

# **Rapid forgetting results from competition over time between items in visual working memory**

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## **Abstract**

Working memory is now established as a fundamental cognitive process across a range of species. Loss of information held in working memory has the potential to disrupt many aspects of cognitive function. Yet, despite its significance, the mechanisms underlying rapid forgetting remain unclear, with intense recent debate as to whether it is interference between stored items that leads to loss of information, or simply temporal decay. Here we show that both factors are essential and interact in a highly specific manner. While a single item can be maintained in memory with high fidelity, multiple items compete in working memory, progressively degrading each other's representations as time passes. Specifically, interaction between items is associated with both worsening precision and increased reporting errors of object features over time. Importantly, during the period of maintenance, even though items are no longer visible, maintenance resources can be selectively redeployed to protect the probability to recall the correct feature and the precision with which cued items can be recalled, as if it was the only item in memory. These findings reveal that the biased competition concept could be applied not only to perceptual processes but also to active maintenance of working memory representations over time.

### **6 keywords:**

Forgetting, working memory, binding, attention, biased competition.

## 1. Introduction

Most of our memories last very briefly (Muter, 1980; Wixted, 2004) with rapid forgetting – apparent loss of information over just a few seconds – being particularly vulnerable to aging, and now recognized as a potential pathological marker for developing Alzheimer’s disease (Gagnon & Belleville, 2011). Even in young people, the ability to hold onto information over the short-term correlates well with established tests of general intelligence (Conway, Kane, & Engle, 2003). Working memory (WM) is now considered to be a fundamental cognitive process across a range of species (Elmore et al., 2011; Kawai & Matsuzawa, 2000; Light et al., 2010; Wright et al., 2010). However, despite its significance and decades of research (Della Sala, 2010), the mechanisms underlying rapid forgetting, in humans and other animals, are still under intense debate (Barrouillet & Camos, 2009; Lewandowsky, Oberauer, & Brown, 2009a, 2009b).

The controversy about forgetting can be traced back more than a century, to Thorndike's law of disuse: "When a modifiable connection is not made between a situation and a response during a length of time, that connection's strength is decreased" (Thorndike, 1913). The implication is that disuse – and therefore the passage of time – by itself, produces forgetting. The effect of mere temporal decay on short-term forgetting gained prominence with Baddeley's phonological loop model (Baddeley, Thomson, & Buchanan, 1975) which suggested that active rehearsal is needed to overcome time-related decay of memory. Evidence for the passage of time being the major factor in forgetting continues to

be an important feature of several studies (Barrouillet & Camos, 2009; Barrouillet, De Paepe, & Langerock, 2011; Vergauwe, Barrouillet, & Camos, 2009).

On the other hand, not long after the "law of disuse" was formulated, a long debate was initiated with the claim that time itself is not the most important factor behind forgetting (Cason, 1924), with analogies made, for example, to the fact that time alone does not transform iron to rust (McGeoch, 1932). Thus McGeoch (1932) suggested that the significant factors behind forgetting are "interpolated activities and changed stimulating conditions" rather than passage of time. Similar concepts are invoked today by researchers who strongly argue for a crucial role of interference in memory from distracting processes (Lewandowsky, Duncan, & Brown, 2004; Lewandowsky et al., 2009b; Oberauer & Lewandowsky, 2008). As yet, there is no resolution to this debate.

Importantly, most previous studies that have examined this issue have used either verbal stimuli that require participants to remember strings of numbers, letters or words, or visual tasks that require them to detect a change in two successive presentations of an array (Baddeley, 2007; Brockmole, 2009; Della Sala, 2010; Melton, 1963; Posner & Konick, 1966). However, the fact that only two possible outcomes can be registered (correct or incorrect) somewhat constrains the amount of information that might be extracted from these tasks. An alternative type of paradigm, often called "delayed estimation task", requires participants to reproduce a feature in memory on a continuous scale of report (P. M Bays, Catalao, & Husain, 2009; Prinzmetal, Amiri, Allen, & Edwards, 1998; Wilken & Ma, 2004;

Zhang & Luck, 2008) enabling the analysis of the distribution of error in recall. This method has been used successfully to challenge current views regarding capacity limits in visual WM (P. M Bays et al., 2009; P. M Bays & Husain, 2008; Wilken & Ma, 2004) and provides a more sensitive means to probe memory than traditional tasks (Zokaei, Burnett Heyes, Gorgoraptis, Budhdeo, & Husain, 2014).

Two recent studies have addressed forgetting using a delayed estimation task that enabled the analysis of the distribution of errors. Zhang and Luck (2009) asked participants to remember 3 patches of colour or shapes. Following a variable retention intervals of up to 10 seconds participants were required to reproduce the correct feature out of a continuous scale. A mixture model analysis distinguished between random errors (presumably a result of a failure to access the target information at the time of test) and the precision of recall. Forgetting was found to reflect a lower probability of recalling the target, but crucially not in precision.

Another recent study used a similar approach but also manipulated the time between consecutive trials (Souza & Oberauer, 2014). This manipulation turned out to have strong impact on recall accuracy, supporting the “temporal distinctiveness” hypothesis (Brown, Neath, & Chater, 2007). According to this theory, time serves as a retrieval cue for a target event, and when events are crowded close together temporally, they are more difficult to retrieve. Mixture model analysis revealed that temporal distinctiveness affects the probability of correctly retrieving information from WM, but not its precision, somewhat in

agreement with the finding of Zhang & Luck (2009). Critically though both studies did not manipulate the number of items participants were required to remember.

