Updating visual working memory in the change detection paradigm

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An updating version of a visual change detection paradigm was used to investigate the behavioral outcomes and event-related potential (ERP) correlates of visual working memory updating. In each trial, participants were either presented with a memory array followed by a test probe, or with two successive memory arrays. Participants were instructed to update their working memory with the information in the second array. The second array differed from the first one in all, some, or none of the items. When a subset of the items was updated, the probe could appear in the location of a repeated item or of an updated item. Two experiments are reported, using set-sizes of six and two items, respectively. Both experiments show a benefit for probing a repeated item compared to an updated item. This result is consistent with an item-specific updating process. Experiment 2 also revealed two distinct updating-related ERP components, observed in both contralateral and ipsilateral visual hemifields. Frontal electrodes were sensitive to the number of changed items in the array. This ERP component was interpreted as reflecting the modification of information in working memory. Lateral-posterior electrodes only showed a difference between a full repetition of the array and updating, regardless of the number of updated items. This component was interpreted as reflecting attention to task-relevant information rather than the updating process per se. The finding of item-specific updating supports discrete-item architecture models of working memory.

Introduction

Working memory (WM) enables the robust maintenance of information over time, as well as updating the stored information according to new input (e.g., Frank, Loughry, & O'Reilly, 2001). Past research had primarily focused on the maintenance function, aiming to specify the structure of WM representations and the source of its strict capacity limits (for recent reviews see Franconeri, Alvarez, & Cavanagh, 2013; Luck & Vogel, 2013). In addition, much research had been devoted to understanding the processes by which an effective use of this limited capacity is made by filtering out irrelevant information (Vogel, McCollough, & Machizawa, 2005), and by selecting task-relevant representations for action (e.g., Chatham, Frank, &

Badre, 2014; Manza, Hau, & Leung, 2014). However, little is known about the ways by which maintained representations in WM interact with new input. Real-life situations, such as driving, require maintaining several independent items in WM (e.g., locations of the surrounding cars) and updating each of them throughout the situation. The perceptual input is composed of items that are already maintained in WM (repeated items, such as locations of parking cars), as well as items that are new or updated (e.g., new locations of moving cars). The present study aims to examine how WM representations are affected by repetition and updating of information, and to identify the event-related potential (ERP) correlates of WM updating in the visual domain.

Computational models suggest that maintenance and updating are coordinated by a gate that buffers between perceptual representations and WM (for review see O'Reilly, 2006). The default closed state of the gate enables robust maintenance, but can be overridden by transient gate opening that leads to updating. However, it is currently an open question whether WM updating in complex situations, such as described above, is global or selective (Badre, 2012; Kessler & Meiran, 2006, 2008). Selective (item-specific, "local") updating refers to the idea that each item in WM is gated separately and independently of the others. This is achieved by having multiple parallel gates to WM. In contrast, global updating refers to the idea that the entire content of WM is updated as a whole and in synchrony. This implies a single, nonselective gate to the WM system. Global updating provides a lesser degree of control over the contents of WM, and can be triggered by a nonspecific updating signal (Braver & Cohen, 2000).

Previous work on updating declarative WM representations (as opposed to procedural task rules, see Oberauer, 2009) had primarily used verbal materials as stimuli, typically digits or letters (e.g., Artuso & Palladino, 2011, 2014; Carretti, Cornoldi, & Pelegrina, 2007; Ecker, Lewandowsky & Oberauer, 2014; Ecker, Lewandowsky, Oberauer, & Chee, 2010; Garavan, 1998; Kessler & Meiran, 2006, 2008; Lendínez, Pelegrina, & Lechuga, 2014; Oberauer, 2003; Oberauer, Souza, Druey, & Gade, 2013; but see Ko & Seiffert, 2009; Manza et al., 2014; Souza, Rerko, & Oberauer, 2014 for exceptions using visual arrays). For example, Kessler and Meiran (2008) presented participants with a sequence of digit-sets. Each set of digits was either identical to the one presented in the previous trial, or different in part or all of the items. The participants were instructed to update their WM with the information presented in each trial and then press a key to proceed to the following trial. After a few screens, the participants were probed to recall the most recent digit set that was presented. Self-paced reaction times (RTs)

to the updating steps were analyzed as a function of the set-size (one to three items) and the number of updated items in each trial. The results were consistent with both local and global updating. First, RT increased within each set-size as more items were updated. For example, updating two items out of three was slower than updating one item out of three. This result supports the idea of serial item-specific (namely, local) updating. Second, the RT difference between a full repetition and updating a single item increased with the set-size. This finding is consistent with the idea of a global updating process that is carried out on the entire set whenever any of the items was changed, and involving both the repeated and updated items. Finally, updating the entire set-size (e.g., three out of three items) was faster than updating only a subset. This effect was observed when only the updated items were presented in each trial. This finding was taken as evidence for the need to unbind item-to-item associations when updating part of the set (but see Ecker et al., in press, for an alternative account). Based on these results, Kessler and Meiran (2008) suggested that WM updating is carried out by a local, item-specific process that serves to modify each of the items independently of the others, followed by a global updating process that results in a stable higher-order WM representation.

A recent study by Kessler and Oberauer (2014) had challenged these conclusions, as well as previous work on verbal WM updating. Participants performed an updating task, similar to the one devised by Kessler and Meiran (2008), with a constant set-size of four items. The specific positions of updated and repeated items within the set were manipulated, rather than the total number of updated items as done before. For example, when updating two items out of four, the updated items could either be in the two leftmost positions of the set, the two rightmost positions, or in the outer positions (1 and 4). Although the same number of items is updated in all the above conditions, Kessler and Oberauer (2014) showed considerable RT differences among them. The complex pattern of RTs to the various sequences of updated and repeated items was explained by a forward scan model. According to this model, participants performed the task by scanning the set from beginning to end (left to right), and updating each item when needed. RTs were explained by the duration of two independent processes. First, moving from an updated item to a repeated one, or vice versa, lead with a large RT cost. This process reflects the duration of changing the gate state, from updating to maintenance or vice versa, supporting computational models of WM gating. Second, each updated item resulted in an additional cost, reflecting the process of creating a new association between the stimulus and its position within the set.

The findings of Kessler and Oberauer (2014, 2015) provide a direct behavioral evidence for the process of

WM gating, as well as the means to measure the duration of gate opening and closing. Also, their finding of a cost associated with updating each item is consistent with the local updating hypothesis. Accordingly, items are updated independently, one after the other in a serial fashion, with a constant and additive updating cost per item. However, it is still unclear whether this item-by-item updating reflects a specific processing strategy used with verbal materials or a more general property of WM. Using an analogous updating task in visual WM, the goal of the present study was to address this point.

