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Impact of processing demands at encoding, maintenance and retrieval in visual working memory

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ABSTRACT

There has been surprisingly little examination of how recall performance is affected by processing demands induced by retrieval cues, how manipulations at encoding interact with processing demands during maintenance or due to the retrieval cue, and how these are affected with aging. Here, we investigate these relationships by examining the fidelity of working memory recall across two delayed reproduction tasks with a continuous measure of report across the adult lifespan. Participants were asked to remember and subsequently reproduce from memory the identity and location of a probed item from the encoding display. In Experiment 1, we examined the effect of filtering irrelevant information at encoding and the impact of filtering distracting information at retrieval simultaneously. In Experiment 2, we tested how ignoring distracting information during maintenance or updating current contents with new information during this period affects recall.

The results reveal that manipulating processing requirements induced by retrieval cues (by altering the nature of the retrieval foil) had a significant impact on memory recall: the presence of two previously viewed features from the encoding display in the retrieval foil led to a decrease in identification accuracy. Although irrelevant information can be filtered out well at encoding, both ignoring irrelevant information and updating the contents of memory during the maintenance delay had a detrimental effect on recall. These effects were similar across the lifespan, but older individuals were particularly affected by manipulations of processing demands at encoding as well as increasing set size of information to be retained in memory. Finally, analyses revealed that there were no systematic relationships between filtering performance at encoding, maintenance and retrieval suggesting that these processing demands are independent of each other. Rather than filtering being a single, monolithic entity, the data suggest that it is better accounted for as distinctly dissociable cognitive processes that engage and articulate with different phases of working memory.

1. Introduction

It is now generally agreed that there are extremely strong links between processes traditionally subsumed by the terms ‘attention’ and ‘working memory’, WM (Chun & Johnson, 2011; Sean James Fallon, Zokaei, & Husain, 2016; Manohar, Zokaei, Fallon, Vogels, & Husain, 2019; Rhodes & Cowan, 2018). In the visual WM literature, these relationships have typically been probed by investigating the impact on recall performance of processing demands at encoding and during maintenance including studies of feature misbinding, but not generally at retrieval.

Demands on memory resources *at encoding* have often been studied

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by using pre-cues which provide information about the relevant properties of the upcoming task, such as the features of stimuli that are more likely to be probed (Jost, Bryck, Vogel, & Mayr, 2011; Vogel, McCollough, & Machizawa, 2005). For example, spatial cues can direct participants to locations where relevant information will be presented allowing them to encode fewer items and thereby improve performance (Ikkai, McCollough, & Vogel, 2010; Schmidt, Vogel, Woodman, & Luck, 2002; Vogel et al., 2005; Woodman, Vecera, & Luck, 2003).

Manipulations of processing demands on visual WM representations *during maintenance* have also been possible using either retro-cues which increase the likelihood of some items being probed (Griffin & Nobre, 2003; Landman, Spekreijse, & Lamme, 2003; for a review see Souza & Oberauer, 2016) or presenting distractors that need to be ignored during the retention interval (Sean J. Fallon, Mattiesing, Dolfen, Manohar, & Husain, 2018; Souza, Rerko, & Oberauer, 2014; Van Moorselaar, Olivers, Theeuwes, Lamme, & Sligte, 2015; Williams, Hong, Kang, Carlisle, & Woodman, 2013). In this case, remembered information has to be protected from being overwritten by the irrelevant stimuli.

In addition to the use of these strategies to investigate the interaction of processing demands and WM, some authors have also focused on *binding errors* in WM recall, since feature binding has been considered to be one important aspect of attention (Baddeley, Allen, & Hitch, 2011; Johnson, Hollingworth, & Luck, 2008; Luck & Vogel, 1997; Wheeler & Treisman, 2002). However, paradigms used to investigate this issue have usually not been designed to establish at which stage of memory – encoding, maintenance or retrieval – feature binding of stimuli has been affected. Some work has shown that attentional deployment during maintenance makes a contribution to keeping stimulus features correctly bound in WM. First, misbinding rates increase with retention durations particularly with high memory loads (Pertzov, Manohar, & Husain, 2017). Second, presentation of distractors during retention intervals can also increase misbinding, specifically to features in the to-be-ignored distractors (Sean J. Fallon et al., 2018). Finally, consistent with the proposal that high processing demands lead to more misbinding errors, paradigms that employ taxing demands during the maintenance interval have shown an increase in misreporting features of stored items (Brown & Brockmole, 2010; Fougnie & Marois, 2009; Zokaei, Heider, & Husain, 2014).

To the best of our knowledge, most investigations on the role of processing demands in WM, such as the ones described above, have focused on encoding and maintenance periods. However, there has been little research on how recall performance is affected by processing demands induced by the retrieval cue. Theeuwes, Belopolsky, and Olivers (2009) showed that in retrieval from visual WM, observers allocate visual attention to the location in space that contains the information to be retrieved, even if this is not required to solve the task whatsoever. Hence, they concluded that directing attention in WM is similar to selecting actual visual input in form of visual stimuli (Theeuwes et al., 2009; Theeuwes, Kramer, & Irwin, 2011). We are not aware, though, of any study that has attempted to examine the relationships between processing demands at encoding, maintenance and retrieval. This would be important to establish whether there is a generic system that operates at all phases of WM when processing demands are increased or whether there might be dissociable or fractionated systems that operate at different phases in WM.

To investigate these issues, we designed two experiments to systematically examine how processing demands induced at different stages of WM relate to each other. The first experiment required participants on some trials to filter out information at encoding because it would never be probed at retrieval, while manipulating processing demands at retrieval by varying the nature of a distractor foil. Specifically, we altered whether the foil had one or two features that belonged to either another to-be-encoded item in the encoding display or one or two features that belonged to a task-irrelevant item that should have been filtered out at encoding. The second experiment compared the ability to filter out distractors presented during maintenance (*Ignoring*) with performance when new items presented during retention had to be uploaded into WM and older ones jettisoned (*Updating*).

Until now, the effects of filtering demands in most previous studies have relied on quantifying WM capacity by employing change-detection paradigms or using the amplitude of contralateral delay activity (CDA), an electrophysiological marker putatively linked to WM capacity, assuming an item is either stored or not (Cowan & Morey, 2006; Gazzaley, Clapp, Kelley, McEvoy, & Knight, 2008; Jost et al., 2011; Rhodes & Cowan, 2018; Robison, Miller, & Unsworth, 2018; Vogel et al., 2005; Vogel & Machizawa, 2004). For example, Vogel et al. showed that filtering ability correlates very closely with WM capacity and that people who can remember more objects from a spatial array are more efficient at excluding irrelevant information, arguing that individual differences in memory capacity can be predictive of filtering abilities (Vogel et al., 2005). In the current study, memory performance was measured using a delayed reproduction task, which uses a continuous response over an analogue scale. Therefore, instead of solely asking participants to report whether they remember a feature, here they were also requested to reproduce the exact quality of the remembered feature in an analogue response space (Bays, Catalao, & Husain, 2009; Gorgoraptis, Catalao, Bays, & Husain, 2011; Pertzov, Dong, Peich, & Husain, 2012). This method also allowed us to model the source of errors in terms of noisiness or imprecision of recall of the probed item or target, misbinding (reporting the features of a non-probed item that had been presented in the encoding display) and random guessing (Bays et al., 2009; Grogan, Fallon, Zokaei, Husain, & Manohar, 2020).

An ancillary aim of our study was to examine how processing demands at encoding, during maintenance and due to the retrieval cues, vary across the adult lifespan, with aging. Investigations of the effects of aging on storage have shown that the number of items that can be held in WM decreases with age (Chen, Hale, & Myerson, 2003; McNab & Dolan, 2014; Myerson, Emery, White, & Hale, 2003; Peich, Husain, & Bays, 2013; Pertzov, Liang, Heider, & Husain, 2015). Additionally, it has been found that filtering abilities, at least as indexed by the amplitude of the CDA, is worse in older people but only just after encoding, improving over the retention delay (Jost et al., 2011). Another study has concluded that the ability to ignore distracting information at encoding might be a better predictor of age-related decline in WM capacity compared to filtering information at maintenance (McNab et al., 2015). Clearly, it remains to be resolved how processing demands impact on WM performance with aging in adults. Moreover, it is unknown whether processing effects induced by retrieval change with age.

2. Experiment 1: Processing demands at encoding and induced by retrieval cues

The first study investigated the effect of filtering at encoding and the impact of distracting information at retrieval. The key questions we sought to answer were:

1. Is there an impact of the nature of the foil type at retrieval depending upon whether it had one or two features from an item presented in the encoding display which is to be expected in Identification Accuracy?
2. Does the nature of the foil type at retrieval impact upon recall, depending upon whether it had features that came from a task-irrelevant item, i.e., that was supposed to have been filtered out at encoding which is also to be expected in Identification Accuracy in particular?
3. How successful is filtering at encoding (by comparing performance in the set size 2 condition with the filtering condition in which 3 items were presented but one item was task irrelevant, i.e., it had to be filtered out) reflected by Identification Accuracy and Localisation Performance?
4. What is the impact of these performance measures with aging? Does aging simply lead to worse performance across the board or is there

any selective effect of age in the Identification Accuracy or Localisation Performance in 1–3?

2.1. Methods

2.1.1. Participants

We ran two experiments (**Experiment 1** and **Experiment 2**) with the order in which participants performed them randomized. 40 young adults aged between 18 and 34 years (26 females, 14 males) and 61 elderly adults aged between 52 and 81 years (34 females, 27 males) that reported to be neurologically normal were recruited to take part in this Experiment. See further demographics displayed in Table 1. Permission for this study was obtained from the local ethics committee and all subjects gave written informed consent. Cognitive function screening was tested using Addenbrookes Cognitive Examination-III (ACE-III) (Mathuranath, Nestor, Berrios, Rakowicz, & Hodges, 2000).

2.1.2. Stimuli, design and procedure

This experiment investigated the effect of filtering at encoding and the impact of distracting information induced by retrieval cues on recall (Fig. 1). Participants were asked to remember both the identity and location of circles, each of which consisted of semicircles of different colours. The orientation of a white arrow presented in the middle of the screen pointed to the items that had to be remembered. For example, if the arrow pointed left, participants had to recall memoranda presented on the left side of the screen while ignoring the *task-irrelevant item* presented on the opposite side of the screen, i.e., this was the item that had to be filtered out from the encoding display. In half of the trials, the memory array (the items that should be remembered) was presented on the left side of the screen, in the other half it was presented to the right. This arrow manipulation allowed us to examine processing demands *at encoding.*

After a 2 s delay, participants were given a two-alternative choice between a *target* – the correct item to identify which had appeared in the encoding display – and a *foil* – a distractor item that had not appeared in the memory display. They had to touch the target, then drag it to where it originally appeared.

In the “set size 2” and “set size 3” conditions, two or three circles were presented respectively on one half of the screen, indicated by the arrow pointing to that side (Fig. 2, first and last row). In the filtering at encoding condition, two circles were presented on the half of the screen that the arrow pointed towards while a *task- irrelevant item* was presented on the opposite side (Fig. 2, second row).

The amount of information competing *at retrieval* was manipulated by including, in addition to the target item, a foil at retrieval. The foil was a circle which consisted of two semicircles, just like the target. Importantly, it contained either one or two features (coloured semicircles) from an item in the original encoding display. Note that the semi-circle with the same colour as the target always occupied the opposite half of the circle to its location in the original encoding display.

The retrieval foil could consist of:

Features from non-target items:

Table 1
Participant demographics.

Measure	Healthy young controls	Healthy elderly controls
n	40	61
Age (years old)	23.8(±4.1)	68.2(±7.5)
Gender (F/M)	26/14	34/27
Handedness (R/L)	38/2	48/12
Global Cognition (ACE-III score)	96.0(±4.1)	97.1(±2.7)

ACE = Addenbrooke’s Cognitive Examination III; all values are mean (± standard deviation).

