Spatial layout of letters in nonwords affects visual short-term memory load: Evidence from human electrophysiology

DAVID PRIME, ^a ROBERTO DELL'ACQUA, ^b MARTIN ARGUIN, ^a FRÉDÉRIC GOSSELIN, ^a AND PIERRE JOLICŒUR^a

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

Abstract

The sustained posterior contralateral negativity (SPCN) was used to investigate the effect of spatial layout on the maintenance of letters in VSTM. SPCN amplitude was measured for words, nonwords, and scrambled nonwords. We reexamined the effects of spatial layout of letters on SPCN amplitude in a design that equated the mean frequency of use of each position. Scrambled letters that did not form words elicited a larger SPCN than either words or nonwords, indicating lower VSTM load for nonwords presented in a typical horizontal array than the load observed for the same letters presented in spatially scrambled locations. In contrast, prior research has shown that the spatial extent of arrays of simple stimuli did not influence the amplitude of the SPCN. Thus, the present results indicate the existence of encoding and VSTM maintenance mechanisms specific to letter and word processing.

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

Encoding visually displayed letter strings is enabled by complex perceptual processes that are not entirely compatible with the mechanisms underlying visual processing of nonletter stimuli. For example, letter perception violates the acuity gradient principle, according to which the visual stimuli presented at fixation are processed more efficiently than stimuli presented in the periphery. In striking contrast, studies on letter identification have revealed that the first letter of a string is the most accurately perceived, even when the first letter is far from fixation (e.g., Hammond & Green, 1982; Tydgat & Grainger, 2009). This and related findings (see Whitney, 2001) have suggested that processing of letter strings relies on specialized brain and functional subroutines that are particularly influenced by the spatial organization of letters within a string (Blais, Fiset, Arguin, Jolicœur, Bub, & Gosselin, 2009; Tydgat & Grainger, 2009). Interestingly,

This research was made possible by a grant from the Natural Sciences and Engineering Research Council of Canada awarded to PJ, by a grant from the Canadian Institutes of Health Research awarded to PJ, by equipment funded by the Canada Fund for Innovation awarded to PJ, by the Canada Research Chairs program, by infrastructure support from the Fonds Quebécois pour la Recherche en Santé du Québec, by a team research grant from the Fonds Québecois pour la Recherche sur la Nature et la Technologie awarded to MA, FG, and PJ, and by research support from Université de Montréal.

Address correspondence to: David J. Prime, Department of Psychology, Simon Fraser University, 8888 University Drive, Burnaby, BC, Canada, V5A 1S6. E-mail: david_john_prime@yahoo.com

whereas psycholinguists have been concerned with the spatial organization of letters at early stages of processing, much less is known about the issue of whether the spatial organization of letters composing a string also influences how letter strings are retained in visual short-term memory (VSTM).

VSTM is a fundamental memory system that enables us to retain visual features and objects for a short period of time (in the order of several seconds). This memory system appears to be important for efficient perceptual and cognitive processing in tasks that depend on visual input (Jolicœur & Dell'Acqua, 1998; Jolicœur, Sessa, Dell'Acqua, & Robitaille, 2006a, b; Prime & Jolicœur, in press). The ability to transfer letter information to VSTM in an efficient and error-free manner may be particularly important for reading (Bosse, Tainturier, & Valdois, 2007; Goulandris & Snowling, 1991; Valdois, Bosse, Ans, Carbonnel, Zorman, et al., 2003). For these reasons, we investigated interactions between VSTM and the processing of letters in the context of words and nonwords, and the role of the spatial layout of letters for memory.

Predovan, Prime, Arguin, Gosselin, Dell'Acqua, and Jolicœur (2009) investigated the effect of lexical status on the maintenance of letter strings in visual short-term memory. They hypothesized that the lexical status of letter strings that formed words would reduce the load in VSTM in comparison to random letter strings that did not form words, because of the availability of pre-existing long-term memory (LTM) representations for words. In order to test this hypothesis, the sustained posterior



^bDepartment of Developmental Psychology and Center for Cognitive Science, University of Padova, Padova, Italy

Lexical status and VSTM 431

contralateral negativity (SPCN), an electrophysiological marker of storage in VSTM, was used to measure VSTM load for word and nonword letter strings.