Present study

The goal of the present study was to examine updating in visual WM. To this end, we manipulated updating within a visual change detection task (Luck & Vogel, 1997). The advantage of using visual arrays is in the ability to present a large amount of information for a brief duration, in which verbal processing strategies are unlikely to take place. Unlike the findings of Kessler and Oberauer (2014), which were based on self-paced RTs for the updating task, Experiment 1 focused on change detection performance as a dependent variable. This strategy removes the potential methodological problems associated with relying on subjective estimates of processing time, by examining the *product* of updating rather than its duration. In addition, event-related potentials (ERP) were used in Experiment 2 in order to examine the temporal dynamics of the updating process(es).

A visual change detection task was used. Participants were presented with a visual array, followed by a probe to which a same/different decision was required. A second memory array was presented in some of the trials, with the instruction to update WM with the items it held. This array was different in all, some, or none of the items compared to the first array. When a second memory array was presented, this array was the reference to which the following probe had to be compared. Change detection performance was tested as a function of the number of updated items in the second array (see Figure 1). Two experiments are reported, using set-sizes of six and two items, respectively. In addition to the effect of updating on a subsequent change detection task, ERP was recorded in Experiment 2. This enabled us to observe the neural correlates of the updating process as they unfold in time, in addition to their final behavioral output.

Predictions

Both the local and the global updating hypotheses predict a repetition benefit, namely a better change detection performance following a second array in which some or all the items were repeated (Ihssen, Linden, & Shapiro, 2010). However, the exact nature of this repetition benefit (or updating cost) in partial-updating situations differs between the hypotheses. In partial-updating conditions some of the items in the second memory array are presented with the same color as in the first array (repeated items), and others change their color (updated items). In these conditions, either a repeated or an updated item could be probed for a change-detection decision.

According to the local updating hypothesis, each item is accessed and updated independently of the others. Accordingly, the repetition benefit should be item-specific. That is, in the partial-updating conditions, performance would be better when probing an item that was previously repeated compared to an item that was previously updated. In addition, local updating predicts a complete independence among the items. Therefore, performance in the partial-updating conditions should not be sensitive to the overall number of updated items. In other words, change-detection performance should only depend on the repetition or updating of the probed item.

Global updating, on the other hand, is the view that the entire WM set is updated as a whole once any of the items is updated. This idea predicts a set-wise repetition benefit or updating cost. Performance is expected to be better when the entire display is repeated compared to partial- or whole-updating. Moreover, in the partial updating conditions, performance should be worse than a full repetition regardless of whether the probed item was repeated or updated. For this reason, no difference is predicted between probing a repeated and an updated item, and no effect for the number of updated items is expected.

Experiment 1

Method

Participants

Thirty students from Ben-Gurion University of the Negev (22 females; age $M = 23.16$, $SD = 1.34$) participated in the experiment in exchange for course credit. All participants were right-handed and reported having normal or corrected-to-normal vision. None of the participants reported being diagnosed as suffering from learning disabilities or neuropsychological dysfunctions. One participant did not complete the experiment due to a computer failure and was therefore removed from the analysis. Another participant was removed from the analysis due to poor performance (mean accuracy = 22%).
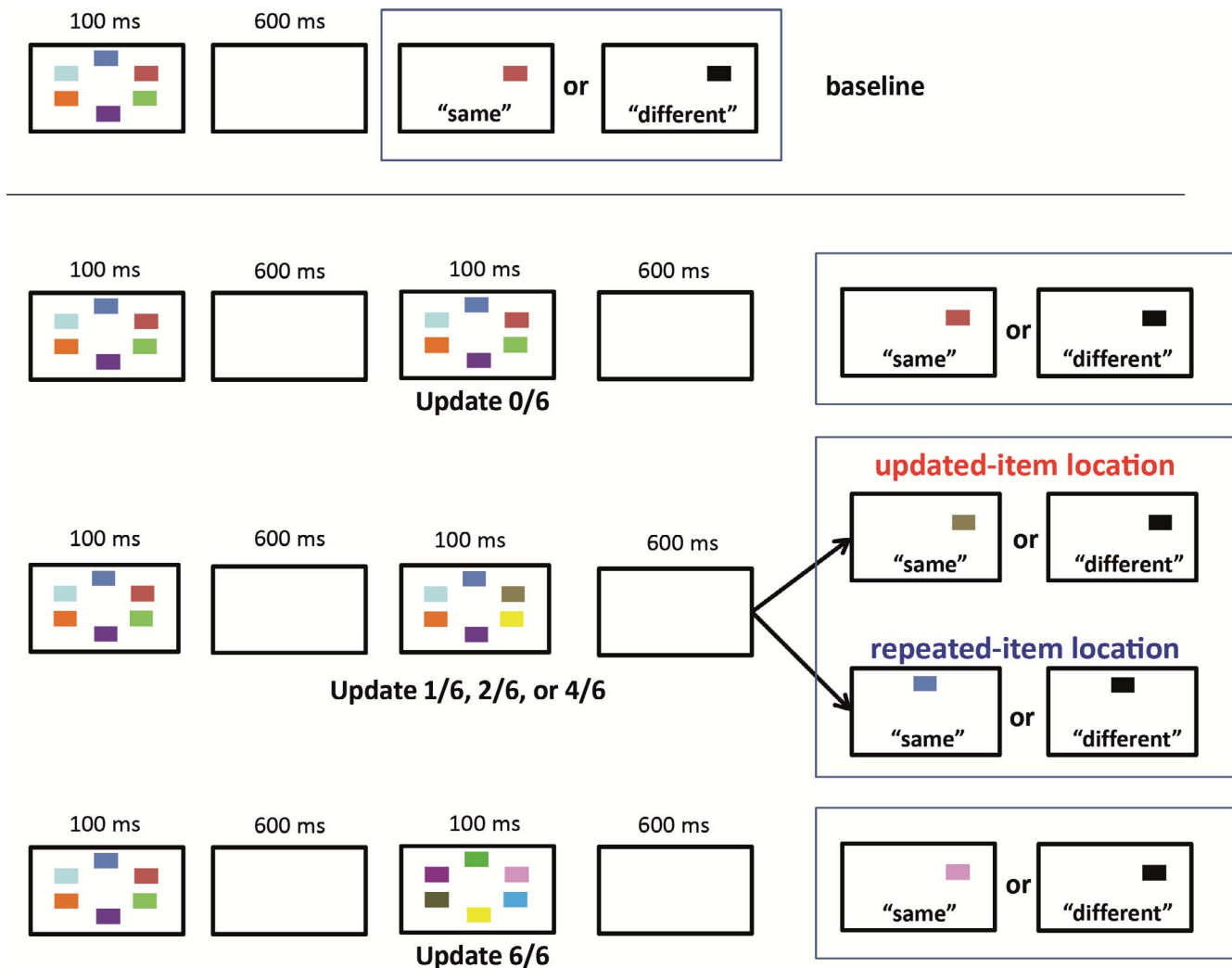
Figure 1. Experimental paradigm for Experiment 1. Half of the trials included a single visual display (baseline). A second visual display was presented in the update condition. The number of updated items in this display was varied. Participants had to indicate whether the color of the probe matched the most recent color in this location.

