What Does Ipsilateral Delay Activity Reflect? Inferences from Slow Potentials in a Lateralized Visual Working Memory Task

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Abstract

■ In the lateralized change detection task, two item arrays are presented, one on each side of the display. Participants have to remember the items in the relevant hemifield and ignore the items in the irrelevant hemifield. A difference wave between contralateral and ipsilateral slow potentials with respect to the relevant items, the contralateral delay activity, can be calculated. As its amplitude varies with the number of items held in working memory (WM) and reaches its asymptote with WM capacity, it is considered a pure neural correlate of visual WM load. However, in addition to this contralateral delay activity, load-dependent activity has also been observed over the hemisphere ipsilateral to the relevant hemifield, suggesting that the ipsilateral hemisphere is also involved in memory-related processes. This ipsilateral activity might either reflect a bilateral processing of relevant or else a lateralized processing of irrelevant, to-be-filtered-out items. As in the lateralized change detection task, the number of items on both sides of the display is typically identical, it was not possible to decide between these alternatives yet. To disentangle the influence of relevant and irrelevant items, we orthogonally varied the number of both types of items. Processing of relevant items caused purely contralateral load-dependent activity. Ipsilateral slow potentials were influenced by the number of irrelevant items only if visual WM load was low, but not if it was high. This suggests that whether irrelevant items are processed or filtered out depends on visual WM load. ■

INTRODUCTION

Temporarily representing objects in visual working memory (WM) is a key ability in daily life. However, because this store's capacity is highly limited, we can only represent some of the objects in our environment. It is possible to exert some control over which information to select and which information to ignore, with selection mechanisms that regulate access to visual WM. The properties of visual WM have been extensively examined via the so-called change detection task. In this task, participants see a memory array of several objects that they have to store in memory for a short retention interval. In the ensuing test array, participants have to detect whether one object changed a feature or not. From change detection performance, it is possible to estimate how many items a tested person is able to hold in visual WM (Cowan, 2000). Sustained electrophysiological activity (slow potentials) can be measured during the retention period of this task (e.g., Rämä et al., 1997; Mecklinger & Pfeiffer, 1996; Ruchkin, Canoune, Johnson, & Ritter, 1995; Ruchkin, Johnson, Grafman, Canoune, & Ritter, 1992). The amplitudes of these negative slow potentials increase with visual WM load (e.g., Rämä et al., 1997; Mecklinger & Pfeiffer, 1996; Ruchkin et al., 1992, 1995). The observation that their amplitude is sensitive to visual WM load constitutes important evidence for the claim that these slow potentials reflect the maintenance of items in visual WM.

However, it is also possible that these slow potentials might partially reflect non-mnemonic task-general processes, such as anticipation of the test stimulus, preparation for an upcoming response, or arousal (McCollough, Machizawa, & Vogel, 2007). To extract pure memory-related activity, the lateralized change detection task was employed (e.g., McCollough et al., 2007; Vogel & Machizawa, 2004). Participants fixate the center of a bilateral display of items. The same amount of items is briefly presented in both hemifields. However, in a given trial, participants only have to remember items in one hemifield. Visual information from the relevant items is first processed in the hemisphere contralateral to the relevant hemifield, whereas information from the irrelevant items is first processed in the hemisphere ipsilateral to the relevant hemifield, which is, of course, contralateral to the irrelevant hemifield. In the following, *contralateral activity* always refers to neural activity that is observed over the hemisphere, which is contralateral to the relevant hemifield and consequentially receives the relevant items (first), and *ipsilateral activity* always refers to neural activity that is observed over the hemisphere, which is ipsilateral to the relevant hemifield and consequentially receives the irrelevant items (first). Throughout the retention interval of the lateralized

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change detection task, a posterior sustained negative slow potential over the hemisphere contralateral to the relevant hemifield has been reported (Vogel & Machizawa, 2004; Klaver, Talsma, Wijers, Heinze, & Mulder, 1999). By computing a difference wave—that means by subtracting ipsilateral from contralateral slow potentials—the nonspecific activity should be subtracted out (McCollough et al., 2007). Although both (difference wave and contralateral slow potential) are delay activity over the contralateral hemisphere to differentiate between both measures, we here reserve the term "contralateral delay activity" (CDA) for the difference wave. The amplitude of this negative component increases with increasing load and reaches its asymptote with the subject's personal memory capacity (Vogel & Machizawa, 2004). For these reasons, the CDA's amplitude is thought to directly reflect the amount of items kept in visual WM. It consequently is also possible to estimate how efficiently items are filtered out (e.g., Fukuda & Vogel, 2009; Vogel, McCollough, & Machizawa, 2005).

However, one aspect of this measure has recently been challenged. In the retention period of a lateralized change detection task, load effects on posterior parietal slow potentials over the contralateral as well as ipsilateral hemisphere, with regard to the relevant hemifield, were found (Robitaille, Grimault, & Jolicoeur, 2009). Because the observed bilateral activity is disguised when only the CDA is considered, Robitaille et al. (2009) caution not simply to use the ipsilateral activity as a means to control for unspecific contralateral activity. They assume that both lateralized activity and bilateral activity are related to the process of maintaining information in visual WM. As the standard lateralized change detection paradigm was employed, the number of items in the relevant hemifield was always identical to the number of items in the irrelevant hemifield, that is, their numbers were perfectly correlated. Therefore, it cannot be decided whether ipsilateral neural activity that covaries with memory load is caused by the relevant or irrelevant items. We now describe the two possible explanations in detail.

