

To appear in *Memory* (Author accepted version)

Time Manages Interference in Visual Short Term Memory

Amy V. Smith, Denis McKeown and David Bunce

University of Leeds

Author Note

Amy V. Smith, Denis McKeown and David Bunce, School of Psychology, University of Leeds.

This work was supported by the Economic and Social Research Council grant 1359029 awarded to Amy V. Smith.

Correspondence concerning this article should be addressed to Denis McKeown, School of Psychology, University of Leeds, Leeds, LS2 9JT, UK. Email: D.McKeown@leeds.ac.uk

Abstract

Emerging evidence suggests that age-related declines in memory may reflect a failure in pattern separation, a process that is believed to reduce the encoding overlap between similar stimulus representations during memory encoding. Indeed, behavioural pattern separation may be indexed by a visual continuous recognition task in which items are presented in sequence and observers report for each whether it is novel, previously viewed (old), or whether it shares features with a previously viewed item (similar). In comparison to young adults, older adults show a decreased pattern separation when the number of items between ‘old’ and ‘similar’ items is increased. Yet the mechanisms of forgetting underpinning this type of recognition task are yet to be explored in a cognitively homogenous group, with careful control over the parameters of the task, including elapsing time (a critical variable in models of forgetting). By extending the inter-item intervals, number of intervening items, and overall decay interval, we observed in a young adult sample ($N=35$, $M_{age}=19.56$ years) that the critical factor governing performance was inter-item interval. We argue that tasks using behavioural continuous recognition to index pattern separation in immediate memory will benefit from generous inter-item spacing, offering protection from inter-item interference.

Keywords: Visual memory, consolidation, interference, pattern separation, pattern completion.

Time Manages Interference in Visual Short Term Memory

Theoretical explanations of forgetting in human memory have contrasted mechanisms of time-based decay on the one hand and interference-based corruption of the memory trace on the other (Barrouillet & Camos, 2014). Indeed recently, there has been a growing consensus that *both* decay and interference play a role in forgetting, with slow time-based decay processes acting as a form of 'eraser' for redundant memory content (Altmann & Gray, 2002; Altmann & Schunn, 2012). Decay of the trace since encoding in this view is an adaptive process which removes residual representations, and by doing so reduces proactive interference (Hardt, Nader & Nadel, 2013; Mercer & Duffy, 2015). Decay also plays an important role in an influential current model of attention-based memory, the time-based resource sharing model (TBRS; Barrouillet, Bernardin, & Camos, 2004; Barrouillet, Bernardin, Portrat, Vergauwe, & Camos, 2007; Vergauwe, Dewaele, Langerock, & Barrouillet, 2012; Vergauwe, Hartstra, Barrouillet, & Brass, 2015). Here, though it is not time since encoding itself that produces a degrading of the memory trace, but rather the proportion of that temporal interval where attention is otherwise captured and therefore is unable to maintain the memory trace. Yet others have argued that time-based decay plays no role in forgetting, but rather loss of information in memory is due to event-related interference (e.g. Lewandowsky, Oberauer, & Brown, 2009), or to the overwriting of features of the memoranda by distracting material presented post-encoding (Oberauer & Kliegl, 2006). Time in such conceptions does not provide an opportunity for decay but rather beneficially isolates memoranda within psychological space and protects them from being confused with other events entering into memory.

Consistent with this conception of the vital role of time in *protecting* the memory trace from interference, the present study reveals that indeed, providing a generous temporal interval between memoranda to be later recalled appears to protect the items from interfering

with one another. In this very real sense 'time manages interference.' As we describe below the continuous recognition task where we demonstrate this vital role for time-based protection of the memory trace may be important for uncovering aspects of forgetting in an ageing population.

When we encode visual images into memory, we need to ensure that similar or overlapping images are stored as distinct representations in order to reduce retrieval errors (McClelland, McNaughton & O'Reilly, 1995). Evidence has converged from many sources, behavioural, anatomical, and neurophysiological and from computational modelling, that the hippocampus supports distinct encoding and retrieval via the processes of pattern separation and pattern completion (Hunsaker & Kesner, 2013). Pattern completion is the retrieval of a memory for an item based on a degraded or partial stimulus cue (Hunsaker & Kesner, 2013). Such a memory process may rely on the auto-associative properties of hippocampus (notably the recurrent collaterals of region CA3) to achieve pattern retrieval based on partial activations across a network (e.g. Rolls, 2007). Pattern separation in contrast, is the process whereby similar or overlapping representations are stored as distinct orthogonal memories, reducing the overlap and interference from previously stored items (Yassa & Stark, 2011). It is believed to occur in the hippocampal dentate gyrus and CA3 region (Deuker, Doeller, Fell & Axmacher, 2014).