The most direct way to study how additional items in memory influence forgetting is by comparing forgetting slopes when participants try to remember different memory loads. Such a strategy has been deployed previously in pioneering studies using verbal material (Melton, 1963; Posner & Konick, 1966). Those experiments concluded that interference between items held in memory plays a crucial role in their recall, with greater memory loads leading to greater attrition of recall over time. Thus, manipulating the number of items in the memory array as well as the retention duration is crucial for understanding how items interact in memory. However, previous studies have relied on binary report (correct / incorrect) and, to the best of our knowledge, combined manipulation of load and retention interval has not been examined for visual objects using the delayed estimation method.

Here we test memory for variable number of visual items over different durations to examine how interaction between items in memory contributes to rapid forgetting. First, we tested the fidelity of WM recall by using a delayed estimation task and also subjected the results to a mixture model analysis. Using this technique, we show that a single item can be maintained in memory with high fidelity over the short-term. However, if further items are added they degrade each other's representation as time passes: competing with each other in memory, just as one prominent theory suggests objects compete for visual processing resources when they are visible (Desimone & Duncan, 1995). Our findings reveal that for visual WM, this competition specifically results in increasing variability in recall *as well as* progressive loss of feature bindings – information that correctly holds together the component features that belong to particular objects.

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111 **Second, we compared our findings to a recent investigation of ‘retro-cuing’** – cuing one item  
112 long *after* the memory array has been removed – to examine how forgetting is influenced  
113 by directing attention towards a single representation in memory (Pertsov, Bays, Joseph, &  
114 Husain, 2013). **In that study, we used identical stimuli to the ones used in the current one**  
115 **and** showed that the selected or attended memory representation is forgotten **far** more  
116 slowly than the other items in memory. Again, analogous to the concept of biased  
117 competition in visual attention (Desimone & Duncan, 1995), it seems that rapid forgetting  
118 could be prevented by biasing memory to a cued item and, importantly, simultaneously lead  
119 to *faster forgetting* of uncued items. We were able to compare the forgetting slopes for one  
120 and 4 items to the rate of forgetting slopes for the retro-cued item in our previous research  
121 to determine whether the retro-cued item is protected as if it was the only item in memory.

122 The results show that rapid forgetting involves an interaction between time and the number  
123 of items to be held in memory, with competition between stored objects leading to  
124 accelerated degradation of their representations. Furthermore, biasing memory resources  
125 to a specific item in memory can protect it from loss, with the same fidelity as if it was the  
126 only item in WM.

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## 128 **2. Method**

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### 130 ***2.1 Experimental procedure***

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Ten neurologically normal participants (age range 19–35 yrs) participated after giving informed consent. All reported normal or corrected-to-normal visual acuity. Stimuli were presented at a viewing distance of 60 cm on a 21" CRT monitor. Each memory array consisted of oriented bars ( $2^\circ \times 0.3^\circ$  of visual angle) presented on a grey background on an imaginary circle (radius  $4.4^\circ$ ) around fixation with equal inter-item distances (centre to centre). The colours of the bars in each trial were randomly selected out of eight easily-distinguishable colours. Bars within the same trials differed by at least  $10^\circ$  in orientation, which was otherwise random.

Each trial began with the presentation of a central fixation cross (white,  $0.8^\circ$  diameter) for 500 milliseconds, followed by a memory array. Each of the participants performed 10 practice trials and between 11 and 15 blocks of 80 trials. Each block consisted of 20 trials for each of the 4 possible set-sizes (1, 2, 4 and 6 bars), consisting of 5 trials for each delay duration (0.1, 1, 2 and 3 seconds). At the end of each sequence, recall for one of the items was tested by displaying a 'probe' bar of the same colour with a random orientation. Subjects were instructed to rotate the probe using a response dial (PowerMate, Griffin Technology, Nashville, TN) to match the remembered orientation of the item of the same colour in the sequence – henceforth termed the target. Note that we use the term 'target' here simply to distinguish from other items, or non-targets, that were not probed.

## **2.2 Analysis**

For each trial, a measure of *raw error* was obtained by calculating the angular deviation between the orientation reported by the subject and the orientation of the target item. These values were averaged separately for the different trial conditions and durations of



delay. The raw error values for each participant and condition were divided into bins of 20° and presented as histograms in **Fig1C** and **Fig1D**.

To quantify the contribution of different sources of error to overall errors, we applied a *probabilistic mixture model* introduced previously by Bays et al (P. M Bays et al., 2009; P. M Bays, Wu, & Husain, 2011) which elaborated an earlier model by Zhang and Luck (Zhang & Luck, 2008).