A growing body of evidence (e.g., Jolicœur, Brisson, & Robitaille, 2008; Klaver, Talsma, Wijers, Heinze, & Mulder, 1999; McCollough, Machizawa, & Vogel, 2007; Perron, Lefebvre, Robitaille, Brisson, Gosselin, et al., 2009; Robitaille, Grimault, & Jolicœur, 2009; Vogel & Machizawa, 2004) supports the hypothesis that the SPCN reflects neural activity specifically related to the maintenance of information stored in VSTM. The SPCN is observed following the encoding of laterally presented visual stimuli. In order to avoid confounding effects 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 field. The SPCN is observed as a relatively more negative event-related potentials (ERP) at posterior electrodes contralateral to the encoded visual field (e.g., the voltage is more negative at electrode PO8 than at PO7 for stimuli encoded from the left visual field). In tasks that require the maintenance of visual information for short retention intervals, an SPCN effect is observed during the retention interval beginning at about 300 ms from the onset of the memory array. Importantly, the amplitude of the SPCN increases as the number of target items increased (Dell'Acqua, Sessa, Toffanin, Luria, & Jolicœur, 2010; Luria, Sessa, Gotler, Jolicœur, & Dell'Acqua, 2010; McCollough et al., 2007; Perron et al., 2009; Robitaille et al., 2009; Vogel & Machizawa, 2004), reaching a maximum when the number of stimuli to be encoded equals or exceeds the estimated capacity of VSTM (Vogel & Machizawa, 2004).

Predovan et al. (2009) thus predicted that the SPCN elicited by horizontal letter strings that formed words would be attenuated relative to the SPCN elicited by equal length horizontal strings that did not form words. The 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 (word condition), the amplitude of the SPCN was reduced relative to when the target string did not form a word (nonword condition). The reduced SPCN for words relative to that for nonwords suggested that reliance on a low-level visual memory system was reduced when the task could be performed on the basis of rapidly activated higher-level representations. Furthermore, this effect of lexical status on the amplitude of the SPCN suggested that the SPCN could become a powerful tool to study basic mechanisms of attention, perception, and memory, supporting reading and individual differences in reading ability (Valdois et al., 2003).

For exploratory purposes, Predovan et al. (2009) also included a condition in which the target string did not form a word, and each letter was randomly displaced either upwards or downwards from the horizontal meridian (*scrambled* condition). Surprisingly, the amplitude of the SPCN was affected by the spatial configuration of the target letters. The amplitude of the SPCN was substantially larger in the scrambled condition than in either of the other two conditions. In contrast, McCollough et al. (2007) found that the SPCN for colored squares was 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. Thus, the results from the scrambled letter condition suggest that there may be important differences in the manner in which VSTM encodes letter and nonletter stimuli, even when the letters do not form a word.

Here we examine a possible alternative explanation for the results of the scrambled letter condition from Predovan et al.

(2009) that arises because the spatial positions of the target letters differed between conditions. In the word and nonword conditions, the horizontal letter strings were always on the horizontal midline. In the scrambled condition, each target letter could appear in either the upper or lower visual field as well as on the horizontal midline. Perron et al. (2009) found that the SPCN elicited by equivalent stimuli was larger for stimuli presented in the lower visual field than for stimuli presented in the upper visual field. However, to our knowledge, a comprehensive mapping of SPCN amplitude across the visual field has not been performed. It is possible that letters encoded from lower visual field positions may have produced a larger SPCN than letters encoded from upper and midline visual field positions, and these effects may be non-linear, leading to a net increase in SPCN amplitude for the scrambled condition.

