = 1.3$, $p > .26$, nor the interaction effect, $F < 1$, approached significance. Subsequent analyses revealed that the SPCN onset earlier in the scrambled condition (332 ms) than either the word (398 ms), $F(1,45) = 7.3$, $p < .01$, or the nonword (380 ms), $F(1,45) = 13.4$, $p < .001$, conditions. The difference in SPCN onset between the word and nonword conditions was not significant, $F < 1$.

The present results were clear-cut in demonstrating that the lexical status of a letter string modulated activity in VSTM during the retention interval of a VSTM task. When the target string formed a word, the amplitude of the SPCN was reduced relative to when the target string did not form a word. At the functional level, one viable explanation for this effect is that the storage of target letters that form words is facilitated by a lexically driven grouping or chunking mechanism that reduces the information load in VSTM (e.g., Martin, Nazir, Thierry, Paulignan, & Demonet, 2006). In this view, the availability of an alternative memory code, already stored in LTM, would reduce the need to rely on an earlier, lower level visual representation of the letters by, for instance, providing supplementary top-down activation support to word representations in VSTM. A second possibility is that horizontal letter strings may make contact with specialized letter detectors that are tuned for horizontally aligned sets of letters (e.g., Dufau, Grainger, & Holcomb, 2008; Grainger, Granier, Farioli, Van Assche, & van Heuven, 2006). The output of these detectors may reduce the need to maintain a low-level visual representation in VSTM, which is, in turn, reflected in the smaller SPCN for words than for nonwords, observed in the present empirical context. At the neurophysiological level, it is natural to hypothesize that the present selective attenuation of an SPCN response to words versus nonwords may arise from the short-range bidirectional connections between the extrastriate

portion of the visual cortex, the lower part of the parietal lobes (which are held to be primary sources of SPCN activity) and regions in the surroundings of the left lingual and fusiform gyri, these latter regions known to be involved in early visual processing of word-like stimuli (e.g., Nobre, Allison, & McCarthy, 1994; Puce, Allison, Asgari, & McCarthy, 1996).

At first blush, the absence of an effect of pronounceability on the SPCN amplitude, despite the large sample of subjects tested in each of the present experimental conditions. However, if this were not lack of power, a different possibility is that VSTM mechanisms are not subject to the influence mediated by phonological recoding, and this may not be surprising given the long studied sensitivity of this memory subsystem to spatial, and not verbal, information about objects. Evidence concerning the neurophysiology of word processing may help to corroborate this view. Contrary to the topographical proximity and massive interconnection of cortical regions in the human brain devoted to early orthographic processing and the hypothesized substrate of SPCN activity, regions devoted to the assembly of phonological codes (i.e., primarily, cortical regions in the left inferior frontal cortex; e.g., Mado Proverbio, Vecchi, & Zani, 2004) seem to entertain short-range connections with regions in the left temporal lobe and, however, a restricted bandwidth reentrant circuitry to the occipito-parietal areas under scrutiny in the present context.

One note of caution is in order, however, concerning the proposed model for the effects found in our study. We are interpreting the lexical-status effects on SPCN as evidence for interactions between lexical status and VSTM. An alternative interpretation could be formulated on the basis of results suggesting that other ERP components, such as the “recognition potential” (RP) are also sensitive to the difference between words

and nonwords (e.g., Martín-Loeches, Hinojosa, Gomez-Jarabo, & Rubia, 1999; Rudell & Hua, 1997). The RP is usually observed as an occipito-parietal negativity peaking in a time window of 200–250 ms following the presentation of words at fixation. The RP to word stimuli is particularly pronounced over left posterior occipito-parietal regions (e.g., at P7), probably originating from the left portion of basal extrastriate cortex labeled visual word form area (Cohen et al., 2000). Could the SPCN results we report in this article be a reflection of the RP component? This possibility appears to be remote in light of the known functional properties of the RP and the time course of that component. Similar to the MEG activity reported by Pulvermüller et al. (2001), the RP tends to be larger as the semantic richness of word stimuli is increased (e.g., Hinojosa, Martín-Loeches, Muñoz, Casado, & Pozo, 2004; Martín-Loeches, Hinojosa, Fernández-Frías, & Rubia, 2001), with the degree of semantic association (or semantic redundancy) of specific word stimuli positively correlated with the negativity in the RP time range. This appears incompatible with the present results, given that lexical activation (words relative to nonwords) in the present case produced a decrease in SPCN amplitude, rather than an increase. Furthermore, the RP component has a time course that is relatively short compared with the sustained nature of the SPCN, and a topographical distribution (larger over left posterior recording sites) that is not consistent with the symmetrical distribution of SPCN activity we have documented. Although it is clear that there are other ERP components that are sensitive to the lexical status of letter strings, the present results appear to be a novel manifestation of processing differences between words and nonwords that is specifically related to differences in VSTM processing efficiency (or load) for words and nonwords.