This model attributes the distribution of responses on the estimation task to a mixture of three components (illustrated in Figure 2) corresponding to: reporting the target orientation (Fig 2B), mistakenly reporting one of the other (nontarget) orientations in the memory array (Fig 2C), and responding at random (Fig 2D). Orientations of all memory array items are recalled with a Gaussian variability. Mathematically, the model is described by the following equation:

$$p(\hat{\theta}) = \alpha \phi_{\kappa}(\hat{\theta} - \theta) + \beta \frac{1}{m} \sum_{i=1}^m \phi_{\kappa}(\hat{\theta} - \varphi_i) + \gamma \frac{1}{2\pi}$$

where  $\theta$  is the true orientation of the target item,  $\hat{\theta}$  is the orientation reported by the subject, and  $\phi_{\kappa}$  is the von Mises distribution (the circular analogue of the Gaussian) with mean zero and concentration parameter  $\kappa$ . The probability of reporting the correct target item is given by  $\alpha$ . The probability of mistakenly reporting a non-target item is given by  $\beta$ , and  $\{\varphi_1, \varphi_2, \dots, \varphi_m\}$  are the orientations of the  $m$  non-target items. The probability of responding randomly is given by  $\gamma = 1 - \alpha - \beta$ . Maximum likelihood estimates of the parameters  $\alpha, \beta, \gamma$  and  $\kappa$  were obtained separately for each subject, condition and time-point using an expectation maximization algorithm. Concentration parameter  $\kappa$  was converted to the more familiar standard deviation (Fig2 A) according to the method of Fisher (1995).

(MATLAB code available at: <http://www.paulbays.com/code/JV10/index.php>). A 4x4 repeated-measures ANOVA with factors *set-size* (1, 2, 4 and 6 items) x *delay-duration* (0.1, 1, 2 and 3 sec) was conducted on the subjects' errors and estimated parameters related to the 3 types of error. We performed a linear regression to calculate the slope of error across time for the different delay intervals for each participant.

### 3. Results

#### ***3.1 Temporal delay and number of items both modulate working memory precision***

Participants were briefly presented with randomly-oriented coloured bars and, after a variable delay, were asked to reproduce from memory the orientation of one of the bars, specified by its colour (**Fig. 1A**). The number of stimuli presented (set size) varied between 1, 2, 4 and 6 in a randomized, interleaved manner.

<<Figure 1 >>

The error with which subjects recalled an item's orientation (**Fig. 1B**) increased with delay duration ( $F(3,27) = 65.76, p < 0.001$ ) as well as with set size ( $F(3,27) = 56.23, p < 0.001$ ). Importantly, the interaction between these factors was also significant: the gradient of the error function showed a clear increase in the rate of forgetting with increasing set size (**Fig. 1B,  $F(9,81) = 19.02, p < 0.001$** ).

With a large number of items held in memory, longer delays led to a decrease in the number of very precise responses (e.g. 6 items, responses with < 10 degrees of error, effect of delay:

F(3,36) = 6.15,  $p = 0.002$ ) and a corresponding increase in the number of trials with large errors (e.g. 6 items, responses between 30-50 degrees of error, effect of delay: F(3,36) = 5.43,  $p = 0.004$ ). **Fig. 1C** shows for set size of 6 how the distribution of responses, aligned to the true target orientation, alters with increasing delay durations (marked in different shades). By contrast, when only a single item had to be remembered, delay duration had little influence on the distribution of responses (**Fig. 1D**; 1 item, responses with < 10 degrees of error, effect of delay: F(3,36) = 1.32,  $p = 0.3$ ; responses between 30-50 degrees of error: F(3,36) = 0.21,  $p = 0.9$ ).

The increased errors with larger delay durations and set sizes might be attributable to three different factors: noisier representation of the target (or probed) object; higher probability of reporting non-target orientations (indicating erroneous binding – or misbinding – of the target colour with the orientation of another item that appeared in the array); or finally an increase in random responses, guessing unrelated to any of the orientations shown in the array.

### **3.2 Decomposing errors into three sources**

To investigate the different sources of error we applied to the data a probabilistic mixture model that assumes these three potential *sources of error* (P. M Bays et al., 2009; Fougny, Asplund, & Marois, 2010). **Fig. 2** presents the results of the mixture model analysis. The standard deviation parameter (STD) which is proportional to the *width of the underlying memory distribution* (**Fig 2A**) was significantly modulated by both delay ( $F(3,27) = 15.48$ ,  $p < 0.001$ ) and set size ( $F(3,27) = 19.00$ ,  $p < 0.001$ ). This is consistent with the view that higher memory load as well as longer delays lead to broader distribution of responses. The

interaction was also significant ( $F(9,81) = 3.70, p < 0.001$ ), consistent with a more stable precision for a single memorized item but worsening variability with time at larger set sizes.

**Fig. 2B** shows the probability that the response was drawn from the distribution centred on the correct *target* orientation. Again, *both* delay ( $F(3,27) = 9.41, p < 0.001$ ) and set size ( $F(3,27) = 31.70, p < 0.001$ ) significantly influenced the likelihood of participants responding with the correct target orientation, with the interaction between these factors being significant ( $F(9,81) = 3.18, p = 0.002$ ). Thus, longer delays as well as larger set sizes decreased the probability that a response reflected noisy recall of target orientation, as opposed to a non-target or random response.

What about misbinding target colour with a non-target's orientation? We can examine this issue by assessing the probability that the response is centred on the orientation of one of the *non-target items* (items presented in the original array but not probed). Such misbinding was found to be a key ingredient, with this type of error increasing with set size and delay duration (main effect of set-size:  $F(3,27) = 26.55, p < 0.001$ , delay-duration:  $F(3,27) = 3.39, p = 0.032$ ), with a significant interaction between these factors ( $F(9,81) = 2.53, p = 0.013$ ).