One possibility is that the relevant items might be processed bilaterally because of advantages that might arise from processing information in both hemispheres over processing in only one hemisphere. Umemoto, Drew, Ester, and Awh (2010) reported a bilateral advantage effect for storage of information in visual WM. If the visual input was provided in both hemifields, participants' visual WM performance was found to be better than if the same visual input was presented unilaterally. In the lateralized change detection design, use of both hemispheres, that is, to transfer the information from the contralateral to the ipsilateral hemisphere, might also improve the processing of the relevant items. Gratton and colleagues (Shin, Fabiani, & Gratton, 2006; Gratton, Corballis, & Jain, 1997) examined the hemispheric organization of visual memory. Similar to the lateralized change detection task, stimuli were initially presented lateralized. Critically, however, the test array was presented centrally. Despite the central presentation of the test array, the amplitude difference between old and new items of ERPs measured during the test interval were larger over the hemisphere contralateral to the hemifield of initial encoding as compared with the ipsilateral hemisphere. This finding indicates that information was stored in both hemispheres, but with a contralateral bias. These distinct yet converging lines of research indicate that bilateral processing of to-be-remembered information might, in some cases, be beneficial for task performance.

The second possibility is that irrelevant items that the underlying neural network received as perceptual input might cause neural activity over the hemisphere ipsilateral to the relevant hemifield. It is well established that, under some conditions, irrelevant, to-be-ignored stimuli are processed to a certain extent (Eriksen & Eriksen, 1974), even when they are presented rather far away from the relevant stimuli (Gatti & Egeth, 1978). However, in line with the well-examined, selective attention effect in perception (e.g., Hopfinger, Luck, & Hillyard, 2004; Hillyard, Vogel, & Luck, 1998; Moran & Desimone, 1985), attention might amplify processing of the relevant items. Allocation of attention toward a certain location might increase the number of neurons that process the stimuli at that location (Bundesen, Habekost, & Kyllingsbaek, 2005). This might lead to both an enhancement in processing and a higher cortical activation level. Concerning the lateralized change detection paradigm, the contralateral slow potentials should show a higher load-dependent activation level than the ipsilateral slow potentials.

As previously mentioned, within the lateralized change detection task, it is impossible to unravel the effects of the amount of items presented in the relevant and irrelevant hemifield, because their numbers are typically identical. We orthogonally varied the number of items in both hemifields to examine the effect of the number of relevant items independent of the effect of the number of irrelevant items and vice versa. This allows us to determine how processing of the relevant and irrelevant items influences the amplitudes of slow potentials over the contralateral and ipsilateral hemisphere, respectively.

Slow potentials contralateral to the relevant hemifield should increase with the number of relevant items, because these slow potentials are supposed to reflect the maintenance of items in visual WM. This prediction is in line with earlier research on the lateralized change detection task, as reviewed above (Robitaille et al., 2009; Vogel & Machizawa, 2004; Klaver et al., 1999). In comparison with contralateral slow potentials, the behavior of slow potentials ipsilateral to the relevant hemifield is not well understood.

(1) If irrelevant items are completely filtered out and relevant items are only processed laterally, the slow potentials over the hemisphere ipsilateral to the relevant hemifield are neither influenced by the relevant nor the irrelevant items, and their amplitude should be of equal size in all conditions.

(2) Alternatively, relevant items might be processed bilaterally. In this case, both the amplitudes of the contralateral and ipsilateral slow potentials would be a function of the number of relevant items. However, the contralateral hemisphere receives the visual input first and might therefore hold a more distinct or enhanced representation. The number of relevant items, therefore, might influence the amplitude of slow potentials over the contralateral hemisphere more strongly than over the ipsilateral one.

According to Hypotheses 1 and 2, irrelevant items are completely filtered out of visual WM, meaning that the number of irrelevant items should not influence the amplitude of the slow potentials.

(3) If irrelevant items are not filtered out but are processed to a certain degree, the amplitude of slow potentials over the hemisphere ipsilateral to the relevant hemifield should increase with the number of irrelevant items. However, because attention is focused on the relevant hemifield, processing of relevant items should be enhanced and, therefore, cause a stronger amplitude modulation in slow potentials measured over the contralateral hemisphere then processing of irrelevant items causes in slow potentials over the ipsilateral hemisphere.

In all three activation patterns described above, the amplitude modulations of the slow potentials ipsilateral to the relevant hemifield are either weaker than those of the contralateral slow potentials or even absent. In all cases, therefore, subtracting ipsilateral from contralateral slow potentials always results in a negative-going difference wave (CDA), the amplitude of which is a function of the number of relevant items. However, the three hypotheses lead to different implications concerning the interpretation of the CDA. (1) If only contralateral effects of the number of relevant items are observed, the CDA is influenced only by processing of relevant items. (2) If ipsilateral effects of the number of relevant items are also observed, the CDA reflects the degree of lateralization of processing of relevant items. (3) In the case that the ipsilateral potentials show effects due to processing of irrelevant items, the CDA reflects the amount of processing bias toward the attended hemifield. Crucially, the CDA does not differentiate between these three predictions. However, we can test these assumptions against each other by analyzing contralateral and ipsilateral slow potentials.

