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Filtering performance in visual working memory is improved by reducing early spatial attention to the distractors

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Abstract

We investigated the underlying processes that enable improving filtering irrelevant items from entering visual working memory (WM). To this end, participants performed a bilateral change-detection task in which either targets or targets along with distractors (i.e., the filtering condition) appeared in the memory array while ERPs were recorded. In the cue-present condition, we provided a spatial cue coupled with a temporal cue regarding where and when the distractors would appear. On some of the filtering trials, after the offset of the memory array, task-irrelevant probes were briefly flashed either at the locations of the targets or at the locations of the distractors. This enabled measuring whether reactivating the filtering settings resulted in reducing spatial attentional resources to the distractors, allocating additional spatial attentional resources to the targets, or both, as was measured by the P1/N1 amplitude. Results revealed that, relative to the cue-absent condition, in the cue-present condition the P1/N1 amplitude was reduced for probes at the distractors and was similar for probes at the targets. In addition, the reduction in the P1/N1 amplitude was accompanied by a reduced filtering cost in accuracy performance in the cue-present condition relative to the cue-absent condition. These findings suggest that reactivating the distractor filtering settings improved filtering performance in visual WM by reducing the allocation of spatial attention to the distractors already at early processing stages, and not by allocating additional spatial attentional resources to the targets.

KEYWORDS

ERPs, filtering ability, N1, P1, spatial attention, visual working memory

1 | INTRODUCTION

Working memory (WM) is our temporary storage that can hold a limited amount of information in an active online state in the face of ongoing cognitive tasks (for a review, see Luck & Vogel, 2013). Many studies suggested that visual WM has a very limited capacity of about 3–4 objects (Awh, Barton, & Vogel, 2007; Luck & Vogel, 1997; Pashler, 1988; Vogel & Machizawa, 2004; Vogel, Woodman, & Luck, 2001; Xu & Chun, 2006). Nonetheless, there are robust individual differences in visual WM capacity (e.g., Vogel & Awh, 2008; Vogel & Machizawa, 2004; Vogel, McCollough, & Machizawa, 2005) that predict performance in assortment of aptitude measures. For instance, studies have shown that individuals with high visual WM capacity tend to get higher scores in fluid intelligence measures (Fukuda, Vogel, Mayr, & Awh, 2010; Johnson et al., 2013; Unsworth, Fukuda, Awh, & Vogel, 2014, 2015) and in complicated cognitive tasks such as problem solving and verbal learning (Cowan et al., 2005). Furtheremore, old age (Cashdollar et al., 2013) and psychiatric disorders such as schizophrenia (Gold et al., 2006; Gold, Wilk, McMahon, Buchanan, & Luck, 2003) and

Alzheimer's (Parra et al., 2009, 2010) were found to be associated with deficits in visual WM functioning as measured by capacity estimates. This evidence indicates that visual WM is a pillar mechanism in guiding behavior, and therefore studies have focused on characterizing the underlying mechanisms that aid visual WM to handle such extreme limitations in its capacity.

The ability to properly allocate attentional resources to encode only the task-relevant information and filter out task-irrelevant information from being encoded into the visual WM workspace has been suggested to be a fundamental mechanism in handling WM capacity limitations (Allon & Luria, 2017; Arnell & Stubitz, 2010; Awh & Vogel, 2008; Fukuda & Vogel, 2009, 2011; Gaspar, Christie, Prime, Jolicœur, & McDonald, 2016; Jost & Mayr, 2016; Liesefeld, Liesefeld, & Zimmer, 2014; McNab & Klingberg, 2008; Vogel & Awh, 2008; Vogel et al., 2005). Furthermmore, it has been demonstrated that filtering ability underlies individul differences in visual WM capacity (e.g., Fukuda & Vogel, 2009; McNab & Klingberg, 2008; Vogel et al., 2005). Since filtering ability is highly important for visual WM functioning, in a recent study (Allon & Luria, 2017) we investigated the mechanisms that can improve filtering of irrelevant information from entering the limited visual WM workspace. Our findings support the notion that the distractor filtering settings are short-lived and therefore need to be reactivated in order to improve filtering performance.

Specifically, in Allon and Luria (2017), participants performed a change-detection task (Luck & Vogel, 1997) in which they were briefly presented with a memory array consisting of either colored circles with a small cut-out (targets) or a memory array with targets along colored circles (distractors, i.e., the filtering condition). Participants were asked to remember the colors of the target items and to ignore the distractors. The memory array was followed by a retention interval (of about 1 s), and then a test item appeared and participants indicated whether the test item had the same or a different color relative to the corresponding memory array item. We used a spatial cue (i.e., placeholder) to mark the positions of the distractors such that their positions were fixed and clearly marked throughout the task, making the distractors' positions perfectly predictable. Yet, the filtering cost (calculated as the difference in accuracy rates between the three targets and the filtering condition) was not reduced relative to a cue-absent condition. Next, we applied the same spatial cue, but this time coupled with a temporal cue (i.e., a warning cue), appearing right before a filtering trial. Thus, participants knew both where and when the distractors would appear. This time, the filtering cost was reduced, and thus we reasoned that the temporal cue helped in reactivating the filtering settings.

To support the reactivation argument, we once again used the spatial cue but this time changed the placeholder positions on every trial. Although changing the placeholder positions on every trial made the task harder relative to the experiment in which the placeholders were fixed, it reactivated the filtering settings since the new positions had to be updated on each trial. Importantly, this manipulation resulted in better filtering performance relative to the cue-absent condition, supporting the idea that the filtering settings had to be reactivated in order to improve the filtering performance. Given the importance of the filtering ability in determining individual differences in visual WM capacity, these results open a new direction to ameliorate filtering ability and perhaps WM performance in general. However, while there were several investigations regarding the neural mechanisms of why the filtering process fails in encoding only targets (described below), it is still unknown what are the underlying processes involved in the improvement of filtering performance, and this was the goal of the current study.

1.1 | The current study

We measured early visually evoked ERP components (i.e., P1 and N1) to index the allocation of spatial attention, as these components are modulated by spatial attention such that higher amplitudes are observed to stimuli at attended locations relative to amplitudes observed to stimuli at unattended locations. The common assumption is that the P1 and N1 waves are thought to reflect the initial modulation of sensory attentional activity passing through the extrastriate of the visual cortex (Hillyard, Vogel, & Luck, 1998; Luck & Kappenman, 2013). This measurement provided neural evidence to whether improving the filtering ability (Allon & Luria, 2017) resulted in reducing spatial attentional resources to the distractors, allocating additional spatial attentional resources to the targets, or both. The P1 wave typically begins 70–100 ms after stimulus offset and is usually illustrated in lateralized displays as a larger positive voltage over the contralateral hemisphere to the attended stimulus. The N1 wave typically begins 50 ms afterward and is usually observed as a larger negative voltage over the ipsilateral hemisphere to the attended stimulus.