Apparatus and stimuli

Participants performed an updating version of the change detection task (Luck & Vogel, 1997). The memory array consisted of six colored squares (0.95 × 0.95° each, assuming a 60-cm viewing distance), arranged in a circle. The locations of the items were fixed both within a trial and across trials, to ensure that any benefit from presenting a second array would be attributed to the colors, rather to learning the locations of the items. The color of each square was selected randomly from a set of 16 different colors. The colors did not repeat within the array. All the stimuli were presented against a gray background. A black fixation cross was presented on in the center of the screen throughout the experiment, and the participants were instructed to fixate their eyes on it during the entire course of the trial. The experiment was programmed in E-Prime 2.0 (Psychology Software Tools, Pittsburgh, PA).

Procedure

Each trial sequence began the presentation of a memory array for 100 ms, followed by a 600 ms blank retention interval (see Figure 1). In half of the trials the probe screen was then presented (baseline condition). In the other half, a second memory array was presented followed by another 600 ms retention interval and a probe screen. The equal proportions of trials with and without a second array prevented a strategy of attending only to the second memory array, that could have been adopted if all or most of the trials included two memory displays. The probe appeared until a response was indicated, for a maximum of 2000 ms. Responses were indicated by pressing the left index finger for "same" response and the right index finger for "different" response. The responses were collected using a serial response box.

The second memory array conditions consisted of a full repetition (0 updated items out of 6), partial updating (1/6, 2/6, 4/6), or full updating (6/6). Only one item was presented in the probe screen, and the participants were required to indicate whether the color of this item was the same as the color of the square that most recently appeared in this location. Accordingly, the reference for comparison was the initial memory array in the control condition, and the second memory array in the update conditions. In each of the partial updating conditions, the probe could either appear in the location of an updated or a repeated item, with equal probabilities.[1]

The experiment was composed of 10 blocks including 40 trials each. The baseline condition included 200 trials, and the other 200 trials were equally divided among the five update conditions (0/6 through 6/6). Within each condition, the probe was matching in half of the trials and nonmatching in the other half. All the conditions were intermixed within the experimental blocks. The experiment was preceded by a short practice phase. Feedback was given during practice only.

Results

Bayesian analysis of variance (ANOVA) was used for data analysis (Rouder, Morey, Speckman, & Province, 2012). The analysis was conducted using the BayesFactor package of the R statistical programming language. Bayesian statistics enables comparing between models based on the Bayes Factor (BF) statistic. Specifically, BF expresses the ratio between the likelihoods of the data under two compared models. For example, testing for a main effect is done by calculating the ratio between the likelihood of a model that includes the main effect and the likelihood of the null model. The value of BF is interpreted as the degree by which the prior belief in the tested model should be updated. In our example, $BF = 100$ means that the main-effect model is 100 times more likely than the null model, and that the prior belief in it should be updated accordingly. An important virtue of Bayesian statistics is its ability to assess the evidence also for the null hypothesis, and hence to examine hypotheses regarding null effects.

The Update (baseline, 0/6 through 6/6) and Probe-Location (whether or not the probe appeared in an updated- or repeated-item location) variable do not create a full factorial design, since the latter only refers to the partial updating conditions. Accordingly, two separate analyses were conducted. First, an analysis of variance (ANOVA) was conducted on the accuracy data with Update (baseline, 0/6, 6/6) as within-subject independent variable, in order to examine how the

presentation of a second memory array affected performance. Performance differed among the conditions, $BF_{Update/Null} = 20.73$ (using Jeffreys' 1961 classification scheme of *BFs*, $10 < BF < 30$ indicates "strong evidence"). Comparisons were conducted in order to examine the source of this effect. Accuracy did not differ between the baseline and 6/6 condition, $BF = 0.32$. This is expected, given the fact that in both conditions the probe appears after a completely new memory array was presented. By contrast, performance in the full repetition condition (0/6) was better than in the baseline and 6/6 conditions (combined), $BF = 62.36$ ($30 < BF < 100$ is interpreted as reflecting "very strong evidence"; see Figure 2). This finding implies that a second presentation of the entire memory array leads to improved performance. Next, a second Bayesian ANOVA was conducted on the accuracy data of the partial updating conditions only, with Update (1/6, 2/6, 4/6) and Probe-Location (probe in updated- vs. repeated item-location) as within-subject independent variables. Performance was better for probe in repeated-item locations compared to updated-item locations, $BF_{Probe-Location/Null} = 5.03$ ("substantial evidence"). Accuracy was unaffected by neither Update, $BF_{Update/Null} = 0.22$, nor the two-way interaction, $BF_{Update*Update-Location/Null} = 0.21$.

Discussion

Repeating the entire memory array led to improved performance compared to the baseline and whole-update (6/6) conditions. This result replicates a similar finding by Ihssen, Linden, & Shapiro (2010). Notably, repetition benefit is not observed when displays are repeated from one trial to another (Logie, Brockmole, & Vandenbroucke, 2009), but only when repetition is done within a trial, namely before the presentation of the probe array. Taken together, these findings suggest that the content of WM is not completely overridden when new information is presented, but only after the probe presentation. This is compatible with the view that WM representations are continuously and gradually updated within events, but replaced at event boundaries (Zacks, Speer, Swallow, Braver, & Reynolds, 2007).

