Neuropsychologia 50 (2012) 1748–1758

Contents lists available at SciVerse ScienceDirect

Neuropsychologia

journal homepage: www.elsevier.com/locate/neuropsychologia

Contralateral cortical organisation of information in visual short-term memory: Evidence from lateralized brain activity during retrieval

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ARTICLE INFO

Article history:
Received 11 October 2011
Received in revised form
8 March 2012
Accepted 30 March 2012
Available online 30 April 2012

Keywords:
Visual short-term memory
EEG
TCN

ABSTRACT

We studied brain activity during retention and retrieval phases of two visual short-term memory (VSTM) experiments. Experiment 1 used a balanced memory array, with one color stimulus in each hemifield, followed by a retention interval and a central probe, at the fixation point that designated the target stimulus in memory about which to make a determination of orientation. Retrieval of information from VSTM was associated with an event-related lateralization (ERL) with a contralateral negativity relative to the visual field from which the probed stimulus was originally encoded, suggesting a lateralized organization of VSTM. The scalp distribution of the retrieval ERL was more anterior than what is usually associated with simple maintenance activity, which is consistent with the involvement of different brain structures for these distinct visual memory mechanisms. Experiment 2 was like Experiment 1, but used an unbalanced memory array consisting of one lateral color stimulus in a hemifield and one color stimulus on the vertical mid-line. This design enabled us to separate lateralized activity related to target retrieval from distractor processing. Target retrieval was found to generate a negative-going ERL at electrode sites found in Experiment 1, and suggested representations were retrieved from anterior cortical structures. Distractor processing elicited a positive-going ERL at posterior electrodes sites, which could be indicative of a return to baseline of retention activity for the discarded memory of the now-irrelevant stimulus, or an active inhibition mechanism mediating distractor suppression.

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1. Introduction

Visual short-term memory (VSTM) is an important fundamental mechanism in the human cognitive architecture. By establishing a bridge between early sensory input to various cognitive operations, VSTM performs an essential temporary maintenance function that enables the integration of multiple or complex visual input, and is thus critical in many everyday activities. Recent work provides some evidence concerning the cortical networks implicated during the retention of visual information in VSTM (e.g., Grimault et al., 2009; Robitaille et al., 2010; Todd & Marois, 2004). Much of this evidence has focused on manipulations of memory load and examined brain activity during the retention interval. These studies are based on the assumption that brain regions mediating the retention of information will be more active when they hold a higher memory load. This activity will increase until the individual memory capacity is reached, at which point, the activity will stop increasing for further attempted load increases, creating a plateau in corresponding brain activity. This assumption has been very useful, but it could overlook brain mechanisms that participate in memory but are not modulated by memory load. Another approach may be to examine brain activity related to memory and attention because the retention of information in VSTM has been suggested to interact with attention (Awh & Jonides, 2001; Baddeley, 1993; Gratton, 1998; Gratton, Corballis, & Jain, 1997; Nobre et al., 2004; Lepsien & Nobre, 2006) through an increase in performance in the recall of information and in activity in areas believed to be implicated in VSTM. Interactions between VSTM and attention are so intricate and pervasive that some propose that both may be different manifestations of the same attentional process directed at different representations (Chun, 2011); VSTM would be attention directed to stable internal representations while visual attention would be attention directed toward volatile sensory representations. The identification of attentional electrophysiological effects during the completion of a memory task would establish a direct relation between attention and VSTM as well as provide a new approach to identify brain activity of

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http://dx.doi.org/10.1016/j.neuropsychologia.2012.03.032

interest. This latter approach may pave the way to a different paradigm by focusing on a subset of the information that is most relevant to the participant, instead of the total amount of information retained in memory. This is the approach we explored in the present research, as explained below.

The deployment of attention to an object in the left or right visual field provokes an imbalance in the activity of contralateral versus ipsilateral cortical visual areas in the posterior part of the brain. This cortical imbalance is believed to be created by a greater activation of the cortical areas directly implicated in the visual search task and it can be measured in EEG as the difference in potential observed at posterior electrodes sites across corresponding left and right electrode sites. A peak in this difference is typically found about 250 ms after the onset of a visual stimulus display requiring an attentional deployment to a lateral stimulus. This difference in potential has been coined N2 posterior contralateral (or N2pc), due to its timing in the N2 time range, negative polarity, and posterior contralateral scalp distribution (Luck & Hillyard, 1994). Usually this component is measured as the difference in activity at electrode sites PO7 and PO8, which are at or near the peak of the voltage distribution on the scalp for the component. Recent research has revealed a new imbalance in brain activity, similar in latency and aspect to an N2pc, but this time related to the delayed recall of information in memory (Dell'Acqua, Sessa, Toffanin, Luria, & Jolicœur, 2010; Eimer & Kiss, 2010; Nobre, Griffin, & Rao, 2008). Dell'Acqua et al., in their experiments, presented a memory display containing an equal number of geometric forms in left and right hemifields simultaneously. After a retention period, the participants were presented a geometric form at fixation and they had to determine if it was present or absent from the initial memory array by a key press. This task introduced an imbalance in voltage scalp activity when the centrally-presented probe matched one of the original forms. This imbalance produced a negative difference wave at electrode sites more anterior than for the N2pc, namely at P7–P8 and T3–T4. These findings have led to the hypothesis that at least part of the visual memory trace is likely to be located in the hemisphere contralateral to the hemifield from which the visual information was initially encoded.

The N2pc component is normally elicited in experimental protocols in which visual arrays are balanced physically, by presenting a target singleton in one visual hemifield and a distractor singleton in the opposite hemifield, to remove possible confounds associated with sensory imbalance, as illustrated in Fig. 1(Top). This approach, while most commendable, makes it difficult to disentangle brain activity related to target processing from activity related to distractor processing. A partial solution to this issue has been to isolate lateralized activity to just the target or just the distractor by placing one of them in a lateral visual-field location and the other on the vertical mid-line, as illustrated in Fig. 1(Bottom). Stimuli on the mid-line, due to the lateralization calculation, cannot produce differential lateralized activity (Woodman & Luck, 2003), enabling a more precise interpretation of observed lateralized activity to the processing of the lateral item. In such displays, processing is usually restricted to items that are salient relative to other background distractors, which still provide a sensory input balance in term of lateral overall luminance. Using a similar approach, Hickey, Di Lollo, and McDonald (2009) argued that the N2pc could be decomposed into two subcomponents, a negativity contralateral to the target (N_T) and a positivity contralateral to the distractor (P_D) by alternatively positioning the distractor and the target on the vertical mid-line and by observing the difference waveform resulting from the activity related to the lateral target and to the lateral distractor separately. They argued that the sum of these two effects would produce the N2pc wave typically observed in the presence of displays that contain a salient target in one visual field and a salient distractor in the opposite hemifield (e.g., Jolicœur, Brisson, & Robitaille, 2008).

