Orienting attention to objects in visual short-term memory

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ABSTRACT

We measured electroencephalographic activity during visual search of a target object among objects available to perception or among objects held in visual short-term memory (VSTM). For perceptual search, a single shape was shown first (pre-cue) followed by a search-array, and the task was to decide whether the pre-cue was or was not in the search-array. For search of VSTM, a search-array was shown first followed by a single shape (post-cue), and the task was to decide whether the post-cue was or was not in the previously displayed search-array. We focused on early lateralized electrical brain activity over posterior and temporal areas time-locked to search-arrays in pre-cue trials and to post-cues in post-cue trials. In Experiment 1, search-arrays were composed of two lateralized shapes, displayed in the upper/lower two quadrants of the monitor. In Experiment 2, search-arrays were composed of four shapes, displayed at the corners of an imaginary square centered on fixation. In pre-cue trials, we observed an N2pc of about equal amplitude and latency for search-arrays composed of two or four shapes. In post-cue trials, we observed N2pc-like activity with search-arrays composed of two shapes, that was however substantially attenuated with search-arrays composed of four shapes. For many aspects, attending to a perceptual object was functionally and neurally analogous to attending to an object held in VSTM, suggesting that spatial selective attention biases search of objects during both ongoing perception and retention.

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1. Introduction

An important feature of the visual system is the retinotopic organization of the primary visual cortex, in which nearby points on the retina activate nearby cells in the primary visual cortex. This retinotopic coding becomes coarser but is still generally preserved as visual processing continues in higher level, extra-striate visual areas (Aguirre, Zarahn, & D'Esposito, 1998; Jack et al., 2007; Zeki, 1993). It is possible that this early retinotopy has contributed to some degree of isomorphism between visual representations and objects in the world, such that distinct and adjacent parts of the physical world are represented as distinct and adjacent parts in isomorphic visual representations (Shepard, 1984). At the coarsest level, the left and right halves of visual space are represented in distinct cerebral hemispheres (in a crossed fashion due to the crossing of the neural projections from the retina to the primary visual cor-

tex). The contralateral organization of the visual space seems to be generally retained in the lower portion of the dorsal visual stream up to and including the intra-parietal sulcus (IPS; Sereno, Pitzalis, & Martinez, 2001), and in inferior regions of the temporal cortex (Chelazzi, Miller, Duncan, & Desimone, 1993).

Sensory representations are temporally fleeting and subject to decay or erasure by newly incoming visual input (e.g., Coltheart, 1980; Sperling, 1960), such that further processing is needed to consolidate them in a more durable representational format, usually referred to as visual short-term memory (VSTM; Averbach & Coriel, 1961; Jolicœur & Dell'Acqua, 1998). VSTM representations are more resistant to visual masking, and temporally more stable, with a duration that outlasts the physical availability of visual input by several seconds (Phillips, 1974). The transition of visual input representation from sensory to VSTM status implies a substantial information reduction, since VSTM capacity is demonstrably a minuscule fraction of the information available at early stages of processing, with a limit in storage that is, on average, of only about 3–4 objects (Cowan, 2001; Stevanovski & Jolicœur, 2007; Vogel, Woodman, & Luck, 2001).

Given the very high capacity of early visual processes and the very limited storage capacity of VSTM, most models of visual pro-

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cessing postulate a critical role for spatial selective attention (e.g., Desimone & Duncan, 1995; Duncan & Humphreys, 1989), which is hypothesized to bias information processing towards portions of the visual world relevant for goal-directed behavior (e.g., Folk, Remington, & Johnston, 1992; Leblanc, Prime, & Jolicœur, 2008). Although much remains to be discovered about the neural realization of attention mechanisms and the algorithms for the selection of objects and/or locations, whether by target activation, distractor suppression, or both, recent work suggests a clear interdependence between spatial attention mechanisms and mechanisms involved in the generation of both sensory and VSTM representations. In general, these results, which we review briefly in the forthcoming sections, converge to support the hypothesis proposed by Awh and Jonides (2001) that attention mechanisms operating at the perceptual level and attention mechanisms operating at the VSTM level overlap to a large extent, both functionally and neuroanatomically (e.g., Coull & Nobre, 1998; DeFockert, Rees, Frith, & Lavie, 2001; LaBar, Gitelman, Parrish, & Mesulam, 1999; Lepsien, Griffin, Devlin, & Nobre, 2005; Nobre et al., 2004; Nobre, Griffin, & Rao, 2008; Olivers, 2008; Yantis et al., 2002).

Two studies have tracked the event-related potential (ERP) response associated with attention deployment to sensory objects and compared it with the ERP response associated with attention deployment to VSTM objects. Eimer and Kiss (in press) instructed subjects to search a visual array for the presence of a target diamond, with the top or bottom corner cut off, among distracting circles, and to indicate via button press the position of the cut corner (top or bottom). The shapes in the array were arranged circularly around fixation, with the shapes in one visual hemifield all colored red and those in the opposite visual hemifield all colored green. In pre-cue trials, subjects were cued about the color of the target before the appearance of the visual array, by having the visual array preceded by a centrally displayed colored square (pre-cue) matching either color in the visual array. In post-cue trials, subjects were cued about the color of the target after the visual array, by displaying the central colored square (post-cue) after the offset of the visual array. In pre-cue trials, the ERP response was time-locked to the onset of the visual array. In post-cue trials, the ERP response was time-locked to the onset of the post-cue color cue. Not surprisingly, an N2pc response was found in pre-cue trials. The N2pc is a greater negativity recorded between 200 and 300 ms at occipito-parietal sites contralateral to an attended stimulus (Brisson & Jolicœur, 2007, 2008; Dell'Acqua, Pesciarelli, Jolicœur, Eimer, & Peressotti, 2007; Dell'Acqua, Sessa, Jolicœur, & Robitaille, 2006; Eimer, 1996; Hickey, Di Lollo, & McDonald, 2008; Hopf et al., 2000; Jolicœur, Sessa, Dell'Acqua, & Robitaille, 2006a,b; Kiss, Jolicœur, Dell'Acqua, & Eimer, 2008; Luck & Hillyard, 1994; Luck, Woodman, & Vogel, 2002; Woodman & Luck, 1999, 2003a,b). The ERP response in post-cue trials was, however, mainly in the form of sustained posterior-contralateral negativity (SPCN, e.g., Jolicœur, Brisson, & Robitaille, 2008; Klaver, Talsa, Wijers, Heinze, & Mulder, 1999; McCollough, Machizawa, & Vogel, 2007; Vogel & Machizawa, 2004), namely, a later – with respect to N2pc – and more protracted enhanced negativity recorded between 300 and 600 ms at occipito-parietal sites contralateral to the target. Notably, the lateralized ERP response in post-cue trials was elicited by the central post-cue colored square, and this suggested that the spatial arrangement of the colors in the visual array was retained in VSTM (Gratton, 1998; Hommel, 2002; Jiang, Olson, & Chun, 2000), and was effective in biasing the responses of neurons in cortical areas surrounding IPS (e.g., Todd & Marois, 2004) during search of VSTM.

Using a similar logic, Kuo, Rao, Lepsien, and Nobre (2009) instructed subject to search a visual array of random shapes or colored squares for a target (shape in one condition, and color in a different condition) that was either shown before the visual array in pre-cue trials, or after the visual array in post-cue trials. The visual array could be composed of either two or four eccentric shapes or colors, in order to evaluate the impact of varying the number of items in a visual array on search efficiency in the sensory and VSTM domains. The ERP response in pre-cue trials was characterized by an N2pc (i.e., a negativity contralateral to the target shape or color that arose between 200 and 300 ms post-array onset). A similar response was observed in post-cue trials, where an N2pc-like response was time-locked to the post-cue shape or color. In both the shape and color conditions, variations in the visual array set-size produced no modulations of the N2pc response, either in pre-cue or post-cue trials.

2. The present study

An important goal of the present work was to determine whether the scalp distribution of the lateralized ERP response during search of VSTM is identical to, or different from, the scalp distribution observed during search in perception. Interestingly, the results of Kuo et al. (2009) suggest a possible difference on the basis of their published isovoltage contour-maps comparing the distribution of N2pc activity between pre-cue and post-cue trials. Although the perspective offered by their maps is from a posterior view only, their figures suggest an anterior shift of the contralateral negativity in the post-cue condition relative to the pre-cue condition. This issue deserves a particular consideration because of expected differences in neural circuitry involved in perceptual and mnemonic search. It seems indeed established that, in addition to important similarities/overlap of cortical regions involved in visual and VSTM search, there are also some notable differences. For instance, signal increases in the insula, inferior frontal gyrus, and more in generally, ventro-lateral prefrontal regions, have been selectively described during VSTM search only (Courtney, Ungerleider, Keil, & Haxby, 1997; Nobre et al., 2004), and not in visual search. Perhaps, the slightly different topographical distributions of the N2pc-like responses in pre-cue vs. post-cue trials of Kuo et al.'s experiments – although not statistically significant – reflect different contributions of memory-related activity in the two conditions. On the basis of this observation, we set out to determine to what extent the scalp distributions of the lateralized ERP responses, N2pc for visual search and N2pc for search of VSTM, would differ, and most particularly whether search of VSTM would be associated with a more anterior scalp distribution than visual search.