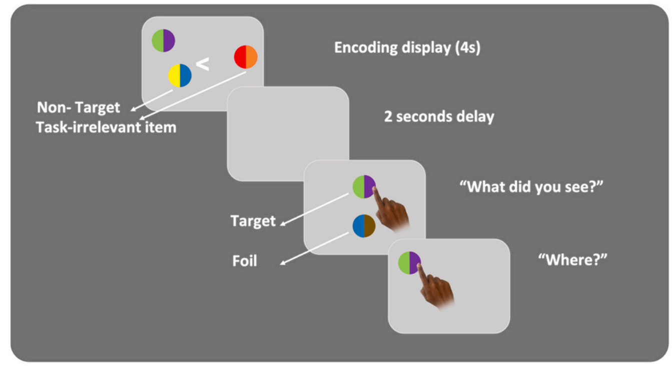

Fig. 1. Schematic of Experiment 1: manipulations of retrieval and filtering. Participants were required to remember only the circles on that half of the screen that the arrow (< or >) pointed towards. After a 2 s delay, they were given a choice between a target and a foil. They needed to select the target and then drag it to where they remembered it to have originally appeared (please find a modified greyscale version of this figure in Appendix, Supplementary Fig. 1).

- A semicircle filled with a colour that had appeared in one of the non-targets in the encoding display (one old feature from non-filtered items), with the other half of the circle filled with a colour that had not appeared in the encoding display (one old feature from non-filtered items: Fig. 2, second column).
- A semicircle filled with a colour that had appeared in one of the non-targets in the encoding display, but with the other half of the circle filled with a colour that had appeared in the *target item* (two old features from non-filtered items; Fig. 2, third column).

Features from task-irrelevant items:

- A semicircle filled with a colour that had appeared in the task-irrelevant item that had to be filtered out in the encoding display (one old feature from the task-irrelevant item), with the other half of the circle filled with a colour that had not appeared in the encoding display (one old feature from the task-irrelevant item: Fig. 2, fourth column).
- A semicircle filled with a colour that had appeared in the task-irrelevant item that had to be filtered out in the encoding display, but with the other half of the circle filled with a colour that had appeared in the *target item* (two old features from the task-irrelevant item: Fig. 2, fifth column).

In total, there were eight different conditions: two manipulations of the number of features competing at retrieval (one old feature vs two old features from the encoding display) x four manipulations of set size (memory array composed of 2 items vs memory array composed of 3 items) and filtering (distracter composed of features from the task-irrelevant item vs distracter composed of features from the non-filtered items). Participants performed ten trials of each of these eight conditions. Each trial began with the presentation of either two or three circles (4000 ms) that appeared in separate spatial locations, with the symbol “<” or “>” appearing in the centre of the screen. These memoranda either had to be encoded or filtered from working memory. The symbol “<” or “>” pointed to which memoranda had to be encoded (Fig. 1). Then, after a delay period (2000 ms) came the probe phase. In the probe phase a dual choice was presented. After touching the target shape, participants had to drag the shape to its original location and confirm by pressing a ‘Done’ button.

Participants sat in front of an interactive touch-sensitive screen (tablet Samsung, model Galaxy Tab S3, 2.15Ghz + 1.6Ghz Quad Core Processor, 9.7 in.,) with a 2048 × 1536 pixel matrix. Stimuli were presented on a grey background (RGB [171,171,171]). In Experiment 1,

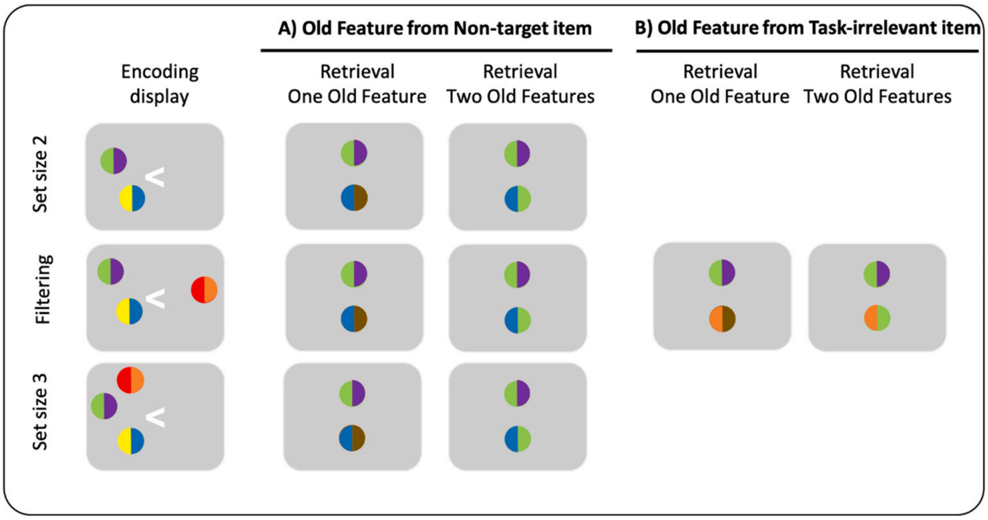

Fig. 2. Schematic of all conditions for Experiment 1.
Encoding was manipulated by varying the number of items to be stored (*Set size 2* and *Set size 3*) and processing demands at encoding were manipulated by asking participants to filter irrelevant information (*Filtering*). Retrieval was manipulated across all conditions in two main ways: A) retrieval cues had features from the non-filtered item or B) retrieval cues had features belonging to the task-irrelevant item. Additionally, in both A) and B), the retrieval foil could have either one or two old features from the encoding display (a modified greyscale version of the figure can be found in Appendix, Supplementary Fig. 2).

colours were selected from a total of seven equally spaced-out colours on the same colour wheel, avoiding identical trial and colour-combinations. The stimuli were presented at a viewing distance of approximately 30 cm and subtended a visual angle of approximately 2.3°.

2.1.3. Behavioural recall analysis

Data and analysis script are available on OSF: https://osf.io/75mju/. Identification performance was computed by taking the proportion of times participants touched the correct shape in the dual choice per condition. Localisation error was calculated by taking the distance between the centre of the reported location and the centre of the original location of the probed item. This was measured for only correctly identified targets. Errors due to misreporting the location of an item occurred as a result of different factors, either misbinding errors or guessing. Misbinding errors refer to the proportion of times subjects misreport the location of the correctly identified item by dragging it to the location of another item presented in the encoding display (Fig. 3). Imprecision was calculated based on the distance to the nearest neighbour, i.e., the closest distance between the response (where the participant placed the chosen item) and the location of any item in the encoding display (either a target, non-target or a task-irrelevant item).

Here, we calculated misbinding, using a permutation analysis approach based on the mixture model (Bays et al., 2009) as follows: Per trial, distances between the response location and **i**) the target location, **ii**) the location of the closest non-target (the closest item that is not being probed) and **iii**) the location of another, randomly chosen trial's non-target were calculated. The locations of each of the target and non-target locations were randomly determined per trial, thus leading to a range of possible locations that is equal to the number of all non-targets in the experiment. Depending on which of these distances was the shortest, the response was either counted as target (**i**), non-target (**ii**, "misbinding") or random/guessing response (**iii**, "uniform"). We repeated this procedure 5000 times per trial, thus introducing a non-target from a randomly chosen trial (see **iii**) each time. This procedure allowed us to calculate proportions for these three sources of response per trial (absolute amount of response type/5000). The introduction of a non-target that was randomly chosen from another trial (**iii**) allowed us to differentiate whether an error was systematically linked to the very specific trial's non-target or whether it could be accounted for even by a randomly chosen non-target that was not present at trial. Guessing, quantifies the proportion of times an item is completely forgotten. This corresponds to the proportion of responding randomly to the target

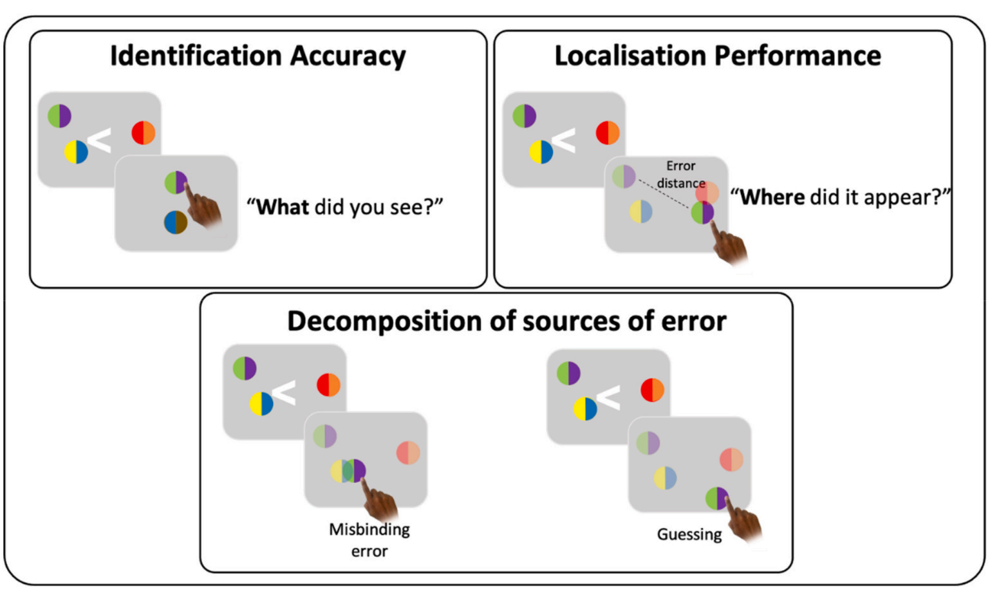

Fig. 3. Recall measures.
Identification performance is the frequency with which participants touched the target in the two-alternative forced choice (**top left**). *Localisation performance* is the distance between the centre of the reported location and the original location of the target (**top right**). *Decomposing the sources of error* allowed extraction of two types of error due to misreporting the location of an item": 1) Misbinding errors, that occur when the participant dragged the correct item to the location of another item presented in the encoding display (**bottom left**) and 2) Errors due to guessing when a participant dragged the correct item to a random location (**bottom right).**

location. To assess the performance of this permutation analysis, we simulated synthetic data and compared the simulation input to the results calculated using this analysis which can be found in the Appendix (see also Supplementary Fig. 3). They show that for misbdinding, the overall average of calculations will land on the true value without any particular bias towards over- or underestimating the parameter. But every single calculation will on average deviate about 0.03 from the true value and, thus, results of small magnitudes should be considered with due caution.

Data were analysed using *MATLAB* (The MathWorks inc., version 2018a) and *JASP* (JASP Team, 2020).

2.2. Results

2.2.1. Effect of set size, retrieval foil type and age group

2x2x2 repeated measures ANOVAs of set size (two vs three) x number of old features in the foil (one vs two) x group (young vs old participants) were first conducted to investigate the effects of set size and number of old features (from items in the encoding display) that appeared in the foil at retrieval on:

- Identification accuracy (proportion of correctly identified items)
- Localisation error
- Model parameters: misbinding, guessing and imprecision
- Reaction time (time taken to initiate the response)

Identification accuracy and Localisation performance were the variables of interest which were followed up with the model parameters and reaction time. The findings are depicted in Fig. 4 and details are summarized in Supplementary Tables 1–9.

2.2.2. Set size

As expected, increase in set size from 2 to 3 items both decreased identification accuracy ($F(1,99) = 50.39$, $p < 0.001$, $\eta_p^2 = 0.34$) and increased localisation error ($F(1,99) = 82.62$, $p < 0.001$, $\eta_p^2 = 0.46$). With respect to modelling parameters, increase in set size led to a significantly higher misbinding ($F(1,99) = 73.27$, $p < 0.001$, $\eta_p^2 = 0.43$) and imprecision ($F(1,99) = 16.11$, $p < 0.001$, $\eta_p^2 = 0.14$) as well as slower reaction time ($F(1,99) = 74.71$, $p < 0.001$, $\eta_p^2 = 0.43$). However, there was no significant main effect on guessing.