In contrast to the results obtained by McCollough et al. (2007) for simple geometric shapes, the amplitude of the SPCN was affected by the spatial configuration of the target letters in the present experiment. The amplitude of the SPCN was substantially larger in the scrambled condition than in either of the other two conditions and particularly than in the nonword condition, despite the use of letter strings with identical left-to-right structure (e.g., consonant, consonant, vowel, as in SPI). This result is open to a number of interpretations. One of the regions held to contribute to SPCN activity (i.e., the intra-parietal sulcus, IPS) has been shown to increase in activity when scrambled objects are displayed relative to objects possessing a regular structure (Xu, 2008). In this perspective, the increment in SPCN activity with scrambled letters could be taken to reflect the likely increase in activation of neurons in IPS for scrambled letters versus aligned letters. This possibility, considering the verbal material used in the present study, is in accord with the idea that special encoding algorithms are used to process letter strings arrayed horizontally (i.e., via activation of letter detectors that are tuned for horizontally aligned sets of letters). A second interpretation, which relates to the topographical distribution of neurons in the visual cortex, is that differences in absolute spatial locations across the scrambled and nonscrambled conditions had an effect on the amplitude of the SPCN. To clarify, it is possible that letters encoded from upper visual field positions (with early projections to the ventral portion of the occipital lobes) may have produced a smaller SPCN than letters encoded from lower visual field positions (with early projections to more dorsal portions of the occipital lobes), and these effects may be nonlinear, leading to a net increase in SPCN amplitude when positions off the horizontal midline are used. The horizontal letter strings were always

on the horizontal midline, and thus caution is mandatory under these circumstances.

An intriguing aspect of the present results is that the SPCN elicited by scrambled letters began earlier than the SPCN elicited by horizontally aligned letter strings. Furthermore, there was also an increase in SPCN amplitude for scrambled letters relative to horizontally aligned letter strings. One possibility is that these differences were not tied to the SPCN per se, but rather arise from differences in the amplitude of the attention-sensitive N2pc component that is typically observed in the latency range preceding the onset of the SPCN (e.g., Jolicœur, Brisson, & Robitaille, 2008). On two thirds of the trials, in the word and nonword conditions, the three target letters were presented at known and adjacent locations. In contrast, in the less frequent scrambled condition, the letters were presented at nonadjacent and unpredictable locations. Consequently, when scrambled, the letters were less likely to fall in the same receptive field of infero-parietal neurons (Jack et al., 2007). These considerations raise two possibilities. The first possibility is that attention needed to be oriented to each of the target letters in the scrambled condition, in contrast with a single attentional shift for horizontal letter strings. Such an increase in attentional demands may have resulted in an increase in N2pc amplitude, which, in turn, would have given the impression of an earlier onset for the SPCN. The second possibility is that scrambled letters were processed as distinct objects more frequently than horizontally aligned letters, which may have been processed as a group. If the amplitude of the SPCN varies as a function of the number of encoded groups, rather than as a function of the number of letters, then we would expect the amplitude of the SPCN to be higher for the scrambled condition relative to the other two conditions (as was found). Perhaps a larger number of distinct objects to be encoded lead to a stronger activation of the neurons giving rise to the SPCN, and a more rapid rise in the activity of these neurons (leading to an earlier SPCN). An additional and interesting perspective is to consider the SPCN onset latency difference between scrambled versus aligned letters not as an effect of onset anticipation for scrambled letters, but rather as a delay in onset latency for word-like stimuli. This alternative perspective would not be incongruent with the view proposed above that the activation of letter detectors may be triggered upon the presentation of horizontally aligned letter strings, on the assumption that this additional stage may be time-consuming.

Conclusions

From the point of view of encoding and maintenance in VSTM, all letter strings are not equal. Letter strings forming words elicit a smaller SPCN than strings forming nonwords, suggesting strongly that maintaining word representations taxes VSTM mechanisms to a lesser extent relative to nonword representations. In addition, the spatial layout of letter strings may also affect ensuing retention loads in VSTM. Both effects are interesting and suggest that the SPCN component may provide a powerful new tool to study interactions between early sensory and memory systems (i.e., VSTM) and processes that interpret stimuli in the context of rich lexical and semantic representations in long-term memory engaged during reading. We expect that the present findings will lead to important discoveries concerning the representation of words and nonwords in individuals with and without reading difficulties.