A second motivation to carry out the present study relies on the inconsistency between the results obtained by Eimer and Kiss (in press) and Kuo et al. (2009). In both studies, a close-to-standard N2pc was observed in pre-cue trials. However, whereas an SPCN was observed in post-cues by Eimer and Kiss (in press), an N2pc similar to that observed in pre-cue trials was observed in post-cue trials by Kuo et al. (2009). One explanation may arise from differences in the task requirements in these two studies. In Eimer and Kiss (in press) case, subjects first had to decode the post-cue color, to orient attention towards the visual hemifield containing the target, and then inspect the target within the color-matching hemifield to determine which corner was missing. It might be that this two-step process (find the target, identify the response-relevant feature) extended the duration of processing of the lateralized memory representation held in VSTM, leading to a sustained response observed as an SPCN instead of an N2pc. The task in Kuo et al. (2009) study required a present/absent response, which may have required a shorter engagement on the target, and this may have yielded an N2pc without the later sustained response (i.e., no SPCN). Given that our Experiment 1, whose design is schematically illustrated in Fig. 1, used a present/absent judgment, we expected to find an N2pc response in both the pre-cue

Experiment 1: Pre-cue condition
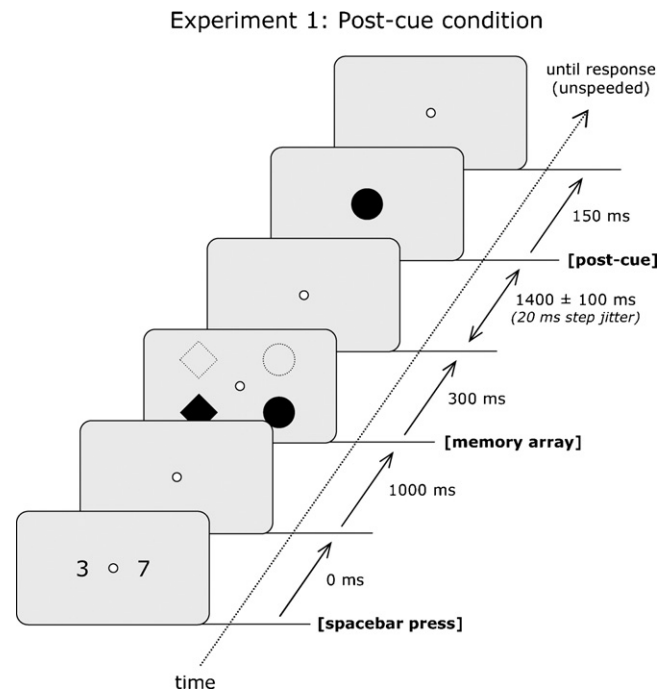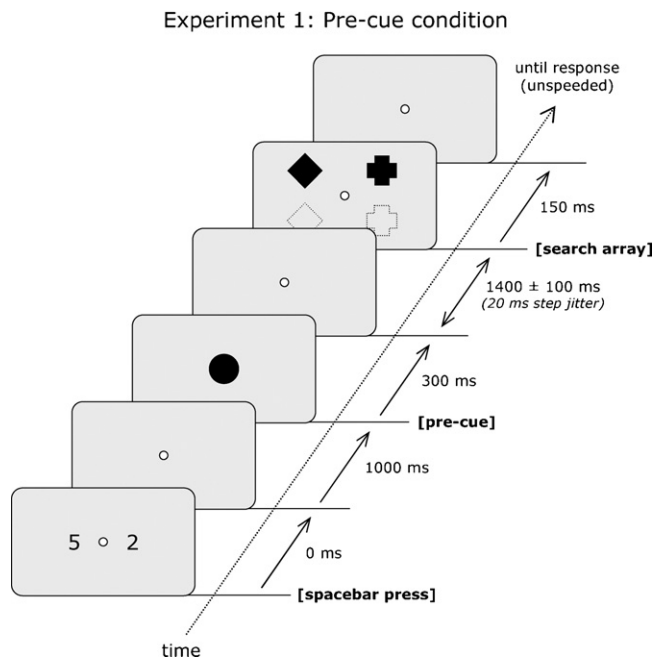
Fig. 1. Sequence of events on a pre-cue trial of Experiment 1. A white fixation dot was presented at the center of the screen, flanked by two digits. Subjects were instructed to start rehearsing the names of the digits aloud before pressing the spacebar on the computer keyboard to start the trial, and continue to rehearse the digits throughout the trial. Upon trial initiation, the digits disappeared and a fixed blank interval of 1000 ms preceded the onset of a centrally displayed shape (i.e., pre-cue), which was exposed for 300 ms. Following the pre-cue offset, a variable interval (1300–1500 ms) elapsed before the presentation of two lateralized shapes (i.e., search-array), that were displayed in the upper (as is the case in the figure) or lower (as indicated by the dotted contours, which were not displayed on screen) two quadrants of the screen. The search-array was exposed for 150 ms, and replaced with a blank screen that lasted until subjects responded by pressing one of two keys of the numeric keypad of the computer keyboard (i.e., either "1" or "2," counterbalanced across subjects) to indicate, without speed pressure, whether the pre-cue was present or absent in the search-array. Following a response, a blank interval of 1500 ms preceded the beginning of the next trial. During the inter-trial interval, a response feedback was provided to subjects by displaying centrally a "+" or a "−" in case of a correct or incorrect response, respectively. In the specific trial illustrated in the figure, the correct response is "absent.".

Experiment 1: Post-cue condition

Fig. 2. Sequence of events on a post-cue trial of Experiment 1. A white fixation dot was presented at the center of the screen, flanked by two digits. Subjects were instructed to start rehearsing the names of the digits aloud before pressing the spacebar on the computer keyboard to start the trial, and continue to rehearse the digits throughout the trial. Upon trial initiation, the digits disappeared and a fixed blank interval of 1000 ms preceded the onset of two lateralized shapes (i.e., memory-array), that were displayed for 300 ms in the lower (as is the case in the figure) or upper (as indicated by the dotted contours, which were not displayed on screen) two quadrants of the screen. Following the memory-array offset, a variable interval (1300–1500 ms) elapsed before the presentation of a centrally displayed shape (i.e., post-cue). The post-cue was exposed for 150 ms and replaced with a blank screen that lasted until subjects responded by pressing one of two keys of the numeric keypad of the computer keyboard (i.e., either "1" or "2," counterbalanced across subjects) to indicate, without speed pressure, whether the post-cue was present or absent in the memory-array. Following a response, a blank interval of 1500 ms preceded the beginning of the next trial. During the inter-trial interval, a response feedback was provided to subjects by displaying centrally a "+" or a "−" in case of a correct or incorrect response, respectively. In the specific trial illustrated in the figure, the correct response is "present." Note that, apart from the reverse order of pre-/post-cues and search/memory-arrays, the sequence of events in pre-cue trials (Fig. 1) and post-cue trials (Fig. 2) was identical.

and post-cue conditions (Fig. 2), as found in Kuo et al. (2009) study.