The results of the partial updating conditions (1/6 through 4/6) are fully consistent with the predictions of local updating. Accuracy was higher when probing repeated items compared to updated items. Importantly for our hypothesis, this repetition benefit (or updating cost) was independent of the number of updated items in the array. These findings speak against global updating. If the entire WM content is removed when any of the items is modified, as suggested by global updating, then all the items presented subsequently should be encoded as new. In
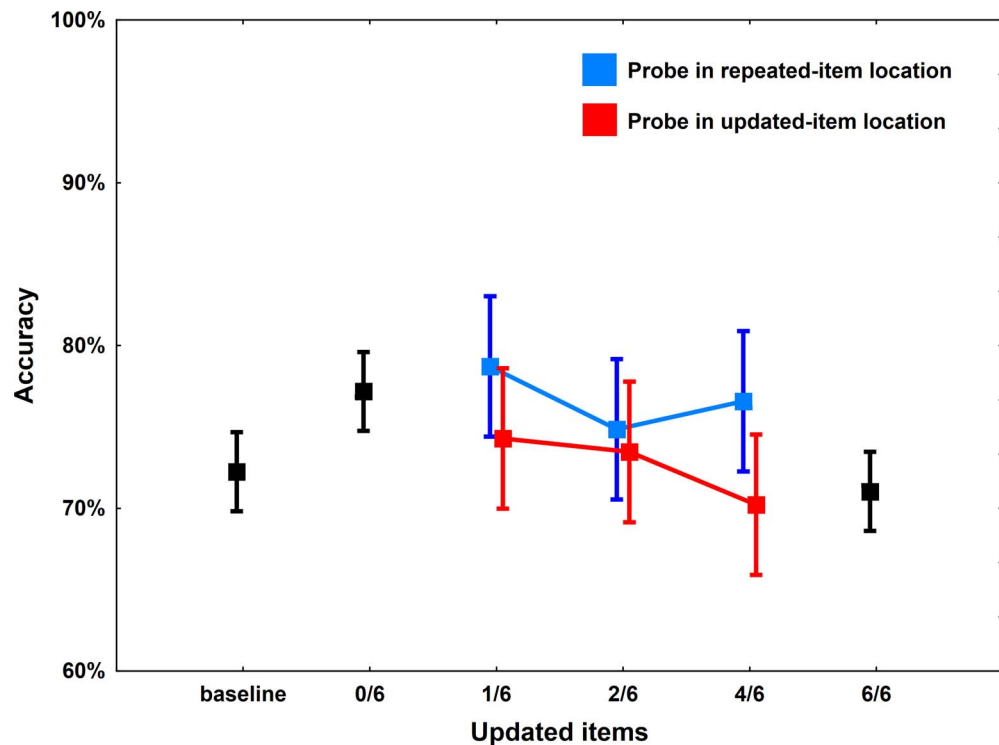
Figure 2. Experiment 1: Performance was better for probes that appeared in repeated-item locations compared to updated-item locations, as predicted by local updating. Performance did not vary across the update conditions. *X*-axis labels represents the number of updated items out of the entire set-size (e.g., 0/6 = full repetition; 6/6 = full updating). Error bars indicate 95% confidence intervals.

this case, no benefit for probing repeated items is expected. This prediction is clearly unconfirmed.

Two corollary predictions follow from supporting local updating. First, if updating is only item-specific, then no benefit is expected for repeating the entire array compared to partial-set updating, as long as a repeated item is probed. Comparing performance in the 0/6 condition to probes in repeated-item locations (in the 1/6, 2/6 and 4/6 conditions together) confirmed this hypothesis, *BF = 0.23*. Second, probing updated-item locations should not differ from probing items in the baseline or 6/6 conditions. In all these situations, the probed items were only presented once. This prediction was also confirmed, *BF = 0.22*.

Experiment 2

Experiment 2 was aimed to extend and replicate these findings, while dealing with one potential limitation of Experiment 1. Specifically, Experiment 1 used a memory set of six items, which exceeds the typical estimated capacity limit of around three to four items (Cowan, 2001). This implies that changes in the second display were not always detected due to a failure to maintain all the items from the first display.

Accordingly, it is difficult to be certain that the participants were sensitive to the updating versus repetition manipulation in all trials. Note, however, that this shortcoming worked against us, since we demonstrated a difference between these conditions despite this problem. Still, a replication with a smaller set-size is needed to overcome this issue. Experiment 2 was conducted with a set-size of two items, being the minimal number of items that enables testing a partial updating condition (one updated and one repeated item).

In addition, this experiment aimed at identifying the ERP correlates of updating, in order to gain a better understanding of the time course of the updating process in addition to its end products (namely, change detection performance). To this end, the effects of updating on the contralateral delay activity (CDA; Vogel & Machizawa, 2004) were examined. The CDA is a lateral-posterior negativity during the delay period, which is sensitive to WM set-size and to individual differences in WM capacity. It is still unknown, however, whether, and in which way, the CDA is sensitive to updating (and hence to the sequential history of the stimuli). Experiment 2 aimed at addressing this issue. The experimental design of Experiment 1 was used with two changes. First, the set-size was two items. This enabled testing four condi-

tions: baseline, 0/2, 1/2, and 2/2. Second, as standard in CDA experiments, visual displays were presented in both sides of the screen, preceded by a cue that indicates which side is relevant. The CDA was calculated as the difference between contralateral and ipsilateral activity over lateral-posterior electrodes.

Method

Participants

Twenty-nine students from Ben-Gurion University of the Negev (10 females; age $M = 24.73$, $SD = 1.67$) participated in the experiment in exchange for monetary compensation. All the participants were right-handed and reported having normal or corrected-to-normal vision. None of the participants reported being diagnosed as suffering from learning disabilities or neuropsychological dysfunctions. Seven participants were excluded from the analysis: two due to technical problems with the ERP recording, four due to a high ERP artifact rate ($>30\%$), and one due to failure to follow the updating requirement, as indicated by near zero accuracy in the 1/2 and 2/2 conditions. All the analyses were conducted on the data of the remaining 22 participants.

Procedure

Two colored squares were presented, one above the other, on each side of the fixation cross. Each trial began with the presentation of an arrow cue (200 ms), pointing to the left or to the right, followed by a 300 to 400 ms delay interval. The memory array was then presented for 100 ms, followed by a 600 ms delay interval. A second memory array was presented in 75% of the trials, which consisted of a full repetition (0/2), partial updating (1/2), or full updating (2/2). These conditions appeared in equal probabilities. In the 1/2 condition, the probe could either appear at the location of the updated item or at the location of the repeated item, with equal probability. Responses to the probe were indicated by pressing left index finger for "same" response and right index finger for "different" response, using a serial response box.

The experiment was composed of 30 blocks with 20 trials each. Seventy-five trials appeared in each of the eight (4 Update × 2 Probe) conditions. The conditions were intermixed within the blocks. The experiment was preceded by a short practice phase.