The sustained posterior contralateral negativity (SPCN; Jolicœur, Sessa, Dell'Acqua, & Robitaille, 2006), observed by Klaver, Talsma, Wijers, Heinze, and Mulder (1999) and called the contralateral negative slow wave (CNSW), was later also studied further under the rubric contralateral delay activity (CDA; Vogel & Machizawa, 2004), is an electrophysiological component believed to reflect the representations held in VSTM (Klaver et al., 1999). For the duration of the retention interval, the SPCN has been shown to increase in amplitude proportionally to the number of items held in VSTM (McCollough, Machizawa & Vogel, 2007; Robitaille, Grimault, & Jolicœur, 2009; Robitaille et al., 2010; Vogel & Machizawa, 2004). The SPCN is typically observed over posterior electrode (typically

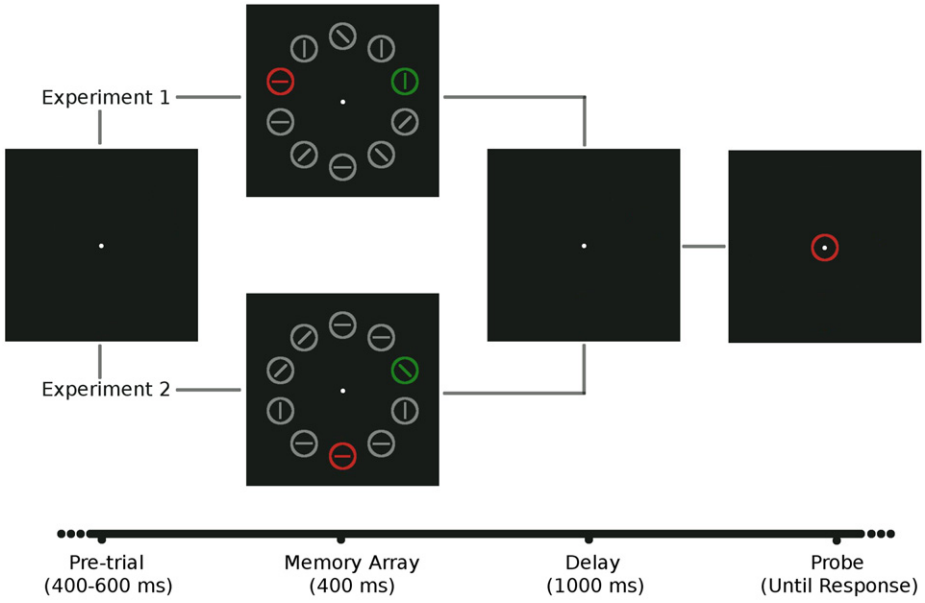

Fig. 1. Timecourse of each trial for Experiment 1 (Top) in which the colored circles to be remembered were both lateral, in opposite hemifields, and for Experiment 2 (Bottom) in which one colored circle was on the vertical midline and the other was in a lateral position.

PO7–PO8) suggesting a posterior site for the brain structures holding representations in VSTM. We hypothesize that the event-related lateralization found by Dell'Acqua et al. (2010) is due to a reactivation, or an increase in activation, of a memory representation that preserves structural properties of the original sensory input, most notably the visual field at the time of encoding. When attention is deployed to such a memory representation at the time of a search through VSTM, a lateralized ERP reflecting the structural properties of the representation emerges. It is not entirely clear why the scalp distribution of this activity is more anterior than the distribution typically observed for the SPCN for visual information retention, but some brain structures implicated in retrieval from VSTM are likely to be more anterior than the structures involved in visual search or visual information retention (Chun, 2011). Overall, the patterns of results suggest that a careful study of the brain activity observed during retrieval is likely to reveal distinct brain structures from those involved primarily in pure maintenance of representations in VSTM.

In the present work, we used the approach developed by Woodman and Luck (2003) and Hickey et al. (2009) to isolate target-related and distractor-related processing during VSTM retention and subsequent retrieval. The paradigm allowed us to demonstrate that the N2pc-like component observed during memory recall by Dell'Acqua et al. (2010) is related to an attentional bias toward the target rather than the distractors, and that the results support a view of VSTM as holding the representations of a visual scene items with a dominance in the cortical hemisphere contralateral to the hemifield from which a specific item representation was encoded (Gratton et al., 1997).

2. Method

2.1. Participants

Participants completed the experiments voluntarily and received monetary compensation. They had normal or corrected to normal vision, were neurologically normal, and were not taking neurologically-active medication. There were 26 participants in Experiment 1, 16 of which were kept for analysis (8 women) with a mean age of 23.1 (19 to 29 years old). Forty-six participants completed Experiment 2, 19 of which were kept for analysis (11 women) with a mean age of 23.1 (18 to 32 years old). The large amount of discarded participants was due to very strict rejection criteria for maintaining strict fixation on a central point during the trials, for technical reasons that will be detailed later. All participants signed an informed consent form following the Université de Montréal ethics committee guidelines.

2.2. Stimuli

Each search display consisted of ten equiluminant circles (13.0 ± 0.1 cd/m^2) positioned on a larger circle around the fixation point. Each circle had a diameter of 1.5° of visual angle and the center of each circle was positioned at 4° of visual angle from the fixation point. Two circles were on the central vertical meridian and two circles were in each quadrant, with no circle on the horizontal mid-line (Fig. 1). Each circle contained a line with a length of 0.9° of visual angle at one of four possible orientations (horizontal, vertical, 45° oblique to the left oblique, or 45° oblique to the right). All circles were gray with the exception of two circles, one red and one green. The positions of the red and green circles were varied from trial to trial. In Experiment 1, the red and green circles were aligned horizontally on opposite sides of the central fixation in mirror-symmetric positions immediately above or below the horizontal mid-line (illustrated in Fig. 1(Top)). In Experiment 2, one of the colored circles was on the vertical meridian, at the 12 o'clock or the 6 o'clock position, and the other one was in the left or right hemifield, at the position closest to the horizontal mid-line in one of the quadrants on the opposite side to the circle on the vertical meridian (i.e., always a distance of 3 positions in the array of circles, as illustrated in Fig. 1(Bottom)).

2.3. Task

The participant started each trial by pressing the space bar. Trials started with the disappearance of feedback from the previous trial and the presentation of a fixation point. The fixation point remained visible throughout the trial until the feedback was presented. The search display (Fig. 1) appeared 400 ms to 600 ms after the space-bar press and was presented for 400 ms. The participant had to remember the stimuli for 1000 ms, from memory array offset, before a colored circle (probe) was shown at fixation. This empty probe circle had the same color as one of the two colored circles presented in the search display and remained in view until a response was recorded. The task was to recall the orientation of the line inside the circle in memory that matched the color of the probe circle and to press a response key corresponding to this orientation with instructions to answer quickly and accurately. Across this paper we will refer to the probed singleton as the target while the other singleton will be referred as the distractor though both singletons had the same status until the probe was presented, both needing to be encoded and maintained in VSTM. Hand of response was counterbalanced between participants; left hand answers were given with the {*x*, *c*, *v*, *b*} keys while right hand answers were given with the {*n*, *m*, ',', '.'} keys on a North American QWERTY keyboard, each key corresponding, respectively, to the line orientations {tilted to the left, vertical, horizontal, tilted to the right}. The participants were given 3000 ms to answer. Once they answered, accuracy feedback was presented at fixation until the next trial and for a minimum duration of 500 ms. Participants completed 1 block of 32 practice trials followed by 8 blocks of 128 experimental trials (for a total of 1024 experimental trials).