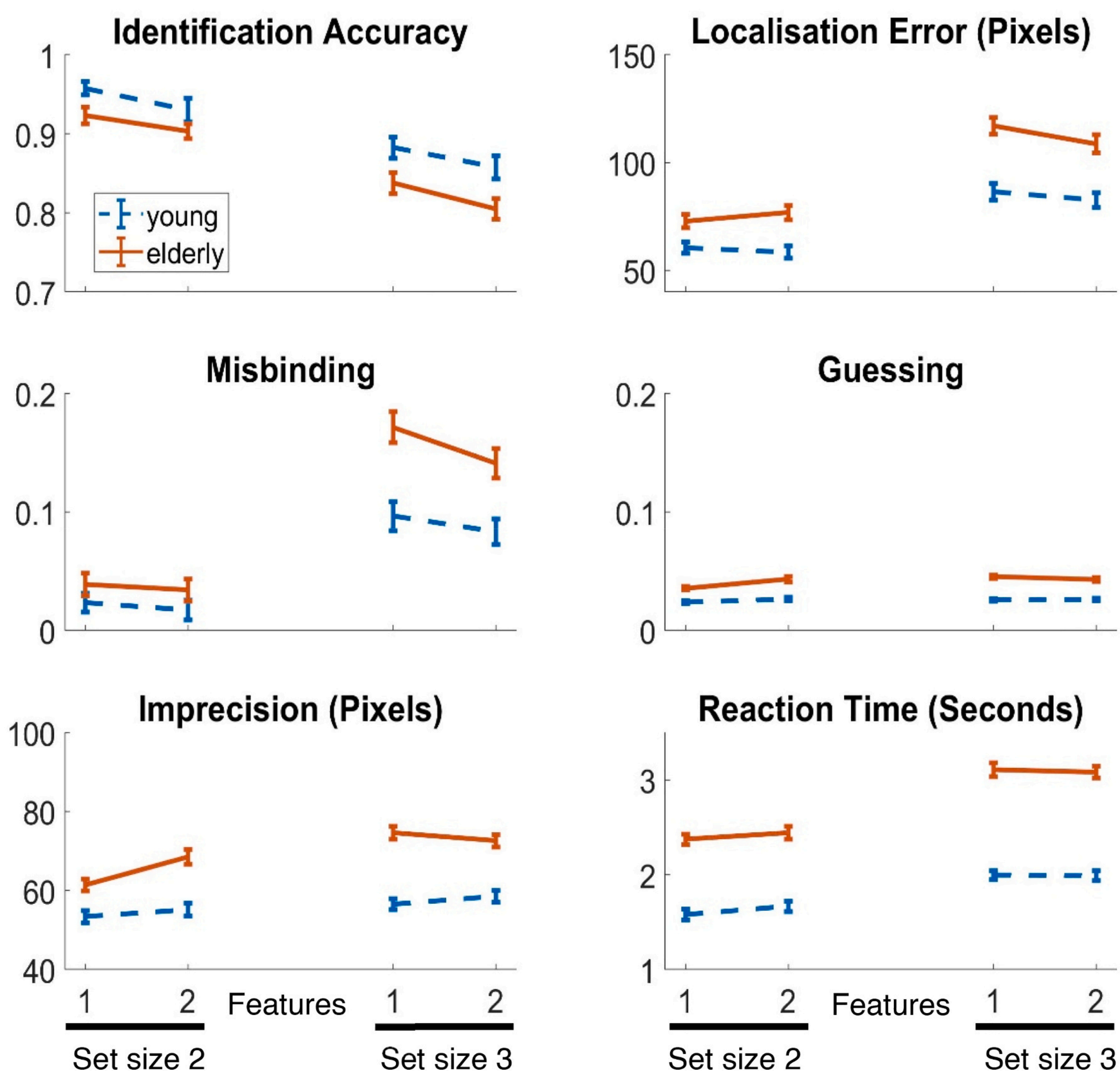

Fig. 4. Impact on memory recall of number of old features in the foil at retrieval.
An increase of old features from 1 to 2 decreased Identification Accuracy. This was independent of Set Size. Higher set size led to an increase of Localisation Error driven by higher imprecision and higher misbinding, additionally participants responded significantly slower. Elderly participants generally performed worse than young controls. Error bars were calculated by subtracting each subject's grand mean away from their individual per-condition values and showing ± standard error (Loftus & Masson, 1994).

2.2.3. Number of old features in foil at retrieval

Increase in the number of features from the memory display in the foil at retrieval from 1 to 2 significantly decreased identification accuracy ($F(1,99) = 7.06$, $p = 0.009$, $\eta_p^2 = 0.07$). However, it had no impact on localisation error, misbinding, guessing, imprecision or reaction time. Thus, the critical impact of number of features in the foil at retrieval was mainly on item identification. In addition, there was also a significant interaction between number of features and set size in guessing ($F(1,99) = 5.49$, $p = 0.021$, $\eta_p^2 = 0.05$): Holm-corrected post-hoc *t*-tests show that participants performed worse for two features in the set size 2 condition compared to one feature ($t(100) = 2.924$, $p = 0.022$), but this was not the case in set size 3 ($t(100) = 0.540$, $p = 1.00$). There was also a significant difference between set size 2 and set size 3 for one feature ($t(100) = 2.940$, $p = 0.022$) but not for two features ($t(100) = 0.166$, $p = 1.00$). However, Fig. 4 suggests that the numeric value of this effect is marginal.

2.2.4. Young vs older participants

Younger participants performed significantly better on all metrics. Their identification accuracy was higher ($F(1,99) = 6.11$, $p = 0.015$, $\eta_p^2 = 0.06$), localisation error was smaller ($F(1,99) = 14.22$, $p < 0.001$, $\eta_p^2 = 0.13$), misbinding ($F(1,99) = 8.83$, $p = 0.004$, $\eta_p^2 = 0.08$) and guessing ($F(1,99) = 9.13$, $p = 0.003$, $\eta_p^2 = 0.08$) were less, and they were more precise ($F(1,99) = 18.21$, $p < 0.001$, $\eta_p^2 = 0.16$) and reacted faster ($F(1,99) = 49.02$, $p < 0.001$, $\eta_p^2 = 0.33$). There was a significant interaction of age group with the set size in misbinding (Supplementary Table 3). This was further explored by two independent ANOVAs for each group on misbinding. In both young and older age groups there were significant main effects of set size (respectively $F(1,39) = 30.82$, $p < 0.001$, $\eta_p^2 = 0.44$); ($F(1,60) = 56.77$, $p < 0.001$, $\eta_p^2 = 0.49$), indicating greater misbinding when 3 items had to be remembered compared to 2. Holm-corrected post-hoc *t*-tests on the original ANOVA revealed that elderly participants were significantly worse than young controls in the 3 item condition but not in the 2 item condition ($t(99) = 8.608$, $p < 0.001$, $t(99) = 0.911$, $p = 0.363$, respectively; Supplementary Table 4). In addition, there was an interaction of group and set size in the reaction time (Supplementary Table 8), which was followed up in an analogous manner. Both young and older people were slower on recall when there were 3 items (respectively $F(31.02$, $p < 0.001$, $\eta_p^2 = 0.44)$; ($F(1,60) = 59.72$, $p < 0.001$, $\eta_p^2 = 0.50$). Holm-corrected post-hoc t-tests following up on the original interaction showed that elderly controls are slower than young controls in both, the set size 2 ($t(99) = 5.30$, $p < 0.001$) and the set size 3 conditions ($t(99) = 7.44$, $p < 0.001$; Supplementary Table 9).

In summary, regarding our first research question, the results show that the nature of the foil type – manipulation of processing demands

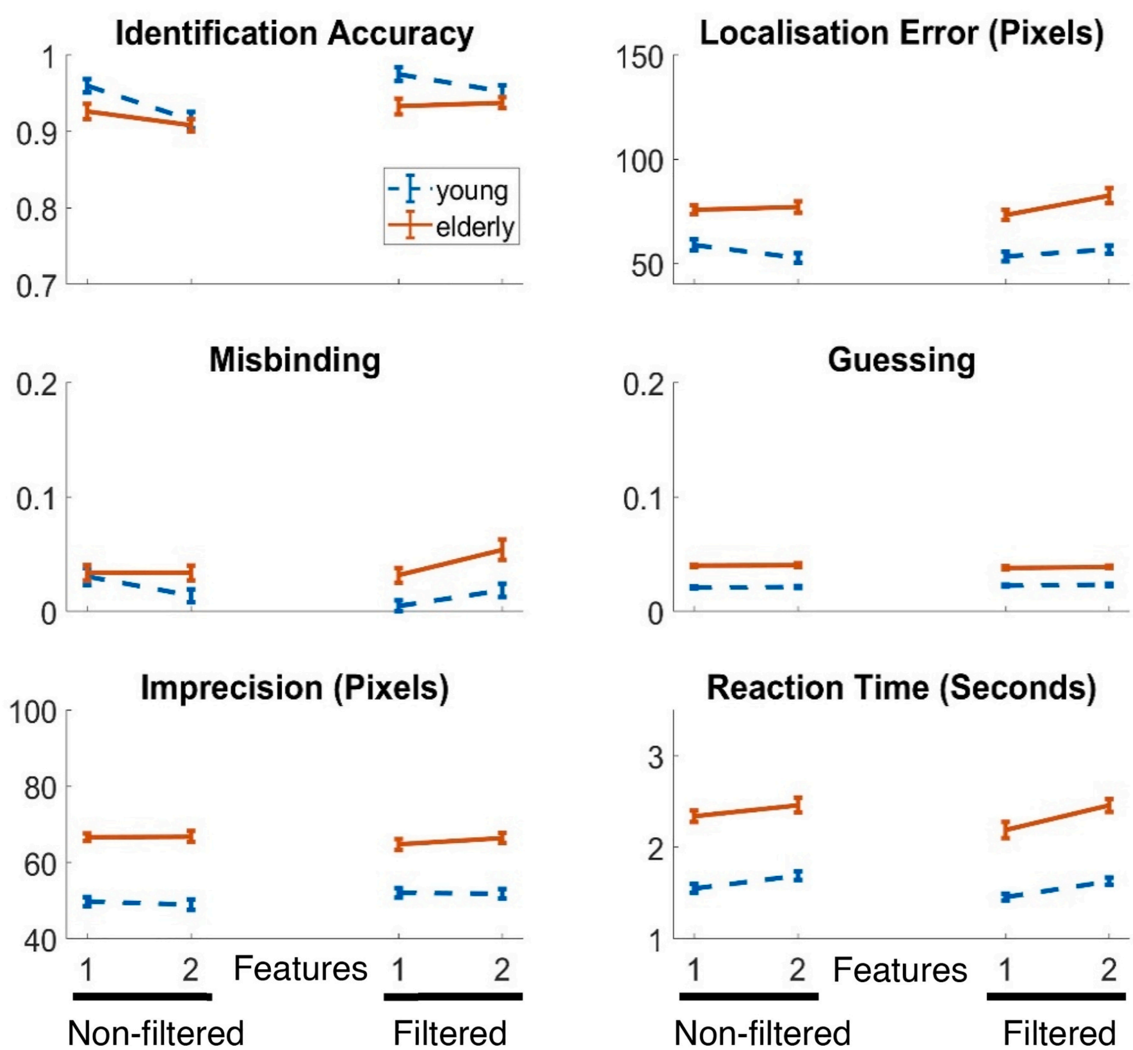

Fig. 5. Impact on memory recall of filtered versus non-filtered features at retrieval.
If the retrieval foil's features were taken from the item that was to be filtered out at encoding, participants were faster and identified the correct item more often. Error bars were calculated by subtracting each subject's grand mean away from their individual per-condition values and showing ± standard error (Loftus & Masson, 1994).

induced by retrieval cues – had a significant impact on memory recall. Presenting two old features in the retrieval foil significantly decreased identification accuracy, independent of set size or age. The latter did not reveal any specific impairment but generally reduced performance over all metrics.

2.3. Impact of filtered vs non-filtered features at retrieval

Next, we examined the data from the filtering trials (Fig. 3, **Filtering condition)** by looking at the effects on recall performance of *filtering at encoding*, as a function of the number of old features from the encoding display present in the foil *at retrieval*. A 2x2x2 ANOVA of the number features x non-filtered vs filtered features in the foil x age group was performed (Fig. 5, Supplementary Tables 10–15).