Electroencephalogram (EEG) recordings and analysis

EEG was recorded using a BioSemi Active Two 64-electrode system (Biosemi, Inc., Amsterdam, The Netherlands). Additional electrodes were placed at the outer left canthus and below the left eye to measure ocular activity. Data was recorded using a 0.01–100 Hz bandpass filter, and was offline filtered at 30Hz low-pass. The sampling rate was 512Hz. The signal was digitized using a 24-bit A/D converter. The EEG data was processed using EEGLAB (Delorme & Makeig, 2004) and ERPLAB (http://erpinfo.org/erplab). Segmented epochs were subjected to an automatic bad-channels, eye blinks, or movement-detection procedures, followed by manual verification. Bad channels were interpolated in the remaining segments. The segments were then averaged, re-referenced to a linked mastoid electrode, and baseline-corrected relative to a 200-ms prestimulus baseline. For the CDA analysis, the potential in lateral-posterior electrodes was calculated by averaging electrodes O1/O2, PO3/PO4, PO7/PO8, P3/P4, P5/P6, P7/P8, and P9/P10.

Results and discussion

Behavioral results

As in Experiment 1, Update and Probe-Location do not create a full factorial design, since the latter variable is nested within the partial-updating condition, namely 1/2. For this reason, two separate analyses were conducted. First, a Bayesian ANOVA was conducted on the accuracy data with Update (baseline, 0/2, and 2/2) as a within-subject independent variable. Accuracy differed among the Update conditions, $BF_{Update/Null} = 680.86$. As in Experiment 1, performance in the full repetition condition was better than the baseline and full-update (2/2) conditions, $BF = 2004.22$. These latter conditions did not differ in accuracy, $BF = 0.42$. A second analysis examined the effect of Probe-Location (updated, repeated) on the partial update condition (1/2) only. As in Experiment 1, unequivocal evidence was found for better performance in repeated-item locations, $BF = 2720.56$ (see Figure 3). As before, accuracy in repeated-item locations in the partial updating condition (1/2) did not differ from the full-repetition condition (0/2), $BF = 0.62$. These findings are again consistent with the prediction of local updating.

Unlike Experiment 1, performance was substantially poorer in updated-item locations compared to the baseline and 2/2 conditions, $BF = 759.33$. Although the latter finding was unexpected, it is hard to ignore the strength of the evidence supporting it. Notably, this effect cannot be merely explained by proactive interference of outdated information, since such interference must also take place in the 2/2 condition. Ecker, Oberauer, and Lewandowsky (2014) recently suggested that updating a subset of the items in WM requires removing previously relevant information and creating associations between the relevant items and their context in WM (e.g., spatial locations). By contrast, updating the entire WM set is faster since no item-
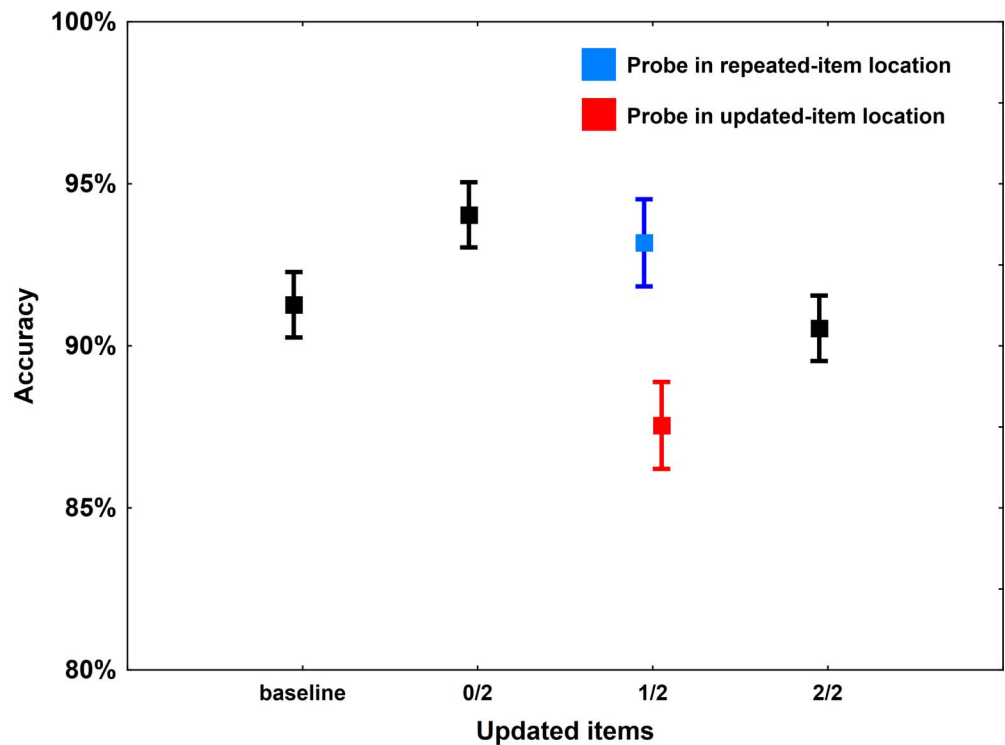
Figure 3. Experiment 2: Performance was better for probes that appeared in repeated-item locations compared to updated-item locations, as predicted by local updating. Error bars represent 95% confidence intervals.

specific removal is needed, but rather a complete "wiping" of the WM set (see Kessler & Meiran, 2008, for similar findings, and Kessler & Oberauer, 2014, for an alternative account). This account suggests a larger interference in updated-item locations compared to the 2/2 condition, consistent with our finding. It is possible that this effect was obscured in Experiment 1 due to using supracapacity set-sizes.

ERP results

We started by examining the effect of update on the CDA. For this analysis, the EEG was segmented between 200 ms prestimulus (baseline) and 1400 ms poststimulus. The CDA was calculated as the difference between contralateral and ipsilateral channels, in lateral-posterior electrode sites. The CDA was calculated as the mean amplitude between 300 and 650 ms after the first memory array presentation (first retention interval), and between 300 and 650 ms after the second memory array presentation (second retention interval). A two-way Bayesian ANOVA was conducted with Update (0/2, 1/2, and 2/2) and Retention-Interval (first, second) as within-subject and CDA amplitude as a dependent variable. The CDA was larger in the second retention-interval compared to the first, $BF_{Retention-Interval/Null} = 42157.10$. No evidence was found for the effect of Update on the CDA, $BF_{Update/Null} = 0.18$, nor for the two-way

interaction, $BF_{Retention-Interval*Update/Null} = 0.17$. Accordingly, the update condition did not affect the CDA amplitude. This finding suggests that the CDA is only sensitive to the number of items in WM, regardless of their update/repetition history (see Figure 4).