METHODS

Participants

Sixteen students of Saarland University (one left-handed, mean age = 22.4 years, range = 20–25 years, eight women) participated in this experiment. All participants had normal or corrected-to-normal vision. One participant had to be excluded from further analysis because of excessive EEG artifacts. Participants were paid for their participation.

Stimuli

Stimuli were seven colored squares (red, blue, green, yellow, black, white, and purple) with a size of $0.65° \times 0.65°$ and were presented against a gray background. The stimuli appeared in two rectangular regions ($4° \times 7.3°$ each) that were centered 3° to the right and the left of the center of the screen.

Design and Procedure

Participants performed a lateralized change detection task (see Figure 1). Before the presentation of the memory array, an arrow was presented for 200 msec. This arrow indicated which of the two hemifields was relevant and consequently had to be remembered. In 50% of the trials, the arrow pointed to the left; in the remaining 50% of the trials, it pointed to the right. Between the presentation of the arrow and the memory array, a blank screen (only containing the fixation cross) was presented for 100–200 msec (randomly) to prevent a systematic timing between processing the arrow and processing the memory array. The memory array was presented for 100 msec and consisted of two rectangular regions, one in each hemifield. In each of these regions, one to three colored squares were presented. Participants were instructed that the best method to encode the stimuli was to fixate on the central fixation cross and covertly move their attention to

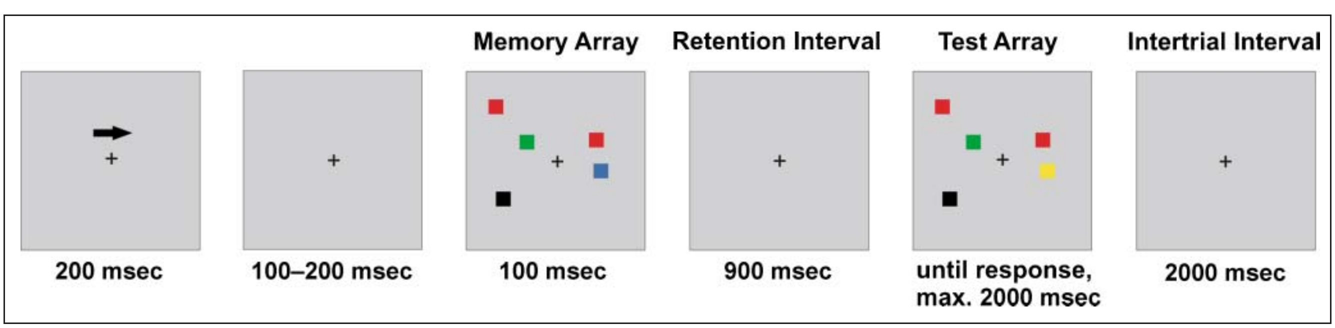

Figure 1. Schematic illustration of the task procedure.

the side indicated by the arrow. The retention interval lasted 900 msec. In 50% of the trials, one of the squares in the relevant hemifield changed its color from memory to test array; in the other half of trials, all colors remained the same. Participants had to press one key to indicate a color change and another key when no color had changed. The assignment of keys to response class was counterbalanced across participants. The test array lasted for 2000 msec, maximally, but was terminated with participants' keypress. The number of relevant, to-be-remembered items and the number of irrelevant items were varied orthogonally between one and three. This resulted in 900 trials, 100 for each number of relevant × the number of irrelevant items-condition.

Within the rectangular regions, item positions were set at random with the limitation that the minimal distance between the centers of each pair of items was at least 2°. Within one trial, colors were randomly chosen with the constraint that a specific color could appear only once within one hemifield. Participants were seated at a distance of 70 cm from the monitor.

ERP Recording and Analysis

The experiment was run in a sound-shielded and electromagnetically shielded chamber. EEG activity was recorded continuously from 28 Ag/AgCl electrodes (Easy Cap, Falk Minow Services, Herrsching-Breitbrunn, Germany) arranged according to the extended international 10–20 system. We recorded at parietal and occipital electrode sites: CPz, CP2, CP4, CP6, TP8, Pz, P2, P4, P6, P8, POz, PO4, PO8, Oz, and O2 (and left sides). Impedances were kept below, at least 10 kΩ for EOG electrodes and 5 kΩ for other electrodes. Signals were amplified with an AC coupled amplifier (Brain Amps, Brain Products, Munich, Germany); sampling rate was 1000 Hz with a 250-Hz analog low-pass filter and a time constant of 10 sec. A left mastoid reference was used during recording, and signals were rereferenced off-line to the averaged mastoids. Vertical and horizontal ocular artifacts were monitored by four ocular electrodes (above and below the right eye and at the outer canthi of both eyes) and corrected according to Gratton, Coles, and Donchin (1983). If the number of blinks was small, no correction was applied, but the blink-contaminated trials were excluded.