<< Figure 2>>

Increasing set size and delay duration also led to an increase in uniformly-distributed or random responses (i.e. centred neither on target nor non-target orientations; main effect of set-size:  $F(3,27) = 6.24, p = 0.002$ , delay-duration:  $F(3,27) = 3.73, p = 0.023$ ), but with no significant interaction in this case ( $F(9,81) = 1.21, p > 0.3$ ). Overall, the more prominent type

of error was a systematic biasing of responses to the orientation of non-targets: misbinding responses. For example: for a memory load of 6 items and > 1 second delay the probability of responding with the orientation of a non-target item was twice as high as responding at random (19% vs 9%; **Figs. 2C and D**).

### ***3.3 Biasing competition in working memory***

WM is not simply a passive storage buffer, but rather a system capable of processing and manipulating ("working") with stored representations (Baddeley, 1992, 2007). We have previously investigated how high level goals change the temporal dynamics of memory representations. In analogy to the biased-competition account of visual processing, we investigated whether forgetting slopes could be biased by top-down processes using a procedure called "retro-cuing" (e.g. Griffin & Nobre, 2003). In this design a cue is presented well after sample stimuli have been extinguished, typically leading to enhanced detection of a change in later test stimuli (e.g. Gazzaley & Nobre, 2012; Griffin & Nobre, 2003; Kuo, Rao, Lepsien, & Nobre, 2009; Lepsien & Nobre, 2006). In a previous study we combined retro-cuing (of 70% validity) with the same delayed estimation task we used here, across variable delays, to study whether forgetting slopes could be biased by retro-cueing. In our previous investigation we used an identical setup (stimuli dimension, screen, report methods etc) to compare the forgetting slopes of retrocued items to the forgetting slopes of items without cueing. We can now ask whether a retrocued item is forgotten at the same rate as if it was the only item displayed and held in working memory.

<< Figure 3 >>

**Figs. 3A and 3C** illustrate the experimental design we used in two previous tasks (Pertsov et al., 2013), based on probing memory either by colour or by location. In 70% of trials a retro-cue was presented 1 second after the sample stimuli had been extinguished. When a cue was presented, it corresponded to the item that was subsequently probed (*valid condition*) on 70% of trials, and one of the other items (*invalid condition*) on the rest. The probe in no-cue trials was presented at various delays following the stimuli presentation. These delays matched the delays of the cued trials with the addition of two further time-points 0.1 and 1 second after the stimuli was extinguished (for more detailed experimental settings please see Pertsov et al., 2013).

In both experiments, the fidelity with which the *cued* item was recalled was relatively stable across time (**Fig. 3** blue line; mean slope of 0.47 deg/sec for the probe-by-colour task and 0.22 deg/sec for the probe-by-location task). These slopes were not significantly different from zero (**Fig. 4**;  $t(11) < 1.5$ ;  $p > 0.16$ ). Crucially, they were comparable to the slope of 1 memorized item in the current experiment (mean slope of 0.35 deg/sec; dotted grey line in **Fig. 3**;  $t(20)s < 0.7$ ;  $ps > 0.5$ ) as illustrated in **Fig. 4**. Importantly, despite the fact that 4 items were displayed prior to the cue, the retro-cued forgetting slopes were significantly lower than the slopes of four items in our experiment ( $t(20)s > 2.6$ ;  $ps < 0.015$ ).

<< Figure 4>>

The fact that the temporal gradient of the cued representation's fidelity is similar to that observed when only one item is held in memory (despite the fact that 4 items were actually displayed) suggests that maintenance resources can indeed be dynamically reallocated according to new task goals and thereby bias competition-based forgetting towards a selected memory representation.

### **3.4 Model effects: Deployment of resources to a cued item leads to stable SD and misbinding**

Next we applied the mixture model analysis to the responses gathered from the retro-cue tasks and plotted it on top of the mixture model results of the current experiment (grey dotted lines in Fig. 2). Consistent with the raw error analysis (Fig. 3), model parameters of cued items were stable across time, just as if one item had been presented in the to-be-remembered array (compare *slopes* of grey dotted lines to blue lines in Fig. 2). Note that comparisons across experiments are meaningful only by examining *gradients* of performance over time, as the *absolute* values of the retro-cue results are determined by the encoding stage (in which 4 items were always presented) and the time that passed before the cue was extinguished (1.1 sec). We conclude from this analysis that selective deployment of maintenance resources can provide protection from the progressive deterioration in precision *as well as* misbinding that results from holding multiple items in memory (Fig. 2B).

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## 316 4. Discussion

317 We studied the fidelity with which visual items are retained in WM, manipulating both set  
318 size and delay duration, and using precision of recall as an index. Studying the forgetting  
319 slopes enabled us to assess the dynamics of maintenance in WM representations without  
320 confounds related to visual processing or encoding of the memory array. First, we found  
321 that greater temporal delays increase forgetting, but crucially only when multiple items  
322 must be remembered (**Fig. 1**). This is inconsistent with the hypothesis that time alone  
323 determines forgetting – at least over the intervals we have studied – which predicts a similar  
324 rate of forgetting for different numbers of objects in memory. The fact that forgetting slopes  
325 are steeper for larger number of items in memory is not trivial: it provides strong evidence  
326 for interaction between different items held in memory, a concept that would not be an  
327 obvious prediction of pure “slot” models of WM (e.g. Luck & Vogel, 1997) in which each  
328 object is assumed to be stored independently, without cross-talk between those  
329 representations. Note, however, that the “slot” model could be consistent with our results  
330 by adding a limited supporting process that is shared between all items, such as a serial  
331 rehearsal or reactivation process (see below).