2.3.1. Filtered vs non-filtered features in retrieval foil

Identification accuracy was significantly affected by whether features in the foil at retrieval were from the non-filtered vs filtered object at encoding ($F(1,99) = 8.23$, $p = 0.005$, $\eta_p^2 = 0.08$). Thus, participants identified the correct item more often when the foil's features were taken from the task-irrelevant item, compared to when they were taken from the non-filtered item. This suggests that if at encoding participants successfully filtered out an item, they were less affected by features from it appearing in the foil. No other significant main effects of the task-irrelevant versus non-filtered item were observed: for localisation error, misbinding, guessing, imprecision or reaction time.

2.3.2. Number of old features in foil at retrieval

Increasing the number of old features in the foil at retrieval significantly decreased identification accuracy ($F(1,99) = 6.08$, $p = 0.015$, $\eta_p^2 = 0.06$) but also slowed participants down ($F(1,99) = 10.11$, $p = 0.002$, $\eta_p^2 = 0.09$). There was, however, no significant effect on localisation error, misbinding, guessing or imprecision. There was a significant interaction for misbinding between filtered/non-filtered feature and number of features in the retrieval foil ($F(1,99) = 4.71$, $p = 0.032$, $\eta_p^2 = 0.05$). Holm-corrected post-hoc *t*-tests showed that participants were significantly more likely to misbind in the two-previously-seen-features condition when one foil's feature was taken from the non-filtered item ($t(100) = -2.18$, $p = 0.032$), but not if it was from the task-irrelevant item ($t(100) = 0.85$, $p = 0.396$).

2.3.3. Young vs older participants

Older participants performed at the levels of young participants in correctly identifying the memoranda ($F(1,99) = 3.25$, $p = 0.074$, $\eta_p^2 = 0.03$)), but showed significantly higher localisation error ($F(1,99) = 26.16$, $p < 0.001$, $\eta_p^2 = 0.21$), more misbinding ($F(1,99) = 7.09$, $p = 0.009$, $\eta_p^2 = 0.07$), more guessing ($F(1,99) = 12.55$, $p < 0.001$, $\eta_p^2 = 0.11$) and higher imprecision ($F(1,99) = 32.55$, $p < 0.001$, $\eta_p^2 = 0.25$) as well as being slower to react ($F(1,99) = 51.32$, $p < 0.001$, $\eta_p^2 = 0.34$). There were no significant interactions between age group with any of the factors or interactions outlined above.

In summary, with respect to our second research question, when previously presented features that were present in the foil originated from the task-irrelevant item, Identification Accuracy was better than when they were from the non-target, indicating they were likely filtered out. This suggests that irrelevant information is filtered out well at encoding. There was no evidence that age modified these effects.

2.4. Effects of filtering at encoding

A 2x2x2 ANOVA of set size (two vs three) x number of old features in the foil (one vs two) x group (young vs old participants was conducted to compare directly the set size 2 condition with the condition in which participants were asked to filter out one of three items. If filtering was perfect, the results of this analysis should show no difference in performance between these conditions. In both cases, the retrieval foil's features were taken from the items that were to be remembered (Fig. 6, Supplementary Tables 16–22).

2.4.1. Two items vs filter condition

There was no significant main effect of filtering between the conditions with respect to identification accuracy, localisation error, misbinding, guessing, imprecision or reaction time. In line with the previous analyses, the number of old features in the foil did, however, have a significant impact on identification accuracy ($F(1,99) = 12.19$, $p < 0.001$, $\eta_p^2 = 0.11$), as well as the reaction time ($F(1,99) = 5.37$, $p = 0.023$, $\eta_p^2 = 0.05$). In this ANOVA, the number of features also increased guessing ($F(1,99) = 4.41$, $p = 0.038$, $\eta_p^2 = 0.04$). All other measures–localisation error, misbinding and imprecision –were unaffected, as previously. There were also no significant interactions with identification accuracy, localisation error, misbinding, guessing or reaction time. However, there was a significant interaction of the two main factors in the imprecision measure ($F(1,99) = 3.98$, $p = 0.049$, $\eta_p^2 = 0.04$). Participants performed significantly better with one repeated feature in the retrieval cue with set size 2 ($t(100) = -2.61$, $p = 0.011$) but not with the filtering condition ($t(100) = 0.13$, $p = 0.898$). The three-way interaction (group x set size x number of features) was not significant but visual inspection of Fig. 6 shows that elderly adults were generally less precise in the filtering condition and it is possible that their precision was already at floor in the set size two, two features condition.

2.4.2. Young vs older participants

Young participants did not differ significantly from older people on identification accuracy but were significantly better on localisation error ($F(1,99) = 16.39$, $p < 0.001$, $\eta_p^2 = 0.14$). They also guessed significantly less ($F(1,99) = 10.06$, $p = 0.002$, $\eta_p^2 = 0.09$), were more precise ($F(1,99) = 23.22$, $p < 0.001$, $\eta_p^2 = 0.19$) and faster ($F(1,99) = 52.14$, $p < 0.001$, $\eta_p^2 = 0.35$) than their elderly counterparts.

However, there was no significant difference between the groups on misbinding. Age group interacted significantly with the number of features in localisation error (Supplementary Table 17, $F(1,99) = 4.20$, $p = 0.043$, $\eta_p^2 = 0.04$) and filtering with respect to imprecision of recall (Supplementary Table 20, $F(1,99) = 7.15$, $p = 0.009$, $\eta_p^2 = 0.07$), but with none of the other factors or interactions.

Following up on the first of these interactions, neither within the group of young nor in older participants was there any significant difference between the filtering and set size two conditions ($F(1,39) = 2.13$, $p = 0.153$; $F(1,60) = 0.30$, $p = 0.588$, respectively) or between one or two repeated features in the retrieval cue ($F(1,39) = 2.61$, $p = 0.114$; $F(1,60) = 1.57$, $p = 0.215$, respectively). With regard to the second interaction, within the young group, imprecision was significantly lower with the filtering condition ($F(1,39) = 10.87$, $p = 0.002$, $\eta_p^2 = 0.22$), but the number of repeated features did not affect imprecision. In the older group, however, although filtering did not affect imprecision, the number of old features in the foil did ($F(1,60) = 4.55$, $p = 0.037$, $\eta_p^2 = 0.07$). In addition, there was an interaction of these two factors ($F(1,60) = 4.56$, $p = 0.037$, $\eta_p^2 = 0.07$) which shows that older participants did worse with two repeated features in the set size two condition ($t(60) = -2.66$, $p = 0.010$) but not in the filtering condition ($t(60) = -0.10$, $p = 0.924$, Supplementary Table 22). However, Fig. 6 (bottom left graph) suggests that this might originate from performance being generally low in the filtering condition.

In summary, concerning our third research question, participants successfully filtered out irrelevant information at encoding, performing at equal levels for the set size 2 and the filtering condition (3 items with one item to be filtered out) in all metrics. Yet, filtering diminished the advantage of one repeated feature in the retrieval foil compared to two repeated features in precision. With respect to our fourth question, as for the previous analyses, there was mostly no selective main effect of age. Aging did lead to overall worse performance, except for the identification accuracy and misbinding which were not significantly different between age groups.

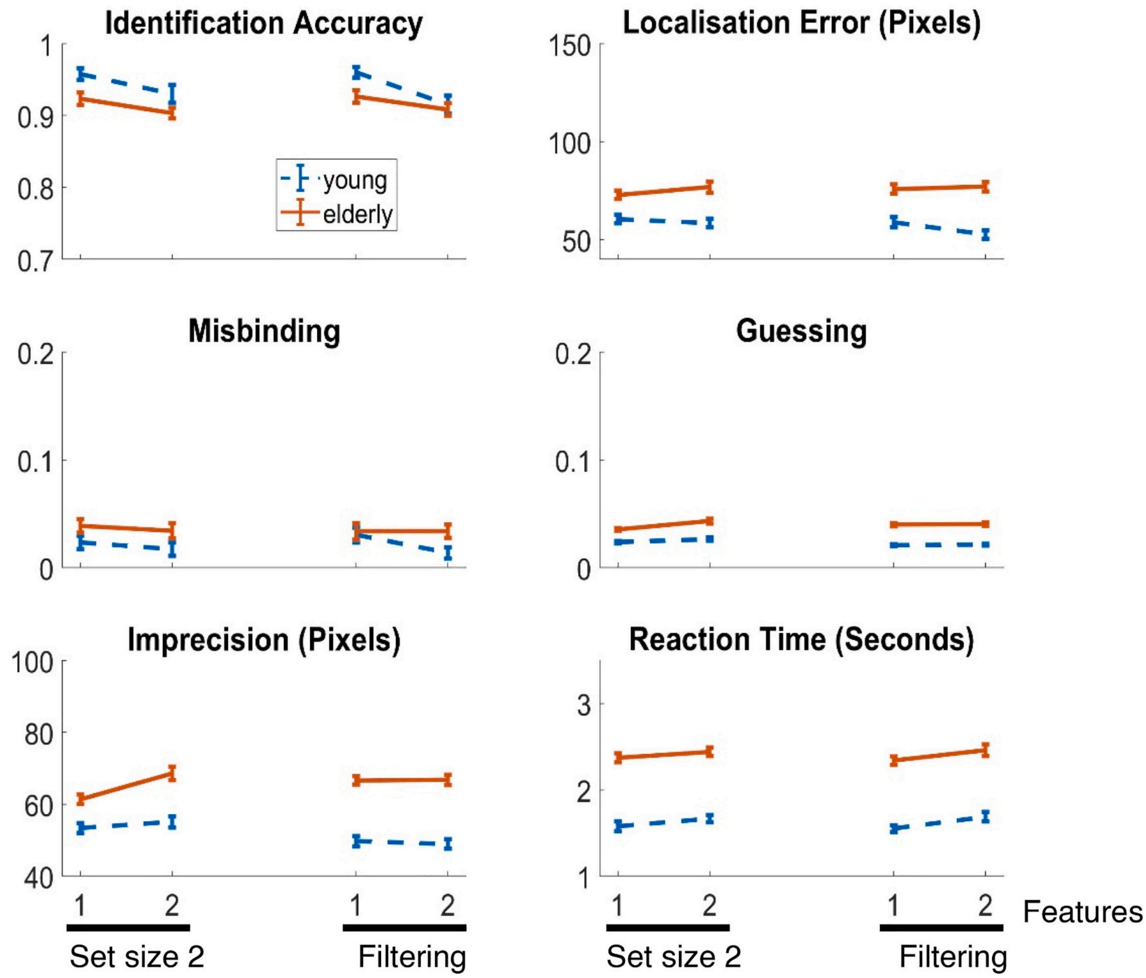

Fig. 6. Impact on memory recall of filtering out one out of three items.
Participants performed at the same level when seeing only two items compared to when three items were presented of which one item was to be filtered out. Hence, they were able to successfully filter out an item at encoding. Error bars were calculated by subtracting each subject's grand mean away from their individual per-condition values and showing ± standard error (Loftus & Masson, 1994).

3. Experiment 2: Effects of ignoring and updating

In the second experiment we focused on processing demands during maintenance. The key questions we sought to answer were:

1. Does ignoring during maintenance (filtering irrelevant items presented during retention) have a detrimental effect on recall measured in Identification Accuracy and Localisation Performance?
2. How does updating the contents of memory during retention affect recall measured in Identification Accuracy and Localisation Performance?
3. What is the impact of ignoring (filtering during maintenance) or updating with aging in Identification Accuracy and Localisation Performance?

3.1. Methods

3.1.1. Participants

Participants in this experiment were the same as in Experiment 1 (see Table 1 **for demographics**).