Because of the relevance of Predovan et al.'s (2009) results for our understanding of the role of the spatial layout of letters in words and nonwords in VSTM and for our understanding of basic mechanisms of letter encoding and reading, a re-examination of this issue was particularly important. Here we attempted to replicate their results using an experimental design that eliminated the potentially confounding effect of letter position on SPCN amplitude. We varied the location of the target letters in all three conditions and equated the mean frequency of use of each position across conditions. In the word and nonword conditions, the target strings were presented equally often in one of three positions: on the horizontal meridian or displaced downwards by 0.95° or 1.90°. In the scrambled condition, each letter was displaced downwards from the horizontal meridian by 0°, 0.95°, or 1.90°. Furthermore, letters were assigned to spatial positions such that, averaged across trials, the target letters appeared equally often in each spatial position. If, as suggested by Predovan et al.'s results, the spatial arrangement of target letters does affect VSTM load, the scrambled condition should produce a larger SPCN than either of the other two conditions. However, if the larger SPCN observed in the scrambled condition by Predovan et al. was due to the absolute spatial positions of the target letters, then there should be no difference in the amplitude of the SPCN between the nonword and the scrambled conditions.

Method

Participants

Forty-four native French speakers (ages 19–35 years, mean = 23.1) participated in this experiment. All participants were naïve volunteers and were paid \$20 Cdn. All participants reported normal or corrected-to-normal vision and no history of neurological problems. Seven participants were excluded from data analysis because an excessive number of trials were rejected, mainly due to a tendency to shift their gaze towards the attended hemifield but also due to electroencephalogram (EEG) artifacts. On average, the 37 remaining subjects moved their eyes less than .15° of visual angle in the direction of the target (based on averaged horizontal electro-oculogram (EOG) results; see Hillyard & Galambos, 1970; Lins, Picton, Berg, & Scherg, 1993).

Task and Design

The experimental task required participants to encode and retain the identity of three visually presented letters. The target letters were equally likely to be presented in the left or right visual field. D. Prime et al.

A retention period of one second 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. There were three within-participant conditions based on the lexical status and spatial layout 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 target letters in the nonword and scrambled conditions 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 addition, bigram and trigram frequency were matched between the nonword and scrambled conditions.

Stimuli

The visual field cue was a centrally presented 0.2° grey arrow pointing towards the left or right. Target displays consisted of three letters presented on each side of the vertical meridian (6 letters total). The letter stimuli were $\sim 0.7^{\circ}$ tall capital letters (A-Z) presented in grey on a black background. In the word and nonword conditions, the letter strings were centered 2.4° to the left and right of fixation. The horizontal center-to-center distance between each letter was 1.3°. The letter strings in these two conditions were presented equally often in one of three positions: on the horizontal meridian or displaced downwards by 0.95° or 1.90°, which is illustrated in Figure 1. In the scrambled condition, the same spatial locations of letters used in the other conditions were used but, on any given trial, there was one letter in each row and column of the 3×3 matrix of possible positions, yielding 6 possible layouts that were used equally often across trials. 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 centered 0.35° above and below the center of the former location of the probed letter (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 grey 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 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. Half of the subjects responded with the right hand (key 'j' to select the top letter and 'n' to select the 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

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 one and a half hours.

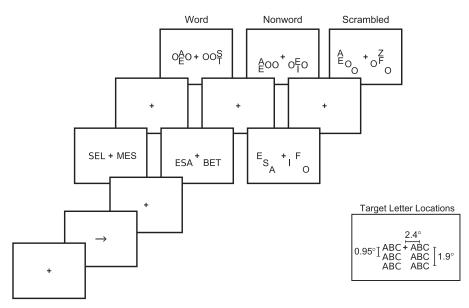


Figure 1. Sequence of events in each trial for the word, nonword, and scrambled conditions.

Lexical status and VSTM 433

Electrophysiological Recording and Analysis

The EEG was recorded with active Ag/AgCl electrodes (BioSemi Active Two, Amsterdam, The Netherlands) mounted on an elastic cap at standard 10–10 scalps 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 EOG. The vertical EOG was recorded as the voltage between Fp1 and an electrode placed below the left eye. The horizontal EOG was recorded 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 cut-off).

Trials containing blinks, eye movements and EEG artefacts were removed prior to ERP averaging by applying automated artefact detection routines (Luck, 2005). Blinks and eye movements were detected by a function that detects rapid steps in the voltage of the EOG channels. Artefacts in EEG channels were identified by functions that detect flat sections of EEG and sudden rapid changes in voltage. 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 8 Hz and baseline corrected relative to mean voltage of the 200-ms pre-stimulus interval. In order 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 signalto-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. The SPCN amplitude for each condition was quantified as the mean voltage of the pooled SPCN wave in the 400 ms to 1000 ms latency range.