ERPs were extracted by stimulus-locked signal averaging from −200 to 1000 msec, relative to the onset of the memory array for each number of relevant items × the number of irrelevant items-cell. Data were baseline-corrected with respect to the 200-msec prestimulus interval and digitally low-pass filtered at 20 Hz. Epochs containing artifacts were excluded from further analysis. Analysis was based only on trials with correct responses. Data were averaged over matches and nonmatches, because we were interested in the retention interval, a period in which these two types of trials are not yet discriminable for the subjects, and so processing is the same.

We calculated contralateral slow potentials for each electrode by averaging activity over right (left) electrodes when the relevant stimuli were presented in the left (right) hemifield. We calculated ipsilateral slow potentials equivalently by averaging activity over right (left) electrodes when the relevant stimuli were presented in the right (left) hemifield. To obtain the CDA, we calculated the difference waves between contralateral and ipsilateral activities with regard to the attended hemifield. Consequently, we differentiated electrodes with respect to the relevant hemifield and not with respect to hemispheres. Therefore, in the following, we refer to electrode positions, contralateral and ipsilateral: CP1/2, CP3/4, CP5/6, TP7/8, P1/2, P3/4, P5/6, P7/8, PO3/4, PO7/8, and O1/2.

RESULTS

All data were analyzed by ANOVA and, if applicable, corrected for nonsphericity using the Greenhouse–Geisser correction (Greenhouse & Geisser, 1959). If the correction was adopted, we report Greenhouse–Geisser ε and corrected p values (p_{corr}) together with the original F values and original degrees of freedom. Effects and interactions were further decomposed by nested ANOVAs and testing of polynomial trends and contrasts. In all graphs, 95% confidence intervals are calculated according to the procedure described by Jarmasz and Hollands (2009) and are based on the error term of the respective effect of interest. We corrected the critical t values' *df*s appropriately if εs were too low, as suggested by Loftus and Masson (1994). The effects on which the confidence intervals are based on can be found below each figure.

Behavioral Data

Mean performance accuracy for all conditions is shown in Table 1. Performance declined with increasing the number of relevant items. A 3 (Number of Relevant Items) × 3 (Number of Irrelevant Items) ANOVA on mean accuracy confirmed a significant effect of the number of relevant items, $F(2, 28) = 23.22$, $\varepsilon = .63$, $p_{corr} < .001$, $\eta^2_{partial} = .62$, indicating a decrease in accuracy with higher memory load. There was no effect of the number of irrelevant items nor an interaction of the number of irrelevant by the number of relevant items, $F(2, 28) = 1.33$, $\varepsilon = .94$, $p_{corr} = .28$, $\eta^2_{partial} = .09$ and $F(4, 56) = 1.84$, $\varepsilon = .75$, $p_{corr} = .16$, $\eta^2_{partial} = .12$, respectively. All levels of the factor number of relevant items differed significantly from each other (all ps $< .05$).

ERP Data

Analyses were based on mean voltage amplitudes averaged over the time window from 350 to 700 msec after the onset of the memory array.

As anticipated, the number of relevant items had the strongest effect on activity measured over electrodes at

Table 1. Mean Accuracies (*M*) and Standard Errors (*SE*) as a Function of the Number of Relevant and Irrelevant Items

Number of Irrelevant Items	Number of Relevant Items		
	1	2	3
1			
M	0.965	0.941	0.923
SE	0.009	0.014	0.016
2			
M	0.961	0.966	0.924
SE	0.009	0.010	0.016
3			
M	0.964	0.952	0.921
SE	0.012	0.013	0.016

posterior recording sites, especially at P3/4, P5/6, P7/8, PO3/4, and PO7/8. We consequently pooled over these five electrode sites separately for contralateral and ipsilateral activity and for the CDA.

Effects of the number of relevant and irrelevant items were analyzed for contralateral slow potentials, ipsilateral slow potentials, and the CDA separately by three 3 (Number of Relevant Items) × 3 (Number of Irrelevant Items) ANOVAs.

The contralateral slow potentials are shown in Figure 2. A 3 (Number of Relevant Items) × 3 (Number of Irrelevant Items) ANOVA on the mean amplitude of slow potentials over the hemisphere contralateral to the relevant hemifield revealed a main effect of Number of Relevant Items, $F(2, 28) = 26.45$, $\varepsilon = .65$, $p_{\mathrm{corr}} < .001$, $\eta^2_{\mathrm{partial}} = .65$, and a significant interaction of the Number of Relevant Items by the Number of Irrelevant Items, $F(4, 56) = 5.12$, $\varepsilon = .84$, $p_{\mathrm{corr}} < .01$, $\eta^2_{\mathrm{partial}} = .27$. A clear linear increase in the slow potentials' negativity as a function of the number of relevant items is evident in Figure 3. As can be seen in Figure 3, this increase is absent for the number of irrelevant items. Linear trend analyses confirmed this picture: Contralateral slow potentials showed a significant linear trend for the Number of Relevant Items, $F(1, 14) = 31.16$, $p < .001$, but no linear trend for the Number of Irrelevant Items, $F(1, 14) = 0.43$, $p = .52$. Deconstructing the interaction, when only one relevant item is presented, there was an effect of the number of irrelevant items $F(2, 28) = 5.68$, $\varepsilon = .85$, $p_{\mathrm{corr}} < .05$, $\eta^2_{\mathrm{partial}} = .29$, namely, the slow potential amplitude for one irrelevant item was significantly more positive than for two or three irrelevant items, $F(1, 14) = 5.02$, $p < .05$ and $F(1, 14) = 7.88$, $p < .05$, respectively. Amplitudes were not influenced by the number of irrelevant items for two and three relevant items, $F(2, 28) = 2.45$, $\varepsilon = .86$, $p_{\mathrm{corr}} = .11$, $\eta^2_{\mathrm{partial}} = .15$ and $F(2, 28) = 0.01$, $p = .99$, $\eta^2_{\mathrm{partial}} < .01$, respectively.