2.4. Recordings and analysis pre-processing

The electroencephalogram (EEG) was recorded with 64 active scalp Ag/AgCl electrodes (BioSemi ActiveTwo system) mounted on an elastic cap. Positioning and naming of the electrodes followed the International 10/10 System (Sharbrough et al., 1991). Data was digitized at a sampling rate of 256 Hz, low-pass filtered online at 67 Hz, and band-pass filtered offline between 0.05 Hz and 30 Hz. The EEG was re-referenced to the average of left and right mastoid electrodes. Trials with a correct response were segmented and averaged for both experiments as 2200 ms long waveforms aligned to the presentation of the memory array, with the preceding 200 ms as baseline for the analysis of pre-probe waveforms, permitting an analysis of the topography of the N2pc/SPCN for the memory array. For post-probe analysis, an 800 ms segmentation was time-locked to the probe presentation, with a 200 ms baseline preceding the probe to remove any previous lateralization not directly related to processing of the probe. Horizontal oculogram (HEOG) was recorded and computed as the difference between signals at additional two electrodes located on the external canthi of each eye. Vertical oculogram (VEOG) was recorded and computed as the difference between signals at an electrode located above (FP1) and an additional electrode below the left eye. Two additional electrodes were used to record signals at the left and right mastoids, and all signals were re-referenced in post-recording analysis to the average of the voltage at the mastoids. Trials with blinks were rejected based on VEOG variations of more than 50 μV in a 200 ms time-window scrolled throughout each trial segment duration. Trials with eye movements, defined as HEOG variations larger than 35 μV in a 200 ms time-window scrolled through each trial segment, were rejected. We rejected data from participants who had less than 50% trials retained after removing incorrect responses and trials with blinks or eye movements, or who had a mean HEOG difference larger than 4 μV across left and right lateral stimulus trials when trials were split across experimental conditions (that would indicate a deviation of the eyes of about 1/4 degrees of visual angle towards the lateral stimulus (Luck, 2005). It was important to be especially stringent on the rejection criterion because current research suggests involuntary eye saccades away from remembered singletons position in memory (Belopolsky & Theeuwes, 2011), which could have lateralized the probe, which should be at fixation. In Experiment 1, seven participants were rejected due to the eye blinks and three due to the HEOG residuals suggesting eye movements toward a remembered lateral item. In Experiment 2, six participants could barely do the task (less than 70% success rate), nine were rejected due to blinks during the trials duration and twelve had residual HEOG values suggesting eye movements toward a remembered lateral singleton.

2.5. Statistical analysis

Test values for statistical analysis were obtained by averaging the time-point measurements over a time period surrounding a period of interest for each electrode. This period of interest was usually centered on the time of peak amplitude, for the grand averaged waveform across participants, for a particular component. The width of the averaging period was set to 50 ms to ensure good stability of the estimated waveform amplitude on a subject-by-subject basis. *T*-tests were performed individually for each electrode pair in order to confirm the reliability of the apparent topography of the components.

3. Results

We were principally interested in lateralized ERPs, elicited by the probe stimulus, as a function of the side of presentation of the memory singleton that matched the color of the probe. A first

objective was to determine if a central probe would induce a lateralized brain response, similar to the N2pc or SPCN, depending on which memory representation matched the color of the probe (Dell'Acqua et al., 2010). When the probed memory singleton had been shown to the left of fixation, right-sided electrodes were considered as contralateral and left-sided electrodes as ipsilateral. These designations were reversed for trials on which the probed memory singleton had been encoded from the right visual hemifield. In Fig. 2(a), we show the grand average of the subtraction of the ipsilateral waveforms from the contralateral waveforms recorded at electrodes CP5 and CP6. The scalp distribution of the lateralized response, computed from the contralateral minus ipsilateral waves for all lateralized electrodes pairs is shown in Fig. 2(b).

These analyses revealed a component that peaked around 300 ms post probe that was more negative contralateral to the

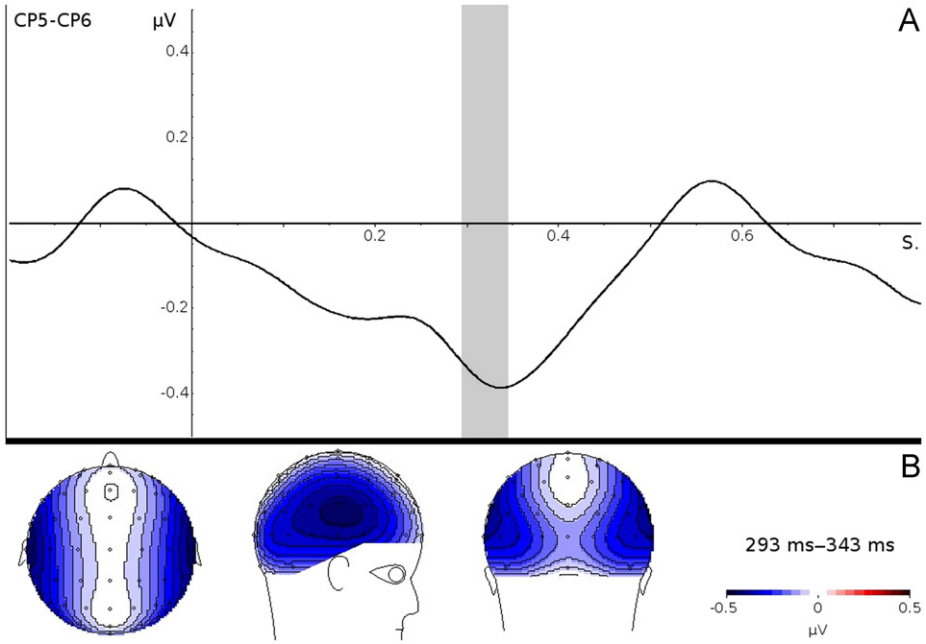

Fig. 2. Experiment 1. (a) Grand average of the ERLs recorded at electrodes CP5 and CP6 timelocked to the presentation of the probe band pass filtered between 0.1 Hz and 6 Hz. (b) Scalp distribution of the lateralized response, computed from the contralateral minus ipsilateral waves for all lateralized electrodes pairs, showing the mean voltage between 293 ms and 343 ms post-probe.

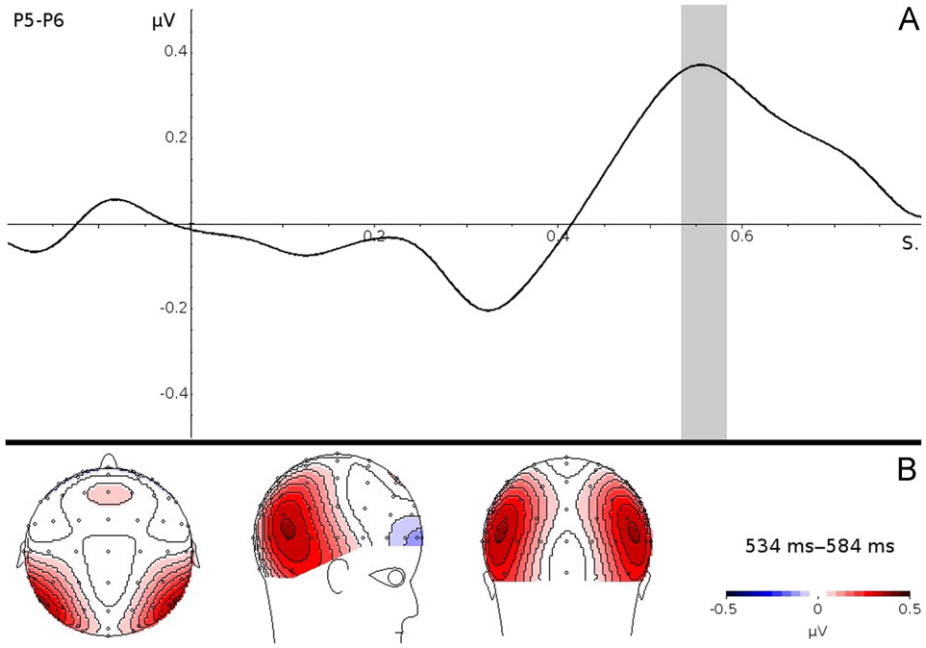

Fig. 3. Experiment 1. (a) Grand average of the ERLs recorded at electrodes P5 and P6 timelocked to the presentation of the probe band pass filtered between 0.1 Hz and 6 Hz. (b) Scalp distribution of the lateralized response, computed from the contralateral minus ipsilateral waves for all lateralized electrodes pairs, showing the mean voltage between 534 ms and 584 ms post-probe.

probed memory singleton with a scalp distribution similar to the one found by Dell'Acqua et al. (2010). Bonferroni-corrected *t*-tests against zero considering all 27 electrodes pairs, revealed a significantly negative ($p < .05$) mean activity during the period between 293 ms and 343 ms post-probe[1] at electrodes pairs P3–P4, F5–F6, and CP5–CP6. The most significant electrode was CP5–CP6, with $t(15) = 5.38$, $p < .00008$, $M = -.415$ μV, $\sigma = .3083$.