Results

Mean percent correct and mean SPCN amplitude measures for each condition were submitted to separate repeated measures analyses of variance (ANOVAs). 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 94%, 92%, and 88%. The ANOVA of accuracy rates revealed that the lexical status of the target letters has a significant effect on performance, F(2,72) = 41.1, p < .001, $\varepsilon = 0.94$, $\eta_p^2 = 0.53$. Subsequent paired comparisons revealed that response accuracy was higher in the word condition than either the nonword condition, F(1,36) = 11.8, p < .002, $\eta_p^2 = 0.25$, or the scrambled condition, F(1,36) = 64.7, p < .001, $\eta_p^2 = 0.64$. Furthermore, response accuracy was higher in the nonword condition than in scrambled condition, F(1,36) = 35.9, p < .001, $\eta_p^2 = 0.50$.

Figure 2 shows grand average waveforms for stimuli encoded from the left and right visual fields at representative lateral occipital electrode sites. The word condition is shown in Panel A, the nonword condition in Panel B, and the 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 was observed in all three conditions for stimuli encoded from both visual fields.

Figure 3, Panel A, shows the scalp distributions of the SPCN for each type of letter string. 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 typical SPCN topography with a voltage peak in the vicinity of electrodes PO7/PO8 (e.g., Brisson & Jolicœur, 2007; Jolicœur et al., 2008; McCollough et al., 2007; Perron et al., 2009; Predovan et al., 2009). 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.

Figure 3, Panel B, shows the SPCN subtraction waves (contralateral—ipsilateral) pooled over electrode pairs O1/O2, PO7/PO8, and P7/P8, for each condition. The lexical status of the target letters has a significant effect on the amplitude of the SPCN, F(2,72) = 14.2, p < .001, $\varepsilon = 0.98$, $\eta_p^2 = 0.28$. The amplitude of the pooled SPCN wave was highest for the scrambled condition, intermediate for the nonword condition, and smallest for the word condition.

Replicating the principal finding of Predovan et al. (2009), the SPCN observed in the word condition was significantly smaller than that observed in the nonword condition, F(1,36) = 7.0, p < .02, $\eta_p^2 = 0.16$. Of more relevance to the present study, paired comparisons also revealed that the scrambled condition elicited a significantly larger SPCN than either the word condition, F(1,36) = 24.8, p < .001, $\eta_p^2 = 0.41$, or the nonword condition, F(1,36) = 8.3, p < .01, $\eta_p^2 = 0.19$. Thus, the spatial configuration of the target letters affected SPCN amplitude even when the letters were presented in the same spatial positions (on average) in all conditions.

Discussion

The present results, combined with those of Predovan et al. (2009), show that the degree of involvement of VSTM for visually presented letters depends both on the lexical and spatial context in which the letters are encoded. Letters that form a word lead to the smallest SPCN amplitude, which we interpret as a reflection of a smaller load in VSTM. A skilled reader, as most of our subjects undoubtedly were, can encode words very quickly, and there is good evidence that letters in the context of a word can be perceived more accurately than letters in a nonword (cf. word superiority effect; Reicher, 1969). We hypothesize that subjects were able to rely on abstract representations of words to reduce the need for a literal visual representation of letters, as would be required in the nonword and scrambled conditions. Abstract representations cannot be excluded for the latter conditions, but they would presumably be limited to shape-independent representations of letter identity. In contrast, a higher-order representation must be available for words, and this is likely to have helped. Interestingly, there is some evidence that even poor readers can show a significant word superiority effect in the perception of letters (Grainger, Bouttevin, Truc, Bastien, & Ziegler, 2003).