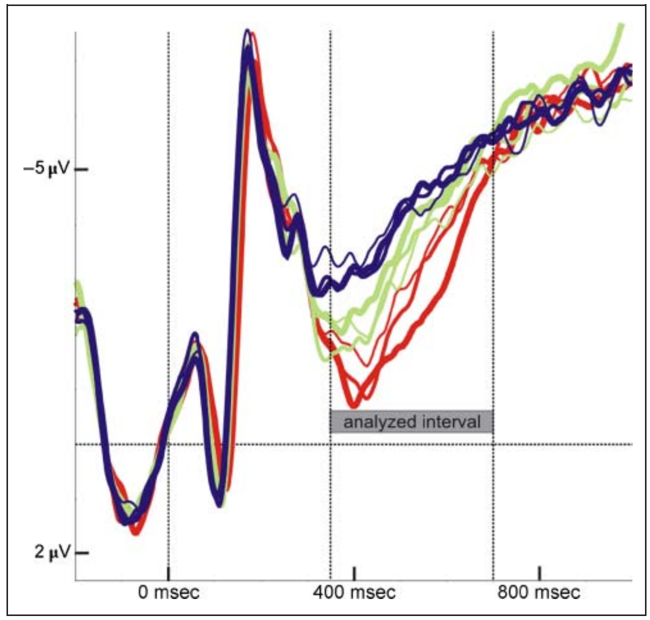

Figure 2. Grand averaged contralateral slow potentials relative to the onset of the memory array at posterior ROI (P3/4, P5/6, P7/8, PO3/4, and PO7/8). Colors code the number of relevant items (red, one relevant item; green, two relevant items; blue, three relevant items), and line thickness codes the number of irrelevant items (thick, one irrelevant item; middle, two irrelevant items; thin, three irrelevant items).

A 3 (Number of Relevant Items) × 3 (Number of Irrelevant Items) ANOVA on mean amplitudes of slow potentials over the hemisphere ipsilateral to the relevant items (see Figures 4 and 5) yielded a significant interaction for

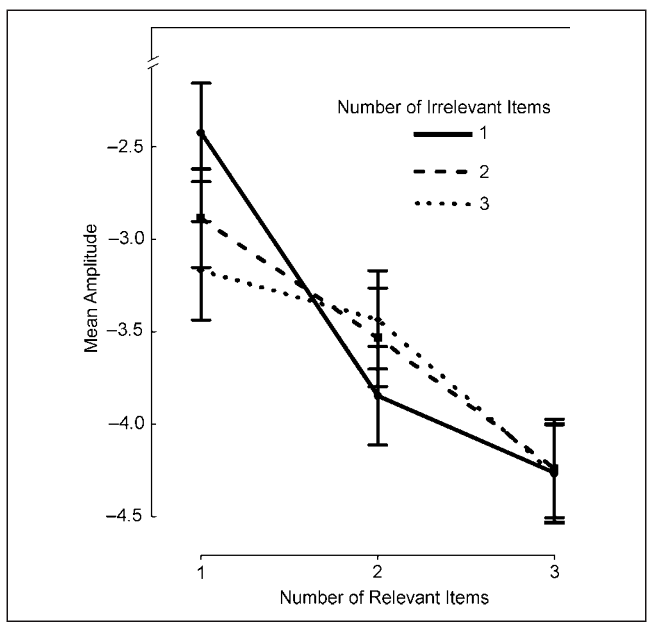

Figure 3. Contralateral slow potentials as a function of the number of relevant and irrelevant items averaged 350–700 msec after onset of memory array. The displayed 95% confidence intervals are based on the interaction between the number of relevant and irrelevant items.