To index the reactivation of the filtering settings, we followed a procedure by Fukuda and Vogel (2009). Namely, on 66% of the filtering trials (on each of the cue-present and cue-absent conditions) after the offset of the memory array, task-irrelevant probes were briefly flashed either at the locations of the targets or at the locations of the distractors. The underlying assumption by Fukuda and Vogel was that the P1/N1 amplitude to the task-irrelevant probes reflected whether individuals could overcome attentional capture by the distractors. Fukuda and Vogel found that large P1/N1 amplitude at the distractors' locations was related to encoding more distractors into the visual WM workspace. Furthermore, there was a strong positive correlation between the attentional capture effect (measured by the difference between the P1/N1 amplitude for probes at the targets and the P1/N1 amplitude for probes at the distractors) and the individual visual WM capacity. They concluded that the allocation of spatial attention at early processing stages has a significant toll at more advanced stages of processing, such that a failure in the initial allocation of attention resulted in distractor information entering the visual WM limited workspace.

Thus, former studies supported the notion that the key process for effective filtering is suppressing the distractors rather than enhancing processing of the targets (Allon & Luria, 2017; Fukuda & Vogel, 2009). Therefore, we hypothesized that reactivating the filtering settings by spatially and temporally cuing the distractors will result in reducing spatial attentional resources to the distractors.

Similar to Fukuda and Vogel (2009), we measured the P1/N1 amplitude within a wider window to include both components (i.e., 100–300 ms locked to the probe array). This is because the P1 may extend to the N1 range (Livingstone, Christie, Wright, & McDonald, 2017). Specifically, measuring the P1/N1 amplitude to the probes enabled us to see whether, relative to the cue-absent condition, in the cue-present condition reactivation of the filtering settings by the distractor cues reduced spatial attention to the distractors, enhanced spatial attention to the targets, or both. That is, if reactivating the filtering settings helps direct spatial attention away from the distractors already at an early processing stage, then the P1/N1 amplitude should be smaller for probes at the distractors relative to the P1/N1 amplitude for probes at the distractors in the cue-absent condition. However, if the reactivation results in allocating additional spatial attentional resources to the targets, then the P1/N1 amplitude for probes at the targets should be higher than the P1/N1 amplitude for probes at the targets in the cue-absent condition. Another possibility is that the reactivation results in both reducing spatial attentional resources to the distractors and allocating additional spatial attentional resources to the targets. In this case, we should expect both a decrease in P1/N1 amplitude for probes at the distractors and an increase in P1/N1 amplitude for probes at the targets relative to the cue-absent condition.

Following Vogel et al. (2005; see also Fukuda & Vogel, 2009), we also measured the contralateral delayed activity, also known as the CDA, which reflects the number of items that are encoded and maintained in visual WM (for a review, see Luria, Balaban, Awh, & Vogel, 2016; McCollough, Machizawa, & Vogel, 2007; Vogel & Machizawa, 2004). The CDA was measured during the memory array and the retention interval to examine whether reactivating the filtering settings in the cue-present condition reduced the number of distractors that entered visual WM as measured by the CDA amplitude. Vogel et al. (2005) found that high-capacity individuals successfully filtered out the distractors, such that their CDA amplitude did not differ when comparing a condition with only targets to a filtering condition containing distractors in addition to the same number of targets. Conversely, low-capacity individuals were less able to filter out the distractors from entering the visual WM workspace, and their CDA amplitude in a filtering condition that included both targets and distractors was higher than a condition with the same number of targets (without distractors).

Based on our previous findings (Allon & Luria, 2017), we predicted that, relative to the cue-absent condition, in the cue-present condition the CDA amplitude in the filtering condition would be more similar to the CDA amplitude in a condition that includes the same number of targets (without distractors), reflecting better filtering ability. As for behavioral measures, we predicted that, in accordance with Allon and Luria (2017), the filtering cost (calculated as the difference in accuracy rates between the two targets and the two targets with three distractors condition) will be smaller in the cue-present condition relative to the cue-absent condition.

2 | METHOD

2.1 | Participants

Nineteen students from Tel Aviv University (14 female, $M = 24.36$ years, $SD = 3.61$) participated in two EEG experimental conditions (i.e., cue-absent condition and cue-present condition, with each condition lasting between 180–195 min) conducted on 2 separate days with a time interval of 3 days and up to 3 weeks between the two conditions. Participants performed the experiment for either course credit, payment of 40 shekels per hour plus a bonus of 20 shekels for each condition due to the EEG recordings (approximately \$10.50 per hour and \$5.50 bonus), or volunteered to the experiment in exchange for EEG training (there were three volunteers). All participants gave their informed consent after the procedures of a protocol approved by the Ethics Committee at Tel Aviv University. All participants had normal or corrected-to-normal visual acuity and reported normal color vision. One participant was excluded from the experiment because of more than 25% rejection rate due to eyeblinks or eye movements in one of the cue-present or cue-absent conditions.

2.2 | Apparatus

Stimuli were presented on 23-inch light emitting diode monitor with a 120 Hz refresh rate, using 1,920 × 1,080 resolution graphics mode. Participants were seated approximately 60 cm from the monitor.

2.3 | Stimuli and procedure

2.3.1 | Filtering change-detection task

We used a bilateral change-detection task (Vogel & Machizawa, 2004; Vogel et al., 2005). Each trial started with a black fixation cross (+) presented in the middle of the screen for 200 ms. Then, two black arrows were presented for 400 ms above and below the fixation cross, indicating on which side to perform the upcoming task while ignoring the other side (right or left, with equal probabilities). The arrows were followed by a black fixation cross that appeared for a random interval (300, 400, or 500 ms). Then, a memory array containing colored circles with a small cut-out size (i.e., targets) in different orientations appeared for 200 ms, and participants were asked to remember only the colors of the targets that appeared on the side indicated by the arrows. Then, the memory array disappeared for 900 ms (retention interval), followed by a test array in which a test item appeared at each side of the fixation at one of the previous locations of the targets in the memory array. The test array remained on the screen until a response was emitted, followed by a blank screen for 1,000 ms until the beginning of the next trial.

Participants made an unspeeded response via button press (*Z* and */* on the computer keyboard, counterbalanced across participants) to indicate whether the color of the test item on the side indicated by the arrows was the same color or not (with equal probability for same and different test item) as the color of the target that appeared there in the memory array. The test item on the side not indicated by the arrows was always the same color as the color of the item that appeared there in the memory array. Participants were informed that only the color of the target could change and that the orientation of the test item was always the same as the orientation of the target that appeared at that location in the memory array. On 70% of the trials (approximately 840 trials), on each side of the fixation cross two targets were presented along with three colored circles used as distractors, (i.e., the filtering condition; 2T3D). On the rest of the trials, arrays of either two targets (2T) or five targets (5T) were presented (with equal probability, nonfiltering conditions, resulting in approximately 180 trials per each nonfiltering condition). On about two thirds of the filtering trials, two task-irrelevant probes in the form of a white triangle (with each side of the triangle subtending 0.85^{o} of visual angle) were presented on each side of the display 50 ms after the offset of the memory array. On half of these trials, the probes appeared at the targets' locations (2T3D target-probe, approximately 280 trials), and on the other half they appeared at the distractor locations (randomly selected, 2T3D distractor-probe, approximately 280 trials). The probes appeared for 50 ms. On the rest of the filtering trials, no probes appeared (2T3D no-probe, approximately 280 trials; see Figure 1).