REFERENCES

- Brisson, B., & Joliceur, B. (2007). A psychological refractory period in access to visual short-term memory and the deployment of visual-spatial attention: Multitasking processing deficits revealed by event-related potentials. *Psychophysiology*, *44*, 323–333.
- Cattell, J. M. (1886). The time it takes to see and name objects. *Mind*, *11*, 63–65.
- Cohen, L., Dehaene, S., Naccache, L., Lehéry, S., Dehaene-Lambertz, G., Hénaff, M. A., et al. (2000). The visual word form area: Spatial and temporal characterization of an initial stage of reading in normal subjects and posterior split-brain patients. *Brain*, *123*, 291–307.
- Coltheart, M. (1980). Iconic memory and visible persistence. *Perception & Psychophysics*, *27*, 183–228.
- Cowan, N. (1996). Short-term memory, working memory, and their importance in language processing. *Topics in Language Disorder*, *17*, 1–18.
- Dell'Acqua, R., Pesciarelli, F., Joliceur, P., Eimer, M., & Peressotti, F. (2007). The interdependence of spatial attention and lexical access as revealed by early asymmetries in occipito-parietal ERP activity. *Psychophysiology*, *44*, 436–443.
- Dell'Acqua, R., Sessa, P., Joliceur, P., & Robitaille, N. (2006). Spatial attention freezes during the attentional blink. *Psychophysiology*, *43*, 394–400.
- Dufau, S., Grainger, J., & Holcomb, P. J. (2008). An ERP investigation of location invariance in masked repetition priming. *Cognitive Affective and Behavioral Neuroscience*, *5*, 222–228.
- Grainger, J., Granier, J. P., Farioli, F., Van Assche, E., & van Heuven, W. (2006). Letter position information and printed word perception: The relative-position priming constraint. *Journal of Experimental Psychology: Human Perception and Performance*, *32*, 865–884.
- Hauk, O., Davis, M. H., Ford, M., Pulvermüller, F., & Marslen-Wilson, W. D. (2006). The time course of visual word-recognition as revealed by linear regression analysis of ERP data. *NeuroImage*, *30*, 1383–1400.
- Heil, M., Rolke, R., & Pecchinenda, A. (2004). Automatic semantic activation is no myth. *Psychological Science*, *15*, 852–857.
- Hinojosa, J. A., Martín-Loeches, M., Muñoz, F., Casado, P., & Pozo, M. A. (2004). Electrophysiological evidence of automatic early semantic processing. *Brain and Language*, *88*, 39–46.
- Holcomb, P. J. (1993). Semantic priming and stimulus degradation: Implications for the role of N400 in language processing. *Psychophysiology*, *30*, 47–61.
- Holcomb, P. J., & Grainger, J. (2006). On the time-course of visual word recognition: An ERP investigation using masked repetition priming. *Journal of Cognitive Neuroscience*, *18*, 1631–1643.
- Holcomb, P. J., & Grainger, J. (2007). Exploring the temporal dynamics of visual word recognition in the masked repetition priming paradigm using event-related potentials. *Brain Research*, *1180*, 39–58.
- Jack, A. I., Patel, G. H., Astafiev, S. V., Snyder, A. Z., Akbudak, E., Shulman, G. L., et al. (2007). Changing human visual field organization from early visual to extra-occipital cortex. *PLoS ONE*, *5*, e452.
- Joliceur, P., Brisson, B., & Robitaille, N. (2008). Dissociation of the N2pc and sustained posterior contralateral negativity in a choice response task. *Brain Research*, *1215*, 160–172.
- Joliceur, P., Sessa, P., Dell'Acqua, R., & Robitaille, N. (2006a). Attentional control and capture in the attentional blink paradigm: Evidence from human electrophysiology. *European Journal of Cognitive Psychology*, *18*, 560–578.
- Joliceur, P., Sessa, P., Dell'Acqua, R., & Robitaille, N. (2006b). On the control of visual spatial attention: Evidence from human electrophysiology. *Psychological Research*, *70*, 414–424.
- Kiesel, A., Miller, J., Joliceur, P., & Brisson, B. (2008). Measurement of ERP latency differences: A comparison of single-participant and jackknife-based scoring methods. *Psychophysiology*, *45*, 250–274.
- Klaver, P., Talsma, D., Wijers, A. A., Heinze, H.-J., & Mulder, G. (1999). An event-related brain potential correlate of visual short-term memory. *NeuroReport*, *10*, 2001–2005.
- Kutas, M., & Hillyard, S. A. (1980). Reading senseless sentences: Brain potentials reflect semantic incongruity. *Science*, *207*, 203–205.