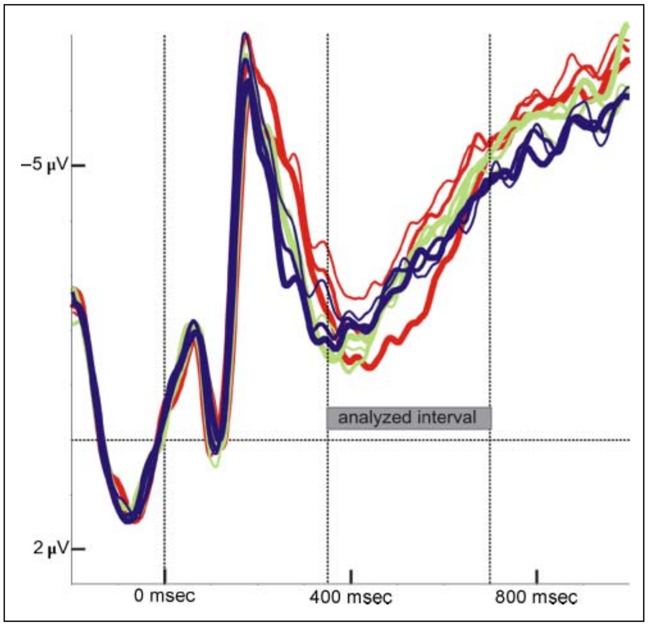

Figure 4. Grand averaged ipsilateral slow potentials relative to the onset of the memory array at posterior ROI (P3/4, P5/6, P7/8, PO3/4, and PO7/8). Colors code the number of relevant items (red, one relevant item; green, two relevant items; blue, three relevant items), and line thickness codes the number of irrelevant items (thick, one irrelevant item; middle, two irrelevant items; thin, three irrelevant items).

the Number of Relevant Items by the Number of Irrelevant Items only, $F(4, 56) = 7.32$, $\varepsilon = .75$, $p_{corr} < .001$, $\eta^2_{partial} = .34$. Notably, there was no main effect for the Number of Relevant Items, $F(2, 28) = 0.71$, $\varepsilon = .86$, $p_{corr} = .48$, $\eta^2_{partial} = .05$. Deconstructing the interaction, when only one relevant item was presented, the number of irrelevant items modulated the amplitude of slow potentials over the ipsilateral hemisphere, $F(2, 28) = 13.89$, $p < .001$, $\eta^2_{partial} = .50$. This effect was because of slow potential amplitudes for one irrelevant item being more negative than two or three irrelevant items, $F(1, 14) = 12.51$, $p < .01$ and $F(1, 14) = 26.56$, $p < .001$, respectively. This ipsilateral amplitude modulation was absent when two or three relevant items were presented, $F(2, 28) = 0.18$, $\varepsilon = .89$, $p_{corr} = .81$, $\eta^2_{partial} = .01$ and $F(2, 28) = 0.08$, $p = .92$, $\eta^2_{partial} = .006$, respectively.

The mean amplitude of the CDA as a function of the number of relevant and irrelevant items is shown in Figure 6. As can be seen from Figure 6, the CDA is clearly modulated by the number of relevant items; its amplitude becomes more negative with higher memory load. To estimate the effects of the number of relevant and irrelevant items, we computed a 3 (Number of Relevant Items) × 3 (Number of Irrelevant Items) ANOVA. The main effect of the Number of Relevant Items, $F(2, 28) = 33.97$, $\varepsilon = .65$, $p_{corr} < .001$, $\eta^2_{partial} = .71$, reflects the increasing negativity of CDA amplitude with increasing the number of relevant items. Linear trend analysis confirmed this picture, $F(1, 14) = 40.03$, $p < .001$. Furthermore, a main effect of the Number of Irrelevant Items, $F(2, 28) = 3.68$, $\varepsilon = .98$, $p_{corr} < .05$, $\eta^2_{partial} = .21$, was present. CDA amplitude was more negative for one irrelevant item as compared with two or three irrelevant items, $F(1, 14) = 5.71$, $p < .05$ and $F(1, 14) = 5.94$, $p < .05$, respectively.[1]

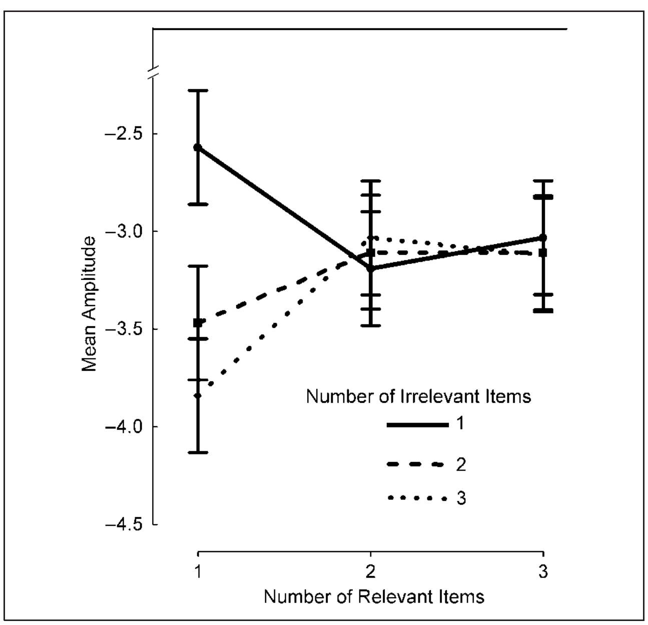

Figure 5. Ipsilateral slow potentials as a function of the number of relevant and irrelevant items averaged 350–700 msec after onset of memory array. The displayed 95% confidence intervals are based on the interaction between the number of relevant and irrelevant items.