The targets and the distractors had a radius of approximately 0.75^{o} of visual angle, and the triangle opening of the targets was one sixth of the size of the targets. All stimuli were randomly positioned independently on each side within a 5.25^{o} × 16.15^{o} visual angle region on the video monitor upon a gray background (RGB values: 179, 179, 179), with the constraint that the minimum distance between each two stimuli was at least 2.85^{o} of visual angle (center to center). The color of each stimulus was randomly selected (without replacement and independently on each side) from a set of eight colors (dark green: 0, 104, 56; red: 255, 0, 0; green: 0, 255, 0; blue: 0, 0, 255; yellow: 255, 255, 0; cyan: 0, 255, 255; pink: 255, 0, 255; brown: 102, 51, 0). On changed trials, the changed item was replaced with a color not presented in the memory array on that side. On each cue-present and cue-absent condition, a total of 1,200 trials were presented in 20 experimental blocks of 60 trials each with all conditions (2T, 2T3D no-probe, 2T3D target-probe, 2T3D distractor-probe, 5T) randomly intermixed. Stimuli were randomly selected at the beginning of each trial, with the restrictions that the same type of conditions must appear on each side of the fixation and that any color could appear no more than once on each side of fixation.

In the cue-present condition, to cue the appearance of the upcoming filtering trial, the fixation cross that appeared along with the arrows appeared in orange (255, 153, 51), instead of in black (i.e., warning cue). In addition, to cue the spatial positions of the distractors, the distractors appeared within placeholders in the form of black frames (see Figure 1a). The placeholders appeared at fixed locations (i.e., location cue) in all conditions of the cue-present condition (2T, 2T3D no-probe, 2T3D target-probe, 2T3D distractor-probe, 5T; the fixed locations were randomly determined for each participant). Namely, in the cue-present condition, the placeholders appeared continuously on filtering and nonfiltering trials. Note that the targets never appeared within the placeholders. Thus, the spatial positions of the distractors, but not the targets, were known in advance. The spatial positions of the targets were randomly determined on each trial, with the restriction that there would be no overlap between the positions of the placeholders and the positions of the targets. All placeholders had a radius of approximately 1^{o} of visual angle and had a thickness of about 0.02^{o} of visual angle, and the distractors were positioned in the center of the placeholder. Participants were told that the placeholders will appear at fixed positions throughout all of the cue-present blocks, that only the distractors will appear within the placeholders, and that the targets will never appear within the placeholders. Moreover, participants were highly encouraged to use the location cue and the warning cue in order to maximize their performance in the filtering trials. Thus, participants were cued about the appearance of the upcoming filtering trial and knew in advance where the distractors, but not the targets, will appear.

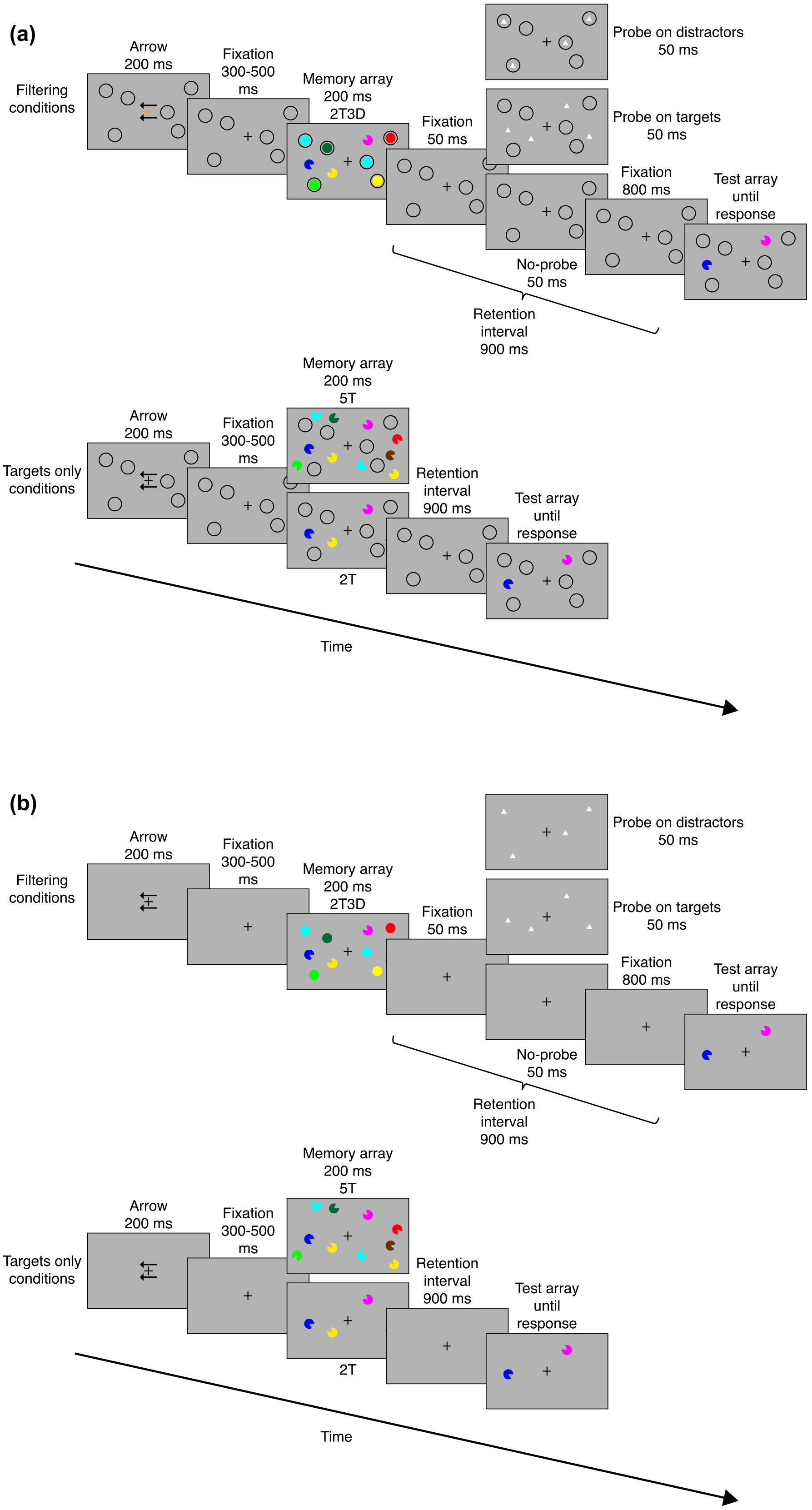

FIGURE 1 Trial sequence in the (a) cue-present and (b) cue-absent conditions. (a) Example for a filtering (i.e., two targets with three distractors) and targets-only trial (i.e., two targets or five targets) in the cue-present condition. To cue the locations of the distractors, the distractors appeared within black frames (i.e., placeholders). The placeholders appeared in fixed locations in all three conditions (i.e., two targets, five targets, or two targets with three distractors). To cue the appearance of the upcoming filtering trials, the fixation cross that appeared along with the arrows appeared in orange instead of in black (i.e., warning cue). (b) Example for a filtering and targets-only trial in the cue-absent condition. In both cue-present and cue-absent conditions on two thirds of the filtering trials, 50 ms after the offset of the memory array, two task-irrelevant probes in the form of white triangles appeared on each side of the memory array for 50 ms

Participants were asked to focus on the fixation cross throughout the whole trial and to minimize blinking and eye movements as much as possible. They were encouraged to blink and move their eyes during the 1,000-ms intervals between the trials and in the breaks between the blocks. Order of the conditions (i.e., cue-absent condition first or cue-present condition first) was counterbalanced between participants. Analysis showed that the order of the conditions did not interact with the Cue × Condition interaction in either of the cue-present and cue-absent conditions. Therefore, we analyzed the data across the order of the conditions. Fifteen practice trials were given before each session.