The initial contralateral negativity was followed by a contralateral positivity to the target with a different scalp distribution, shown in Fig. 3. This other component peaked around 559 ms after the presentation of the probe. A *t*-test against zero (Bonferroni-corrected for multiple comparisons across five candidate electrode pairs selected from the scalp distribution) for the mean activity of the period between 534 ms and 584 ms post-probe revealed that only P5–P6 reached significance, $t(15) = 3.32$, $p < .0047$, $M = .4316$ μV, $\sigma = .5209$.

4. Discussion

The results of Experiment 1 show that retrieval from VSTM is associated with lateralized brain activity that depends on the side of visual space from which the memory representation was initially encoded. Importantly, the retrieval cue for this search of VSTM (the probe) was presented at fixation, and could not, by itself, have produced a lateralized brain response. The present results thus highlight an interaction between the retrieval cue and a lateralized representation in VSTM.

The results replicate and extend those of Dell'Acqua et al. (2010) and similar suggestions by others (Gratton, 1998; Gratton et al., 1997; Lepsien & Nobre, 2006; Nobre et al., 2004). In the study by Dell'Acqua and colleagues the probe matched a representation in VSTM in term of shape, or did not match any representation, and the task was to report whether the item was in memory or not. We extend previous results by showing that color can act as the retrieval cue for a shape feature (line orientation), and thus the phenomenon appears to have some generality in terms of basic visual features. We also performed recordings with about twice as many electrodes as in the Dell'Acqua et al. (2010) study, enabling a more detailed mapping of the voltage distribution on the scalp (Figs. 2 and 3). The results confirm that the scalp distribution of the contralateral negativity observed during retrieval of a lateralized object in VSTM is clearly more anterior than that found during the initial retention of information in VSTM (Brisson & Jolicœur, 2007; Jolicœur et al., 2008), which we have called the SPCN elsewhere (Brisson & Jolicœur, 2007; Dell'Acqua, Sessa, Jolicœur, & Robitaille, 2006; Jolicœur et al., 2008, 2006; Robitaille, & Jolicœur, 2006; Robitaille, Jolicœur, Dell'Acqua, & Sessa, 2007). Given the clear difference in distribution from the SPCN, and also N2pc, we will refer to this brain response as the TCN, for temporal contralateral negativity.

4.1. Experiment 2

In Experiment 2, we aimed to determine if the TCN observed during retrieval in Experiment 1 was due to retrieval of target information from VSTM, per se, to activation and/or suppression of the distractor in VSTM, or to some combination of both. We achieved this by placing either the target or the distractor on the vertical meridian at the time of encoding. With only one lateral singleton in each trial, we expected to see a contralateral negativity associated with singleton processing shortly after initial encoding (Hickey et al., 2009), and later during the retention interval. Until the probe was presented, however, the participants did not know which of the two singletons would be the target. Hence, we expected to detect an initial N2pc (or N_T, Hickey et al., 2009) and an SPCN, when either the distractor or the target was lateral, until the presentation of the probe. Once the probe was presented, if the TCN activity was related to the target rather than the distractor, we expected to see a negative component for the lateral target condition and, either no activity or positive-going activity in the condition with the lateral distractor, given that Hickey et al. (2009) argued that processing related to distractor suppression is observed as a contralateral positive component (P_D).

4.2. Results

The results immediately following the presentation of the memory array were clearcut: lateral colored circles, that later became either target or distractor, generated an N2pc followed by an SPCN at posterior electrodes, with a maximum near PO7–PO8 and P7–P8. Prior to the presentation of the probe, these waveforms should be equivalent, and this was confirmed by a *t*-test against 0 of the difference in mean voltage of the lateralized waves for targets and distractors which showed no significant results, the most significant electrode pair FC1–FC2 failed to reach significance, $t(18) = 1.80$, $p < .09$.

In order to distinguish the topography of the TCN component from the initial N2pc and SPCN observed during the retention interval, we compared their voltage scalp distributions. We can see from Fig. 4(a), showing the activity of the electrode pair CP5–CP6 during the retention period for both experiments, that there was an N2pc/SPCN only for Experiment 2. In Fig. 4(b), we can see that the topography of the SPCN for Experiment 2 was more posterior than the TCN. Although the TCN is similar to the N2pc/SPCN in timing, the topography of the TCN is more anterior on the scalp based on visual inspection. Confirming this topography difference is important because it would contribute to the demonstration that they may reflect distinct underlying processes. We used the mean voltage around the peak amplitude time-point, across lateral target and distractor trials, from 227 ms to 277 ms for the N2pc and from 641 ms to 691 ms for the SPCN, after the presentation of the memory display to compare them with the mean voltage for the TCN component from Experiment 1. We compared the TCN from Experiment 1 with the N2pc/SPCN from Experiment 2 because in Experiment 1 the balanced memory array did not generate any N2pc or SPCN, while Experiment 2 do not produce, in a single condition, a complete TCN (as is shown below). We normalized the voltage of the electrodes sites by component (McCarthy & Wood, 1985). An ANOVA, Greenhouse–Geisser corrected, with the factors Electrode × Component showed no significant Electrode × Component interaction between the N2pc and the SPCN ($F(26\ (6.9), 936\ (249.6)) = 0.48$, $p < .85$) indicating that both components had a similar scalp distribution. We averaged the N2pc and SPCN voltages to compare them to the TCN voltage on four diagnostic electrodes pairs: PO7–PO8, P3–P4, F5–F6, and CP5–CP6. These electrode pairs were chosen because they captured activity at the peak of the N2pc/SPCN (PO7–PO8) and the peak for the TCN in Experiment 1 (P3–P4, F5–F6, and CP5–CP6). An ANOVA, Greenhouse–Geisser corrected, with the factors Electrode × Component showed a significant Electrode × Component interaction ($F(3\ (2.8), 99\ (91.8)) = 2.96$, $p < .04$) confirming what was visible by eye, namely that the TCN had a more anterior/temporal distribution than the typical N2pc or SPCN. While the normalization technique may provide some hint toward separation of brain processes, this technique still has limitations that demand restraint in the conclusions that can be drawn, particularly for inferences about brain generators (Urbach & Kutas, 2002).

[1] The apparent discrepancy between peak amplitude in the figure and the selected time window for analysis is due to the filtering applied to the figure, which smoothed out a peak that was slightly earlier in the unfiltered data.