D. Prime et al.

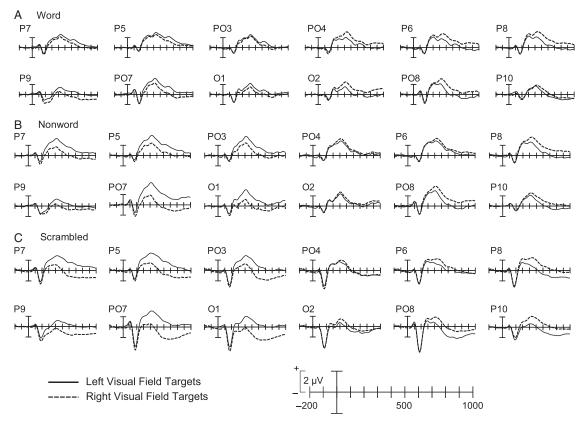


Figure 2. Grand averaged waveforms for representative posterior electrodes. Separate waveforms are shown for stimuli encoded from the left and right visual fields. (A) Word condition. (B) Nonword condition. (C) Scrambled condition.

Most interestingly, however, was the fact that we again found a significantly lower VSTM load for nonwords presented in a typical horizontal array (nonword condition) compared with the load observed for the same letters presented in a spatially scrambled set of locations (scrambled condition). Because we varied the location of the target letters in all three conditions and equated the mean frequency of use of each position across con-

ditions, this difference in SPCN amplitude cannot be due to the effects of visual field location on SPCN amplitude found by Perron et al. (2009). This result, anticipated by Predovan et al. (2009), and confirmed here, suggests that, even for nonwords, there is a significant encoding advantage for letters presented in a word-like structure, over letters presented in spatially scrambled positions. One possibility is that there are specialized encoding

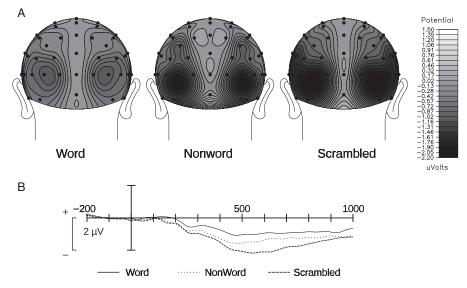


Figure 3. (A) Scalp distributions of the SPCN for each condition (mean activity from 400–1000 ms post memory stimulus onset). (B) Contralateral minus ipsilateral waveforms showing the SPCN for the pooled response at three posterior electrode sites for each condition.

Lexical status and VSTM 435

routines for word-like letter strings, and that these routines can be deployed on horizontal letter strings and confer an encoding advantage even for nonword letter strings. This would be consistent with a set of sub-lexical letter combinations (Grainger et al., 2003), which may be accessed more efficiently when letters are presented in a horizontal array than when presented in a scrambled array. Results from Peressotti and Grainger (1995) and Humphreys, Evett, and Quinlan (1990) suggest that readers encode multi-letter units (even when they occur in nonwords) that can prime subsequent processing of letter strings (see also Mayall & Humphreys, 1996; Mayall, Humphreys, & Olson, 1997). The present results suggest that such higher-order units can support VSTM by reducing the need to encode visual representations at the individual letter level. However, the efficient encoding of such multi-letter units may not be possible when the letters are presented in a spatially scrambled display.

Alternatively, the encoding advantage observed for the word and nonword conditions over the scrambled condition may have arisen because the horizontal layout of the letters in the word and nonword conditions provided structure and reduced ambiguity. The disordered layout of the scrambled condition may have increased the attentional and working memory load required to encode the target letters, and this may have given rise to an increase in SPCN amplitude. According to this account, a reduction in SPCN amplitude relative to the scrambled condition should be observed for any orderly arrangement of letters (e.g., vertical). Further research will be required to test these possible accounts.

The present results, for letters, contrast with those of McCollough et al. (2007), who found that the spatial extent of arrays of simple colored stimuli did not influence the amplitude

of the SPCN. The present results, therefore, suggest that the spatial layout of letters may be more critical than the spatial layout of simple colored stimuli. One possible explanation for this difference is that letter detectors tuned for horizontally aligned sets of letters may allow for special encoding algorithms that reduce the information load in VSTM for letter strings by facilitating a grouping or chunking of the letters (Grainger, 2008; Grainger & Jacobs, 1996).