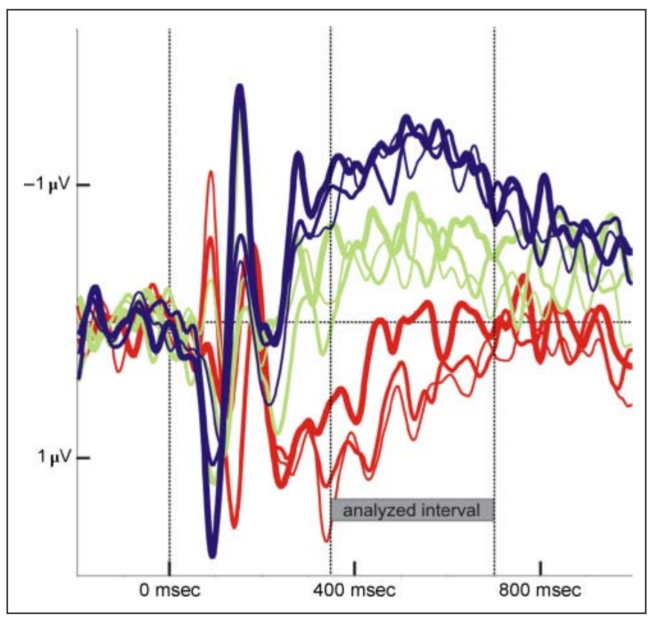

Figure 6. Grand averaged difference wave (CDA) relative to the onset of the memory array at posterior ROI (P3/4, P5/6, P7/8, PO3/4, and PO7/8). Colors code the number of relevant items (red, one relevant item; green, two relevant items; blue, three relevant items), and line thickness codes the number of irrelevant items (thick, one irrelevant item; middle, two irrelevant items; thin, three irrelevant items).

As was expected based on the results of the analyses of the contralateral and ipsilateral slow potentials, a 2 (two vs. three relevant items) × 3 (number of irrelevant items) ANOVA revealed an effect of the number of relevant items only, $F(1, 14) = 27.29, p < .001, \eta^2_{\text{partial}} = .66$. CDA amplitude was more negative for three relevant items compared with two relevant items. In contrast, an effect of the number of irrelevant items and an interaction were absent, $F(2, 28) = 1.33, p = .28, \eta^2_{\text{partial}} = .09$ and $F(2, 28) = 0.38, p = .69, \eta^2_{\text{partial}} = .03$, respectively.

DISCUSSION

The amplitude of posterior slow potentials, measured during the retention interval of change detection tasks, is sensitive to the amount of processed items. We exploited this fact to find out whether, in addition to contralateral activity, ipsilateral delay activity occurs in a lateralized change detection task, and if so, whether it reflects processing of the relevant or irrelevant items. An influence of the amount of items on ipsilateral slow potentials was observed earlier (Robitaille et al., 2009). However, in lateralized change detection tasks, the numbers of items in the relevant and irrelevant hemifields are usually the same. Therefore, the variation of the number of relevant or irrelevant items might have caused these amplitude modulations. By independently manipulating both numbers, we were able to separately examine the influence of relevant and irrelevant items on slow potentials over the contralateral and ipsilateral hemispheres.

In line with earlier studies (Robitaille et al., 2009; McCollough et al., 2007; Robitaille & Jolicoeur, 2006; Vogel & Machizawa, 2004; Klaver et al., 1999), during the retention interval, contralateral slow potentials as well as the CDA were modulated by the number of relevant items. Notably, in the present study, the amplitude of the ipsilateral slow potentials was not modulated by the number of relevant items. This pattern of data suggests a completely lateralized memory effect for the relevant items.

In contrast to the strong electrophysiological effect of the number of relevant items, the number of irrelevant items had no effect on slow potentials. One exception is the condition in which only one item was to be remembered, which will be discussed shortly. The absent effect of the number of irrelevant items suggests that, as instructed, participants ignored irrelevant items and focused on the relevant hemifield. Consequently, irrelevant items were filtered out and did not enter visual WM. Indeed, in the lateralized change detection task, the specific filtering mechanism might be the allocation of attention toward the relevant hemifield. Accordingly, Hillyard et al. (1998) assume that selective attention biases the strength of a perceptual representation. Bundesen et al. (2005) theorize that more processing resources are available for objects that have gained a higher attentional weight. Consequently, these objects are more likely to be encoded into visual WM. This is similar to Awh's hypothesis that attention works as a rehearsal mechanism in WM (Awh & Jonides, 2001). When more than one item had to be processed in the present study, participants appear to have efficiently directed attention toward the relevant hemifield and biased processing in favor of the relevant items.

There was one important exception where the number of irrelevant items had an impact. When only one relevant item had to be processed, we observed amplitude modulations due to the number of irrelevant items over the hemisphere ipsilateral to the relevant hemifield, that is, over the hemisphere that received these items. This suggests that, in this condition, irrelevant items were not filtered out but were processed to some extent. Critically, this effect cannot be explained by increased effort or task difficulty, because the amplitude of ipsilateral slow potentials should depend on the amount of relevant items, if this were the case. Obviously, when only one item is memorized, memory load is far from its capacity limit. In this case, all information seems to be processed without filtering out irrelevant information. The processing of irrelevant information might also cause the effect of the amount of irrelevant items on the slow potentials contralateral to the relevant hemifield when only one item has to be memorized because the available capacity is shared between relevant and irrelevant information.