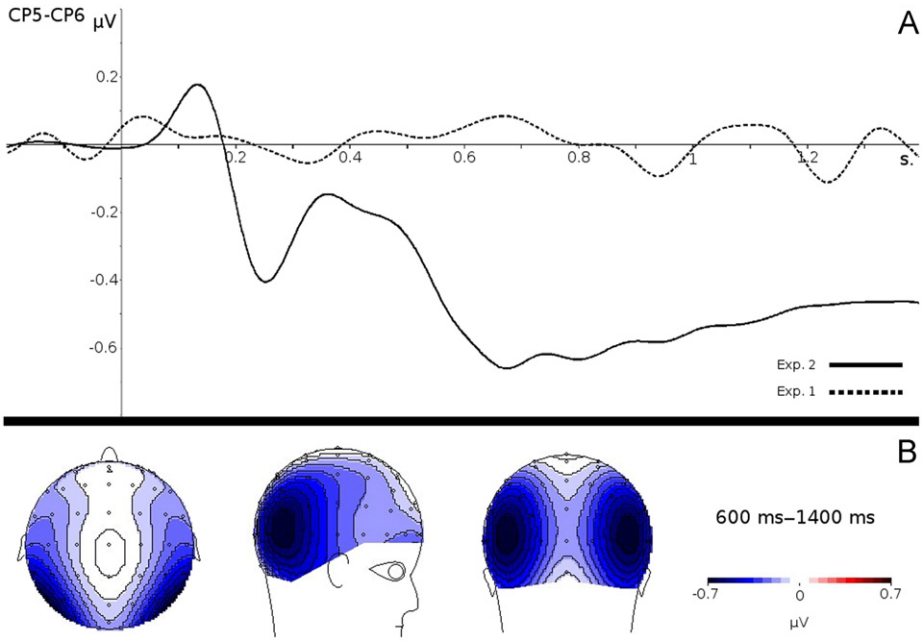

Fig. 4. (A) Grand average of the ERLs recorded at electrodes CP5–CP6 during retention, timelocked to the presentation of the memory array band pass filtered between 0.1 Hz and 6 Hz, in Experiment 1 (dashed line) and in Experiment 2 (solid line). An N2pc and SPCN can be seen for Experiment 2 in which one of the stimuli was lateral and the other was on the midline, but is absent for Experiment 1 in which the two items to be memorized were in opposite hemifields. (B) Scalp distribution of the lateralized response (SPCN) in Experiment 2, computed from the contralateral minus ipsilateral waves for all lateralized electrodes pairs, showing the mean voltage between 600 ms and 1400 ms after the presentation of the memory array.

When we inspected the voltage maps in Experiment 2 as a function of the type of lateral singleton (target vs. distractor), a clear difference between conditions (Fig. 5(b)) at the time corresponding to the TCN component in Experiment 1 (293–343 ms post-probe) emerged. In the condition with a lateral target, we saw a large fronto-temporal negative component and a small positive component near P7–P8, whereas in the other condition, with a lateral distractor, there was only a large positive component near P7–P8, and no hint of a fronto-temporal negativity. A Bonferroni correction over all electrode pairs was too conservative for the amplitude of the components observed in the Experiment 2. However, because the components under study had the same general topography as in Experiment 1, and as in previous publications (e.g., Dell'Acqua et al., 2010), we argue statistical reliability is well supported by examining electrode pairs in the same area covered by the TCN in Experiment 1 or at the expected peak of the N2pc. An uncorrected *t*-test against zero showed for the lateral target condition that negative activity was significantly non-null at T7–T8, C5–C6, FC5–FC6, F7–F8, and CP5–CP6, with peak significance at T7–T8 ($t(18)=2.45$, $p<.025$, $M=-.3529\ \mu V$, $\sigma=.5326$). For the lateral target condition the positive component failed to reach significance on an uncorrected *t*-test against zero. The most significant electrode pair was PO7–PO8 ($t(18)=1.58$, $p<.133$). In the lateral distractor condition, positive activity was significantly non-null at TP7–TP8, PO7–PO8, P5–P6, P7–P8, and O1–O2, according to an uncorrected *t*-test with the peak of significance at P7–P8 ($t(18)=4.97$, $p<.0001$, $M=.6777\ \mu V$, $\sigma=.5946$). On a paired *t*-test, we found that P7–P8, near the peak of the positive component in the lateral distractor condition, was not significantly different between the two conditions ($t(18)=1.79$, $p<.09$, $M_D=.6777\ \mu V$, $\sigma=.5946$, $M_T=.2787\ \mu V$, $\sigma=.7969$), while the difference between conditions at T7–T8, the peak of the negative component in the lateral target condition, was well above significance ($t(18)=3.73$, $p<.002$, $M_D=.2086\ \mu V$, $\sigma=.5443$, $M_T=-.3529\ \mu V$, $\sigma=.5326$). Paired *t*-tests also showed that conditions differred significantly at electrode pairs TP7–TP8, CP5–CP6, P5–P6, FC5–FC6, F3–F4, and C5–C6, with a peak significance at C5–C6 ($t(18)=3.023$, $p<.007$). The lateralization of the distractor produced a positivity at P7–P8, while the lateralization of the target produced a negativity at T7–T8. We note that the target lateralization also produced a near significant positivity at P7–P8. Fig. 5(a) shows the waveforms for electrode pairs CP5–CP6, which was the peak of the TCN in Experiment 1 and which reveals a similar negative going component for the lateral target trials as the peak at electrode pair T7–T8 (not shown), and P7–P8, which is the most significant electrode pair for the positive going component when we had a lateral distractor.

In order to compare the ERLs of the Experiment 1 TCN with the results obtained in Experiment 2, we subtracted the ERLs of the lateral distractor condition from the ERLs of the lateral target condition. This provided the algebraic equivalent to the Experiment 1 ERLs calculation where both target and distractor were positioned in opposite visual hemifields. When we computed this difference waveform, between 293 ms and 343 ms we found a scalp voltage topography that was very similar to the one obtained for the TCN component in Experiment 1, as can be seen in Fig. 6. In this case, the P7–P8 positivity found in both the lateral target and distractor conditions disappeared. The lateral target condition positivity being smaller than the lateral distractor condition positivity, the subtraction actually turned these positivities into a negativity contralateral to the target when algebraically reconstituting the balanced condition of Experiment 1. This clearly illustrates the difficulty of allocating a sign to ERLs without a methodology for isolating the activity source; a negativity contralateral to a target could in fact be a positivity contralateral to a distractor, the other way around, or a combination of both. When we tested the most significant pair of electrodes in Experiment 1 (CP5–CP6) for the difference waveform of the two conditions with a *t*-test against zero, we found that the mean voltage of the difference waveform was significantly negative ($t(18)=2.39$, $p<.014$, $M=-.449\ \mu V$, $\sigma=.8175$).