3.1.2. Stimuli, Design and Procedure

Stimuli and procedure were similar as to those in Experiment 1, except for the following changes. In Experiment 2, information during the maintenance interval was manipulated (Fig. 7). As per Fallon et al. (2018) each trial began with the presentation of two-coloured circles (4

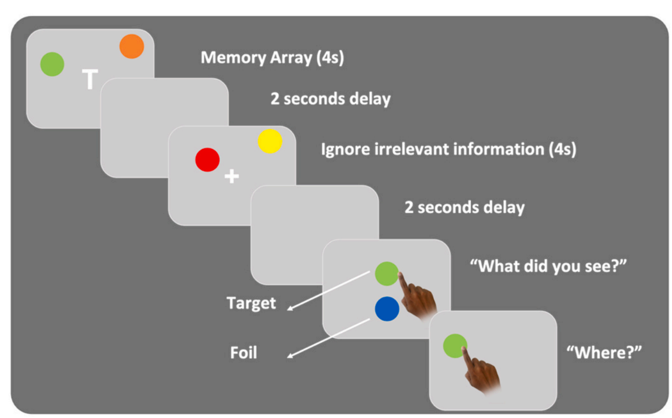

Fig. 7. Schematic of Experiment 2: Manipulations of retrieval and filtering.
Participants were required to remember only the coloured circles when the letter 'T' (for 'targets') was present at screen centre. Moreover, they were told that only the most recent circles presented with a 'T' needed to be kept in memory. Later, they had to select the circle which was last presented with a 'T' and drag it to its remembered location (a modified greyscale and colour-blind friendly version of this can be found in Appendix, Supplementary Fig. 4).

s) that appeared in separate spatial locations, with the letter "T" appearing in the centre of the screen. After a blank screen delay (2 s), two different circles appeared on the screen. These could be accompanied either by a central "T" or simply a fixation cross. The presence of a central letter "T" indicated that the original stimuli held in memory should now be jettisoned, and these new circles remembered (**Update** condition). Conversely, the presence of a fixation cross meant that these new circles had to be ignored, i.e., ignore the new set of items and continue to remember the previous set (**Ignore** condition). Then, after another delay period (2 s) two further circles were presented, one of which was a circle that had to be remembered (target) and the other one a foil, the colour of which was not presented before within the trial (Fig. 8). As in Experiment 1, after touching the target shape, participants had to drag the circle to its remembered location. We also included two control conditions with only one set of items and a short or long delay that matched the delays following the stimuli ultimately to be remembered in both ignore and update conditions (**maintain long** and **short** conditions). In total, there were 4 randomized conditions of which participants performed 10 trials each, adding up to one block of 40 trials.

In this experiment, unlike to Experiment 1, six equally spaced-out colours were taken from a different colour wheel, avoiding same combinations across all trials.

3.2. Results

3.2.1. Impact of ignoring items during retention delay

A 2 × 2-ANOVA was conducted comparing performance in the ignoring versus the long maintenance delay conditions between the two age groups (Fig. 9). When participants were asked to ignore two items during the retention period, their performance suffered significantly on several parameters: identification accuracy was lower ($F(1,99) = 7.63$, $p = 0.007$, $\eta_p^2 = 0.7$), they guessed more ($F(1,99) = 6.50$, $p = 0.012$, $\eta_p^2 = 0.06$) and misbinding increased ($F(1,99) = 69.89$, $p < 0.001$, $\eta_p^2 = 0.41$). On average, misbinding increased from 4.67% in the simple maintenance condition (when participants dragged the correctly identified target to the location of the other item that had appeared in the memory display) to 16.51% in the ignore condition. Most of the misbinding in the ignore condition (mean 66.4%; SD = 18.2%) was to the location of one of the to-be-ignored items, demonstrating the significant effect of these distractors, even on trials in which the target was correctly identified. Paradoxically there was a slight decrease in imprecision in the ignore condition compared to simple maintenance ($F(1,99) = 4.84$, $p = 0.030$, $\eta_p^2 = 0.05$). Neither localisation error nor reaction time were significantly different between the two conditions.

Unlike in Experiment 1, there was no significant difference between young and old participants for any of our metrics (identification accuracy, localisation error, misbinding, guessing, imprecision or reaction time). The between subject factor group did not interact significantly with the factor ignore in any of these measures. Thus, ignoring was not significantly affected by age, under these experimental conditions (Supplementary Tables 23–28).

In summary, with respect to our first question, the findings show that ignoring information during the maintenance delay has a significant detrimental effect on recall. Filtering irrelevant items during retention affects identification accuracy, misbinding and guessing. With respect to our third research question, age did not interact with these effects; in this experiment, both age groups performed similarly.

3.2.2. Effect of updating contents of memory during retention delay

As for the Ignore condition, we conducted another 2 × 2-ANOVA of updating versus maintaining (this time for the short retention delay) and the between subject factor group (Fig. 10). When participants were asked to update the contents of memory, there was no effect on identification accuracy but there was a significant increase in localisation error ($F(1,99) = 4.46$, $p = 0.037$, $\eta_p^2 = 0.04$), due to greater misbinding ($F(1,99) = 10.55$, $p = 0.002$, $\eta_p^2 = 0.10$). But participants were faster ($F(1,99) = 4.57$, $p = 0.035$, $\eta_p^2 = 0.04$). In 82.42% (SD = 9.34%) of the cases, the item that was misbound to was *from the initial display*,

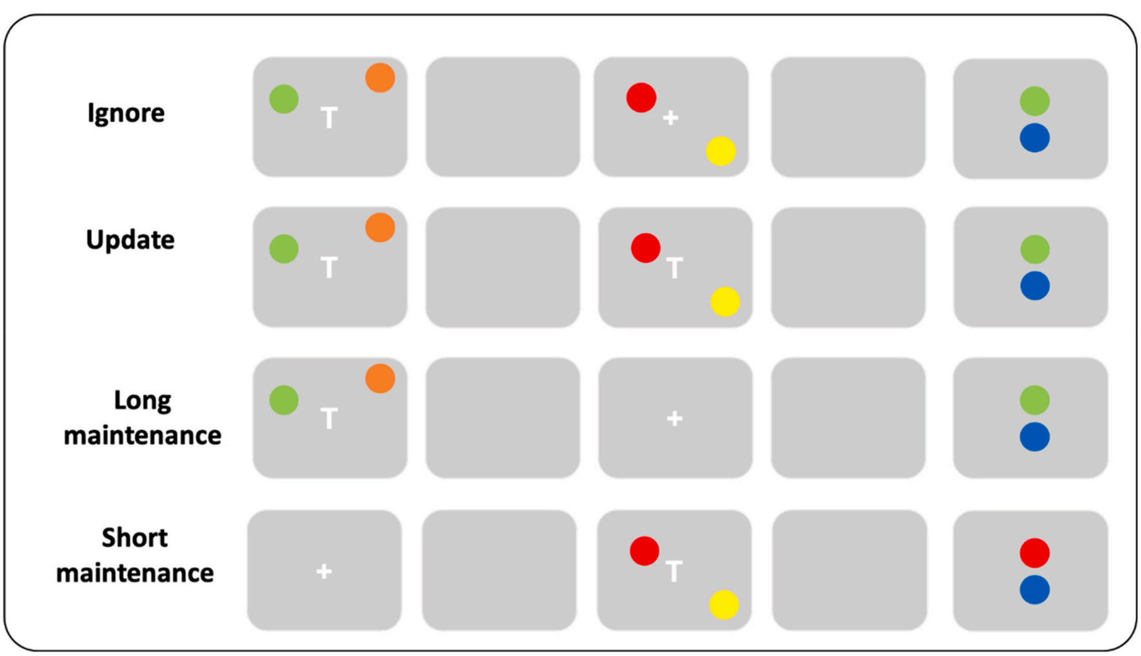

Fig. 8. Schematic of all conditions for Experiment 2.
In the *Ignore* condition, participants had to retain information whilst ignoring an irrelevant pair of circles presented during maintenance. In contrast, in the *Update* condition, participants were presented with two pairs of circles consecutively, both of which are presented with the letter "T". They had to remember the last pair of circles and discard the previous pair. Two temporal control conditions were also used. They did not feature any irrelevant memoranda but differed only in the length of time for which items needed to be retained. The *Long maintenance* condition served as the temporal control for the Ignore condition, whereas the *Short maintenance* condition served as the temporal control for the *Update* condition. (a modified greyscale and colour-blind friendly version of this can be found in Appendix, Supplementary Fig. 5).

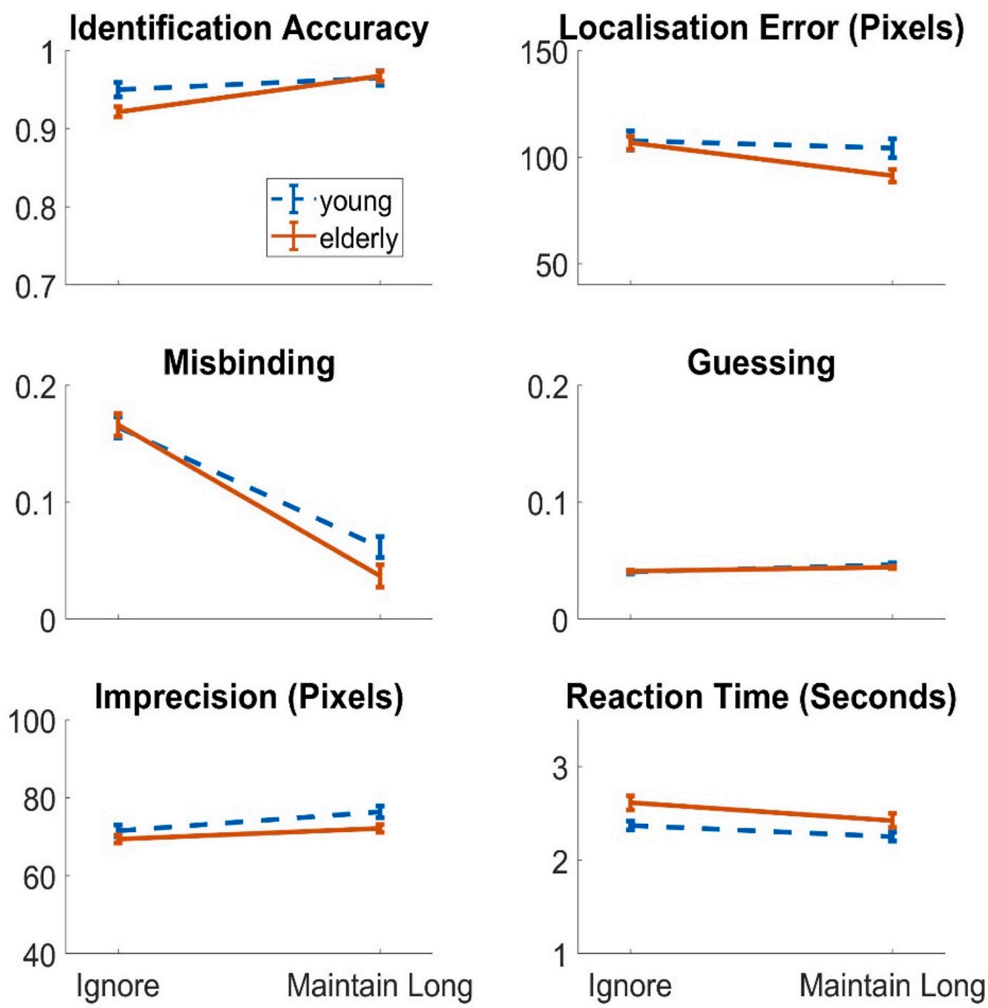

Fig. 9. Impact on memory recall of filtering during maintenance (Ignoring).
Ignoring decreased identification accuracy, but increased misbinding and guessing. Effects were independent of age with elderly and young participants performing at similar levels. Error bars were calculated by subtracting each subject's grand mean away from their individual per-condition values and showing ± standard error (Loftus & Masson, 1994).

demonstrating lingering effects of a previously retained (but now jettisoned) item on recall. Updating did not significantly impact on guessing or imprecision. As in the ignore condition, both groups performed at similar levels for identification accuracy, localisation error, misbinding, guessing, imprecision and reaction time. The between subject factor group did not interact with the factor update in any of the measures. Thus, like ignoring, updating was not significantly affected by age (Supplementary Tables 29–34).