- Mado Proverbio, A., Vecchi, L., & Zani, A. (2004). From orthography to phonetics: ERP measures of grapheme-to-phoneme conversion mechanisms in reading. *Journal of Cognitive Neuroscience*, *16*, 301–317.
- Martin, C. D., Nazir, T., Thierry, G., Paulignan, Y., & Demonet, J.-F. (2006). Perceptual and lexical effects in letter identification: An event-related potential study of the word superiority effect. *Brain Research*, *1098*, 153–160.
- Martín-Loeches, M., Hinojosa, J. A., Fernández-Frías, C., & Rubia, F. J. (2001). Functional differences in the semantic processing of concrete and abstract words. *Neuropsychologia*, *39*, 1086–1096.
- Martín-Loeches, M., Hinojosa, J. A., Gómez-Jarabo, G., & Rubia, F. J. (1999). The recognition potential: An ERP index of lexical access. *Brain and Language*, *70*, 364–384.
- McClelland, J. L., & Rumelhart, D. E. (1981). An interactive activation model of context effects in letter perception: Part I. An account of basic findings. *Psychological Review*, *88*, 375–407.
- McCullough, A. W., Machizawa, M. G., & Vogel, E. K. (2007). Electrophysiological measures of maintaining representations in visual working memory. *Cortex*, *43*, 77–94.
- Morsella, E., & Miozzo, M. (2002). Evidence for a cascade model of lexical access in speech production. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *28*, 555–563.
- Nobre, A. C., Allison, T., & McCarthy, G. (1994). Word recognition in the human inferior temporal lobe. *Nature*, *372*, 260–263.
- Pesciarelli, F., Kutas, M., Dell'Acqua, R., Peressotti, F., Job, R., et al. (2007). Semantic and repetition priming within the attentional blink: An event-related brain potential (ERP) investigation. *Biological Psychology*, *76*, 21–30.
- Puce, A., Allison, T., Asgari, M., Gore, J. C., & McCarthy, G. (1996). Differential sensitivity of human visual cortex to faces, letterstrings, and textures: A functional magnetic resonance study. *Journal of Neuroscience*, *16*, 5205–5215.
- Pulvermüller, F. (2001). Brain reflections of words and their meaning. *Trends in Cognitive Science*, *5*, 517–524.
- Pulvermüller, F., Assadollahi, R., & Elbert, T. (2001). Neuromagnetic evidence for early semantic access in word recognition. *European Journal of Neuroscience*, *13*, 201–205.
- Pulvermüller, F., Shtyrov, Y., & Ilmoniemi, R. (2005). Brain signatures of meaning access in action word recognition. *Journal of Cognitive Neuroscience*, *17*, 884–892.
- Reingold, E. M., & Joliceur, P. (1993). Perceptual versus postperceptual mediation of visual context effects: Evidence from the letter-superiority effect. *Perception & Psychophysics*, *53*, 166–178.
- Robitaille, N., Joliceur, P., Dell'Acqua, R., & Sessa, P. (2007). Short-term consolidation of visual patterns interferes with visuo-spatial attention: Converging evidence from human electrophysiology. *Brain Research*, *1185*, 158–169.
- Rolke, B., Heil, M., Streb, J., & Hennighausen, E. (2001). Missed prime words within the attentional blink evoke an N400 semantic priming effect. *Psychophysiology*, *38*, 165–174.
- Rudell, A. P., & Hua, J. (1997). The recognition potential, word difficulty, and individual reading ability: On using event-related potentials to study perception. *Journal of Experimental Psychology: Human Perception and Performance*, *23*, 1170–1195.
- Sereno, S. C., Rayner, K., & Posner, M. I. (1998). Establishing a timeline of word recognition: Evidence from eye movements and event-related potentials. *NeuroReport*, *9*, 2195–2200.
- Thorpe, S., Fize, D., & Marlot, C. (1996). Speed of processing in the human visual system. *Nature*, *381*, 520–522.
- Ulrich, R., & Miller, J. (2001). Using the jackknife-based scoring method for measuring LRP onset effects in factorial designs. *Psychophysiology*, *38*, 816–827.
- Vogel, E. K., Luck, S. J., & Shapiro, K. L. (1998). Electrophysiological evidence for a postperceptual locus of suppression during the attentional blink. *Journal of Experimental Psychology: Human Perception and Performance*, *24*, 1656–1674.
- Vogel, E. K., & Machizawa, M. G. (2004). Neural activity predicts individual differences in visual working memory capacity. *Nature*, *428*, 748–751.
- Xu, Y. (2008). Representing connected and disconnected shapes in human inferior intraparietal sulcus. *NeuroImage*, *40*, 1849–1856.

(RECEIVED January 7, 2008; ACCEPTED May 5, 2008)