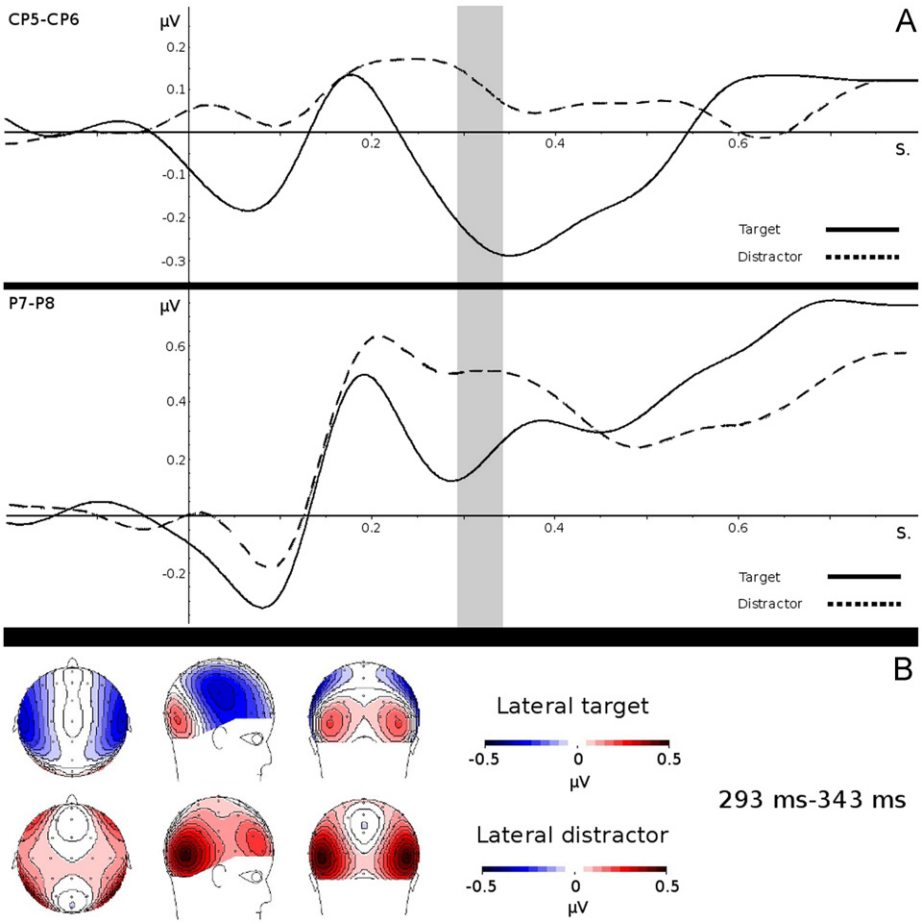

Fig. 5. Experiment 2. (A) Grand average of the ERLs recorded at electrodes CP5–CP6, to illustrate the target-related negativity, as well as P7–P8, to illustrate the distractor-related positivity, both timelocked to the presentation of the probe, band pass filtered between 0.1 Hz and 6 Hz. (B) Scalp distribution of the lateralized response showing the mean voltage between 293 ms and 343 ms post-probe for the lateral target condition (top) and the lateral distractor condition (bottom).

This confirmed that we had a greater negativity contralateral to the lateral item at electrode pair CP5–CP6 when we lateralized the target than when we lateralized the distractor. The electrodes with the largest difference between the two conditions in this experiment for this time period was T7–T8 ($M_T = -.32$ μV, $\sigma = .57$; $M_D = .27$ μV, $\sigma = .57$; $t(18) = 3.53$, $p < .001$).

We again found a positive component in the period between 534 ms and 584 ms post-probe, as we had in Experiment 1, for both the lateral target and the lateral distractor conditions scalp distributions. We do not show separately the scalp distributions from Experiment 2, which are very similar to the one found in Experiment 1 and shown in Fig. 3. Both maps showed a parietal-occipital positivity, and if anything the lateral distractor condition positive component seemed to be a bit more anterior than the lateral target condition component. An uncorrected *t*-test against zero revealed that the voltage in the lateral target condition was significantly positive at the electrode pairs O1–O2, P1–P2, P3–P4, P5–P6, P7–P8, P9–P10, PO3–PO4, and PO7–PO8, with a significance peak at PO7–PO8 ($t(18) = 5.69$, $p < .00002$, $M = .8589$ μV, $\sigma = .6577$). In the lateral distractor condition, significantly positive activity was found with an uncorrected *t*-test against zero at electrode pairs P3–P4 and P7–P8, with a significance peak at P3–P4 ($t(18) = 2.63$, $p < .017$, $M = .3041$, $\sigma = .5043$). Positive activity was however larger in amplitude in the lateral target condition. The subtraction of both conditions left a scalp voltage distribution with a positive component near PO7–PO8. Positive activity was significantly greater in the lateral target condition than corresponding activity in the lateral distractor condition at the electrode pairs O1–O2, P1–P2, and PO7–PO8, with a significance peak at PO7–PO8, as confirmed by a *t*-test against zero ($t(18) = 3.69$, $p < .002$, $M_D = .1739$ μV, $\sigma = .4176$, $M_T = .8589$ μV, $\sigma = .6577$). One surprising exception was found at F5–F6, where voltage was significantly lower in the lateral target condition than in the lateral distractor condition ($t(18) = 2.2$, $p < .041$, $M_D = .3856$ μV, $\sigma = 1.0502$, $M_T = -.1861$ μV, $\sigma = .613$).

From 141 ms to 191 ms post-probe there was a positive component that was very similar in scalp distribution across the two conditions (Fig. 7). The component was significantly different from zero at PO7–PO8 (post-probe, target: $t(18) = 6.75$, $p < .000002$, $M = .7328$ μV, $\sigma = .473$; post-probe, distractor: $t(18) = 6.42$, $p < .000005$, $M = .5414$ μV, $\sigma = .3678$) when comparing mean activity between 141 ms and 191 ms. A paired *t*-test between conditions showed the conditions to be nearly significantly different ($t(18) = 2.00$; $p < .06$). Also, this component had a similar scalp distribution to a component seen between 141 ms and 191 ms after the presentation of the memory array. We normalized the voltage of the electrodes sites for the post memory array component and the post probe component (McCarthy & Wood, 1985). An ANOVA, Greenhouse–Geisser corrected, with the factors Electrode × Component showed no significant interaction Electrode × Component ($F(26\ (7.1),\ 468\ (1\ 2\ 8)) = 1.89$, $p < .08$) suggesting, since the null hypothesis was not rejected, that both components had a similar scalp distribution.

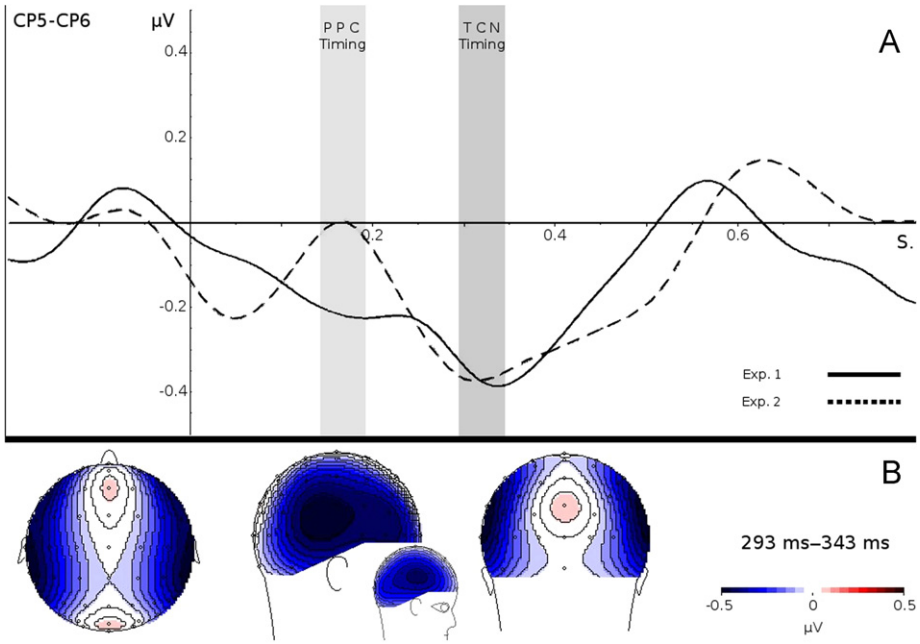

Fig. 6. (A) Grand average of the ERLs recorded at electrodes CP5 and CP6 timelocked to the presentation of the probe, band pass filtered between 0.1 Hz and 6 Hz, in Experiment 1 (solid line) and in Experiment 2 (dashed line), estimated as the sum of the lateral target and lateral distractor conditions. (B) Scalp distribution in Experiment 2 resulting from the the subtraction of the ERLs recorded in the lateral distractor condition from the ERLs recorded in the lateral target condition between 293 ms and 343 ms post-probe for all electrodes pairs. A smaller lateral view of Experiment 1 TCN is provided for comparison.