In summary, pertaining to our second research question, the results show that updating the contents of memory during retention did significantly impair localisation performance, with this being driven by increased misbinding to one of the original memoranda that should have been over-written by a new item.

3.2.3. Effect of time – long vs short delay

A 2 × 2 ANOVA of delay (long vs short) and the between subject factor group was conducted (Fig. 11). A longer delay did not significantly affect identification accuracy but it did increase localisation error ($F(1,99) = 53.94$, $p < 0.001$, $\eta_p^2 = 0.35$), driven by guessing ($F(1,99) = 52.54$, $p < 0.001$, $\eta_p^2 = 0.35$) and imprecision ($F(1,99) = 116.37$, $p < 0.001$, $\eta_p^2 = 0.54$). Misbinding and reaction time were unaffected by a main effect of longer delay. Again, the two groups performed equally well across all the metrics we studied (identification accuracy, localisation error, misbinding, guessing, imprecision or reaction time).

Delay duration interacted significantly with the between subject factor group on localisation error ($F(1,99) = 5.91$, $p = 0.017$, $\eta_p^2 = 0.06$). Therefore, we followed up on this using pairwise *t*-tests within both groups individually. Both older and young participants had a greater localisation error with longer delay (respectively ($t(60) = 3.99$, $p < 0.001$); ($t(39) = 6.10$, $p < 0.001$)). In addition, group also interacted with the delay effect on misbinding ($F(1,99) = 9.90$, $p = 0.002$, $\eta_p^2 = 0.09$). For this reason, we performed pairwise t-tests in each of the groups again. There was no difference between a short and long delay in misbinding for older participants ($t(60) = -1.57$, $p = 0.122$). However, in the young group, misbinding increased more for longer delays ($t(39) = 2.58$, $p = 0.014$) than it did in their older counterparts. In younger controls the increase of misbinding in longer delays could have also contributed to the increase of localisation error for longer delays (Supplementary Tables 35–40).

The results show a significant decay of location memory over longer delays, driven by an increase in guessing and imprecision.

3.2.4. Relationship between updating and ignoring

In a final step, the relationship between Updating and Ignoring performance was examined to assess whether these were correlated. For Identification accuracy, Imprecision and Misbinding: (i) participant-wise difference between the long delay trials and the ignore condition and (ii) participant-wise difference between the short delay trials and the update condition were computed. There were no significant correlations between these indices of Updating and Ignoring for either Identification accuracy or Imprecision (identification accuracy: $r = 0.08$, $p = 0.412$; imprecision: $r = 0.17$, $p = 0.086$), suggesting that effects of ignoring and updating were independent of one another in these measures. However, there was a significant correlation between Updating

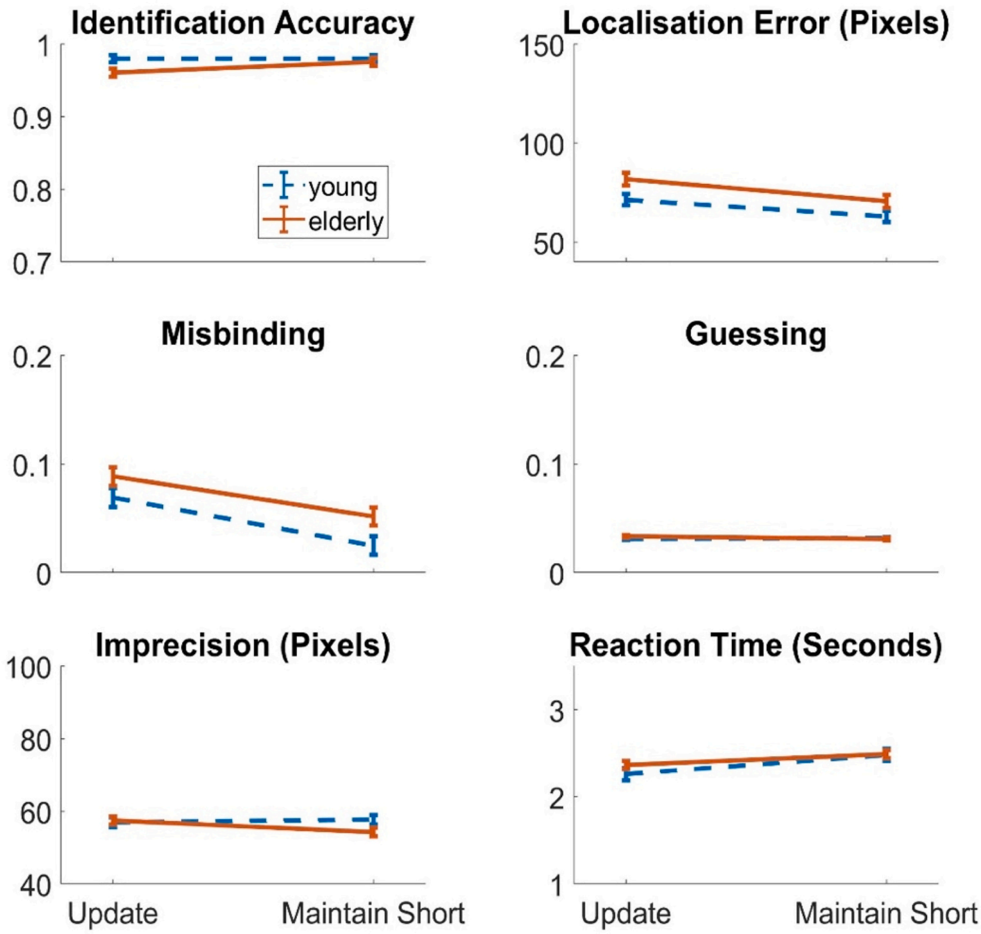

Fig. 10. Impact on memory recall of Updating.
Updating increased localisation error driven by an increase in misbinding. However, participants were faster when updating. These effects were again independent of age. Error bars were calculated by subtracting each subject's grand mean away from their individual per-condition values and showing ± standard error (Loftus & Masson, 1994).

and Ignoring performance for Misbinding ($r = 0.24$, $p = 0.015$). This result suggests that the ability to bind features of an object together might depend on a single system, regardless of whether information has to be protected (Ignore condition) or jettisoned to store new information (Update).

3.3. Filtering at encoding, maintenance and processing requirements induced by retrieval across experiments

In the final analysis step, we examined the relationship between several parameters that pertain to processing demands at encoding, maintenance and processing demands due to retrieval across Experiments 1 and 2. In this analysis, we included the most important investigated measures. These were i) the quantitative working memory result of identification accuracy, ii) misbinding and iii) imprecision which were the main sources of error of the qualitative working memory task.

First, scores were calculated for the effect of the following on different performance measures:

1. **Filtering at encoding** (**Encoding):** Difference between Set Size 2 versus the Filtering condition in which the foil's features were taken from the non-filtered item, collapsed over the number of features, in Experiment 1. *This provides a general measure of filtering at encoding.*
2. **Filtering during maintenance** (**Maintenance):** Difference between the maintain long and the ignore condition in Experiment 2. *This is an index of filtering during maintenance.*
3. **Processing requirements induced by the retrieval cue** (**Retrieval):** Difference between one- and two-repeated-features conditions, collapsed over all other conditions in Experiment 1. *This provides a measure of interference introduced by the retrieval cue.*
4. **Set size:***Difference between Set Size 2 and Set Size 3 conditions, collapsed over the number of features, in Experiment 1. This is an index of the impact of memory load.*

Next, correlation matrices for these four scores were examined separately for the Identification Accuracy, Misbinding and the Imprecision (Fig. 12; details in Supplementary Tables 42–44). Analyses revealed a significant positive correlation between *Set size* and *Encoding* across all three metrics (Identification Accuracy: r (99) = 0.52, $p < 0.001$, Misbinding: r(99) = 0.25, $p = 0.011$ and Imprecision: r(99) = 0.44, $p < 0.001$). Thus, the more participants were affected by a manipulation of set size (difference between *Set Size 2 and 3*) the stronger they were also affected by a manipulation of processing demands at encoding (difference between *Set Size 2* and the filtering condition in which the foil's features were taken from the non-filtered item), and vice-versa. Most importantly, there were no significant correlations between filtering at encoding, maintenance and processing requirement induced by the retrieval cues across any of the three metrics of Identification accuracy, Misbinding and Imprecision. This suggests that, within the limitations of this study, there was independence of filtering performance at encoding, maintenance and retrieval.

4. Discussion

Although several previous investigations have examined the effect on WM of processing demands at encoding and maintenance, there has been little work on such demands induced by the retrieval cue or how

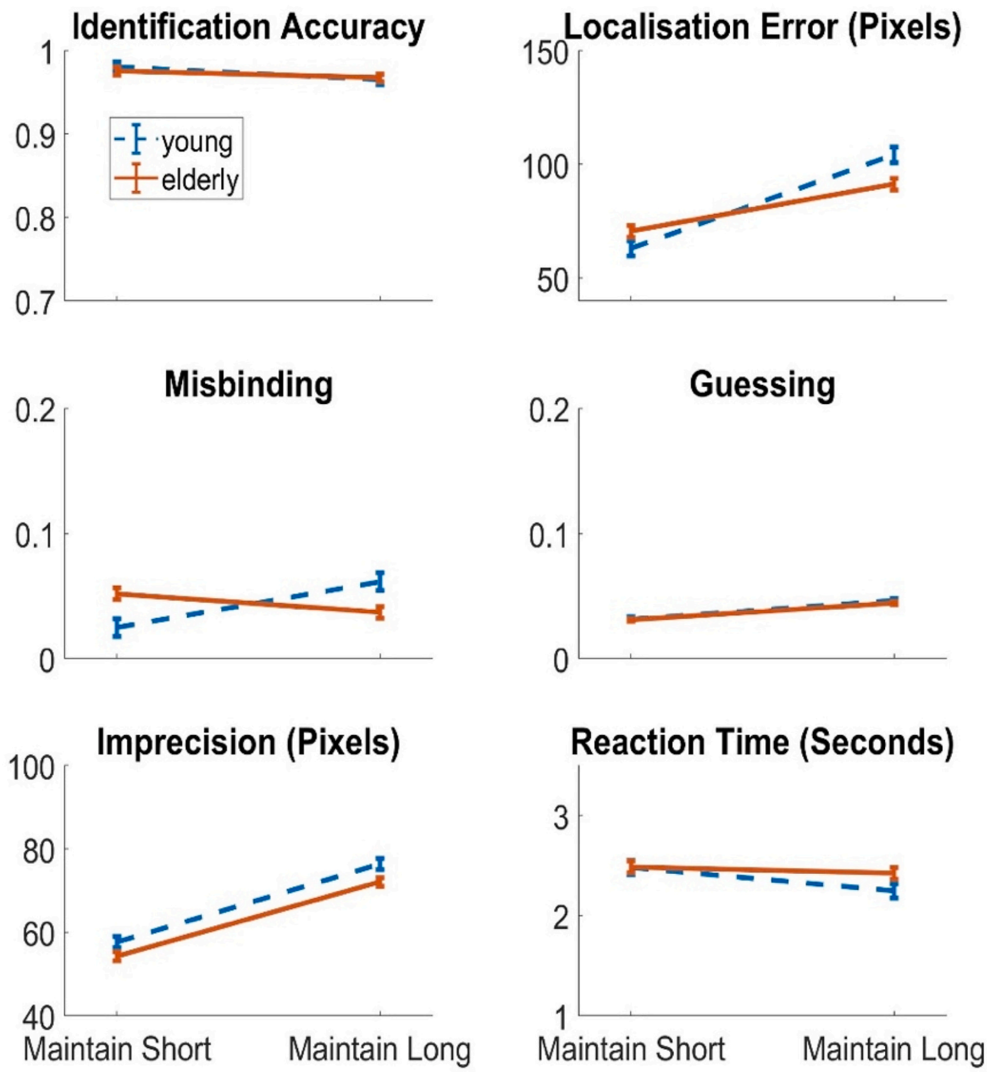

Fig. 11. Impact on memory recall of Delay.
Longer delay increased localisation error in both young and elderly groups. Error bars were calculated by subtracting each subject's grand mean away from their individual per-condition values and showing ± standard error (Loftus & Masson, 1994).

this is related to the impact of processing demands at encoding and maintenance. In the present study, we conducted two experiments to examine how recall performance is affected by processing requirements induced by retrieval and to assess the relationships between such demands at encoding, maintenance and retrieval. In Experiment 1, we investigated the effects of filtering irrelevant information at encoding and the impact of distracting information at retrieval by presenting a foil that could either contain one or two old features from the encoding display (either from the task-irrelevant or a non-filtered item). In Experiment 2, we explored the effect of ignoring - filtering during the retention period - by asking participants to ignore irrelevant information during the maintenance interval. Or, in an updating condition, they were asked to jettison and replace previously stored information. Across the two experiments, a secondary aim of the study was to examine how the effect of filtering at different stages of WM is affected by age.