We continued by exploring whether the lack of updating effect on the CDA reflects similar effects on ipsilateral and contralateral electrodes, which do not show up when subtracting them. This analysis is admittedly exploratory, and more research is needed to establish its results. Since the update conditions did not differ in the first retention interval, both logically and empirically, we resegmented the data and time-locked the segments to the onset of the second memory array interval. Baseline correction was done relative to the 200 ms before the second memory array. We used Guthrie and Buchwald's (1991) procedure to determine the time window in which this effect was significant. This procedure corrects for multiple comparisons by calculating the minimal number of time points in a row (i.e., time window), which are required to make sure that significant difference between conditions are consistent along time rather than spurious. Relying on this method, a minimal sequence of 11 *t* tests was determined based on the sample size, number of time points in the 200 to 400 ms poststimulus window, and assuming a maximal (0.90) autocorrelation in the ERP data. All ERP effects reported below passed this criterion.
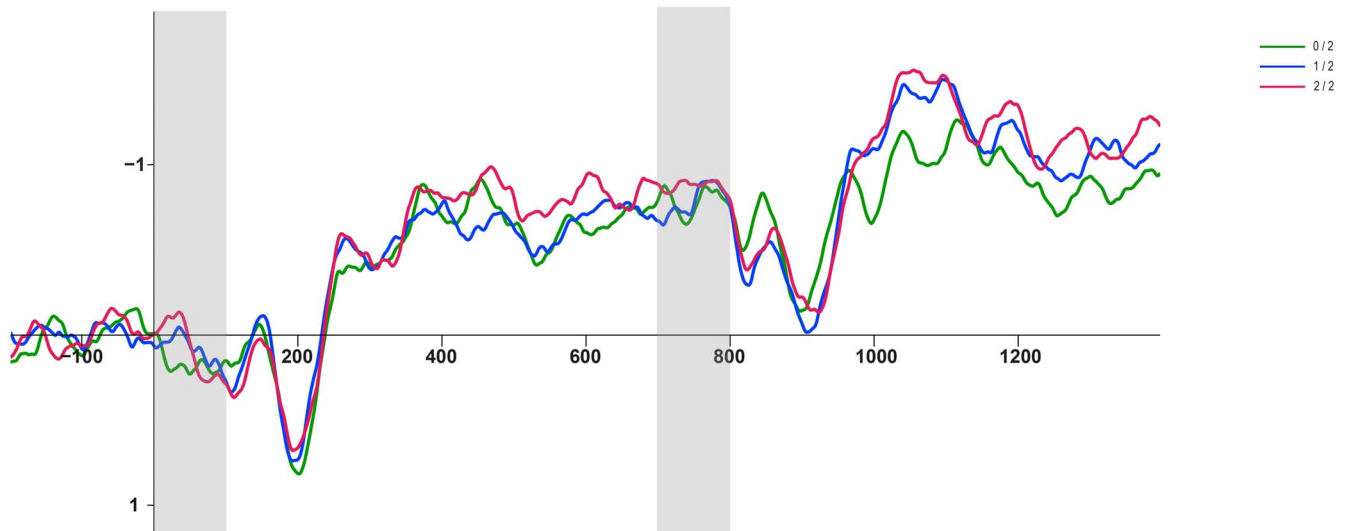
Figure 4. CDA in lateral-posterior electrodes. The CDA did not vary across the update conditions. The visual array presentations are marked in gray.

The lateral-posterior electrodes (calculated as in the CDA analysis) were sensitive to the difference between the full-repetition and the two update conditions (see Figure 5). This difference was significant in the intervals 200 to 250 ms and 273 to 389 ms in the contralateral electrodes, and between 279 and 381 ms in the ipsilateral electrodes. The partial and full update conditions did not differ significantly in these electrodes.

In contrast to lateral-posterior electrodes, activity in anterior electrodes was also sensitive to the number of updated items, namely the difference between conditions 1/2 and 2/2. This ERP component ("local effect") was the largest in electrodes F1/F2, and was significant between 252 and 293 ms in the contralateral electrode and between 258 and 285 ms in the ipsilateral electrode.

The difference between a full repetition and both update conditions ("global effect") was also significant in electrodes F1/F2 at 246 to 322 ms and 252 to 293 ms for the contralateral and ipsilateral hemispheres, respectively.

General discussion

Our behavioral results support the predictions of the local updating hypothesis. While previous findings showed that repeating the memory array benefits retention (Ihssen et al., 2010), the results of Experiments 1 and 2 show that this benefit is item-specific. The ability to recognize a matched probe depended only on whether that item was previously repeated or updated, regardless of what happened to the other items in WM. This finding supports item-based theories of WM representation, including discrete-slots (Luck &

Vogel, 1997; Zhang & Luck, 2008) and variable-resolution (Wilken & Ma, 2004) models.

The CDA amplitude was unaffected by the update manipulation. Specifically, Experiment 2 demonstrates equivalent amplitudes for the 0/2, 1/2 and 2/2 conditions. This suggests that the CDA indexes the amount of information (namely, number of items) in WM, regardless of whether the items were repeated or updated before. An exploratory analysis revealed update-related ERP components at both the contralateral and ipsilateral hemispheres, with a striking similarity between the hemispheres. The effect in electrodes F1/F2 is consistent with local updating, showing a larger negativity as more items are changed. Activity in lateral-posterior electrodes, on the other hand, was sensitive to whether or not an update occurred, regardless of the amount of change. This pattern is consistent with the predictions of global updating, but not with the behavioral results. Importantly, the local effect in the frontal electrodes was shorter than the global effect in the lateral-posterior electrodes, although their onset was roughly similar. This latency overlap of these ERP components presumably reflects parallel processing, as opposed to a serial two-stage model (c.f. Kessler & Meiran, 2008).