A final observation concerns the work of Kuo et al. (2009), and refer specifically to the absence of N2pc modulations in response to visual array set-size variations. An absence of N2pc amplitude variations depending on visual array set-size is not unusual. Since similar N2pc components have been found with visual search-arrays of 2 stimuli (e.g., Dell'Acqua et al., 2006, 2007; Eimer, 1996) up to arrays of 24 stimuli (e.g., Woodman & Luck, 1999; Woodman & Luck, 2003b),[1] an absence of N2pc variations in pre-cue trials of Kuo's et al. when the set-size varied between two and four random shapes or colored squares were somewhat expected in pre-cue trials. What is more surprising was the absence of N2pc variations in post-cue trials when the visual array was varied in set-size. In post-cue trials, increasing the size of the visual array from 2 to 4 objects presumably implied an increase in VSTM load, and we have recently shown that a memory load of 2 random polygons brings VSTM close to capacity (Luria, Sessa, Gotler, Jolicœur, & Dell'Acqua, in press). Interestingly, although much attention has

been devoted to the interaction between search efficiency and VSTM *content* (see Olivers, 2009, for a review), evidence from studies focusing on the interaction between search efficiency and VSTM *load* is scant, and the emerging picture is somewhat contradictory. Whereas some researchers have proposed a dissociation between attention mechanisms underpinning visual search and VSTM maintenance by showing no search slope variations in reaction time (RT) as a function of concurrent visual memory load (Woodman, Vogel, & Luck, 2001), more recent work revisiting this issue has provided evidence of diminished search efficiency with a concurrent VSTM load, when object features to be held in memory overlapped with object features guiding search (Oh & Kim, 2004; Woodman & Luck, 2004). This is precisely the condition implemented in post-cue trials of Kuo et al.'s design. It may be worth mentioning that Kuo et al. also recorded RT in both pre-cue and post-cue trials, observing results that are consistent with the latter view. The effects of set-size on RT (slower RT with visual arrays composed of four shapes than of two shapes) were more pronounced in post-cue trials than pre-cue trials. So set-size effects that were not apparent at the level of N2pc were instead fully manifest behaviorally. It is hard to explain this inconsistency and this provided additional motivation to examine effects of a set-size manipulation on the expected

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[1] At first blush, this prediction appears based more on intuition than on a solid empirical ground. However, it must be noted that, to our knowledge, no studies have ever been published so far describing N2pc variations in visual search generated through systematic manipulations of search-array size.

N2pc in post-cue trials. Thus, in Experiment 2, we replaced the two-shape visual arrays used in Experiment 1 with four-shape arrays. The fact that the N2pc is reduced in amplitude when visual-spatial attention is taxed by an attentional blink (Dell'Acqua et al., 2006; see also Jolicœur et al., 2006a,b; Robitaille, Jolicœur, Dell'Acqua, & Sessa, 2007) suggested to us that search of VSTM under greater load would produce a reduction in N2pc amplitude (Brisson & Jolicœur, 2007). This would be most evident in post-cue trials of Experiment 2 because the requirement to maintain four items in VSTM would fill VSTM to capacity and thus impose the highest processing load relative to other conditions in the study (i.e., pre- and post-cue trials of Experiment 1, pre-cue trials of Experiment 2).

3. Method

3.1. Participants

A total of 31 psychology students at the University of Padova took part in the present study, either as volunteers or in partial fulfillment of course requirements. There were 15 participants (8 females; mean age 22.0 ± 2.2) in Experiment 1, and 16 participants (11 females; mean age 22.4 ± 1.8) in Experiment 2. All participants had normal or corrected-to-normal vision, and none reported a prior history of neurological disorders and/or was under medication at the time of testing. Most of the participants (83%) were right-handed. Each participant provided informed consent prior to the beginning of the experiment. Three subjects were discarded from analyses, one in Experiment 1 and two in Experiment 2, for an excessive rate of ocular artifacts, and so analyses were based on results from 14 participants in each experiment.

3.2. Material

The stimuli were 8 regular shapes (i.e., square, circle, triangle, pentagon, diamond, hexagon, moon, and cross) and the digits 1–9. They were displayed in black ($4 \, cd/m^2$) on a light gray background ($36 \, cd/m^2$) on a 19 in. cathode-ray tube monitor controlled by a Pentium IV CPU and Eprime® software (Psychology Software Tools Inc.). At a distance of 70 cm (set by a chin rest), each shape was scaled to fit inside a square subtending 1.6° of visual angle. The digits were .7° wide and 1° high. A white ($50 \, cd/m^2$) disk with a black contour with a diameter of .3° was used as fixation point. When presented off-center, the center of each shape coincided with the vertex of an imaginary square, centered on the monitor, with a side of 2.8° of visual angle.

3.3. Design

In both experiments, each participant performed two types of trials, pre-cue trials and post-cue trials. In pre-cue trials, one shape (i.e., pre-cue) was displayed for 300 ms at the center of the monitor, followed, at an interval varying from 1300 to 1500 ms (jittered randomly from trial to trial in steps of 20 ms), by an array composed of a variable number of lateralized shapes (i.e., search-array) that was displayed for 150 ms. In pre-cue trials, the task was to indicate, without speed pressure, whether the pre-cue shape was present or absent in the search-array. In post-cue trials, an array composed a variable number of lateralized shapes (memory-array) was displayed for 300 ms, followed, at an interval varying from 1300 to 1500 ms (jittered randomly from trial to trial in steps of 20 ms), by a shape displayed for 150 ms at the center of the monitor (i.e., post-cue). In post-cue trials, the task was to indicate, without speed pressure, whether the post-cue shape was present or absent in the memory-array. Participants responded by pressing one of two keys of the numeric keypad of the computer keyboard (either "1" or "2," with the response mapping counterbalanced across participants), and received visual feedback in the form of a centrally displayed "+" or "−" in case of a correct or incorrect response, respectively. In both pre-cue and post-cue trials, when the target was absent, all shapes used on a particular trial (i.e., cue shape and array shapes) were selected at random, without replacement, from the set of available shapes. When the target was present, one of the shapes in the array (search-array in pre-cue trials or memory-array in post-cue trials) matched the (pre- or post-) cue shape. In both experiments, there were 6 blocks of 80 pre-cue trials and 6 blocks of 80 post-cue trials, for a total of 960 trials. In each experiment, half of the subjects started with 6 consecutive blocks of pre-cue trials, followed by 6 blocks of post-cue trials, and the other half of the subjects performed the trial types in the reverse order. In both experiments, two randomly selected digits (always different) were presented prior to the beginning of the trial, flanking the central fixation point. Participants were instructed to repeat the digits aloud throughout the trial,[2] until a response was emitted. This articulatory suppres-

sion task was adopted to minimize the possibility of phonological recoding of the shapes into their names during retention (e.g., Besner, Davies, & Daniels, 1981; see also Vogel et al., 2001). All experiments were self-paced, with each trial starting with a spacebar press.

3.4. ERP recording and signal processing

Using a head-cap with tin electrodes, EEG activity was recorded continuously from the Fp1, Fp2, Fz, F3, F4, F7, F8, C3, C4, Cz, P3, P4, Pz, O1, O2, T3, T4, T7, T8, P7, P8 sites, and the right earlobe, referenced to the left earlobe (Pivik et al., 1993). Horizontal EOG (HEOG) was recorded bipolarly from electrodes positioned on the outer canthi of both eyes. Vertical EOG (VEOG) was recorded bipolarly from two electrodes, positioned above and below the left eye. EEG, HEOG, and VEOG activities were amplified, filtered using a bandpass of 0.01–80 Hz, and digitized at a sampling rate of 250 Hz. Impedance at each electrode was maintained below 5 kΩ. The EEG was re-referenced offline to the average of the left and right earlobes, and segmented into 700 ms epochs starting 100 ms prior to the onset of the search-array in pre-cue trials or to the onset of the post-cue in post-cue trials. Trials associated with a HEOG exceeding ±30 μV were discarded from analyses. Trials associated with eye blinks, or any other artifact (electrode activity exceeding ±80 μV in a time interval of 400 ms), were also discarded from analyses. In target-present trials, signal-averaged HEOG was used to control for possible eye movements away from fixation during the presentation of the search-array in pre-cue trials and the memory-array in post-cue trials (i.e., when the shapes were presented off-center). The difference between left and right HEOG electrodes was averaged separately for trials in which the target shape (i.e., the shape in the search-array matching the pre-cue or the shape in the memory-array matching the post-cue) was displayed to the right or to the left of the central fixation. A maximum deflection of less than 3 μV was observed for any given subject, ensuring that the average eye position did not deviate by more than .2° towards the target shape included in search/memory-arrays during the ERP epoch. Lateralized activity was monitored at the P7/P8 and T3/T4 sites (i.e., where the lateralized activity was particularly pronounced), and only target-present trials with a correct response were analyzed.

In both pre-cue and post-cue trials, for each electrode pair, the ERP contralateral to the target shape was calculated by averaging the ERP generated at the left-sided electrode when the target shape was displayed in the right visual hemifield and the ERP generated at the right-sided electrode when the target shape was displayed in the left visual hemifield. The ERP ipsilateral to the target shape was calculated by averaging the ERPs at the complementary sites. Isovoltage contour-maps representing differences between brain activity over sites ipsilateral and contralateral to the target shape were generated by spherical spline interpolation (Perrin, Pernier, Bertrand, & Echallier, 1989), after computing difference waves for each lateralized electrode pair and entering a voltage of zero at midline electrodes. To compare the topographic distribution of activity over the scalp, normalization of the activity values was carried out using the algorithm described by McCarthy and Wood (1985). Estimation of the latency of the ERP components of interest was carried out using the jackknife approach (Ulrich & Miller, 2001), by finding the time at which a jackknife waveform reached 50% of peak amplitude. In the ERP analyses, the Greenhouse–Geisser correction for nonsphericity was applied when appropriate.