2.3.2 | Visual working memory capacity estimates: Change-detection task

Before the first session of the filtering change-detection task, participants performed a change-detection task with colored squares (e.g., Fukuda & Vogel, 2009; Luck & Vogel, 1997; Vogel et al., 2001) in order to estimate their visual WM capacity. Participants were presented with arrays of four or eight colored squares for 150 ms (memory array), the squares then disappeared for 900 ms (retention interval), and then a colored square (a test probe) appeared at one of the previous locations of the items in the memory array. Participants made an unspeeded response via button press (*Z* and */* on the computer keyboard, counterbalanced across participants) to indicate whether the color of the test item was the same as the color of the square that appeared at the same location in the memory array (with equal probability for same and different test probes). Sixty trials were presented for each array size in one intermixed block. Each color square subtended approximately $1.24^{\circ} \times 1.24^{\circ}$ of visual angle and was randomly positioned within a $16.6^{\circ} \times 16.6^{\circ}$ region on the video monitor upon a gray background with the constraint that the minimal distance between each two stimuli was at least 2° of visual angle (center to center). The color of each square was randomly selected (without replacement) from a set of nine colors: black, blue, brown, cyan, green, orange, pink, red, and yellow. On changed trials, the changed item was replaced with a color not presented in the memory array. The accuracy for each individual was transformed into a *K* estimate (separately for each set size) following standard formula (Cowan, 2001; Pashler, 1988). The formula is $K = S \times (H - F)$, where K is the memory capacity, S is the size of the memory array, H is the observed hit rate, and F is the false alarm rate. These two values were averaged to form a single visual WM capacity estimate (*K*).

2.4 | Electroencephalography recordings

The EEG was recorded inside a shielded Faraday cage using a BioSemi ActiveTwo EEG recording system (BioSemi B. V., Amsterdam, The Netherlands). Data were recorded from 32 scalp electrodes at a subset of locations out of the extended 10–20 system, including mostly occipital and parietal sites (in which the P1, N1, N2pc, and the CDA are most pronounced): Fp1, Fp2, AF3, AF4, F3, F4, F7, F8, Fz, FCz, C3, C4, Cz, T7, T8, P1, P2, P3, P4, P5, P6, P7, P8, Pz, PO3, PO4, PO7, PO8, POz, O1, O2, and Oz. In addition, the horizontal electrooculogram (EOG) was recorded from electrodes placed 1 cm to the left and right of the external canthi to detect horizontal eye movement, and the vertical EOG was recorded from an electrode below the left eye to detect blinks and vertical eye movements. The single-ended voltage was recorded between each electrode site and a common mode sense electrode (CMS/DRL). Data were digitized at 256 Hz.

Offline signal processing and analysis were performed using EEGLAB Toolbox (Delorme & Makeig, 2004), ERPLAB Toolbox (Lopez-Calderon & Luck, 2014), and custom MATLAB (The Mathworks, Inc.) scripts. All electrodes were referenced offline to the average of the left and right mastoids. For analysis of the P1 and N1 components, the continuous data were segmented into epochs from −100 to +300 ms relative to onset of the probe array, and for analysis of the CDA component, the continuous data were segmented into epochs from −200 to +1,100 ms relative to the onset of the memory array. In the analysis of the P1 and N1 components, data were normalized relative to a 100-ms window before the onset of the probe array. In the analysis of the CDA, data were normalized relative to a 200-ms window before the onset of the memory array. Artifact detection was performed using a pick-to-pick analysis, based on a sliding window of 200 ms wide with a step of 100 ms. Threshold activity for rejecting trials was adjusted for each participant and was either 60 and 80 μV or 80 and 100 μV at the EOG electrodes and at the analyzed electrodes (P7, P8, PO7, PO8, PO3, and PO4, respectively). For each participant, the same rejection thresholds were used in both EEG conditions. In the P1 and N1 analysis, this procedure resulted in a mean rejection rate of 2.69% (*SD* = 2.00) and 3.33% (3.25) for the cue-absent and cue-present conditions, respectively. In the CDA analysis, this procedure resulted in a mean rejection rate of 8.57% (5.09) and 7.41% (6.77) for the cue-absent and cue-present conditions, respectively. The P1 and N1 analysis included at least 218 trials per each relevant condition (2T3D no-probe, 2T3D probe at target, 2T3D probe at distractor) per participant in the cue-absent and cue-present conditions. The CDA analysis included at least 110 trials per each relevant condition (2T, 2T3D no-probe, 5T) per participant in the cue-absent and cue-present conditions. The epoched data were then averaged and low-pass filtered using a noncausal Butterworth filter (12 dB/oct) with a half-amplitude cutoff at 30 Hz. Only correct trials with reaction times (RTs) higher than 100 ms or lower than 3,000 ms were included in the analysis.

2.5 | ERP analysis

2.5.1 | P1/N1 analysis

To isolate the activity resulting from the probe array from the activity resulting from the memory array, we followed the procedures of Fukuda and Vogel (2009). We computed the difference between each of the probe-present conditions (2T3D target probe, 2T3D distractor probe), and the probe-absent filtering condition (2T3D no-probe). Thus, the overlapping activity from the memory array, which was equivalent for the probe-present and probe-absent filtering trials, would be eliminated by the subtraction, resulting in only the ERPs for the probe array. The amplitude of P1/N1 as attentional modulation to the probe was measured as the difference in mean amplitude between the contralateral and ipsilateral waveforms recorded at the analyzed electrodes (PO7/PO8, P7/P8, PO3/PO4) from 100–300 ms after the onset of the probe array.

2.5.2 | CDA analysis

The CDA was measured for each of the relevant conditions (2T, 2T3D no-probe, and 5T) in each condition as the difference in mean amplitude between the ipsilateral and contralateral waveforms recorded at the analyzed electrodes (PO7/PO8, P7/P8, PO3/PO4) from 400–1,000 ms after the onset of the memory array. The CDA amplitude was measured in the probe-absent trials only to avoid any overlap with the probe onset.

2.6 | Behavioral analysis

Trials with RTs lower than 100 ms or higher than 3,000 ms were removed from further analysis, resulting in removal of 0.3% of the trials. Then, mean accuracy rates were calculated for each participant and for each combination of the independent variables to allow statistical analysis. This data preparation was conducted using *prepdat*—an *R* package for preparing experimental data for statistical analysis (Allon & Luria, 2016).