We suggest that frontal activity reflects information modification in WM (for example, by creating new item-location associations), while lateral-posterior activity stems from a separate comparison process between the perceptual input and WM representations. Hyun, Woodman, Vogel, Hollingworth, and Luck (2009) provided evidence for a rapid and parallel process of comparison between perceptual information and WM, which results in shifting attention to the changed item. We suggest that the effect in the lateral-posterior electrodes is similar in nature to the N2pb
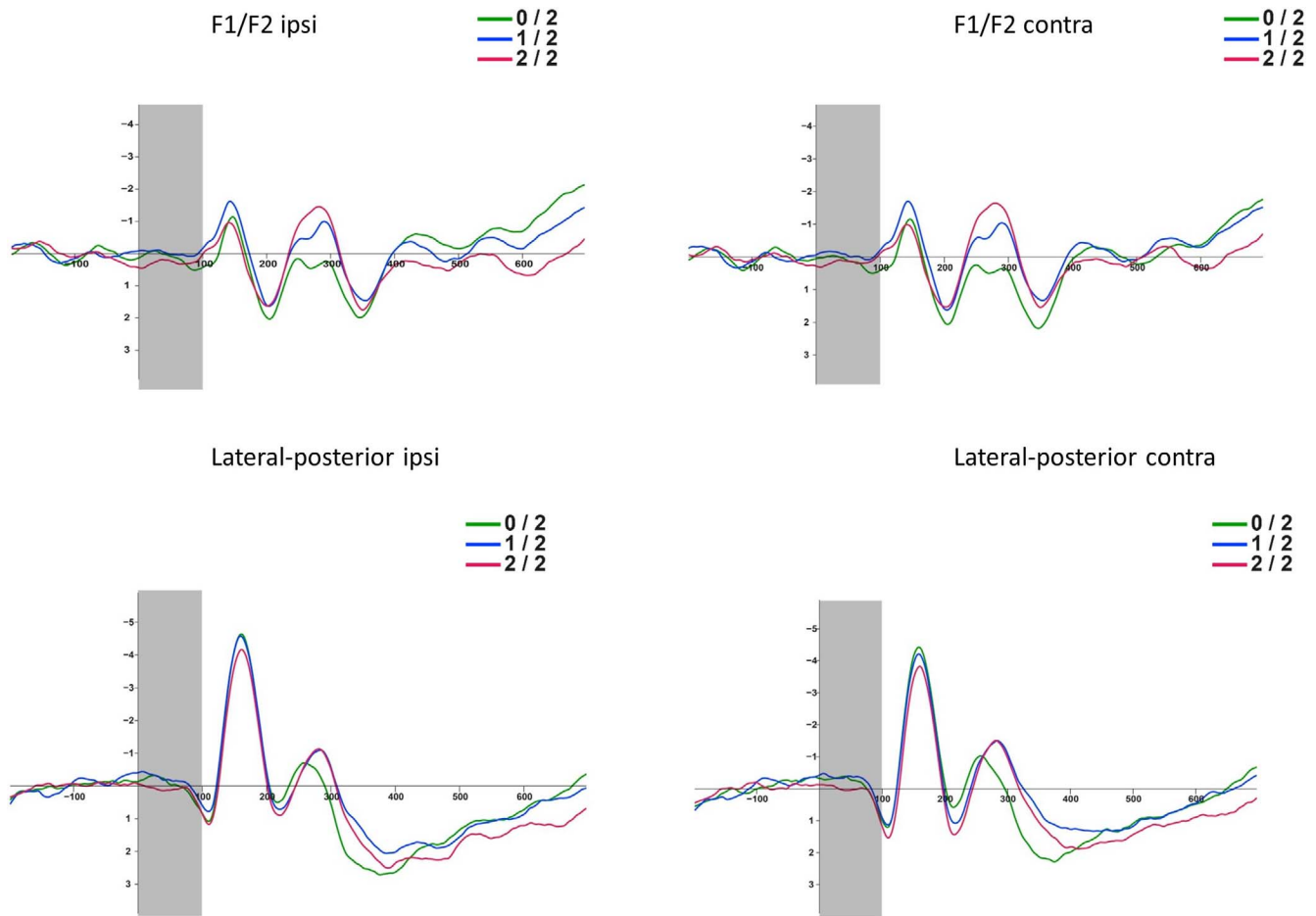
Figure 5. F1/F2 electrodes were sensitive to the number of updated items. In contrast, lateral-posterior electrodes only showed a difference between a full repetition and updating, independently of the number of updated items. Similar effects are observed in the ipsilateral and contralateral hemispheres. The presentation of the second visual array is marked in gray.

that is observed in visual search tasks (Luck & Hillyard, 1994; see Luck & Kappenman, 2011, for review). The N2pb is a bilateral posterior negativity related to the pop-out of task-relevant features. Our findings of a larger posterior negativity in the update conditions (1/2 and 2/2) compared to the full repetition suggests a parallel comparison process that occurs for each item independently. However, detecting a change is necessary but not sufficient for WM. The actual modification of WM contents may involve further processes such as inhibiting the outdated information (Ecker et al., in press; Oberauer, 2001) and establishing new item-position associations (Kessler & Oberauer, 2014). These processes are manifested in the frontal electrodes, and, therefore, predict performance when probing an updated item.

Taken together, our results support item-based models of WM representations, as well as local updating. Items are maintained separately, and can be updated independently, presumably through the operation of item-specific gates. It should be noted that our paradigm does not include irrelevant items, which require an additional mechanism for selecting and gating task-relevant information (c.f. Manza et al., 2014). While we propose that such a selective mechanism must take place in a later processing stage, future work is required to investigate the coordination of selective and nonselective change detection processes, and the way in which only task-relevant changes trigger WM updating.

Keywords: event-related potentials, updating, visual working memory, working memory

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Footnote

[1] Administering these conditions with equal probabilities was done to ensure equal number of trials in each condition. However, this also affects the probability that an updated item will be probed. In the 1/6 condition, for example, the updated item has a 50% probability to be probed, compared to 10% for any of the other items. This might lead to strategically remembering the updated items. However, as demonstrated by the results, performance for updated items was poorer than for repeated items. This made the use of such a strategy unlikely, or at least makes its benefit very limited. This potential bias is corrected in Experiment 2, using a set-size of two items only.

References

Artuso, C., & Palladino, P. (2011). Content-context binding in verbal working memory updating: On-line and off-line effects. *Acta Psychologica, 136,* 363–369.

Artuso, C., & Palladino, P. (2014). Binding and context updating in working memory tasks. *British Journal of Psychology, 105,* 226–242.

Badre, D. (2012). Opening the gate to working memory. *Proceedings of the National Academy of Sciences, USA, 109,* 19878–19879.

Braver, T. S., & Cohen, J. D. (2000). On the control of control: The role of dopamine in regulating prefrontal function and working memory. In S. Monsell & J. Drive (Eds.), *Control of cognitive processes: Attention and performance XVIII,* (pp. 713–737). Cambridge, MA: MIT Press.

Carretti, B., Cornoldi, C., & Pelegrina, S. L. (2007). Which factors influence number updating in working memory? The effects of size distance and suppression. *British Journal of Psychology, 98,* 45–60.