4. Results

4.1. Experiment 1

4.1.1. Behavior

The mean proportion of hits was .97.[3] We submitted to separate analyses of variance (ANOVAs) standard indices of sensitivity (d' and β; Green & Swets, 1974) in which trial type (pre-cue vs. post-cue) and array position (above vs. below the horizontal meridian) were considered as within-subjects factors. Mean d' and β values were 4.1 and 1.7, respectively. Neither factor produced significant effects in any of the analyses (all $Fs < 1$).

4.1.2. ERP

After the exclusion of error trials and trials contaminated by eye movements and/or any other artifact, 92% of trials were retained for analysis. The most important ERP results are shown in Fig. 3. The contralateral (dotted lines) and ipsilateral (solid lines) ERPs

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[2] A microphone inside the recording chamber was used to detect and amplify the digits' rehearsal outside the chamber, in order to monitor whether participants were repeating aloud the digits during each trial. When a participant did not repeat

the digits, the experimenter stopped the experiment, entered the chamber, and reminded the participant to do so.

[3] The high proportion of correct responses did not allow us to compute stable ERP functions, in this experiment (as well as in Experiment 2), based on trials associated with misses.

Experiment 1: ERP results
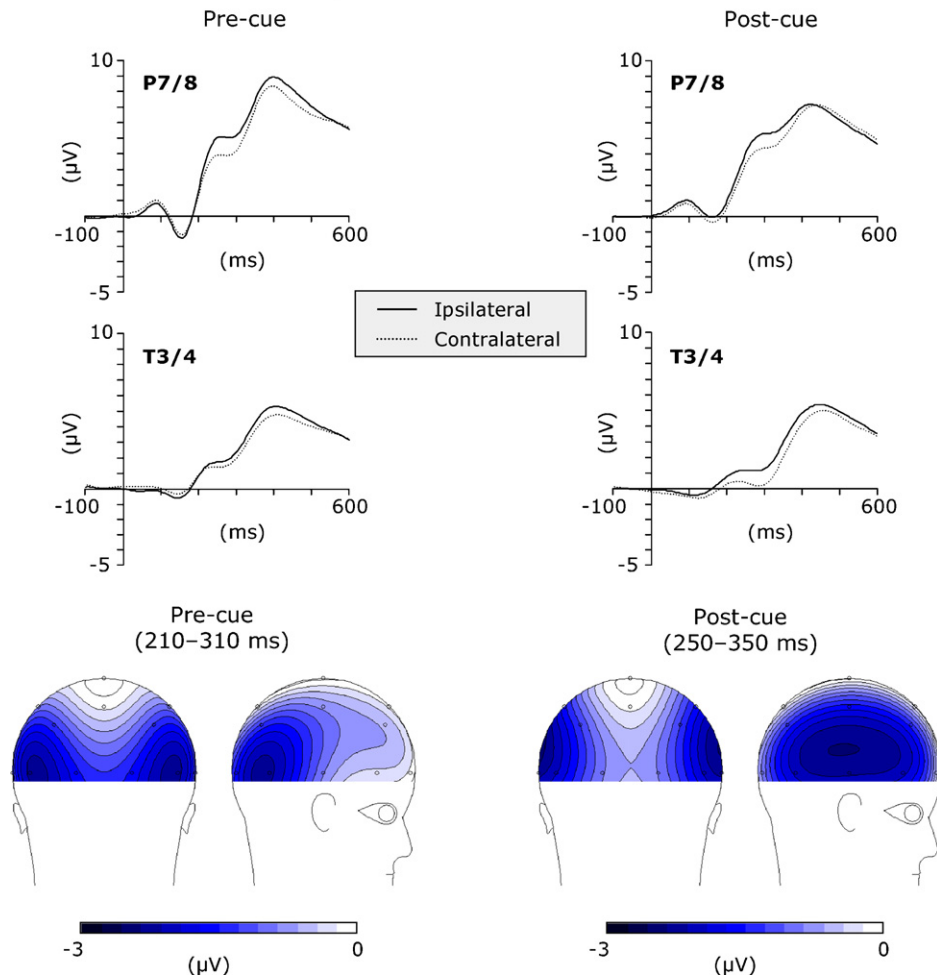
Fig. 3. ERP results of Experiment 1. *Left graphs*: ERP functions recorded at P7/P8 and T3/T4 time-locked to the onset of the search-array on target-present trials, ipsilateral (solid function) and contralateral (dotted function) to the target shape. *Right graphs*: ERP functions recorded at P7/P8 and T3/T4 time-locked to the onset of the post-cue on target-present trials, ipsilateral (solid function) and contralateral (dotted function) to the target shape. *Left maps*: Posterior and lateral views of isovoltage contour-maps generated from activity recorded during a 210–310 ms interval following the onset of the search-array in pre-cue trials. *Right maps*: Posterior and lateral views of isovoltage contour-maps generated from activity recorded during a 250–350 ms interval following the onset of the post-cue in post-cue trials.

recorded at P7/P8 and T3/T4 are shown for pre-cue trials (left graphs) and for post-cue trials (right graphs). ERPs at P7/P8 were characterized by evident P1 and N1 components, though of different amplitudes because pre-cue trials were time-locked to the onset of two lateralized shapes whereas post-cue trials were time-locked to the onset of a single shape at fixation. N1 and P1 components were much less evident at T3/T4. The ERP waveforms were characterized by an increment in positivity starting at about 200 ms post-eliciting events. From 200 ms on, contralateral and ipsilateral waveforms differed, as expected, reflecting the presence of the N2pc component in both pre-cue and post-cue trials.

The lower part of Fig. 3 displays posterior and lateral views of isovoltage contour-maps of the scalp distribution of contra-minus-ipsilateral activity in a 210–310 ms interval for pre-cue trials (left maps) and in a 250–350 ms interval for post-cue trials (right maps). These intervals were centered on the peak of the waveform for each condition for the displayed electrode sites. As can be seen by comparing left and right maps, the distribution of activity on the scalp was different between the pre-cue and post-cue conditions, with a peak of negativity that was localized more anteriorly in post-cue trials than in pre-cue trials. To test whether this difference in scalp topography was reliable, normalized activity values in the mentioned time-windows were submitted to an ANOVA that con-

sidered electrode site (O1/O2, P3/P4, P7/P8, C3/C4, T3/T4, F3/F4, and F7/F8) and trial type (pre-cue vs. post-cue) as within-subjects factors. A significant interaction between electrode site and condition was detected, $F(6, 8) = 8.3$; $p < .005$, suggesting that scalp distributions were indeed different between pre-cue and post-cue trials.

The contra-minus-ipsilateral difference ERPs are shown in Fig. 4. The mean amplitude values, in windows of 210–310 and 250–350 ms for pre-cue and post-cue trials, respectively, were submitted to an ANOVA that considered electrode site (P7/P8, T3/T4), target position (above vs. below the horizontal meridian), and trial type (pre-cue vs. post-cue) as within-subjects factors. The ANOVA revealed significant interactions between target position and electrode site, $F(1, 13) = 6.9$, $p < .05$, and between electrode site and trial type, $F(1, 13) = 16.5$, $p < .005$. Separate t-tests were conducted on the values recorded at each recording site. The t-tests revealed equally large lateralized activity in pre-cue and post-cue trials at P7/P8 (pre-cue: $-1.11\,\mu V$; post-cue: $-.91\,\mu V$), $t(13) = -1.35$, $p > .05$, and reduced lateralized activity in pre-cue trials ($-.48\,\mu V$) compared to post-cue trials ($-.95\,\mu V$) at electrode sites T3/T4, $t(13) = 2.5$, $p < .05$.