3 | RESULTS

3.1 | Behavioral results

3.1.1 | Filtering change-detection task

Accuracy levels for Cue (absent, present) × Condition (2T, 2T3D, 5T) are presented in Figure 2. Accuracy rates were analyzed using a repeated measures analysis of variance (ANOVA) with cue (absent, present) and condition (2T, 2T3D, 5T) as within-subject independent variables. Mauchly's test indicated that the assumption of sphericity was not violated (χ^2 (2) = 0.98, $p = 0.61$; χ^2 (2) = 2.14, $p = 0.34$; for the main effect of condition and the Cue × Condition interaction, respectively). The ANOVA revealed a main effect for condition, $F(2, 36) = 476.63$, $MSE = 0.00136$, $p < 0.001$, $\eta_p^2 = 0.96$. Most importantly, there was a Cue × Condition interaction, $F(2, 36) = 15.59$, $MSE = 0.00126$, $p < 0.001$, $\eta_p^2 = 0.46$. Planned comparisons showed that the filtering cost (i.e., the difference between the 2T and the 2T3D condition) was smaller in the cue-present relative to the cue-absent blocks, $F(1, 18) = 44.33$, $MSE = 0.000852$, $p < 0.001$, $\eta_p^2 = 0.71$, suggesting that the warning cue along with the location cue improved filtering performance, corroborating the results from Allon and Luria (2017). There were no differences in the 2T and 5T conditions between the cue-present and cue-absent blocks, $F(1, 18) = 3.98$, $MSE = 0.000470$, $p = 0.06$, $\eta_p^2 = 0.18$; $F < 1$; in the 2T and 5T conditions, respectively.

The behavioral results showed that the filtering cost in visual WM was reduced when participants knew that distractors are about to appear and where they appear, thus replicating the results from Allon and Luria (2017).

A possible alternative explanation for these findings is that the probes might have created a mask, especially when they appeared within the placeholders (i.e., in the cue-present 2T3D distractor-probe condition). In addition, probes within the placeholders might have been treated as changes to existing items, whereas probes outside the placeholders might have been treated as new items appearing in the display. In order to test these alternative explanations, accuracy rates were reanalyzed while taking the three filtering conditions

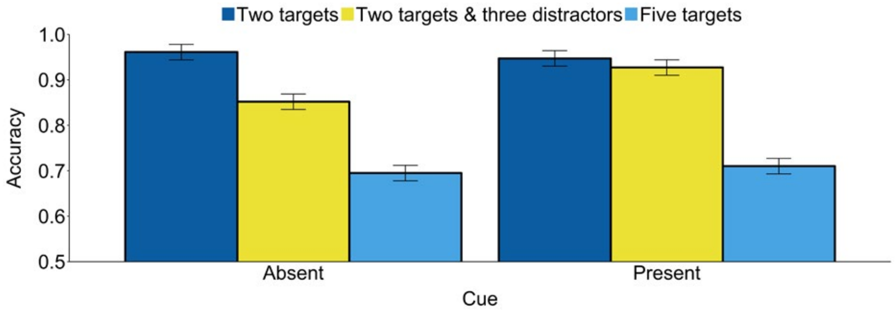

FIGURE 2 Behavioral results. Accuracy as a function of cue and condition. Error bars represent the 95% confidence intervals according to Loftus and Masson (1994)

into consideration instead of collapsing across the three filtering conditions using a repeated measures ANOVA with Cue (absent, present) × Condition (2T, 2T3D no-probe, 2T3D target-probe, 2T3D distractor-probe, 5T) as within-subject independent variables. Means and *SD* can be found in online supporting information, Table S1. Mauchly's test indicated that the assumption of sphericity was violated (χ^2 (9) = 17.08, $p = 0.04$, $\varepsilon = 0.70$; χ^2 (9) = 39.32, $p < 0.001$, $\varepsilon = 0.54$; for the main effect of condition and the Cue × Condition interaction, respectively), so we applied the Greenhouse-Geisser correction. The ANOVA revealed a main effect for condition, $F(2.83, 50.94) = 303.57$, $MSE = 0.486$, $p < 0.001$, $\eta_p^2 = 0.94$, and a Cue × Condition interaction, $F(2.16, 38.99) = 17.35$, $MSE = 0.001262$, $p < 0.001$, $\eta_p^2 = 0.49$. Post hoc comparisons corrected to FDR (false discovery rate) *p* value of 0.0125 (Benjamini & Hochberg, 1995) showed that, in the cue-present, accuracy in the 2T3D distractor-probe condition ($M = 0.92$, $SD = 0.05$) was similar to accuracy in the 2T3D target-probe condition ($M = 0.92$, $SD = 0.04$; $F < 1$), suggesting that probes inside the placeholders did not create a mask relative to probes outside the placeholders and resulted in similar performance. Furthermore, in the cue-present, accuracy in the 2T3D no-probe condition ($M = 0.93$, $SD = 0.05$) was similar to accuracy in the 2T3D probe-present condition ($M = 0.92$, $SD = 0.051$; collapsed across the 2T3D distractor-probe and 2T3D target-probe conditions; $F(1, 18) = 1.61$, $MSE = 0.0003$, $p = 0.22$, $\eta_p^2 = 0.08$, suggesting that the probes did not create a mask.

3.1.2 | Visual WM capacity estimates: Change-detection task

The mean visual WM capacity estimate was 2.12 ($SD = 0.57$) with a range from 0.86 to 3.53. We did not find consistent correlations between *K* and estimates of filtering using the EEG neural markers, and therefore we do not further report this measure. The mean visual WM capacity of participants in the current study was low relative to the mean capacity estimates in previous studies from our lab ($M = 2.69$, $SD = 0.72$ in Allon & Luria, 2017; $M = 2.76$, $SD = 0.82$ in Allon, Vixman, & Luria, 2018; $M = 2.70$, $SD = 0.81$ in Vaskevich & Luria, 2018), suggesting that the current group of participants was relatively a low-capacity group.

3.2 | ERP results

3.2.1 | P1/N1

The P1/N1 waveforms for Cue (absent, present) × Probe (at target, at distractor) are presented in Figure 3a, and the mean P1/N1 amplitudes are presented in Figure 3b. The contralateral and ipsilateral waveforms are presented in supporting information Figure S1. A repeated measures ANOVA with cue (absent, present) and probe (at target, at distractor) as within-subject independent variables on the P1/N1 mean amplitude as a dependent measure revealed a Cue × Probe interaction, $F(1, 18) = 5.33$, $MSE = 0.116227$, $p = 0.03$, $\eta_p^2 = 0.22$. Planned comparisons showed that the P1/N1 amplitude for probes at the targets was similar in the cue-absent and cue-present conditions, $F(1, 18) = 1.48$, $MSE = 0.151$, $p = 0.23$, $\eta_p^2 = 0.076$, indicating that the cue did not enhance allocation of spatial attention to the targets. Importantly and according to our hypothesis, the P1/N1 amplitude for probes at the distractors was lower in the cue-present condition relative to the P1/N1 amplitude for probes at the distractors in the cue-absent condition, $F(1, 18) = 4.75$, $MSE = 0.086$, $p = 0.04$, $\eta_p^2 = 0.209$, indicating that the cue was able to reduce allocation of spatial attention to the distractors. There were no main effects for cue and probe ($F < 1$; $F(1, 18) = 1.40$, $MSE = 0.094909$, $p = 0.25$, $\eta_p^2 = 0.07$, for the cue and probe, respectively).