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333 The results presented here also challenge any time-invariant role of interference in  
334 forgetting, as such accounts by definition predict zero forgetting slopes. Thus short-term  
335 forgetting is mediated by mutual competition between memorized representations that  
336 leads to worse performance *over time*. But time alone is not sufficient: rapid forgetting



requires *both* competition and time. The competition between items is reflected as both increasing variability and increasing probability in reporting the wrong item in memory (**Fig. 2**).

Our conclusion that forgetting is related to time-dependent interference between items in memory is in agreement with two pioneering studies conducted more than 50 years ago using verbal stimuli and binary report (correct/incorrect response). Those investigations showed that either additional (Melton, 1963) or more similar letters (Posner & Konick, 1966) to-be-remembered lead to steeper forgetting curves across filled retention intervals. Posner and Konick concluded colourfully that forgetting was akin to an “acid bath”, with greater degradation occurring with more retained items (analogous to the concentration of acid) and increasing maintenance time (within the acid). To the best of our knowledge though the same conclusions have not been demonstrated for visual memoranda using a delayed estimation task as used here. Moreover, the modelling we employed shows far more directly that the competition is one of interference *between retained features* belonging to different objects, leading to misbinding reports. Previous studies using verbal stimuli did not do this.

In two previous experiments (Pertzov et al., 2013) we found that rapid forgetting is not ‘compulsory’. Subjects were able to bias inter-item competition in favour of one representation – retro-cued either by object colour or location – and protect it from degradation (**Fig. 3**; Pertzov et al., 2013). Strikingly, the forgetting slope of a *retro-cued* item

in a 4-item array was comparable to the rate of forgetting when only a single item was held in memory (comparison of data from the current and previous experiment; **Fig. 3&4**). Thus, top-down processes can bias resources dedicated to the maintenance of each memory representation and counteract the competition induced by other memory representations. Specifically, they maintain the fidelity of memory for the prioritized object, including the associations or bindings between its different features, as if it was the only object in memory.

What is the nature of information that is being degraded over time in our experiments? Is it sensory or categorical? While the longest duration used (3 secs) is too long for iconic memory, recent work has proposed that a high capacity but fragile visual short-term store, different from visual WM, might operate over such a time interval (Pinto, Sligte, Shapiro, & Lamme, 2013; Vandenbroucke, Sligte, & Lamme, 2011). Such a system may be very much a sensory memory since it is erased if similar objects are presented at the same locations (Pinto et al., 2013). The existence of such a longer lasting but fragile store is highly controversial, with some arguing that the effects emerge only after a long period of practice (Matsukura & Hollingworth, 2011).

While it is possible that the competition we have observed between items in memory occur at this level, we consider this unlikely for three reasons. First, we are not aware of any previous data that shows this fragile store is characterized by competition that leads specifically to misbinding of features belonging to different items. By contrast, active

binding of visual features is considered to be a key part of WM (Treisman & Zhang, 2006; Wheeler & Treisman, 2002). Second, the fragile short-term memory system is typically revealed if a retro-cue is presented prior to probing. In the main experiment used here we did not use such a cue. Rather we employed only a probe which is most likely to diminish the contribution of such “fragile memory” traces. Finally, it has been shown that prolonged practice might be required to demonstrate the fragile memory effect (Matsukura & Hollingworth, 2011). In our study, a long period of practice was not made available to participants. Nevertheless, it remains a possibility that the interference we have observed over time might be related to competition within such a sensory memory store.

In visual perception, competition between items in the scene is considered to be crucial (Desimone & Duncan, 1995). More recently, others have suggested that such competition might also operate in WM (Shapiro & Miller, 2011), possibly via a two dimensional map architecture (Franconeri, Alvarez, & Cavanagh, 2013) in which nearby items inhibit each other (Emrich & Ferber, 2012; Kiyonaga & Egner, 2015). Our data is consistent with this approach: items become closer to each other when more of them are displayed, and therefore are expected to interfere more with each other. *Note, however, that we cannot make any conclusions regarding the exact mechanism of inter-item interference that lead to our results. In fact, an alternative interference account that does not rely on spatial based interference but rather on time-sharing might also provide a plausible account (see below).* In any event, the novel contribution of our study is that it provides compelling evidence that inter-item competition, resembling that observed in visual processing, also occurs during maintenance of objects in visual WM. Such maintenance-competition could *only* be

revealed by analysing the forgetting slopes when variable number of items are retained in memory. As far as we are aware, this is the first report which convincingly shows that more items held in visual WM lead to faster forgetting slopes.