We determined whether the contra-minus-ipsilateral waveforms onset at different latencies using a jackknife approach. The mean latency values, in windows of 210–310 and 250–350 ms for pre-cue and post-cue trials, respectively, were submitted to an

Experiment 1: ERP results
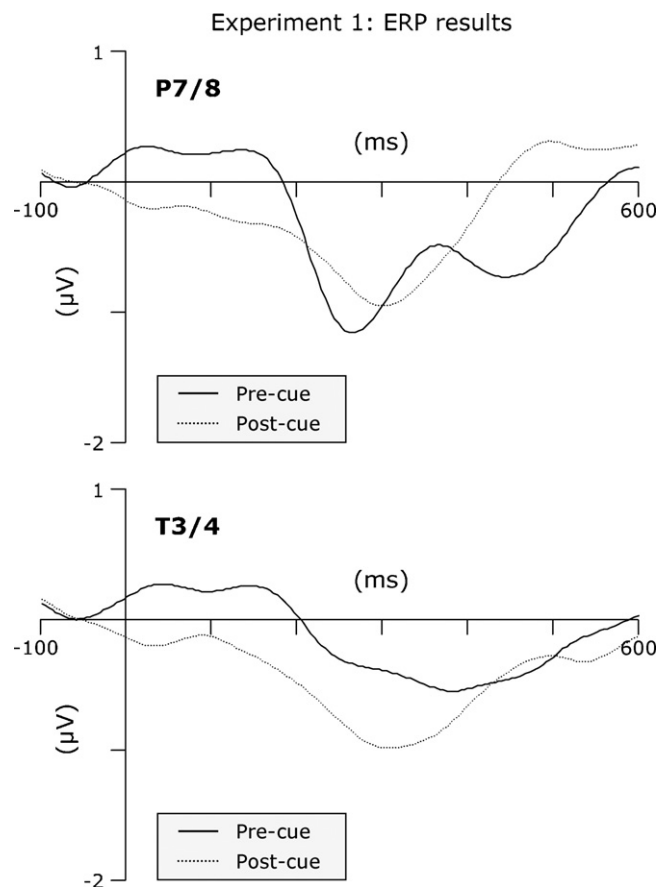
Fig. 4. ERP results of Experiment 1. Difference (contralateral minus ipsilateral) ERP functions recorded at P7/P8 (top graph) and T3/T4 (bottom graph) in pre-cue trials (solid line) and post-cue trials (dotted line).

ANOVA that considered electrode site (P7/P8, T3/T4), and trial type (pre-cue vs. post-cue) as within-subjects factors. With F corrected values, no significant factor effects on difference ERP latency components were detected, all Fs < 1.

4.2. Experiment 2

4.2.1. Behavior

The mean proportion of hits was .87. Separate ANOVAs on d' and β were conducted in which trial type (pre-cue vs. post-cue), horizontal position of the target shape when displayed in search- and memory-arrays (above vs. below the horizontal meridian), and vertical position of the target shape (left vs. right of the vertical meridian) were considered as within-subjects factors. Participants were less accurate in post-cue trials ($d' = 1.8$) than in pre-cue trials ($d' = 3.8$), $F(1, 13) = 168.2$, $p < .001$, and less accurate when targets were displayed in the lower quadrants of the visual field ($d' = 2.7$) than in the upper quadrants of the visual field ($d' = 2.9$), $F(1, 13) = 17.8$, $p < .001$. No other effect was significant in the analysis of d' (all ps > .2). The analysis on β did not reveal any significant effects (all Fs <= 1).

4.2.2. ERP

After the exclusion of error trials and trials contaminated by eye movements and/or any other artifact, 90% of trials were retained for analysis. The most important ERP results are shown in Fig. 5. The contralateral (dotted lines) and ipsilateral (solid lines) ERPs recorded at P7/P8 and T3/T4 are shown for pre-cue trials (left graphs) and for post-cue trials (right graphs).

Similarly to ERPs in Experiment 1, ERPs at P7/P8 were characterized by P1 and N1 components, which were not apparent at T3/T4. All ERP functions were characterized by an increment in positivity starting at about 200 ms post-eliciting events. From 200 ms on, contralateral and ipsilateral waveforms differed, as expected, reflecting the presence of the N2pc component in both pre-cue and post-cue trials. The lower part of Fig. 5 displays posterior and lateral views of isovoltage contour-maps of the scalp distribution of activity in a 210–310 ms interval for pre-cue trials (left maps) and in a 260–360 ms interval for post-cue trials (right maps). Note that in order to maximize the information about the distribution of scalp activity in post-cue trials (where the negativity was strongly attenuated with respect to pre-cue trials, see below), pre-cue maps were color-scaled differently from post-cue maps. As can be seen by comparing the left and right maps in Fig. 5, the distribution of activity over the scalp resembled the distributions observed in Experiment 1, with a peak of negativity in post-cue trials that was localized more anteriorly relative to the peak observed in pre-cue trials. As in Experiment 1, normalized activity values in the mentioned time-windows were submitted to an ANOVA that considered electrode site (O1/O2, P3/P4, P7/P8, C3/C4, T3/T4, F3/F4, and F7/F8) and trial type (pre-cue vs. post-cue) as within-subjects factors. A significant interaction between electrode site and trial type was found, $F(6, 8) = 7.5$, $p < .01$, showing that pre-cue and post-cue conditions caused significantly different scalp distributions.

The contra-minus-ipsilateral difference ERPs are reported in Fig. 6. The mean amplitude values, in windows of 210–310 and 260–360 ms for pre-cue and post-cue trials, respectively, were submitted to an ANOVA that considered electrode site (P7/P8 and T3/T4), target position (above vs. below the horizontal meridian), and trial type (pre-cue vs. post-cue) as within-subjects factors.

The factor target position did not produce significant main or interactive effects (all Fs < 1). The effect of trial type was significant, $F(1, 13) = 17.5$, $p < .01$. Separate t-tests were conducted on the values recorded at each recording site. The t-tests revealed reduced lateralized activity in post-cue trials ($-.40\,\mu V$ and $-.51\,\mu V$, at electrode sites P7/P8 and T3/T4, respectively) than in pre-cue trials ($-1.20\,\mu V$ and $-.93\,\mu V$, at electrode sites P7/P8 and T3/T4, respectively), a difference that was significant at both electrode sites (P7/P8: $t(13) = -4.6$, $p < .01$; T3/T4: $t(13) = -2.9$, $p < .05$). Separate t-tests carried out on post-cue trials revealed that the lateralized activity amplitude was significantly different from 0 at electrode sites T3/T4 ($t(13) = -2.5$, $p < .05$), and only marginally different from 0 at electrode site P7/P8, $t(13) = -2.1$, $p < .06$.

The mean latency values, in windows of 210–310 and 260–360 ms for pre-cue and post-cue trials, respectively, were submitted to an ANOVA that considered electrode site (P7/P8, T3/T4), and trial type (pre-cue vs. post-cue) as within-subjects factors. With F corrected values, no significant factor effects on difference ERP latency components were detected, all Fs < 1.

4.3. Combined analyses of Experiments 1 and 2

4.3.1. Behavior

Combined analysis on d' and β were conducted on the data from Experiments 1 and 2 in which array size (Experiment 1 = 2-object array; Experiment 2 = 4-object array) was added as a between-subjects factor to the factors considered in the separate analyses of Experiments 1 and 2. Participants were generally less accurate with 4-object arrays ($d' = 2.7$) than with 2-object arrays ($d' = 3.5$), $F(1, 26) = 10.7$, $p < .003$; and less accurate in post-cue trials ($d' = 2.5$) than in pre-cue trials ($d' = 3.8$), $F(1, 26) = 199.7$, $p < .0001$. Array size and trial type interacted significantly, $F(1, 26) = 54.6$, $p < .0001$, indicating an accuracy reduction in post-cue trials relative to pre-cue-trials that was more marked with 4-object arrays ($d' = 3.77$ vs. 1.81) than with 2-object arrays ($d' = 4.2$ vs. 4.1). With 2-object