The results indicated a reduction of the P1/N1 amplitude in the cue-present condition relative to the cue-absent condition for probes at distractors. As for the P1/N1 amplitude for probes at targets, the P1/N1 amplitude was similar in the cue-present and in the cue-absent conditions. These findings suggest that reactivating the distractor filtering settings using a combined temporal (i.e., the warning cue) and a spatial (i.e., fixed location cue) cue resulted in a reduction of spatial

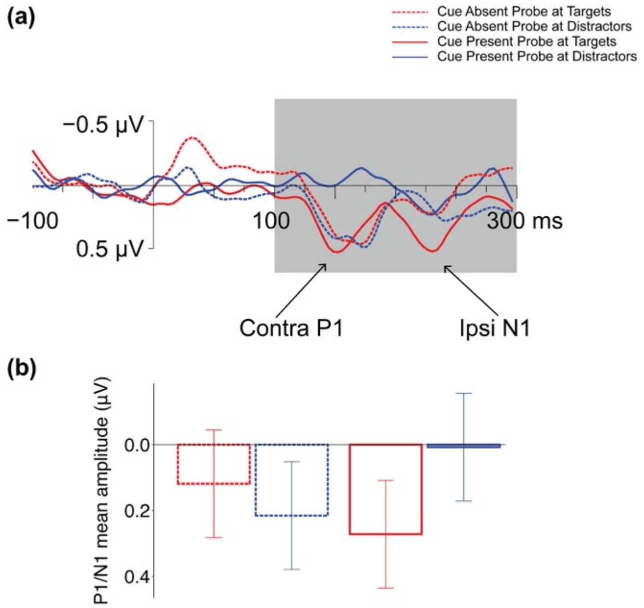

FIGURE 3 (a) Grand-averaged ERP difference waves (contralateral minus ipsilateral) time-locked to the probe array for Cue (absent, present) × Probe (at target, at distractor). Gray shading indicates the time range for calculating the mean amplitude. Negative voltage is plotted upward. (b) Mean P1/N1 amplitude in µV for Cue (absent, present) × Probe (at targets, at distractors). Error bars represent 95% confidence intervals calculated according to Loftus and Masson (1994)

attentional resources to the distractors rather than allocating additional attentional resources to the targets. Furthermore, since we were able to detect this effect in the P1/N1 wave, which is considered as a neural marker for early allocation of spatial attention, these findings suggest that reactivation of the filtering settings also occurs in early stages in the processing stream.

3.2.2 | CDA

The CDA waveforms in the Cue (absent, present) × Condition (2T, 2T3D no-probe, 5T) are presented in Figure 4, and the mean CDA amplitudes are presented in Table S2. As one can see in the waveforms, the filtering cost (calculated here as the difference in the CDA amplitude between the 2T condition and the 2T3D no-probe condition) was smaller in the cue-present condition relative to the cue-absent condition, thus suggesting that indeed the distractor filtering settings activated by the cue resulted in less irrelevant items entering into visual WM and corroborating the behavioral accuracy reduction in the filtering cost. However, this pattern was not significant, perhaps due to a relatively low visual WM capacity sample size in the current study ($M = 2.12$, $SD = 0.57$). The mean CDA amplitude was analyzed in a repeated measures ANOVA with cue (absent, present) and condition (2T, 2T3D no-probe, 5T) as within-subject independent variables. Mauchly's test indicated that the assumption of sphericity was not violated (χ^2 (2) = 4.48, $p = 0.10$; χ^2 (2) = 4.22, $p = 0.12$; for the main effect of condition and the Cue × Condition interaction, respectively). The ANOVA revealed a main effect of condition, $F(2, 36) = 4.47$, $MSE = 0.1814$, $p = 0.01$, $\eta_p^2 = 0.19$. Planned comparisons showed that the CDA amplitude in the 2T3D no-probe condition ($M = -1.34$ µV, $SD = 0.17$) was higher than the CDA amplitude in the 2T condition ($M = -1.18$ µV, $SD = 0.17$; $F(1, 18) = 2.27$, $MSE = 0.22143$, $p = 0.14$, $\eta_p^2 = 0.11$), indicating a filtering cost, and similar to the CDA amplitude in the 5T condition ($M = -1.47$ µV, $SD = 0.17$; $F(1, 18) = 3.35$, $MSE = 0.09418$, $p = 0.08$). In addition, the CDA amplitude in the 5T condition was higher than the CDA amplitude in the 2T condition, $F(1, 18) = 7.06$, $MSE = 0.228616$, $p = 0.01$, $\eta_p^2 = 0.28$, indicating a set size effect (e.g., Vogel & Machizawa, 2004). There was no main effect for the cue, $F(1, 18) = 2.27$, $MSE = 0.4113$, $p = 0.14$, $\eta_p^2 = 0.11$, or a Cue × Condition interaction, $F(2, 36) = 1.79$, $MSE = 0.1459$, $p = 0.18$. Planned comparisons showed that the filtering cost was similar in

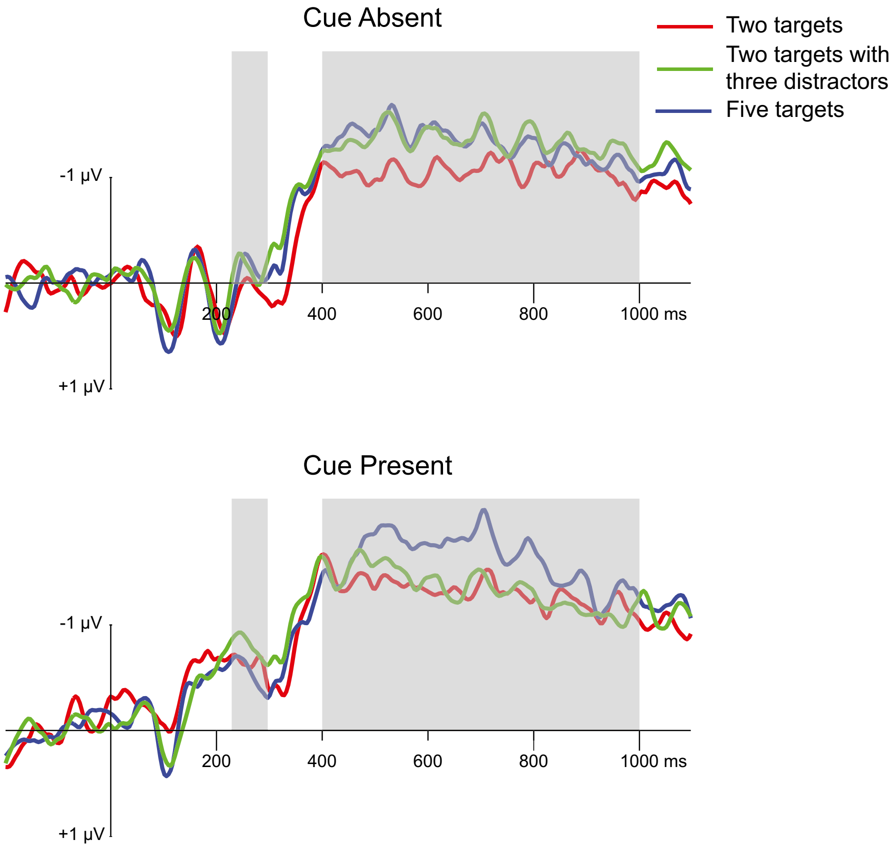

FIGURE 4 N2pc and CDA waveforms (time-locked to the memory array) in µV in the cue-absent and cue-present conditions as a function of condition (2T, 2T3D no-probe, 5T). Left gray shading indicates the time range for calculating the mean N2pc amplitude. Right gray shading indicates the time range for calculating the mean CDA amplitude. Negative voltage is plotted upward

the cue-present condition and in the cue-absent condition, $F(1, 18) = 1.81$, $MSE = 0.181809$, $p = 0.19$. There were no differences in the 2T and 5T conditions between the cue-present and cue-absent conditions, $F(1, 18) = 3.33$, $MSE = 0.184894$, $p = 0.08$; $F(1, 18) = 3.15$, $MSE = 0.267621$, $p = 0.09$; in the 2T and 5T conditions, respectively.