From the results discussed in the two preceding paragraphs, it would appear that irrelevant items are processed when only one relevant item is present but are filtered out when visual WM load is higher. These results are in line with one theory forwarded by Lavie and colleagues (e.g., Lavie, 2005; Lavie, Hirst, De Fockert, & Viding, 2004). They assume that, when perceptual load is low, capacity that is not needed for the processing of relevant information automatically and involuntary spills over to the irrelevant stimuli. In contrast, when perceptual load is high, selective attention reduces distractor perception. In the lateralized change detection task, capacity might also involuntarily spill over to the irrelevant hemifield when one relevant item is shown. With more relevant items on the other hand selective attention might suppress this spread of capacity.

Our design, the orthogonal variation of the number of items in both hemifields, required the creation of a display that was unbalanced in perceptual terms. If perceptual effects on slow potential activity had been present, this aspect of our design would have allowed for an alternative interpretation of our results; then the effects of the number of items might have been driven by perceptual instead of mnemonic processes. However, from our data, we can exclude this alternative. There were no effects of the number of irrelevant items when two or three relevant items were presented, although perceptual effects, if existent, should have been present in all conditions.

Several authors discuss changes in ipsilateral slow potential activity near the end of the retention interval (Robitaille et al., 2010; McCollough et al., 2007). A close look on Figure 4 reveals a modulation of the ipsilateral slow potentials as a function of the number of relevant items in the last section of the retention interval. However, in contrast to all memory-related effects in our study and in contrast to all earlier research on memory processes during the lateralized change detection task, the ipsilateral slow potentials' amplitude becomes more positive with increasing the number of relevant items. Given this pattern, it is rather improbable that the amplitude modulation of ipsilateral slow potentials in this late time window is related to the process of maintaining items in visual WM. McCollough et al. (2007) discuss an increase in ipsilateral activity at the end of the retention interval as an anticipation process for the upcoming test array. Also the late ipsilateral activity observed in the present study might be related to an anticipation of the test array. As these late effects seem not to reflect memory processes, they do not affect our interpretation of the earlier memory-related effects. Further research is necessary to understand these late processes and their contribution to a successful handling of the change detection task.

Recall that the presentation of to-be-remembered items in one hemifield elicits load-dependent activity over the contralateral hemisphere (e.g., Robitaille et al., 2009, 2010; McCollough et al., 2007; Vogel & Machizawa, 2004). Such load-dependent activity was also observed over the ipsilateral hemisphere (Robitaille et al., 2009). When relevant items were presented in the right hemifield, ipsilateral slow potentials were so strongly influenced by the amount of presented items that the effect of the number of items disappeared in the resulting CDA, although it was clearly present in contralateral slow potentials (Robitaille et al., 2009). Up to now, it is not quite clear under which conditions there are stronger contributions of the ipsilateral hemisphere. An additional issue is the kind of method used. Robitaille et al. (2010) observed lateralized load-dependent electrophysiological activity, resulting in a CDA. Applying functional magnetic imaging during the very same lateralized change detection task, these authors observed bilateral load-dependent BOLD responses, not lateralized ones. Furthermore, analyzing the MEG which was also measured during the same task identified both lateralized as well as bilateral activation. There might be several generators contributing to successful performance in the lateralized change detection task. However, that lateralized activity in this task is memory-related remains rather noncontroversial (e.g., Ikkai, McCollough, & Vogel, 2010; Robitaille et al., 2009, 2010; Vogel et al., 2005; Vogel & Machizawa, 2004), emphasizing the importance and utility of the CDA as a measure of WM load.

The present study leads to three important conclusions: (1) Variation of the number of relevant items caused amplitude modulations over the hemisphere contralateral to the relevant hemifield only. This suggests a complete lateralized processing of relevant items. Amplitude modulations ipsilateral to the relevant hemifield are exclusively caused by irrelevant items. (2) The amplitude of slow potentials measured over the hemisphere ipsilateral to the relevant hemifield was influenced by the number of irrelevant items when visual WM load was low, indicating that irrelevant items are not filtered out in this case. This might come about somewhat passively when the bottom–up capturing of attention by the onset of irrelevant stimuli is not prevented. In contrast, the number of irrelevant items did not influence slow potential amplitude when the load was high, indicating that irrelevant items were completely filtered out. Voluntary allocation of attention might work as a filter mechanism when visual WM load is high. (3) For extracting the CDA, these ipsilateral slow potentials are subtracted from contralateral ones. Our findings for ipsilateral slow potentials, therefore, suggest that when memory load is high, the CDA amplitude is only influenced by the number of relevant items; when only one item has to be remembered, the CDA amplitude is also influenced by the number of irrelevant items. Consequently, the CDA amplitudes for low and high memory load might not be directly comparable, because they might reflect only partially overlapping processes. However, according to our data, this problem does not apply to memory loads above one item, because in these cases, the CDA purely reflects processing of relevant items.

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Note

1. The CDA amplitude is more negative for one irrelevant item compared with two or three irrelevant items at three of five electrodes only (P3/4, PO3/4, and PO7/8). For the other two electrodes (P5/6 and P7/8), there is no effect for the irrelevant items on CDA amplitude. In contrast, all five electrodes show clear effects for the number of relevant items.

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