Experiment 2: ERP results
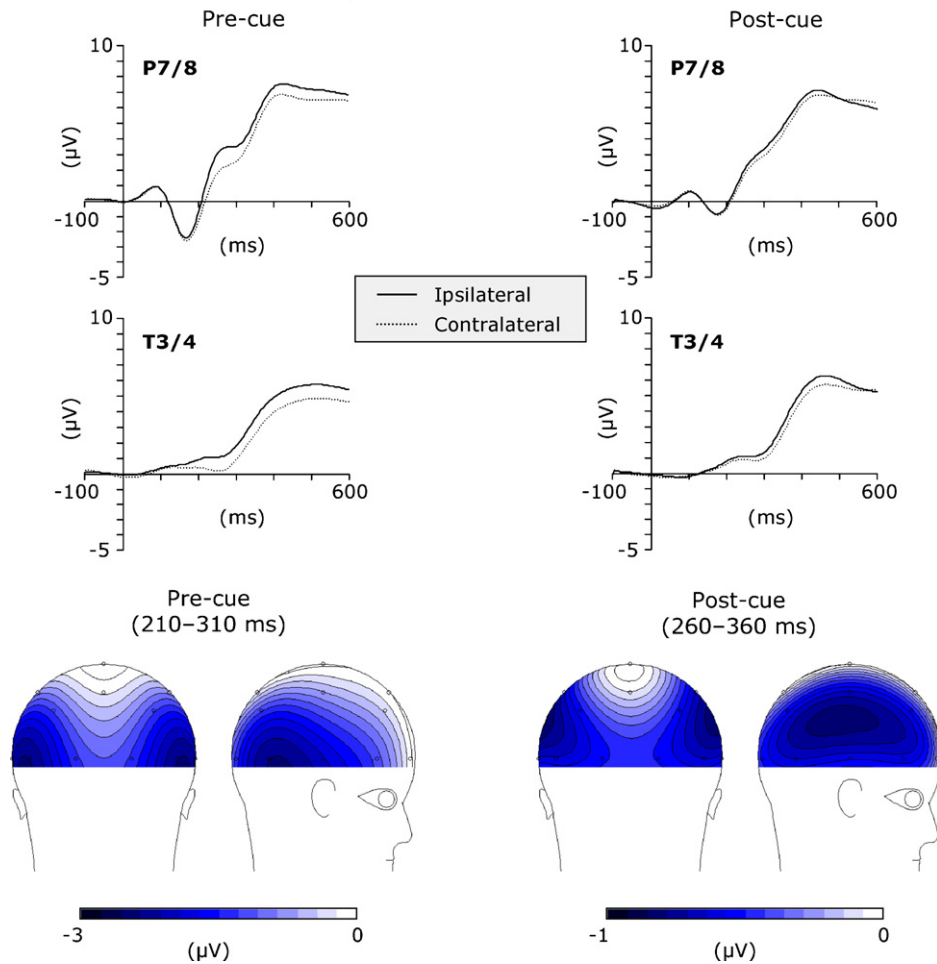
Fig. 5. ERP results of Experiment 2. *Left graphs*: ERP functions recorded at P7/P8 and T3/T4 time-locked to the onset of the search-array on target-present trials, ipsilateral (solid function) and contralateral (dotted function) to the target shape. *Right graphs*: ERP functions recorded at P7/P8 and T3/T4 time-locked to the onset of the post-cue on target-present trials, ipsilateral (solid function) and contralateral (dotted function) to the target shape. *Left maps*: Posterior and lateral views of isovoltage contour-maps generated from activity recorded during a 210–310 ms interval following the onset of the search-array in pre-cue trials. *Right maps*: Posterior and lateral views of isovoltage contour-maps generated from activity recorded during a 260–360 ms interval following the onset of the post-cue in post-cue trials.

arrays, accuracy did not differ between pre-cue and post-cue trials (see results of Experiment 1). No significant effects were detected in the combined analysis on β (all Fs < 1).

4.3.2. ERP

Mean amplitude values of contra-minus-ipsilateral ERPs from Experiments 1 and 2 were submitted to an ANOVA that considered electrode site (P7/P8 and T3/T4) and trial type (pre-cue vs. post-cue) as within-subjects factors, and array size (Experiment 1 = 2-object arrays; Experiment 2 = 4-object arrays) as a between-subjects factor. The ANOVA revealed significant effects of trial type, $F(1, 26) = 5.8$, $p < .05$, and of the interaction between trial type and array size $F(1, 26) = 14.1$, $p < .01$. There were also significant effects of electrode site, $F(1, 26) = 16.5$, $p < .001$, of the interaction between electrode site and trial type, $F(1, 26) = 16.3$, $p < .001$, and of the interaction between electrode site and array size, $F(1, 26) = 6.0$, $p < .05$. The results indicated that, at P7/P8, the amplitude reduction in lateralized activity in post-cue trials relative to pre-cue trials was more pronounced with 4-object than with 2-object array sizes. With F corrected values, no significant factor effects on difference ERP latency components were detected, all Fs < 1.

To check for the topographical consistency of the distribution of lateralized activity between Experiments 1 and 2, mean normalized

amplitude values were submitted to an ANOVA that considered electrode site (O1/O2, P3/P4, P7/P8, C3/C4, T3/T4, F3/F4, and F7/F8) and trial type (pre-cue vs. post-cue) as within-subjects factors, and array size (Experiment 1 = 2-object arrays; Experiment 2 = 4-object arrays) as a between-subjects factor. The ANOVA revealed a significant interaction between electrode site and trial type, $F(6, 8) = 9.7$; $p < .001$, supporting the observation of a more anterior peak of negativity in post-cue trials than in the pre-cue trials. The three-way interaction between electrode site, trial type, and array size was not significant, $F(6, 8) = 1.35$; $p > .25$, suggesting that the anterior shift of the peak of negativity in post-cue trials was similar in Experiments 1 and 2.

5. Discussion

Equal N2pc responses to search-arrays containing 2 or 4 objects were observed in pre-cue trials. These results confirmed our expectations that search of objects in perception would not be strongly affected by array size. Most importantly, search for objects held in VSTM in post-cue trials was also characterized by a strongly lateralized ERP that was temporally, but less so topographically, similar to N2pc activity. This N2pc-like response was quite clear with arrays of 2 objects, but was attenuated with arrays of 4 objects. The attenuation of the N2pc-like response with arrays of 4 objects

Experiment 2: ERP results
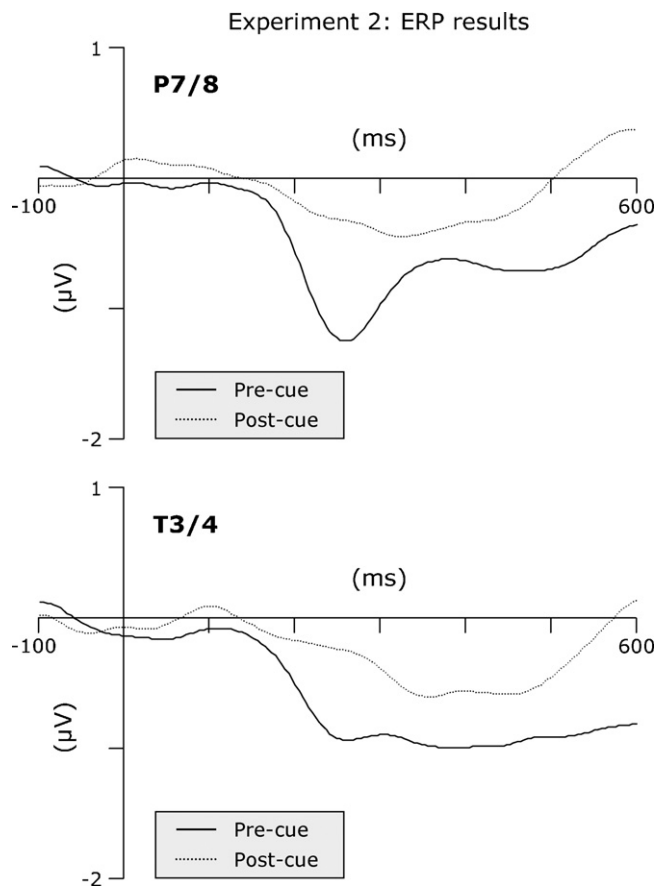
Fig. 6. ERP results of Experiment 2. Difference (contralateral minus ipsilateral) ERP functions recorded at P7/P8 (top graph) and T3/T4 (bottom graph) in pre-cue trials (solid line) and post-cue trials (dotted line).

converges with the observation of a reduced accuracy in post-cue trials observed in this condition.

The observed attenuation of N2pc-like response with increased memory load in search of VSTM is consistent with the hypothesis of an interaction between VSTM and spatial selective attention mechanisms, on the assumption that the suppressed N2pc-like response was caused by a less efficient memory search in post-cue trials. On the other hand, a different proposal is that subjects in post-cue trials found it possible to encode only a subset of the information available in Experiment 2. The behavioral results suggest that about 1.73 (out of 2) items were retained in Experiment 1 and that about 2.32 (out of 4) items were retained in Experiment 2. Clearly, the task requirements of Experiment 2 exceeded the capacity of VSTM, and given this outcome one option that, at present, we cannot exclude is that ERPs were deflated by activity recorded during target-absent trials associated with a proportion of correct guesses (i.e., where an N2pc-like response was likely to be absent). Thus, while the significant N2pc-like response in post-cue trials replicates an important aspect of Kuo et al. (2009) work, the interactive effects – reflected at both behavioral and electrophysiological levels – of set-size and search mode (perceptual vs. mnemonic) found in the present empirical context diverge substantially from Kuo et al.'s findings, and converge nicely instead with recent behavioral investigations in the visual search area (Oh & Kim, 2004; Woodman & Luck, 2004).