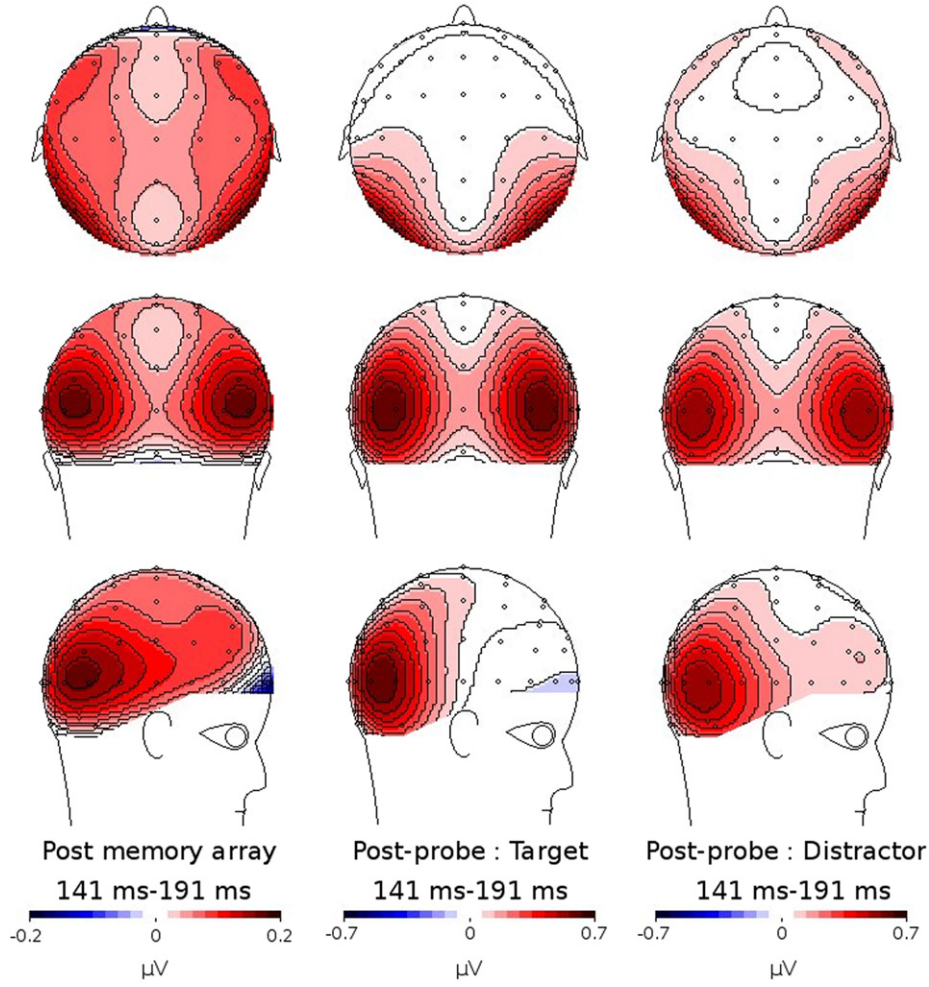

Fig. 7. Results from Experiment 2 showing, from left to right, scalp distributions of ERLs recorded across all electrode pairs showing a Ppc (Positivity posterior contralateral) component between 141 ms and 191 ms post memory array, post-probe in the lateral target condition, and post-probe in the lateral distractor condition.

5. Discussion

Experiment 2 brought several interesting findings. First, we again found a clear contralateral negativity with a more anterior scalp distribution (a TCN) relative to an SPCN, when we probed VSTM with a centrally-presented probe and the target was encoded from a lateral spatial location. This finding extends those of Experiment 1 by showing that the TCN can reflect lateralized activity related to the position of the target, without contamination from distractor processing. The target-related TCN can also be found when retrieval from VSTM is performed on the basis of a color cue, extending the results of Dell'Acqua et al. (2010), who studied a shape-matching retrieval process.

Importantly, Experiment 2 also produced new findings. Relatively early after the presentation of the central retrieval cue (between 141 ms and 191 ms), we observed a posterior positivity contralateral to the lateral item in VSTM, whether that item matched the retrieval cue or not (i.e., was the same for lateral targets as for lateral distractors). A similar component has been observed following the presentation of visual displays containing a lateral item 'of interest' even when that item is balanced by a luminance-matched item 'of lesser interest' on the other side. A visual salience imbalance could be responsible for this component presence. For example, in the present Experiment 2, the two interesting items were those colored red or green, compared to the grey ones, even though they were all equally luminant. We will refer to this component, when observed following the initial presentation of a physical display, as the Ppc (positivity, posterior contralateral). A similar Ppc has been observed in a number of studies (e.g., Leblanc, Prime, & Jolicœur, 2008; Sawaki & Luck, 2010), although it has not been the focus of much research so far. From those studies and our Experiment 1, the Ppc appears to reflect an initial processing of the display based on local feature discontinuities, which may guide later controlled deployment of visual spatial attention, reflected in the N2pc. It is particularly interesting that we observed a similar response following the presentation of the memory cue, at fixation, based on the memorized lateral position of stimuli held in VSTM. This result lends further support for the notion that VSTM can preserve a spatially isomorphic representation of visual stimuli, likely based on a spatiotopic mapping of external space in the brain. The fact that we appeared to find a memory-based Ppc following the presentation of the probe, and that this response was similar for probes that matched a lateral target or a lateral distractor suggests that there was likely an initial reactivation of the entire memory representation (i.e., of both the target and distractor) and that the Ppc may be a spatial index linked to a representation of interest rather than a reflection of a perceptual discontinuity in the visual array information.

6. General discussion

With a balanced display in Experiment 1, we replicated and extended the most important findings of Dell'Acqua et al. (2010). We found a contralateral negativity during retrieval from VSTM that was widespread, spanning from P3–P4 to F5–F6, with a peak near CP5–CP6. Because of the structure of our experiment, in which the retrieval cue was displayed at a central fixation point, this voltage imbalance between the contralateral and ipsilateral hemispheres relative to the position of memorized stimuli could only be the reflection of a differential activation of some of the neural structures implicated in the retention of lateralized information in VSTM. The representation itself must, in some sense, have preserved the differential activation of lateralized brain activity produced by the stimulus at the time of encoding. The results observed by Dell'Acqua et al. (2010) had a component that peaked at more inferior electrode sites than we found in our Experiment 1, and closer to the peaks observed in Experiment 2 at P7–P8 and T7–T8. However, the spatial sparsity of these earlier recordings may explain this discrepancy in peak location. Another possibility is that the variation of the component morphology could reflect the differences in stimulus materials (simple shapes in the Dell'Acqua et al., 2010, study, vs. color and line orientation in the present study). Importantly, the lateralized component observed during retrieval does not match the scalp distribution of the N2pc or SPCN found in typical studies of visual attention (e.g., Brisson & Jolicœur, 2007; Jolicœur et al., 2008) or of the SPCN found during the initial maintenance of representations in VSTM for the retention interval in Experiment 2. Thus, we confirm one of the most important findings of Dell'Acqua et al., namely the more temporal distribution of the lateralized activity related to retrieval, which we now call the TCN. It is likely that the TCN reflects distinct, and possibly more anterior, generators engaged in retrieval from VSTM, than those required for the initial selection, encoding, and maintenance of visual representations. The balanced visual display of Experiment 1 and the baseline correction preceding the presentation of the probe in Experiment 2 both ensure that the observed TCN activity is distinct from the activity related to memory maintenance producing the SPCN. However, there is still a possibility that the activity of the TCN reveals an increased activation of generators already active during the SPCN and that are masked by stronger posterior generators.