3.3 | Post hoc analysis

A visual inspection of the waveforms in Figure 4 suggested that the N2pc amplitude in the cue-present condition was higher than the N2pc amplitude in the cue-absent condition. The only difference in the spatial domain between the cue-present and cue-absent conditions was the presence of the placeholders. Thus, it is reasonable to suggest that the difference in the N2pc between the cue-present and cue-absent reflected the processing of the placeholders. We decided to post hoc compare the N2pc component between the cue-present and cue-absent conditions. The N2pc is characterized by a greater negativity in the contralateral recorded electrodes to the attended stimulus than the negativity when the attended stimulus is ipsilateral and is typically observed within 200–300 ms after the onset of the stimulus. It is relatively accepted to interpret the N2pc as an index of deployment of covert spatial visual attention (Luck & Hillyard, 1994a, 1994b; Woodman & Luck, 1999, 2003).

3.3.1 | N2pc analysis

The N2pc was measured for each of the relevant conditions (2T, 2T3D no-probe, and 5T) in each condition (cue-present, cue-absent) as the difference in mean amplitude between the ipsilateral and contralateral waveforms recorded at the analyzed electrodes (PO7/PO8, P7/P8, PO3/PO4) from 230–290 ms after the onset of the memory array. The N2pc amplitude was measured in the probe-absent trials only to avoid any overlap with the probe onset. The same results of the N2pc mean amplitude were obtained with time windows of 220–280 ms and 240–300 ms, and therefore we decided to present the results of the 230–290 ms analysis, where the effect was maximal.

3.3.2 | N2pc results

The N2pc waveforms in the Cue (absent, present) × Condition (2T, 2T3D no-probe, 5T) are presented in Figure 4. The mean N2pc amplitudes were analyzed in a repeated measures ANOVA as in the CDA analysis. Mauchly's test indicated that the assumption of sphericity was not violated (χ^2 (2) = 0.57, $p = 0.75$; χ^2 (2) = 3.09, $p = 0.21$; for the main effect of condition and the Cue × Condition interaction, respectively). The ANOVA revealed a main effect in the cue, $F(1, 18) = 9.92$, $MSE = 1.12251$, $p = 0.005$, $\eta_p^2 = 0.35$; $M = -0.05$, $SD = 1.01$ and $M = -0.68$, $SD = 1.08$; mean amplitudes for the cue-absent and cue-present conditions, respectively, possibly suggesting that participants were spatially processing the placeholders. There was no main effect for condition, $F(2, 36) = 1.20$, $MSE = 0.27257$, $p = 0.31$, $\eta_p^2 = 0.06$, or Cue × Condition interaction, $F(2, 36) = 1.16$, $MSE = 0.16923$, $p = 0.32$, $\eta_p^2 = 0.06$. Note that, since this comparison was done post hoc after observing the ERP waveforms, one should be particularly careful when interpreting this finding.

4 | DISCUSSION

The purpose of the current study was to investigate the underlying processes involved in improving filtering performance. To the best of our knowledge, the current study is the first to provide neural evidence regarding the processes underlying the improvement of the filtering performance, since previous research mainly focused on understanding the filtering mechanism in itself (e.g., Gaspar et al., 2016; Gulbinaite, Johnson, de Jong, Morey, & van Rijn, 2014; Liesefeld et al., 2014). Participants performed a bilateral change-detection task in which either two targets, five targets, or two targets along with two distractors were presented in the memory array while their ERPs were recorded. In the cue-present condition, a combined spatial and a temporal cue was used to cue the distractors and reactivate the filtering settings, whereas in the cue-absent condition, no cues were provided regarding the distractors. We measured the P1/N1 amplitude to task-irrelevant probes that were briefly flashed during the memory array either on the locations of the targets or on the locations of the distractors. This enabled us to measure whether spatial attention in the cue-present condition, as was reflected by the P1/N1 amplitude to the probes, was distributed more over the locations of the targets or over the locations of the distractors relative to the distribution of spatial attention in the cue-absent condition. In accordance with our hypothesis, the results showed that, relative to the P1/N1 amplitude in the cue-absent condition, in the cue-present condition there was a reduction of the P1/N1 amplitude for probes at distractors and a similar P1/N1 amplitude for probes at targets.

The results of the CDA showed a reduced filtering cost in the cue-present condition relative to the cue-absent condition, yet this pattern did not reach statistical significance. A possible reason could be due to a relatively low visual WM capacity sample size encountered in the current study. A primary characteristic of the CDA is that its amplitude increases as more items are encoded into WM, until it reaches an asymptote. This asymptote was found to relate to individual differences in visual WM capacity (see Luria et al., 2016, for a meta-analysis; Vogel & Machizawa, 2004). Namely, the CDA amplitude further increases for high- relative to low-capacity individuals as more items are encoded, corroborating findings showing higher storage and processing abilities observed among high-capacity individuals (Luck & Vogel, 2013). Therefore, we suggest the relatively low-capacity group observed in the current study did not allow us to detect a significant pattern.

The results from Allon and Luria (2017) suggested that participants hold a "filtering setting" that specifies which are the targets and which are the distractors (e.g., "Ignore the complete circles that appear inside the placeholders, focus on the circles with a small cut-out size"). The filtering setting can be held active to suppress the distractor processing only for a limited duration. A possible explanation for the limited activation of the spatial filtering settings lies in findings from previous studies, which suggested that attentional resources are allocated to expected distractor locations before they can be ignored, constituting a major factor in the failure to filter irrelevant information (i.e., the attentional white bear phenomenon; Benoni, 2018; Humphreys, Stalmann, & Oliviers, 2004; Lahav, Makovski, & Tsal, 2012; Lahav & Tsal, 2013; Tsal & Makovski, 2006). Another option is that the filtering setting may simply deteriorate with time. Presumably, reactivating the filtering settings improves performance by either refreshing the filtering setting or by overcoming the implications of the attentional white bear phenomenon. Importantly, our P1/N1 results indicate that reactivating the filtering setting is an early process that operates mainly on the distractors.