The present results, combined with those of McCollough et al. (2007), indicate the existence of encoding and VSTM maintenance mechanisms specific to letter and word processing. Thus, the SPCN provides a useful index of VSTM processes involved in letter processing and reading. One potential application of the present methodology is in investigating the processing deficits underlying dyslexia. Some researchers have proposed that dyslexia arises from inefficient processing at either the grapheme-to-phoneme conversion stage or the phonological short-term memory buffer (or a mixture of both) as primary determinants of impaired nonword reading (e.g., Goswami, Thomson, Richardson, Stainthorp, Hughes, et al., 2000; Ramus, 2003). Others, however, have emphasized problems in the segmentation of letter strings due to sluggish control of visuo-spatial attention mechanisms (e.g., Hari & Renwall, 2001; see also Facoetti, Trussardi, Ruffino, Lorusso, Catteneo, et al., 2010), or problems in the rapid transfer of ordered representations in VSTM (Valdois et al., 2003). The present differences in VSTM load for words and nonwords revealed by substantial modulations of the amplitude of the SPCN suggests that the SPCN may be a powerful tool to study the mechanisms that mediate efficient reading and deficits in these mechanisms that contribute to dyslexia.

REFERENCES

- Blais, C., Fiset, D., Arguin, M., Jolicœur, P., Bub, D., & Gosselin, F. (2009). Reading between eye saccades. *PLoS ONE*, 4, e6648.
- Bosse, M.-L., Tainturier, M. J., & Valdois, S. (2007). Developmental dyslexia: The visual attention span deficit hypothesis. *Cognition*, 104, 198–230
- Brisson, B., & Jolicœur, P. (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.
- Coltheart, M. (1980). Iconic memory and visible persistence. *Perception & Psychophysics*, 27, 183–228.
- Dell'Acqua, R., Sessa, P., Toffanin, P., Luria, R., & Jolicœur, P. (2010).
 Orienting attention to objects in visual short-term memory.
 Neuropsychologia, 48, 419–428.
- Facoetti, A., Trussardi, A. N., Ruffino, M., Lorusso, M. L., Cattaneo, C., Galli, R., Molteni, M., & Zorzi, M. (2010). Multisensory spatial attention deficits are predictive of phonological decoding skills in developmental dyslexia. *Journal of Cognitive Neuroscience*, 22, 1011–1025.
- Goswami, U., Thomson, J., Richardson, U., Stainthorp, R., Hughes, D., Rosen, S., & Scott, S. K. (2000). Amplitude envelope onsets and developmental dyslexia: A new hypothesis. *Proceedings of the National Academy of Sciences*, USA, 99, 10911–10916.
- Goulandris, N. K., & Snowling, M. (1991). Visual memory deficits: A plausible cause of developmental dyslexia? Evidence from a single case study. *Cognitive Neuropsychology*, 8, 127–154.
- Grainger, J. (2008). Cracking the orthographic code: An introduction. Language and Cognitive Processes, 23, 1–35.
- Grainger, J., Bouttevin, S., Truc, C., Bastien, M., & Ziegler, J. (2003). Word superiority, pseudoword superiority, and learning to read: A comparison of dyslexic and normal readers. *Brain and Language*, 87, 432–440.
- Grainger, J., & Jacobs, A. M. (1996). Orthographic processing in visual word recognition: A multiple read-out model. *Psychological Review*, 103, 518–565.

- Hammond, E. J., & Green, D. W. (1982). Detecting targets in letter and non-letter arrays. *Canadian Journal of Psychology*, 36, 67–82.
- Hari, R., & Renwall, H. (2001). Impaired processing of rapid stimulus sequences in dyslexia. Trends in Cognitive Science, 5, 525–532.
- Hillyard, S. A., & Galambos, R. (1970). Eye movement artifact in the CNV. Electroencephalography and Clinical Neurophysiology, 28, 173– 182.
- Humphreys, G. W., Evett, L. J., & Quinlan, P. T. (1990). Orthographic processing in visual word identification. *Cognitive Psychology*, 22, 517–560.
- Jolicœur, 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.
- Jolicœur, P., & Dell'Acqua, R. (1998). The demonstration of short-term consolidation. *Cognitive Psychology*, 36, 138–202.
- Jolicœur, P., Sessa, P., Dell'Acqua, R., & Robitaille, N. (2006a). On the control of visual spatial attention: Evidence from human electrophysiology. *Psychological Research*, 70, 414–424.
- Jolicœur, P., Sessa, P., Dell'Acqua, R., & Robitaille, N. (2006b). Attentional control and capture in the attentional blink paradigm: Evidence from human electrophysiology. *European Journal of Cognitive Psychology*, 18, 560–578.
- Klaver, P., Talsma, D., Wijers, A. A., Heinze, H.-J., & Mulder, G. (1999). An event-related brain potential correlate of visual short-term memory. *Neuro Report*, 10, 2001–2005.
- Lins, O. G., Picton, T. W., Berg, P., & Scherg, M. (1993). Ocular artifacts in EEG and event-related potentials I: Scalp topography. *Brain Topography*, 6, 51–63.
- Luck, S. J. (2005). An introduction to the event-related potential technique. Cambridge, MA: MIT Press.
- Luria, R., Sessa, P., Gotler, A., Jolicœur, P., & Dell'Acqua, R. (2010).
 Visual short-term memory capacity for simple and complex objects.
 Journal of Cognitive Neuroscience, 22, 496–512.