A second important result of this study is the modelling used to examine the nature of errors made over time. Maintenance competition appears to lead to mutual degradation of item representations in a specific manner. The analysis shows that this is via an increase in probability of misbinding one object's features with another's, relating directly to the concept of attention as a binding mechanism within visual processing (Treisman & Gelade, 1980). Critically, our experimental design controls well for visual processing because the forgetting slopes are not sensitive to the initial stages of visual perception (captured in the shortest delay of 100 ms; reflected in the intercepts of the forgetting functions rather than their gradients). Therefore, maintenance of items in WM seems to be supported by a mechanism which functions similarly to perceptual attention, but even when visual information is no longer present (Chun, 2011; Wheeler & Treisman, 2002), a view inconsistent with new taxonomical definitions of 'internal' or 'reflective' attention (Chun, Golomb, & Turk-Browne, 2011; Chun & Johnson, 2011).

In contrast to the findings we report, a study using a probabilistic model of errors on a recall task concluded that over time there is an increase in the probability of responding randomly, but no increase in variability forgetting (Zhang & Luck, 2009). The authors of that report concluded that forgetting is effectively the result of "sudden death" (complete

erasure) of memory representations (Zhang & Luck, 2009). Critically, however, they tested only small arrays of 3 items. Here we used a wider range of set sizes and found evidence for progressive changes in recall variability over time, i.e., *gradual decay* – not only sudden death – of memory representations. We note also that the “sudden death” observed by Zhang & Luck occurred using a design with a much longer delay than the longest interval employed here (10 vs 3 seconds). It is possible that such errors might gain greater prominence when the retention interval is extended to longer delays. Additionally, the previous analysis assumed that any response not centred on the target orientation was a random guess; misbinding errors were not modelled. The recall task requires not only that a subject correctly remember the target feature of the items in the memory array (i.e. orientation in the present study), but also that each target feature is correctly matched (“bound”) with the corresponding probe feature (i.e. colour) (P. M Bays et al., 2011; Pertzov & Husain, 2013).

Non-target stimuli have been found to act as a strong attractor on the recalled appearance of an accompanying target stimulus (Paul M. Bays, 2016; Huang & Sekuler, 2010). Our analysis also shows that of the responses not centred on the target orientation at larger set sizes, the majority are due to incorrectly reporting a non-target item rather than random responding. Thus, misreporting features that belong to different objects stored in WM (P. M Bays et al., 2011; Ma, Husain, & Bays, 2014) plays a key role in rapid forgetting. In contrast, even the highest frequencies of random responding observed in the present study (~10% in 6-item arrays) is less than that predicted by the complete erasure of one item (16.7%). Thus, using a task with a continuous response permitted us to go beyond the results of previous

seminal studies which showed that more complex visual stimuli are forgotten faster, but based on a binary measure of recall (Phillips, 1974).

Here we specifically found that increases in the *number* of items to-be-held in memory also increases the rate of forgetting, with forgetting manifest as a gradual decline in recall fidelity, caused by increases in both recall variability and misbinding of visual features over time. Such a view of forgetting is consistent, at least in part, with the concept of WM as active binding of visual features (Treisman & Zhang, 2006; Wheeler & Treisman, 2002) and extends findings which report the strong effect of delay interval on object-location binding, across a few seconds (Pertzov, Dong, Peich, & Husain, 2012) and days (Lew, Pashler, & Vul, 2015).

What is the maintenance resource that items in memory compete for? A recent study presented data which shows that while arrays of letters are not forgotten over short intervals, unconventional characters that are hard to name are (Ricker & Cowan, 2010). The authors hypothesized that their results could be explained as a combination of time-based forgetting and refreshing processes which are hampered in the unconventional characters condition. One type of refreshing processes might be covert verbal rehearsal (Baddeley, 2007) which was found to counteract forgetting in a delayed estimation task when only one item had to be retained in memory (Donkin, Nosofsky, Gold, & Shiffrin, 2014). However, in our case, any crude verbal coding is highly unlikely to account for the levels of accuracy (errors < 15 degrees of orientation) reported here. The maintenance resource items

compete for in our type of experiment could instead be attentional refreshing (Barrouillet, Bernardin, & Camos, 2004), 'covert visuospatial rehearsal' (Baddeley, 2007), or visual imagery (Baddeley, 2007). When more items are maintained in memory, the refreshing cycle would be longer, leading to a higher rate of forgetting reflected as loss of accessibility and precision. Indeed, a recent study has shown that items that were taken out of the focus of attention lead to less precise reports compared to items that reside in the focus of attention (LaRocque et al., 2015).

The time-based resource-sharing model (TBRS) provides one possible model of inter-item competition. The TBRS model proposes a *sequential* and time-based sharing of the internal attention resource (Barrouillet et al., 2004; Barrouillet, Bernardin, Portrat, Vergauwe, & Camos, 2007) similar to the way computer's dynamic RAM is refreshed. To the best of our knowledge, TBRS models have not hitherto been discussed in the context of competition between multiple items. However, this model – among others – would be expected to generate faster forgetting slopes when the maintenance resources have to be shared among more items that reside simultaneously in memory. This view is supported by a recent study that reported that the time needed to refresh information in WM increases with the number of retained items (Vergauwe, Camos, & Barrouillet, 2014).

The processes underlying 'attentional refreshing' or 'visual imagery' are currently only vaguely defined (Baddeley, 2007). In this context, we regard the above options as specific probable manifestations of the more general concept of maintenance resources. Importantly, our findings help to characterize and constrain this resource. They suggest that when more items are maintained in memory, they share – and compete for – a limited pool

of maintenance resources over time. Importantly, resources can be rapidly reallocated to a selected representation within WM and protect it from dissolving, as if it is the sole item in memory (Pertzov et al., 2013). Indeed, a recent imaging study (Lewis-Peacock & Norman, 2014) used pattern classification of fMRI data to show that switching between two representations in WM often leads to increased competition that results in strengthening of the winning memory and, crucially, simultaneous weakening of competing memories.