These findings are consistent with previous research indicating that, in the context of visual WM, the essential process for effective filtering of irrelevant items is reducing spatial attentional resources to the distractors rather than allocating additional spatial attentional resources to the targets (Allon & Luria, 2017; Fukuda & Vogel, 2009; Gaspar et al., 2016). The reduction of attentional resources to the distractors was already detected in the P1/N1 component, which is typically considered as a preliminary neural marker for allocation of spatial attention (Hillyard et al., 1998; Luck & Kappenman, 2013). Thus, the findings from the current study suggest that reactivating the filtering settings also occurs at early stages of the processing stream. Another support for reactivation of the filtering settings at early processing stages comes from our previous study (experiment 3 in Allon & Luria, 2017), in which increasing the time available for reactivating the filtering settings did not further improved performance. Additionally, previous findings (Fukuda & Vogel, 2011) provided evidence that the filtering process already fails at an early processing stage. The current study provided evidence that ameliorating the failure of the filtering process improved filtering performance, therefore supporting the notion that improving of filtering performance occurs at early processing stages.

Accordingly, the findings from Fukuda and Vogel (2011), along with the findings from the current study, suggest that the filtering mechanism in general seems to be determined very early in the processing stream. While most of the studies on WM investigate its capacity storage component, in recent years there has been a growing literature demonstrating the importance of controlling what enters WM in determining performance (Allen, Baddeley, & Hitch, 2017; Feldmann-Wüstefeld & Vogel, 2018; Robison & Unsworth, 2017; Unsworth & Robison, 2017; Vissers, Gulbinaite, van den Bos, & Slagter, 2017).

The results of the current study relate to other ERP components involved in the filtering process. For example, the Pd component is considered to be a neural marker for active suppression of distractors, and it appears as an enhanced positive wave in posterior electrodes contralateral to the distractors and starting around 200 ms poststimulus (Hickey, Di Lollo, & McDonald, 2009; see Sawaki, Geng, & Luck, 2012, for a discussion on the variability in the Pd onset). Furthermore, Liesefeld et al. (2014) have found a prefrontal biasing signal in the form of a positive wave in frontal electrodes appearing between 245–288 ms poststimulus. They argued that this positivity at frontal sites is responsible for initiating the filtering process, triggered by an earlier signal in posterior electrodes that is in charge for detecting the distractors. In the current study, the cues helped direct spatial attention away from the distractors, as indicated by the reduction in the P1/N1 waves, which are considered as a neural marker for early allocation of spatial attention mostly pronounced in posterior electrodes. Since the Pd component and the biasing signal appear later than the P1/N1 waves, we suggest that the reduction of the P1/N1 found for probes at distractors in the cue-present condition decreases and possibly eliminates the need to actively suppress the distractor at later processing stages, as indexed by the Pd and the biasing signal.

Unlike previous studies in which a cue was used to mark the one target item in a memory display in which all items were relevant (Ravizza, Uitvlugt, & Hazeltine, 2016; Schmidt, Vogel, Woodman, & Luck, 2002; Woodman, Vecera, & Luck, 2003), the cues in the current study pointed to irrelevant items in a memory display that included both relevant and irrelevant items. Previous studies (e.g., Di Russo, Martínez, & Hillyard, 2003; Hillyard & Anllo-Vento, 1998) have shown that the P1 and N1 components are enhanced in response to an attended location of an upcoming target (i.e., cued target) relative to unattended items. Hence, we suggest that, if the cues in the current study were applied to cue the targets, it would have resulted in enhanced P1/N1 wave as well.

A possible explanation for the difference in the filtering cost between the cue-present and the cue-absent conditions may be due to alerting differences resulting from the location cue being manipulated across blocks rather than within blocks, and the instructions to the participants encouraging them to use the cues in order to improve their performance on filtering trials. However, considering the results from our recent study (Allon & Luria, 2017), we do not think that this explanation is likely to account for the differences in the filtering cost. Namely, in Allon and Luria (2017), we applied a nonbilateral change-detection task with the same experimental design and instructions (i.e., encouraging participants to use the cues in order to maximize performance on filtering trials) as in the current study. Specifically, in experiment 1 and in the cue-present blocks in experiment 5 in which only the location cue was used, we applied only the location cue and kept the placeholders fixed throughout the whole cue-present blocks. The results showed that the filtering cost in the cue-present condition was similar to the filtering cost in the cue-absent condition. If encouraging participants to use the cue to maximize their performance on filtering trials would have caused an alerting difference between the cue-present and cue-absent blocks, then this should have resulted in improved filtering cost in the cue-present blocks already in those experiments. Similar results were received in experiment 4 in which in the cue-present blocks only the temporal cue was applied and the distractors appeared in fixed locations without the placeholders. Therefore, we do not think the results of the current study can be explained by alerting differences.

The results of the current study relate to recent findings by Wang and Theeuwes (2018, experiment 2 and experiment 3). Wang and Theeuwes implemented a visual search task in which the location of a color singleton distractor was explicitly cued on a trial-by-trial basis. The results indicated that this trial-by-trial cueing of the distractor location did not reduce reaction time for finding the target. At first, these findings might seem at odds with the results of the current and our recent study (Allon & Luria, 2017). Importantly, however, there are significant differences between the two studies. First, the paradigm in the current study (i.e., change detection) is somewhat different than the additional singleton paradigm used in Wang and Theeuwes (2018), and different dependent measures were used (i.e., accuracy rates vs. RTs). Second, in a previous study from the same research group (Munneke, Van der Stigchel, & Theeuwes, 2008), they applied a trial-by-trial cueing of the distractor location in a visual search task. Similar to the current findings and in contrast to Wang and Theeuwes (2018), the cue in Munneke et al. (2008) was found to reduce the distractor interference. As pointed out by Wang and Theeuwes, it is possible that the distractor used in Munneke et al. was a nonsilent distractor as opposed to the color singleton used in the Wang and Theeuwes study. The targets and the distractors in the current study were distinguished from each other by their shape, which is known to be a less salient feature than a color singleton (Theeuwes, 1992). Therefore, it is plausible to assume that the distractors used in the current study were not as salient as the color singleton distractor used in Wang and Theeuwes (2018), which can explain the gap between the findings of the two studies, enabling the cues to improve the filtering cost.

Note that previous studies suggested that the P1 and N1 components might reflect the operation of different processes (Hillyard & Anllo-Vento, 1998; Hillyard et al., 1998; Lasaponara, Chica, Lecce, Lupianez, & Doricchi, 2011; Lasaponara et al., 2017; Luck et al., 1994; Luck & Yard, 1995; Mangun & Hillyard, 1991; Slagter, Prinssen, Reteig, & Mazaheri, 2016; Van Voorhis & Hillyard, 1977). For example Luck et al. (1994) have found that the P1 wave was smaller for invalid cued targets relative to neutral trials, and that there was no increase in the P1 in response to valid cued targets, whereas the N1 wave was increased for valid cued targets relative to neutral trials, with no reduction in the invalid cued trials. Luck et al. (1994) suggested that the P1 reflected suppression of the ignored locations and the N1 reflected facilitation of processing at attended locations. Since in the current study we used a lateralized display resulting in positive waveforms for both the P1 and N1 difference waves, it was not possible to dissociate the P1 and N1 in the current study. It might be interesting for future studies to investigate how reactivating the filtering settings affects each of these components separately.

To summarize, research on the filtering mechanism has mainly focused on studying the filtering mechanism per se. The results of the current study add a layer to the existing literature on filtering irrelevant information and visual WM by specifying the underlying processes that enable the improvement of filtering performance.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1

Table S1

Table S2

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