The scalp topography of the lateralized N2pc-like response across pre-cue trials and post-cue trials differed significantly, and this finding represents a further novel aspect of the present investigation with respect to prior work in the field. As can be seen in Figs. 3 and 5, the negativity contralateral to the target shape was more anterior for VSTM search than for perceptual search. We noted that an analogous trend in the same direction emerged from a visual inspection of Kuo et al. (2009) results. Though not corroborated statistically in the Kuo et al. study, a trend in the same direction (again, not statistically significant) was evident in another study bearing some analogy with the present study (Astle, Scerif, Kuo, & Nobre, 2009), in which however the focus was on feature-based, rather than object-based, selection in perceptual vs. mnemonic domains. In these respects, it must be pointed out that fMRI evidence of the overlap of cortical regions involved in perceptual and memorial search is abundant, which however also highlights some crucial differences in neural activity when attention scans sensory vs. VSTM representations of the visual world. Lepsien et al. (2005) described significant signal increases bilaterally in the posterior parietal cortex, including precuneus, SPL, IPS, and the left supramarginal gyrus, together with a frontal activation cluster including the FEF bilaterally, preSMA, and rostral cingulate zone, that was shared between perceptual and memorial search (Nobre et al., 2004). This fronto-parietal circuit is held to be the neural substratum of the intersection between working memory and attention (Corbetta, Kincade, & Shulman, 2002; Gitelman et al., 1999; Hopfinger, Woldorff, Fletcher, & Mangun, 2001; Kastner & Ungerleider, 2000; LaBar et al., 1999; Nee & Jonides, 2009; Nobre, 2001). Signal increases in the insula, inferior frontal gyrus and, more in general, ventro-lateral prefrontal regions have however been shown to be selectively activated during memory search (Courtney et al., 1997; Nobre et al., 2004). These are the regions that have also been proposed to support working memory functions related to active maintenance of information, to transient working memory functions such as updating contents, comparison operations or rehearsal (e.g., Cohen et al., 1997). In relation to the present results, this evidence is suggestive of a different origin of reentrant signals from anterior to posterior regions of the cortex in pre-cue and post-cue trials. In this view, one likely possibility is that N2pc responses were modulated by a local, short-range circuitry confined to posterior parietal regions during perceptual search, whereas N2pc-like responses during mnemonic search were (perhaps in addition to local neural interactions) influenced by ventro-lateral prefrontal activity.

A final observation is related to the distinction between N2pc and SPCN (e.g., Jolicœur et al., 2008). Based on the temporal dynamics of the N2pc-like response in post-cue trials with 2-object arrays (Experiment 1, Figs. 3 and 4), the response was more similar to what is typically observed for the N2pc than for the SPCN, because the SPCN typically lasts longer by at least another several hundred milliseconds. To reiterate an issue raised in Section 1, our hypothesis is that this ERP pattern reflects the nature of the task, which required a present/absent response with the contents of VSTM based on a match with the post-cue. Following a successful match, further processing of VSTM was no longer required, and the enhanced activity could be relatively short-lived. Given the distinctive nature of the shapes, it is likely that the matching operation was efficient and rapid, and did not require much further processing. Eimer and Kiss (in press) also compared ERP responses to a centrally presented post-cue stimulus with the response to a search-array presented after a centrally presented pre-cue stimulus. In their results, however, the lateralized response in search of VSTM appeared to be mainly in the form of an SPCN wave of standard duration, raising the question as to why we and Kuo et al. (2009) observed an N2pc response whereas they found an SPCN. We hypothesize that this difference likely reflects the additional perceptual and cognitive operations required to perform the notch-location task relative to the present/absent task. Another interpretation of the results is that, despite their relatively short durations, the lateralized responses we observed in the post-cue conditions were more like the SPCN observed in previous work (e.g., Klaver et al., 1999;

McCollough et al., 2007) than N2pc. In the present work, prior to the onset of the post-cue, an equal amount of information encoded from left and right visual hemifields was presumably held in VSTM, yielding a sustained bilateral response (e.g., Klaver et al., 1999). Upon onset of the post-cue shape, a match to the contents of VSTM may have triggered a lateralized response. In this view, the present results from post-cue trials may therefore reflect a form of phasic SPCN resulting from a momentary imbalance between sustained VSTM activity in left and right hemispheres. On the other hand, a problem for this line of argument may arise when considering the scalp distribution of the N2pc-like component we observed in post-cue trials, that was characterized by a shift of contra-minus-ipsilateral activity (relative to pre-cue trials) towards lateral temporal regions rather than towards the dorso-parietal regions described by McCollough et al. (2007) for the SPCN. More work will be required to pinpoint the neural generators of this somewhat atypical ERP component and underlying functional significance. Nonetheless, the fact that such ERP was strongly lateralized as a function of location provides strong evidence for the maintenance of spatial information in the representation of visual shape and for a general similarity of mechanisms that search perceptual and memory representations.

References

Aguirre, G. K., Zarahn, E., & D'Esposito, M. (1998). Neural components of topographical representation. *Proceedings of the National Academy of Sciences (USA)*, 95, 839–846.

Astle, D. E., Scerif, G., Kuo, B.-C., & Nobre, A. C. (2009). Spatial selection of features within perceived and remembered objects. *Frontiers in Human Neuroscience*, 3. Article 6.

Averbach, E., & Coriel, A. S. (1961). Short-term memory in vision. *Bell System Technical Journal*, 40, 309–328.

Awh, E., & Jonides, J. (2001). Overlapping mechanisms of attention and spatial working memory. *Trends in Cognitive Sciences*, 5, 119–126.

Besner, D., Davies, J., & Daniels, S. (1981). Reading for meaning: The effects of concurrent articulation. *Quarterly Journal of Experimental Psychology*, 33A, 415–437.

Brisson, B., & Jolicœur, P. (2007). Electrophysiological evidence of central interference on the control of visual-spatial attention. *Psychonomic Bulletin & Review*, 14, 126–132.

Brisson, B., & Jolicœur, P. (2008). Express attentional re-engagement but delayed entry into consciousness following invalid spatial cues in visual search. *PLoS ONE*, 3, e3967.

Chelazzi, L., Miller, E. K., Duncan, J., & Desimone, R. (1993). A neural basis for visual search in inferior temporal cortex. *Nature*, 363, 345–347.

Cohen, J. D., Perlstein, W. M., Braver, T. S., Nystrom, L. E., Noll, D. C., Jonides, J., et al. (1997). Temporal dynamics of brain activation during a working memory task. *Nature*, 386, 604–608.

Coltheart, M. (1980). Iconic memory and visible persistence. *Perception & Psychophysics*, 27, 183–228.

Corbetta, M., Kincade, J. M., & Shulman, G. L. (2002). Neural systems for visual orienting and their relationships to spatial working memory. *Journal of Cognitive Neuroscience*, 14, 508–523.

Coull, J. T., & Nobre, A. C. (1998). Where and when to pay attention: The neural systems for directing attention to spatial locations and to time intervals as revealed by both PET and fMRI. *Journal of Neuroscience*, 18, 7426–7435.

Courtney, S. M., Ungerleider, L. G., Keil, K., & Haxby, J. V. (1997). Transient and sustained activity in a distributed neural system for human working memory. *Nature*, 386, 608–611.

Cowan, N. (2001). The magical number 4 in short-term memory: A reconsideration of mental storage capacity. *Behavioral and Brain Sciences*, 24, 87–185.

DeFockert, J. W., Rees, G., Frith, C. D., & Lavie, N. (2001). The role of working memory in visual selective attention. *Science*, 291, 1803–1806.

Dell'Acqua, R., Pesciarelli, F., Jolicœur, P., Eimer, M., & Peressotti, F. (2007). The interdependence of spatial attention and lexical access as revealed by early asymmetries in occipito-parietal ERP activity. *Psychophysiology*, 44, 436–443.

Dell'Acqua, R., Sessa, P., Jolicœur, P., & Robitaille, N. (2006). Spatial attention freezes during the attentional blink. *Psychophysiology*, 43, 394–400.

Desimone, R., & Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annual Review of Neuroscience*, 18, 193–222.

Duncan, J., & Humphreys, G. W. (1989). Visual search and stimulus similarity. *Psychological Review*, 96, 433–458.

Eimer, M. (1996). The N2pc component as an indicator of attentional selectivity. *Electroencephalography and Clinical Neurophysiology*, 99, 225–234.

Eimer, M., & Kiss, M. (in press). An electrophysiological measure of access to representations in visual working memory. *Psychophysiology*.

Folk, C. L., Remington, R. W., & Johnston, J. C. (1992). Involuntary covert orienting is contingent on attentional control settings. *Journal of Experimental Psychology: Human Perception and Performance*, 18, 1030–1044.

Gitelman, D. R., Nobre, A. C., Parrish, T. B., LaBar, K. S., Kim, Y. H., Meyer, J. R., et al. (1999). A large-scale distributed network for covert spatial attention: Further anatomical delineation based on stringent behavioral and cognitive controls. *Brain*, 122, 1093–1106.