Finally, the findings presented here also have implications for everyday vision. Experiments using naturalistic tasks and free-viewing conditions suggest that participants store only very little task-related information, as they tend to make eye-movements to obtain the required information just prior to the moment they need it, leading to very brief retention intervals (Ballard, Hayhoe, & Pelz, 1995; Hayhoe, Bensinger, & Ballard, 1998). Our results might provide a rationale for such behaviour: because retention of multiple objects leads to mutual degradation of their representations and worse performance, it is most efficient to maintain a small number of items for short durations.

In conclusion, rapid forgetting occurs because items in WM compete and degrade each other's representations as time passes. This competition manifests, in part, as decreased precision and failures in the binding of features that belong to objects held in memory. Maintenance resources can be dynamically reallocated to protect a selected item from competition and hold it with the same fidelity as a single retained item.



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**Figure 1 | Forgetting with time as a function of number of items in memory**

**(A)** Experimental design: 1, 2, 4 or 6 bars with different orientations and colours were presented for 500 msec. Following a variable delay period, a probe item with the colour of one of the items (in this example, blue) was presented, and subjects adjusted the orientation of the probe to match the remembered orientation of the item with the same colour. **(B)** Mean error of recall for increasing set sizes and delays. **(C)** Distribution of responses for increasing delays, plotted with respect to target orientation (aligned at zero) when 6 items were presented. Different shades represent different delays. Note how the distribution of errors in recalling target orientation alters with delay. **(D)** Distribution of responses for one item did not alter with different delays. Error bars denote SEM across participants.

**Figure 2 | Results of probabilistic model of sources of error in responses.**

**(A)** Variability in recall of each item's orientation is shown as standard deviation of the underlying error distribution. Participants' responses were decomposed into three further separate components, illustrated by the coloured regions in the illustrations: **(B)** a circular Gaussian distribution of responses centred on the orientation value of the target; **(C)** circular Gaussian distributions with the same width centred on each non-target orientation value, corresponding to misbinding errors; **(D)** and a uniform distribution, capturing random responses unrelated to any of the sample orientations. Different colours represent different number of items. For comparison, dotted lines in dark and light grey show model results of the single, retro-cued item in the two experiments reported in Pertzov *et al* 2013, respectively. Error bars denote SEM across participants.

**Figure 3 | Retro-cue experiments: biasing within working memory**

**(A)** Previous colour probe, retro-cue experiment. Participants saw 4 bars, each with a different orientation and colour, for 500 ms. In most trials, after 1 second of blank display, the fixation colour changed to match one of the preceding bars (enlargement of fixation point is only for presentation purposes). This signalled the most probable (70%) item to be probed. In a proportion of trials no cue was presented. In all trials, a probe item with the colour of one of the items (in this example, blue) was presented following a variable delay, and subjects adjusted the orientation of the probe to match the remembered orientation of the item with the same colour. **(B)** Error in recall over time for the three different conditions: *Blue*: Valid, cue matches the probe; *Red*: Invalid, cue does not match the probe; *Green*: No Cue, no cue was presented. **Grey dotted lines represent the predicted performance using the slopes calculated from 1 and 4 item conditions in the current experiment.** **(C)** Previous location probe, retro-cue experiment. Similar to (A), but the cue was a grey ring displayed at the location of the probable target. The probe bar was presented in a neutral colour at the location of one of the memory items (70% at cued location). **(D)** Results of probe-by-location experiment. Error bars denote SEM across participants.

**\*\* for production: we probably need to receive approval from JEP HPP to use this figure as it is very similar to the figure in Pertzov et al 2013;**

**Figure 4 | Comparison of forgetting slopes**

The right side of the figure shows slopes of linear regression between averaged error and delay interval for the different number of items in the current experiment. For comparison, we also calculated the forgetting slopes of the retro-cued items from our previous experiments (Pertzov et al., 2013) shown in Fig. 3. These are shown on the left of the graph. Note that the retro-cued items were forgotten similarly to the one item condition and significantly more slowly than the 4 items slope, despite the fact that 4 items were displayed. Error bars denote SEM across participants.\* :  $p < 0.05$ .