In order to ensure that the TCN following the probe was due to attentional and retrieval processes related only to the target rather than a partial contribution to the effect from both target processing and distractor suppression, we isolated lateralized activity related to the target and to the distractor in a second experiment. Experiment 2 was identical to Experiment 1 except that the memory array had one of the two colored circles on the vertical meridian. The lateralized differences we then obtained originated from the singleton that was lateral because any effect that would have been generated by the midline singleton would have been canceled in the subtraction used to compute interhemispheric differences across matched lateral electrodes. Since both colors and positions were randomly attributed, trial by trial, to the target or to the distractor, the only factor that was uniquely associated with our manipulations was the lateralization of representations in the brain, and consequently of the deployment of attention, at the time of retrieval.

The voltage scalp distribution observed in the lateral target condition of Experiment 2 (Fig. 5(B) top) confirmed that the TCN was related to the retrieval of the target item representation in VSTM. A fronto-temporal negative component was only present when the target was lateral, which differentiated the TCN from more perceptual components, such as the N2pc and SPCN. This spread of activity across more anterior electrode sites when the target was lateral suggests that temporal cortical structures may be involved during the retrieval of visual information held in VSTM, because the activity imbalance related to the retrieval of information can only be observed in this condition. In addition to the anterior negativity, we observed a contralateral positivity over the posterior scalp in Experiment 2. This posterior positivity near P7–P8, which was only nearly significant when the target was presented laterally, but fully significant when the distractor was presented laterally, could indicate that part of the activity during retrieval is common to both target and distractor related processing. The relatively small amplitude of the positive component, and to some extent of the negative component as well, in the lateral target trials could be the effect of destructive summation of scalp voltage for the two opposite polarity neighboring components. The fact that the TCN peak is located at electrode sites

between the two lateral target components peaks and the shape of the components could indicate that the TCN originates most likely from the modulation of a single large component that covers the extent of the TCN voltage scalp distribution in Experiment 1. This spatially-large component (but of relatively weak voltage amplitude) would share a part of the scalp surface occupied by another posterior positive component present and constant when the target and the distractor are lateral. An alternate explanation would be that the two components are modulated alternatively in the same direction, the fronto-temporal negative component when the target is lateral and the parieto-occipital positive component when the distractor is lateral, and that this effect is averaged in Experiment 1 to peak between the individual peaks present in the lateral target condition voltage scalp distribution found in Experiment 2. Due to the distance separating the two opposite polarity peaks, this latter explanation is unlikely because the voltage decay over the scalp would most likely lead to an averaged voltage for the observed TCN peak to be inferior to the average of the two individual peaks modulated across the lateral target and lateral distractor conditions.

The voltage scalp distribution observed in the lateral distractor trials of Experiment 2 (Fig. 5(B) bottom) revealed a parieto-occipital positive component and an absence of the fronto-temporal negative component seen in the lateral target condition. This indicates that the TCN represents recall-related activity specifically related to the target that is absent when the distractor was the lateral item. The absence of negative component in the lateral distractor trials is consistent with the need to access lateralized representations only when the target was lateral. The topography of the parieto-occipital positive component resembles that of the N2pc and SPCN with reversed polarity. Although this positive component could reflect an active inhibition of the memory representation in VSTM of the lateral distractor, this component could also be explained by a return to baseline from a state of sustained activity required to maintain the representation of the distractor during the retention interval prior to the probe. Once the probe was presented and found to match the midline object, the maintenance of the lateral object would no longer be required. The baseline correction introduced on the 200 ms pre-probe period make it so that the voltage was actually negative compared to a pre-memory array baseline. A return to this pre-memory array baseline would be seen as a positive going component, sustained while the target is still in use, resembling a positive SPCN. In the time range of the TCN, both possibilities are credible and more research will be needed to disentangle these possibilities.

In addition to the TCN, we isolated a latter positive going component in the difference waveform of Experiment 1 that had a more occipito-parietal distribution with a peak centered near P5–P6. This latter positive component, present between 534 ms and 584 ms post-probe in the balanced experiment, was elicited by bilateral singletons, one a target the other a distractor. Experiment 2 elicited a similar component in the algebraic difference between the waveforms from the lateral target trials and the lateral distractor trials. While Experiment 1 could not indicate whether the positive component was elicited by the activity generated by the processing of the target, Experiment 2 could show us the activity linked to each singleton separately. In Experiment 2, the late posterior positivity was larger on the lateral target trials than on lateral distractor trials, although it was also seen on these latter trials. This difference between conditions would be equivalent in the balanced experiment to a positive component contralateral to the target. This positive component timing and voltage scalp distribution left us wondering if this component could not be an artifact generated by involuntary eye movements toward the target bringing the probe, still present on the screen, toward the distractor hemifield. Our severe eye movements rejection criterion should have prevented such an occurrence, however, which leaves us uncertain as to the nature of this component.

In summary, the individual lateral placement of the target and distractor in our memory task in Experiment 2 made it possible to distinguish two components, between 293 ms and 343 ms after the probe presentation. When we summed these effects we observed a pattern that was undistinguishable from what we found in Experiment 1, in which target and distractor were both lateral (in opposite hemifields). Thus, we consistently found a component, we now call the TCN, which is a broadly distributed negative ERL, following the presentation of a central memory probe. The TCN thus appears to reflect a negative component, more anterior, related to the target and a positive component, more posterior, related mostly to the distractor that both confirm the lateralization of the memory structures in VSTM, as well as indicating a dissimilarity in the processing of the target and the distractor at the time of the retrieval. Whereas the more anterior temporal component related to the target could be related to the structures holding the visual information, the more posterior component is close to the regions already linked to the retention of information in VSTM, notably by the research done on the SPCN. This result, combined with results from curve tracing (Lefebvre, Jolicœur, & Dell'Acqua, 2010) and multiple objects tracking (Drew and Vogel, 2008) studies that find an SPCN in paradigms that do not rely on VSTM, suggests that the SPCN, and the posterior positive component, may be present in tasks that require tracking of visual representations in either perception or memory, representations that would be held in other cortical regions. The positive going component in the lateral distractor condition might indicate the disengagement of the structures contributing to the SPCN for the distractor or an active inhibition mechanism in memory for that item.

The Ppc, an already known component but little-studied, was observed in the lateralized conditions pre-probe waveforms and, as far as we can tell, also post-probe, altering the reconstitution of the balanced waveform by making a positive deflection in the waveform resulting from the subtraction of the two conditions (Fig. 6). The presence of a Ppc like component during retrieval would hint toward a reactivation of cortical structures activated during perception, because the centered probe could not account for an imbalance in salience, which would elicit a Ppc. As can be seen on Fig. 5(a) on the P7–P8 electrode pair, this component is sustained longer during retrieval when the distractor is lateral, which let us wondering if this component could not also be sustained and masked by the overlap in the lateral target condition with the larger negative going component at anterior electrode sites seen on Fig. 5(a) at electrode pair CP5–CP6. This would in turn raise the hypothesis that, in perceptual search tasks, the N_T part of an N_T–P_D pair may be superimposed to the P_D, occupying during perception roughly the same scalp area, whereas during retrieval, in a memory task, the target related component would be more anterior than the positive component. The resulting voltage distribution would reveal both the anterior target related negativity and the posterior positivity that could be a spatial index of representations of interest. The Ppc could be the initial part of a larger posterior positive component that remains active throughout the N2pc or the TCN, whose negative-going inflexion mask the posterior sustained activity until its later part, called the P_D, become visible in distractor related trials, when attention toward the distractor is minimal.

More generally, the present results suggest we can elucidate the nature of the neuronal representation of visual memory representations and retrieval mechanisms that operate on them by careful examination of electrophysiological waveforms during

retrieval, and that event-related lateralizations are likely to be particularly useful in these endeavors.

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