Gratton, G. (1998). The contralateral organization of visual memory: A theoretical concept and a research tool. *Psychophysiology*, 35, 638–647.

Green, D. M., & Swets, J. A. (1974). *Signal detection theory and psychophysics*. Huntington, NY: Krieger.

Hickey, C., Di Lollo, V., & McDonald, J. J. (2008). Electrophysiological indices of target and distractor processing in visual search. *Journal of Cognitive Neuroscience*, 21, 760–775.

Hommel, B. (2002). Responding to object files: Automatic integration of spatial information revealed by stimulus–response compatibility effects. *Quarterly Journal of Experimental Psychology*, 55A, 567–580.

Hopf, J.-M., Luck, S. J., Girelli, M., Hagner, T., Mangun, G. R., Scheich, H., et al. (2000). Neural sources of focused attention in visual search. *Cerebral Cortex*, 10, 1233–1241.

Hopfinger, J. B., Woldorff, M. G., Fletcher, E. M., & Mangun, G. R. (2001). Dissociating top-down attentional control from selective perception and action. *Neuropsychologia*, 39, 1277–1291.

Jack, A. I., Patel, G., Astafiev, S. V., Snyder, A. Z., Akbudak, E., Shulman, G. L., et al. (2007). Changing human visual field organization from early visual to extraoccipital cortex. *PLoS ONE*, 5, e452.

Jiang, Y., Olson, I. R., & Chun, M. M. (2000). The organization of visual short-term memory. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 26, 683–702.

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.

Kastner, S., & Ungerleider, L. G. (2000). Mechanisms of visual attention in the human cortex. *Annual Review of Neuroscience*, 23, 315–341.

Kiss, M., Jolicœur, P., Dell'Acqua, R., & Eimer, M. (2008). Attentional capture by visual singletons is mediated by top-down task-set: New evidence from the N2pc component. *Psychophysiology*, 45, 1013–1024.

Klaver, P., Talsa, D., Wijers, A. A., Heinze, H. J., & Mulder, G. (1999). An event-related brain potential correlate of visual short-term memory. *NeuroReport*, 10, 2001–2005.

Kuo, B. C., Rao, A., Lepsien, J., & Nobre, A. C. (2009). Searching for targets within the spatial layout of visual short-term memory. *Journal of Neuroscience*, 29, 8032–8038.

LaBar, K. S., Gitelman, D. R., Parrish, T. B., & Mesulam, M. (1999). Neuroanatomic overlap of working memory and spatial attention networks: A functional MRI comparison within subjects. *NeuroImage*, 10, 695–704.

Leblanc, É., Prime, D., & Jolicœur, P. (2008). Tracking the location of visuospatial attention in a contingent capture paradigm. *Journal of Cognitive Neuroscience*, 20, 657–671.

Lepsien, J., Griffin, I. C., Devlin, J. T., & Nobre, A. C. (2005). Directing spatial attention in mental representations: Interactions between attentional orienting and working-memory load. *NeuroImage*, 26, 733–743.

Luck, S. J., & Hillyard, S. A. (1994). Spatial filtering during visual search: Evidence from human electrophysiology. *Journal of Experimental Psychology: Human Perception and Performance*, 20, 1000–1014.

Luck, S., Woodman, G. F., & Vogel, E. K. (2002). Event-related potential studies of attention. *Trends in Cognitive Sciences*, 4, 432–440.

Luria, R., Sessa, P., Gotler, A., Jolicœur, P., & Dell'Acqua, R. (in press). Visual short-term memory capacity for simple and complex objects. *Journal of Cognitive Neuroscience*.

McCarthy, G., & Wood, C. C. (1985). Scalp distributions of event-related potentials: An ambiguity associated with analysis of variance models. *Electroencephalography and Clinical Neurophysiology*, 62, 203–208.

McCollough, A. W., Machizawa, M. G., & Vogel, E. K. (2007). Electrophysiological measures of maintaining representations in visual working memory. *Cortex*, 43, 77–94.

Nee, D. E., & Jonides, J. (2009). Common and distinct neural correlates of perceptual and memorial selection. *NeuroImage*, 45, 963–975.

Nobre, A. C. (2001). The attentive homunculus: Now you see it, now you don't. *Neuroscience and Biobehavioral Reviews*, 25, 477–496.

Nobre, A. C., Coull, J. T., Maquet, P., Frith, C. D., Vandenberghe, R., & Mesulam, M. M. (2004). Orienting attention to locations in perceptual versus mental representations. *Journal of Cognitive Neuroscience*, 16, 363–373.

Nobre, A. C., Griffin, I. C., & Rao, A. (2008). Spatial attention can bias search in visual short-term memory. *Frontiers in Human Neuroscience*, 1. Article 4.

Oh, S.-H., & Kim, M.-S. (2004). The role of spatial working memory in visual search efficiency. *Psychonomic Bulletin & Review*, 11, 275–281.

Olivers, C. N. L. (2008). Interactions between working memory and visual attention. *Frontiers in Bioscience*, *13*, 1182–1191.

Olivers, C. N. L. (2009). What drives memory-driven attentional capture? The effects of memory type, display type, and search type. *Journal of Experimental Psychology: Human Perception and Performance*, *35*, 1275–1291.

Perrin, F., Pernier, J., Bertrand, O., & Echallier, J. F. (1989). Spherical splines for scalp potential and current density mapping. *Electroencephalography and Clinical Neurophysiology*, *72*, 184–187.

Phillips, W. A. (1974). On the distinction between sensory storage and short-term visual memory. *Perception & Psychophysics*, *16*, 283–290.

Pivik, R. T., Broughton, R. J., Coppola, R., Davidson, R. J., Fox, N., & Nuwer, M. R. (1993). Guidelines for the recording and quantitative analysis of electroencephalographic activity in research contexts. *Psychophysiology*, *30*, 547–558.

Robitaille, N., Jolicœur, P., Dell'Acqua, R., & Sessa, P. (2007). Short-term consolidation of visual patterns interferes with visuo-spatial attention: Converging evidence from human electrophysiology. *Brain Research*, *1185*, 158–169.

Sereno, M. I., Pitzalis, S., & Martinez, A. (2001). Mapping of contralateral space in retinotopic coordinates by a parietal cortical area in humans. *Science*, *294*, 1350–1354.

Shepard, R. N. (1984). Ecological constraints on internal representation: Resonant kinematics of perceiving, imagining, thinking, and dreaming. *Psychological Review*, *91*, 417–447.

Sperling, G. (1960). The information available in brief visual presentations. *Psychological Monographs: General and Applied*, *74*, 1–29.

Stevanovski, B., & Jolicœur, P. (2007). Visual short-term memory: Central capacity limitations in short-term consolidation. *Visual Cognition*, *15*, 532–563.

Todd, J. J., & Marois, R. (2004). Capacity limit of visual short-term memory in human posterior parietal cortex. *Nature*, *428*, 751–754.

Ulrich, R., & Miller, J. (2001). Using the jackknife-based scoring method for measuring LRP onset effects in factorial designs. *Psychophysiology*, *38*, 816–827.

Vogel, E. K., & Machizawa, M. G. (2004). Neural activity predicts individual differences in visual working memory capacity. *Nature*, *428*, 748–751.

Vogel, E. K., Woodman, G. F., & Luck, S. (2001). Storage of features, conjunctions, and objects in visual working memory. *Journal of Experimental Psychology: Human Perception and Performance*, *27*, 92–114.

Woodman, G. F., & Luck, S. J. (1999). Electrophysiological measurement of rapid shifts of attention during visual search. *Nature*, *400*, 867–869.

Woodman, G. F., & Luck, S. J. (2003a). Dissociation among attention, perception, and awareness during object-substitution masking. *Psychological Science*, *14*, 605–611.

Woodman, G. F., & Luck, S. J. (2003b). Serial deployment of attention during visual search. *Journal of Experimental Psychology: Human Perception and Performance*, *29*, 121–138.

Woodman, G. F., & Luck, S. J. (2004). Visual search is slowed when visuospatial working memory is occupied. *Psychonomic Bulletin & Review*, *11*, 269–274.

Woodman, G. F., Vogel, E. K., & Luck, S. (2001). Visual search remains efficient when visual working memory is full. *Psychological Science*, *12*, 219–224.

Yantis, S., Schwarzbach, J., Serences, J. T., Carlson, R. L., Steinmetz, M. A., Pekar, J. J., et al. (2002). Transient neural activity in human parietal cortex during spatial attention shifts. *Nature Neuroscience*, *5*, 995–1002.

Zeki, S. M. (1993). *A vision of the brain*. Oxford, UK: Blackwell Scientific Publications.