, 2011, 3, Downloaded from https://online/blary.wiley.com/doi/10.1111/j.1469-8986.2010.01072.x by Universitate De Montreal, Wiley Online Library on [1005/2024]. See the Terms and Conditions (https://online/bbary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons

D. Prime et al.

Mayall, K., & Humphreys, G. W. (1996). Case mixing and the task-sensitive disruption of lexical processing. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 22, 278–294.

- Mayall, K., Humphreys, G. W., & Olson, A. (1997). Disruption to word or letter processing? The origins of the case-mixing effect. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 23, 1275–1286.
- McCollough, A. W., Machizawa, M. G., & Vogel, E. K. (2007). Electrophysiological measures of maintaining representations in visual working memory. *Cortex*, 43, 77–94.
- Peressotti, F., & Grainger, J. (1995). Letter-position coding in random consonant arrays. *Perception & Psychophysics*, *57*, 875–890.
- Perron, R., Lefebvre, C., Robitaille, N., Brisson, B., Gosselin, F., Arguin, M., & Jolicœur, P. (2009). Attentional and anatomical considerations for the representation of simple stimuli in visual short-term memory: Evidence from human electrophysiology. *Psychological Research*, 73, 222–232.
- Predovan, D., Prime, D. J., Arguin, M., Gosselin, F., Dell'Acqua, R., & Jolicœur, P. (2009). On the representation of words and nonwords in visual short-term memory: Evidence from human electrophysiology. *Psychophysiology*, 46, 191–199.
- Prime, D. J., & Jolicœur, P. (in press). Mental rotation requires visual short-term memory: Evidence from human electric cortical activity. *Journal of Cognitive Neuroscience*.
- Ramus, F. (2003). Developmental dyslexia: Specific phonological deficit of general sensorimotor disfunction? *Current Opinion in Neurobiology*, 13, 212–218.

- Reicher, G. M. (1969). Perceptual recognition as a function of meaningfulness of stimulus material. *Journal of Experimental Psychology*, 81, 275–280.
- Robitaille, N., Grimault, S., & Jolicœur, P. (2009). Bilateral parietal and contralateral responses during the maintenance of unilaterally-encoded objects in visual short-term memory: Evidence from magnetoencephalography. *Psychophysiology*, 46, 1090–1099.
- Tydgat, I., & Grainger, J. (2009). Serial position effects in the identification of letters, digits, and symbols. *Journal of Experimental Psychology: Human Perception and Performance*, 35, 480–498.
- Valdois, S., Bosse, M.-L., Ans, B., Carbonnel, S., Zorman, M., David, D., & Pellat, J. (2003). Phonological and visual processing deficits can dissociate in developmental dyslexia: Evidence from two case studies. *Reading and Writing*, 16, 541–572.
- Vogel, E. K., & Machizawa, M. G. (2004). Neural activity predicts individual differences in visual working memory capacity. *Nature*, 428, 748–751.
- Whitney, C. (2001). How the brain encodes the order of letters in a printed word: The SERIOL model and selective literature review. *Psychonomic Bulletin & Review*, 8, 221–243.

(RECEIVED February 2, 2010; ACCEPTED April 25, 2010)