# Figure 1

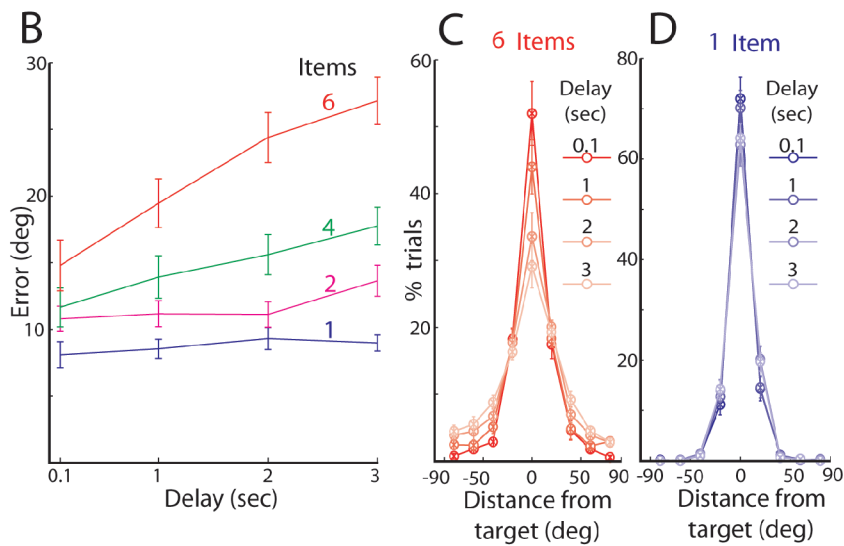
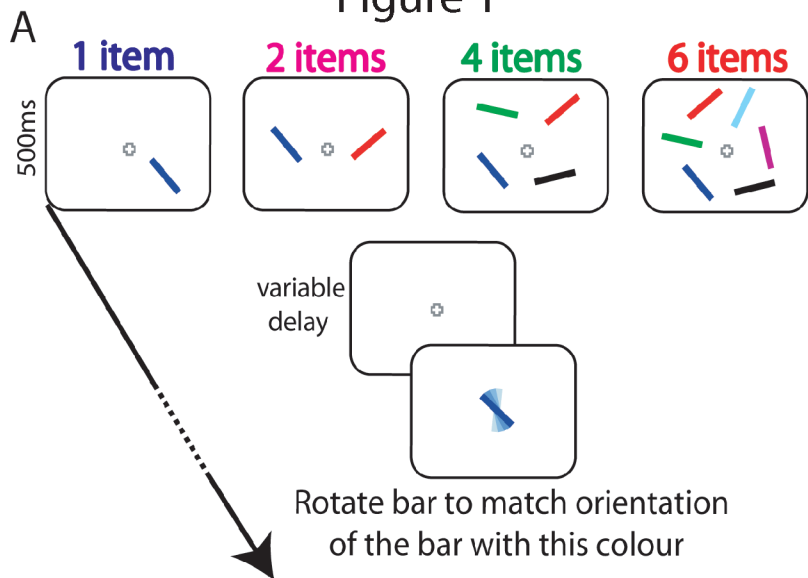




Figure 2

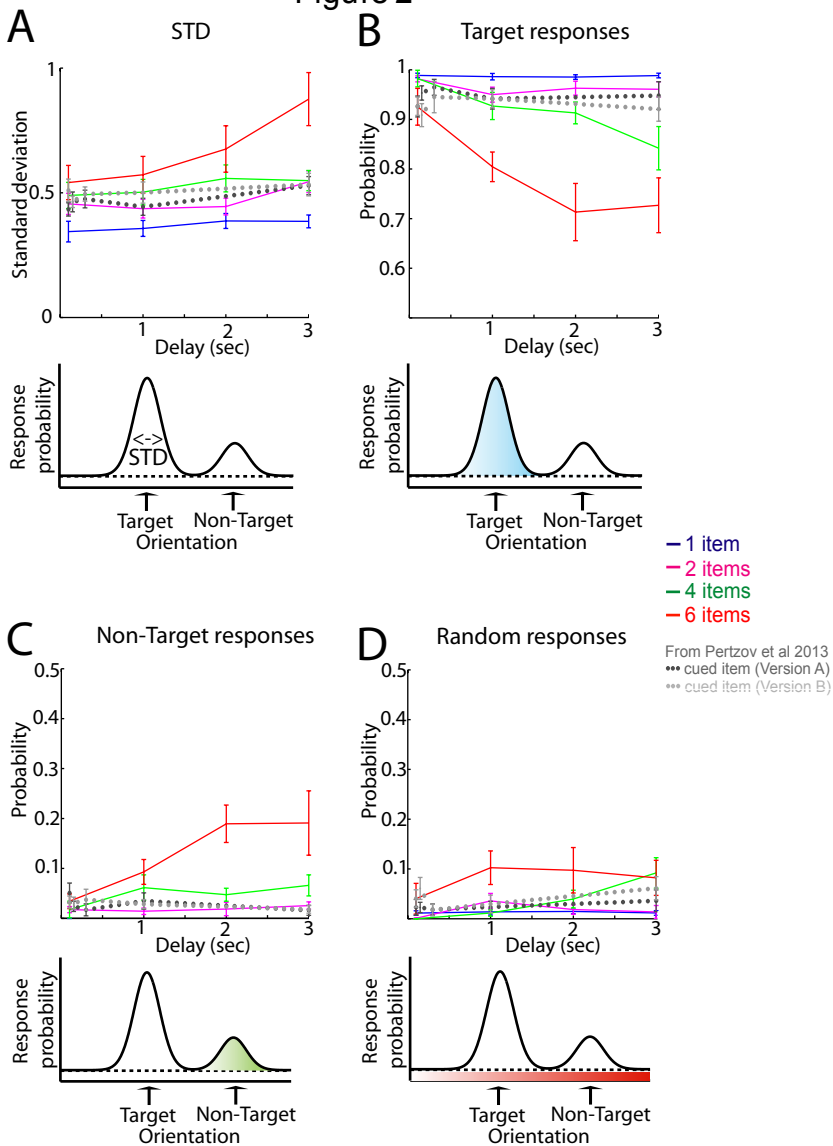


Figure 3