Chatham, C. H., Frank, M. J., & Badre, D. (2014). Corticostriatal output gating during selection from working memory. *Neuron, 81,* 930–942.

Cowan, N. (2001). The magical number 4 in short-term memory: A reconsideration of mental storage capacity. *Behavioral and Brain Sciences, 24,* 87–114.

Delorme, A., & Makeig, S. (2004). EEGLAB: An open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *Journal of Neuroscience Methods, 134,* 9–21.

Ecker, U. K. H., Lewandowsky, S., and Oberauer, K. (2014). Removal of information from working memory: A specific updating process. *Journal of Memory and Language, 74,* 77–90.

Ecker, U. K. H., Lewandowsky, S., Oberauer, K., & Chee, A.E. (2010). The components of working memory updating: An experimental decomposition and individual differences. *Journal of Experimental Psychology: Learning, Memory and Cognition, 36,* 170–189.

Ecker, U. K. H., Oberauer, K., & Lewandowsky, S. (2014). Working memory updating involves item-specific removal. *Journal of Memory and Language, 74,* 1–15.

Franconeri, S. L., Alvarez, G. A., & Cavanagh, P. (2013). Flexible cognitive resources: Competitive content maps for attention and memory. *Trends in Cognitive Sciences, 17,* 134–141.

Frank, M. J., Loughry, B., & O'Reilly, R. C. (2001). Interactions between frontal cortex and basal ganglia in working memory: A computational model. *Cognitive, Affective, and Behavioral Neuroscience, 1,* 137–160.

Garavan, H. (1998). Selective attention within working memory. *Memory and Cognition, 26,* 263–276.

Guthrie, D., & Buchwald, J. S. (1991). Significance testing of difference potentials. *Psychophysiology, 28*(2), 240–244.

Hyun, J. S., Woodman, G. F., Vogel, E. K., Hollingworth, A., & Luck, S. J. (2009). The comparison of visual working memory representations with perceptual inputs. *Journal of Experimental Psychology: Human Perception & Performance, 35,* 1140–1160.

Ihssen, N., Linden, D. E., & Shapiro, K. L. (2010). Improving visual short-term memory by sequencing the stimulus array. *Psychonomic Bulletin & Review, 17,* 680–686.

Jeffreys, H. (1961). *Theory of probability.* New York: Oxford University Press.

Kessler, Y., & Meiran, N. (2006). All updateable objects in working memory are updated whenever any of them are modified: Evidence from the memory updating paradigm. *Journal of Experimental Psychology: Learning, Memory and Cognition, 32,* 570–585.

Kessler, Y., & Meiran, N. (2008). Two dissociable

updating processes in working memory. *Journal of Experimental Psychology: Learning Memory and Cognition, 34,* 1339–1348.

Kessler, Y., & Oberauer, K. (2014). Working memory updating latency reflects the cost of switching between maintenance and updating modes of operation. *Journal of Experimental Psychology: Learning, Memory and Cognition, 40,* 738–754.

Kessler, Y., & Oberauer, K. (2015). Forward scanning in verbal working memory updating. *Psychonomic Bulletin & Review*, e-pub ahead of print.

Ko, P. C., & Seiffert, A. E. (2009). Updating objects in visual short-term memory is feature selective. *Memory & Cognition, 37,* 909–923.

Lendínez, C., Pelegrina, S., & Lechuga, M. T. (2014). The role of similarity in updating numerical information in working memory: Decomposing the numerical distance effect. *Quarterly Journal of Experimental Psychology, 67,* 16–32.

Logie, R. H., Brockmole, J. R., & Vandenbroucke, A. R. E. (2009). Bound feature combinations in visual short-term memory are fragile but influence long-term learning. *Visual Cognition, 17,* 160–179.

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

Luck, S. J., & Kappenman, E. S. (2011). ERP components and selective attention. In S. J. Luck & E. S. Kappenman (Eds.), *The Oxford handbook of event-related potential components* (pp. 295–328). New York: Oxford University Press.

Luck, S. J., & Vogel, E. K. (1997). The capacity of visual working memory for features and conjunctions. *Nature, 390,* 279–281.

Luck, S. J., & Vogel, E. K. (2013). Visual working memory capacity: From psychophysics and neurobiology to individual differences. *Trends in Cognitive Sciences, 17,* 391–400.

Manza, P., Hau, C. L., & Leung, H. C. (2014). Alpha power gates relevant information during working memory updating. *Journal of Neuroscience, 34,* 5998–6002.

O'Reilly, R. C. (2006). Biologically based computational models of high-level cognition. *Science, 314,* 91–94.

Oberauer, K. (2001). Removing irrelevant information from working memory: A cognitive aging study with the modified Sternberg task. *Journal of Experimental Psychology: Learning, Memory and Cognition, 27,* 948–957.

Oberauer, K. (2003). Selective attention to elements in working memory. *Experimental Psychology, 50,* 257–269.

Oberauer, K. (2009). Design for a working memory. *Psychology of Learning and Motivation, 51,* 45–100.

Oberauer, K., Souza, A. S., Druey, M. D., & Gade, M. (2013). Analogous mechanisms of selection and updating in declarative and procedural working memory: Experiments and a computational model. *Cognitive Psychology, 66,* 157–211.

Rouder, J. N., Morey, R. D., Speckman, P. L., & Province, J. M. (2012). Default Bayes factors for ANOVA designs. *Journal of Mathematical Psychology, 56,* 356–374.

Souza, A. S., Rerko, L., & Oberauer, K. (2014). Unloading and reloading working memory: Attending to one item frees capacity. *Journal of Experimental Psychology: Human Perception and Performance, 40,* 1237–1256.

Vogel, E. K., & Machizawa, M. G. (2004). Neural activity predicts individual differences in visual working memory capacity. *Nature, 428,* 784–751.

Vogel, E. K., McCollough, A. W., & Machizawa, M. G. (2005). Neural measures reveal individual differences in controlling access to visual working memory. *Nature, 438,* 500–503.

Wilken, P., & Ma, W. J. (2004). A detection theory account of change detection. *Journal of Vision, 4*(12):11, 1120–1135, doi:10.1167/4.12.11. [PubMed] [Article]

Zacks, J. M., Speer, N. K., Swallow, K. M., Braver, T. S., & Reynolds, J. R. (2007). Event perception: A mind-brain perspective. *Psychological Bulletin, 133,* 273–293.

Zhang, W., & Luck, S. J. (2008). Discrete fixed-resolution representations in visual working memory. *Nature, 453,* 233–235.