The results from Experiment 1 showed that the nature of processing demands induced by the retrieval cue does indeed impact significantly on memory performance. Increasing the number of old features from an item presented in the encoding display in the retrieval foil decreased participants' ability to correctly identify an item (Fig. 4). For example, it was harder for participants to correctly identify an item when the target was presented together with a foil containing the same two colours from another item they saw in the encoding display. These results expand on previous work which shows that adding unnecessary information in the probe (Tabi, Husain, & Manohar, 2019), and the presence of distractors at the time of probe (Makovski, Watson, Koutstaal, & Jiang, 2010; Udale, Farrell, & Kent, 2018), disrupts performance. Including partial information from other representations currently maintained in memory negatively impacts recall performance.

These findings also align well with a recent computational neural model of WM (Manohar et al., 2019) which uses rapid synaptic plasticity to encode combinations of features represented in feature neuron layers as bound objects in flexibly-coding conjunction neurons. During recall, activation of a single feature neuron can trigger pattern completion by guiding the activation down the strengthened synapses to the appropriate conjunction neuron that, in turn, activates the rest of the features from its joined representation. The model predicts that if competing information is presented in the retrieval cue, i.e., information that triggers the activation of multiple conjunction units, retrieval will suffer. However, this should be more evident if the irrelevant information is represented in WM. In line with this prediction, we found that when the retrieval foil had features that came from a task-irrelevant item that was supposed to be filtered out at encoding, participants identified the correct item more often and were faster at making this choice. This shows

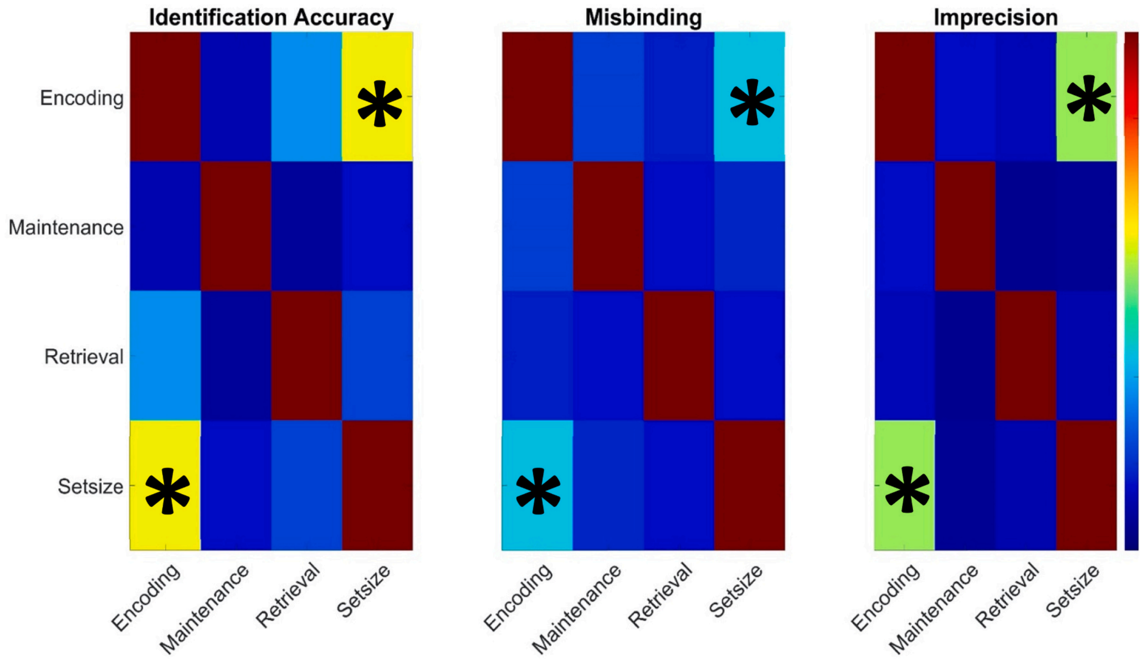

Fig. 12. Correlation matrices of filtering at encoding, maintenance and retrieval, and set size.
Set size and processing demands at encoding were strongly correlated, but there were no significant correlations between filtering at different phases of working memory – encoding, maintenance and retrieval. Significant correlations are indicated with an asterisk and df = 99.

that filtering at retrieval interacts with processing demands at encoding.

A limitation to the retrieval cue manipulation, however, is that the results observed cannot exclusively be linked to effects that are at or due to retrieval. The retrieval cue manipulations affect the degree of similarity between foil and target and, thus, require participants to solve a computational problem that might increase with an increasing similarity of the choices available. In the signal detection framework, for example, similarity between the available choices at retrieval is claimed to explain participants' accuracy in the task (Schurgin, Wixted, & Brady, 2020). Thus, in trials in which target and foil were more similar, an increased number of false-alarms can be expected without any particular effects associated to retrieval. This would also be the case if participants would compute wrong colour-colour bindings at encoding to begin with and then consecutively fail at retrieval.

In Experiment 1, participants were able to successfully filter out an irrelevant item at encoding because they performed just as well as when presented with only two items to encode, compared to when they were presented with three items but one had to be filtered out (task-irrelevant item) (Fig. 5). However, ignoring irrelevant information during maintenance had a detrimental effect on recall (Experiment 2), leading to an increase in identification accuracy, misbinding rates and guessing (Fig. 9). Moreover, updating the contents of memory during retention affected recall: Localisation performance was impaired driven by an increase of misbinding to one of the original memoranda's locations that should have been over-written by a new item (Fig. 10). Unlike the results of a previous study (Fallon et al., 2018) which reported an increase in misbinding solely to the to-be-ignored distractors in the Ignore condition, we also found an increase in misbindings to the to-be-updated item in the Update condition. Furthermore, performance in the Ignore and Update conditions were significantly correlated with respect to misbinding.

In line with previous work in which filtering at encoding has been closely related to working memory capacity (McNab & Dolan, 2014; Vogel et al., 2005; Vogel & Machizawa, 2004), the results presented here show that filtering at encoding is related to the set size effect, i.e., participants with greater WM capacity were less affected by irrelevant information at encoding (Fig. 12). This result is consistent with the proposal that individuals' WM capacity is related to their ability to filter irrelevant information at encoding (McNab & Dolan, 2014; McNab & Klingberg, 2008; Vogel & Machizawa, 2004), suggesting that attention serves as a gatekeeper for WM, biasing the encoding of information towards relevant memoranda (Awh, Vogel, & Oh, 2006). Importantly, these findings assume a direct relation between WM capacity and set size such as a decrease of available resource in the resource model of working memory (Bays et al., 2009) or in the slot model where $K = S\ (H—F)$ where K is the capacity, S the set size, H is hit and f the false alarm rate (McNab & Dolan, 2014; Vogel et al., 2005).

A key finding of the studies reported here is that there were no significant correlations between the ability to filter at encoding, maintenance, or at retrieval (Fig. 12) suggesting that there is no single, monolithic mechanism responsible for all these processes. Thus people who are good at filtering information at one of the memory stages are not necessarily good at filtering at the other two. Of course, although we did not find a significant relationship between filtering at different memory stages, a negative result does not mean that it might not exist if tested for differently. One possible explanation for the lack of correlation between filtering efficiency at encoding, maintenance and retrieval might be the fact that the processing of information has to operate in different ways at each stage and interacts with different types of representation. During encoding, attention is considered to operate on perceptual information to filter out distractors and to selectively encode targets. During maintenance, it has been invoked as a mechanism to protect current WM contents from distraction if the information is irrelevant or to update existing contents if information is relevant. Finally, processing demands induced by the retrieval cues, as tested here, serve to select the appropriate response while filtering out irrelevant information that interferes with the process of recall.

An alternative explanation is that, if these are indeed truly unrelated metrics, different brain mechanisms and regions might be involved in each process. In support of this view, there is some evidence from imaging studies that have investigated neural correlates of protecting the contents of WM that have shown evidence for separate mechanisms for distractor-filtering at encoding and during the maintenance interval (Cools, Miyakawa, Sheridan, & D'Esposito, 2010; Sean James Fallon &

Cools, 2014; Gruber, Dayan, Gutkin, & Solla, 2006; McNab & Dolan, 2014; McNab & Klingberg, 2008; Mehta, Manes, Magnolfi, Sahakian, & Robbins, 2004). For example, some researchers have observed an improvement of distractor filtering during the maintenance delay as a result of a deficit in striatal dopamine (Cools et al., 2010; Mehta et al., 2004), whereas other studies have reported that presenting distractors during encoding is linked to prefrontal and basal ganglia activity, particularly in the globus pallidus (McNab & Klingberg, 2008). In line with this, Gruber et al. (2006) have posited that, since the basal ganglia have a high density of dopamine receptors critical to WM, dopamine can carry out a gating function by transiently strengthening the efficiency of inputs to the frontal cortex, and have modelled the effects of dopamine in the basal ganglia as gating stabilization against distractors by improving specific memories.

Previous studies have also consistently shown that aging is linked to a general deterioration of performance on WM tasks (Chen et al., 2003; Jost et al., 2011; McNab et al., 2015; McNab & Dolan, 2014; Myerson et al., 2003; Peich et al., 2013; Pertzov et al., 2015). We therefore tested whether age similarly correlated with general WM performance decrement. Evidence from manipulations of processing demands during encoding and processing demands due to the retrieval cues (Experiment 1) shows that elderly participants performed generally worse compared to young controls (Figs. 4, 5, 6). When the effects of processing demands at the different memory stages were directly compared between young and elderly, filtering at encoding and set size had a greater negative effect on elderly participants compared to younger ones.

In conclusion, the findings of these studies provide evidence that additional irrelevant information presented at retrieval has a detrimental impact on performance and that the efficiency of filtering during encoding has an impact on recall. Moreover, filtering efficiency is associated with memory capacity. Finally, the findings point to the absence of a unified filtering system that operates across all phases of WM. Instead, evidence from the two experiments suggest that filtering at encoding, maintenance and retrieval are not related and might be underpinned by different cognitive processes.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cognition.2021.104758.

References

Awh, E., Vogel, E. K., & Oh, S. H. (2006). Interactions between attention and working memory. *Neuroscience, 139*(1), 201–208. https://doi.org/10.1016/j.neuroscience.2005.08.023.

Baddeley, A. D., Allen, R. J., & Hitch, G. J. (2011). Binding in visual working memory: The role of the episodic buffer. *Neuropsychologia, 49*(6), 1393–1400. https://doi.org/10.1016/j.neuropsychologia.2010.12.042.

Bays, P. M., Catalao, R. F. G., & Husain, M. (2009). The precision of visual working memory is set by allocation of a shared resource. *Journal of Vision, 9*(10), 7. https://doi.org/10.1167/9.10.7.

Brown, L. A., & Brockmole, J. R. (2010). The role of attention in binding visual features in working memory: Evidence from cognitive ageing. *Quarterly Journal of Experimental Psychology, 63*(10), 2067–2079. https://doi.org/10.1080/17470211003721675.

Chen, J., Hale, S., & Myerson, J. (2003). Effects of domain, retention interval, and information load on young and older adults' visuospatial working memory. *Aging, Neuropsychology, and Cognition, 10*(2), 122–133. https://doi.org/10.1076/anec.10.2.122.14461.

Chun, M. M., & Johnson, M. K. (2011, November 17). Memory: Enduring traces of perceptual and reflective attention. *Neuron.*. https://doi.org/10.1016/j.neuron.2011.10.026.

Cools, R., Miyakawa, A., Sheridan, M., & D'Esposito, M. (2010). Enhanced frontal function in Parkinson's disease. *Brain, 133*(1), 225–233. https://doi.org/10.1093/brain/awp301.

Cowan, N., & Morey, C. C. (2006, April). Visual working memory depends on attentional filtering. *Trends in Cognitive Sciences*. https://doi.org/10.1016/j.tics.2006.02.001.

Fallon, S. J., Mattiesing, R. M., Dolfen, N., Manohar, S. G., & Husain, M. (2018). Ignoring versus updating in working memory reveal differential roles of attention and feature binding. *Cortex, 107*, 50–63. https://doi.org/10.1016/j.cortex.2017.12.016.

Fallon, S. J., & Cools, R. (2014). Reward acts on the pFC to enhance distractor resistance of working memory representations. *Journal of Cognitive Neuroscience, 26*(12), 2812–2826. https://doi.org/10.1162/jocn_a_00676.

Fallon, S. J., Zokaei, N., & Husain, M. (2016). Causes and consequences of limitations in visual working memory. *Annals. New York Academy of Sciences, 1369*, 40–54. https://doi.org/10.1111/nyas.12992.

Fougnie, D., & Marois, R. (2009). Attentive tracking disrupts feature binding in visual working memory. *Visual Cognition, 17*(1–2), 48–66. https://doi.org/10.1080/13506280802281337.

Gazzaley, A., Clapp, W., Kelley, J., McEvoy, K., & Knight, R. T. (2008). Age-related top-down suppression deficit in the early stages of cortical visual memory processing. *PNAS, 2*(35).

Gorgoraptis, N., Catalao, R. F. G., Bays, P. M., & Husain, M. (2011). Dynamic updating of working memory resources for visual objects. *Journal of Neuroscience, 31*(23), 8502–8511.

Griffin, I. C., & Nobre, A. C. (2003). Orienting attention to locations in internal representations. *Journal of Cognitive Neuroscience, 15*(8), 1176–1194.

Grogan, J. P., Fallon, S. J., Zokaei, N., Husain, M., & Manohar, S. G. (2020). A new toolbox to distinguish the sources of spatial memory error. *Journal of vision, 20*(13), 6. https://doi.org/10.1167/jov.20.13.6. PMID: 33289797; PMCID: PMC7726590.

Gruber, A. J., Dayan, P., Gutkin, B. S., & Solla, S. A. (2006). Dopamine modulation in the basal ganglia locks the gate to working memory. *Journal of Computational Neuroscience, 20*(2), 153–166. https://doi.org/10.1007/s10827-005-5705-x.

Ikkai, A., McCollough, A. W., & Vogel, E. K. (2010). Contralateral delay activity provides a neural measure of the number of representations in visual working memory. *Journal of Neurophysiology, 103*(4), 1963–1968. https://doi.org/10.1152/jn.00978.2009.

JASP Team. (2020). JASP (Version 0.13.1)[Computer software]. Retrieved from https://jasp-stats.org/.

Johnson, J. S., Hollingworth, A., & Luck, S. J. (2008). The role of attention in the maintenance of feature bindings in visual short-term memory. *Journal of Experimental Psychology: Human Perception and Performance, 34*(1), 41–55. https://doi.org/10.1037/0096-1523.34.1.41.

Jost, K., Bryck, R. L., Vogel, E. K., & Mayr, U. (2011). Are old adults just like low working memory young adults? Filtering efficiency and age differences in visual working memory. *Cerebral Cortex, 21*(5), 1147–1154. https://doi.org/10.1093/cercor/bhq185.

Landman, R., Spekreijse, H., & Lamme, V. A. F. (2003). Large capacity storage of integrated objects before change blindness. *Vision Research, 43*, 149–164. Retrieved from www.elsevier.com/locate/visres.

Loftus, G. R., & Masson, M. E. J. (1994). Using confidence intervals in within-subject designs. *Psychonomic Bulletin & Review, 1*.

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

Makovski, T., Watson, L. M., Koutstaal, W., & Jiang, Y. V. (2010). Method matters: Systematic effects of testing procedure on visual working memory sensitivity. *Journal of Experimental Psychology. Learning, Memory, and Cognition, 36*(6), 1466–1479. https://doi.org/10.1037/a0020851.

Manohar, S. G., Zokaei, N., Fallon, S. J., Vogels, T. P., & Husain, M. (2019). Neural mechanisms of attending to items in working memory. *Neuroscience and Biobehavioral Reviews. Elsevier Ltd.*. https://doi.org/10.1016/j.neubiorev.2019.03.017.

Mathuranath, P. S., Nestor, P. J., Berrios, G. E., Rakowicz, W., & Hodges, J. R. (2000). A brief cognitive test battery to differentiate Alzheimer's disease and frontotemporal dementia. *Neurology, 55*(11), 1613–1620. https://doi.org/10.1212/01.wnl.0000434309.85312.19.

McNab, F., & Dolan, R. J. (2014). Dissociating distractor-filtering at encoding and during maintenance. *Journal of Experimental Psychology: Human Perception and Performance, 40*(3), 960–967. https://doi.org/10.1037/a0036013.

McNab, F., & Klingberg, T. (2008). Prefrontal cortex and basal ganglia control access to working memory. *Nature Neuroscience, 11*(1), 103–107. https://doi.org/10.1038/nn2024.

McNab, F., Zeidman, P., Rutledge, R. B., Smittenaar, P., Brown, H. R., Adams, R. A., & Dolan, R. J. (2015). Age-related changes in working memory and the ability to ignore distraction. *Proceedings of the National Academy of Sciences of the United States of America, 112*(20), 6515–6518. https://doi.org/10.1073/pnas.1504162112.

Mehta, M. A., Manes, F. F., Magnolfi, G., Sahakian, B. J., & Robbins, T. W. (2004). Impaired set-shifting and dissociable effects on tests of spatial working memory following the dopamine D2 receptor antagonist sulpiride in human volunteers. *Psychopharmacology, 176*(3–4), 331–342. https://doi.org/10.1007/s00213-004-1899-2.

Myerson, J., Emery, L., White, D. A., & Hale, S. (2003). Effects of age, domain, and processing demands on memory span: Evidence for differential decline. *Aging, Neuropsychology, and Cognition, 10*(1), 20–27. https://doi.org/10.1076/anec.10.1.20.13454.

Peich, M. C., Husain, M., & Bays, P. M. (2013). Age-related decline of precision and binding in visual working memory. *Psychology and Aging, 28*(3), 729–743. https://doi.org/10.1037/a0033236.

Pertzov, Y., Dong, M. Y., Peich, M. C., & Husain, M. (2012). Forgetting what was where: The fragility of object-location binding. *PLoS One, 7*(10). https://doi.org/10.1371/journal.pone.0048214.

Pertzov, Y., Liang, Y., Heider, M., & Husain, M. (2015). Effects of healthy ageing on precision and binding of object location in visual short term memory. *Psychology and Aging, 30*(1), 26–35. https://doi.org/10.1037/a0038396.supp.

Pertzov, Y., Manohar, S., & Husain, M. (2017). Rapid forgetting results from competition over time between items in visual working memory. *Journal of Experimental Psychology. Learning, Memory, and Cognition, 43*(4), 528–536. https://doi.org/10.1037/xlm0000328.

Rhodes, S., & Cowan, N. (2018). Attention in working memory: Attention is needed but it yearns to be free. *Annals of the New York Academy of Sciences. Blackwell Publishing Inc.*. https://doi.org/10.1111/nyas.13652.

Robison, M. K., Miller, A. L., & Unsworth, N. (2018). Individual differences in working memory capacity and filtering. *Journal of Experimental Psychology: Human Perception and Performance, 44*(7), 1038–1053. https://doi.org/10.1037/xhp0000513.

Schmidt, B. K., Vogel, E. K., Woodman, G. F., & Luck, S. J. (2002). Voluntary and automatic attentional control of visual working memory. *Perception & Psychophysics, 64*(5), 754–763. https://doi.org/10.3758/BF03194742.

Schurgin, M. W., Wixted, J. T., & Brady, T. F. (2020). Psychophysical scaling reveals a unified theory of visual memory strength. *BioRxiv*. https://doi.org/10.1101/325472.

Souza, A. S., & Oberauer, K. (2016). In search of the focus of attention in working memory: 13 years of the retro-cue effect. *Attention, Perception, & Psychophysics, 78* (7), 1839–1860. https://doi.org/10.3758/s13414-016-1108-5.

Souza, S. A., Rerko, L., & Oberauer, K. (2014). Unloading and reloading working memory: Attending to one item frees capacity. *Journal of Experimental Psychology: Human Perception and Performance*. https://doi.org/10.1037/a0036331.supp.

Tabi, Y. A., Husain, M., & Manohar, S. G. (2019). Recall cues interfere with retrieval from visuospatial working memory. In *, vol. 110. British Journal of Psychology* (pp. 288–305). John Wiley and Sons Ltd.. https://doi.org/10.1111/bjop.12374

Theeuwes, J., Belopolsky, A., & Olivers, C. N. L. (2009). Interactions between working memory, attention and eye movements. *Acta Psychologica, 132*(2), 106–114. https://doi.org/10.1016/j.actpsy.2009.01.005.

Theeuwes, J., Kramer, A. F., & Irwin, D. E. (2011). Attention on our mind: The role of spatial attention in visual working memory. *Acta Psychologica, 137*(2), 248–251. https://doi.org/10.1016/j.actpsy.2010.06.011.

Udale, R., Farrell, S., & Kent, C. (2018). Task demands determine comparison strategy in whole probe change detection. *Journal of Experimental Psychology: Human Perception and Performance, 44*(5), 778–796. https://doi.org/10.1037/xhp0000490.

Van Moorselaar, D., Olivers, C. N. L., Theeuwes, J., Lamme, V. A. F., & Sligte, I. G. (2015). Forgotten but not gone: Retro-cue costs and benefits in a double-cueing paradigm suggest multiple states in visual short-term memory. *Journal of Experimental Psychology. Learning, Memory, and Cognition, 41*(6), 1755–1763. https://doi.org/10.1037/xlm0000124.

Vogel, E. K., & Machizawa, M. G. (2004). Neural activity predicts individual differences in visual working memory capacity. *Nature, 428*(6984), 748–751. https://doi.org/10.1038/nature02447.

Vogel, E. K., McCollough, A. W., & Machizawa, M. G. (2005). Neural measures reveal individual differences in controlling access to working memory. *Nature, 438*(7067), 500–503. https://doi.org/10.1038/nature04171.

Wheeler, M. E., & Treisman, A. M. (2002). Binding in short-term visual memory. *Journal of Experimental Psychology: General, 131*(1), 48–64. https://doi.org/10.1037/0096-3445.131.1.48.

Williams, M., Hong, S. W., Kang, M. S., Carlisle, N. B., & Woodman, G. F. (2013). The benefit of forgetting. *Psychonomic Bulletin and Review, 20*(2), 348–355. https://doi.org/10.3758/s13423-012-0354-3.

Woodman, G. F., Vecera, S. P., & Luck, S. J. (2003). Perceptual organization influences visual working memory. *Psychonomic Bulletin and Review, 10*(1), 80–87. https://doi.org/10.3758/BF03196470.

Zokaei, N., Heider, M., & Husain, M. (2014). Attention is required for maintenance of feature binding in visual working memory [The Quarterly Journal of Experimental Psychology, (2013), 67, 6, (2013), (1191-1213), DOI 10.1080/17470218.2013.852232]. *Quarterly Journal of Experimental Psychology, 67*(6). https://doi.org/10.1080/17470218.2015.1049873. i–i.