As noted, the theoretical framework supporting pattern completion (retrieval) and pattern separation (encoding) relies on diverse experimental methodologies, and recent reviews (Hunsaker & Kesner, 2013) broadly support the current operational descriptions of the processes, and their realization within hippocampal circuits. The human behavioural index of these forms of memory encoding and retrieval has been measured in human studies using the Behavioural Pattern Separation Task (BPS) (Kirwan and Stark, 2007). In the task, pictures of everyday objects (a wheelbarrow, an apple, a table) are presented one by one in

sequence on a computer screen and observers report for each item whether it is novel (new), previously viewed in the sequence (old), or whether it shares features with a previously viewed item (similar). The index of "behavioural pattern separation" is calculated as the difference between the rates of 'similar' responses to similar items minus 'similar' responses to novel items. Pattern completion is, strictly, recall of an item following presentation of a partial cue, but within the BPS task is taken to be captured by the rate of similar items incorrectly identified as 'old' (Toner, Pirogovsky, Kirwan & Gilbert, 2009). The reasoning here is that when a similar item is identified as old, it has acted as a partial cue for the recall of a prior item.

Renewed recent interest in pattern completion and pattern separation arises from attempts to understand older adults' memory and forgetting. Indeed, a growing body of evidence suggests that older adults exhibit a deficit in encoding new memories so that they are distinct from previously stored items. In other words, they show impaired pattern separation (Carr, Castel & Knowlton, 2015; Holden, Toner, Pirogovsky, Kirwan & Gilbert, 2013). For example, recent research suggests that visual recognition impairments in older adults are due to an impaired ability to identify stimulus novelty (Yassa & Stark, 2008). As we age, false recognition of everyday objects increases (Norman & Schacter, 1997), which can result from novel images being viewed as though they had been previously seen (Koutstaal & Schacter, 1997). Yeung, Ryan, Cowell and Barense (2013) presented older adults with a series of everyday objects in an initial study phase. They then recorded their eye tracking behaviour whilst they viewed some of the objects from the study phase amongst new objects, which shared either high or low similarity with previously viewed objects. Commonly, mean eye fixation is greater for the exploration of a novel object (Henderson & Hollingworth, 2003). Yet Yeung et al. found that mean eye fixations in their older adults did not differ across old repeated items and items sharing high similarity; apparently new items

were falsely viewed as old. This may have reflected either impoverished encoding in the study phase (Molitor, Ko, Hussey & Ally, 2014) or failure to identify novel visual features.

Importantly, evidence of impaired object recognition in healthy older adults has been found using the BPS task (Yassa et al., 2011). For example, Toner et al. (2009) used the BPS to compare pattern separation performance between young adults and healthy older adults, aged over 65. Groups did not differ in their performance for 'old' and 'new' items; but for 'similar' items the older adults performed more poorly. Toner et al. argued that age related changes to the hippocampus in older adults may result in inefficient pattern separation, rather than a recognition memory deficit per se. Stark, Yassa, Lacy & Stark (2013) demonstrated that behavioural pattern separation scores in the BPS gradually decline across the lifespan. Based on this, it could be suggested that diminished ability to recognize the novel features of objects results from neurocognitive ageing, (i.e. Wilson, Gallagher, Eichenbaum & Tanila, 2006), where in older adults the formation of new memories is hindered by interference from prior memories.

Some claim that the BPS is a neuropsychological test capable of identifying the early behavioural markers of cognitive impairment related to neuropathological conditions, such as amnesic mild cognitive impairment (aMCI; Yassa et al., 2010) and Alzheimer's disease (AD; Stark et al., 2013). Yet it is unclear how this behavioural task might differentiate between aMCI, AD and normal ageing. One suggestion has been to manipulate the number of intervening items (and necessarily therefore, the temporal interval elapsing) between 'old' and 'similar' item presentations. Ally, Hussey, Ko and Molitor (2013) measured pattern separation performance in healthy older adults, and aMCI or AD groups, at differing numbers of intervening items (4, 12 or 40), a variable the authors termed 'lag'. As expected, pattern separation performance was lowest for AD patients. However, in comparison to healthy older adults, pattern separation performance in the aMCI group decreased significantly with

increasing lag, whilst AD showed flat, poor or chance performance at each lag. Ally et al. suggested that performance in aMCI is evidence of rapidly degrading visual representations in immediate memory.

Although very interesting, the differing patterns of performance in pattern separation on the behavioural task demonstrated by Ally et al. (2013) across normal ageing, aMCI and AD individuals must remain very tentative since their manipulation confounded two critical dimensions identified within theories of forgetting (Altmann & Gray, 2002): namely the temporal interval elapsing (that is, between encoding of an 'old' item into memory and its reintroduction later as a 'similar' item) and the number of intervening items occurring within this temporal interval. Time based forgetting in short term memory is well documented both in our own laboratory (McKeown, Holt, Delvenne, Smith & Griffiths, 2014; McKeown & Mercer, 2012; Mercer & McKeown, 2014) and elsewhere (Zhang & Luck, 2009), yet the underlying mechanisms of such decline in memory over time are fiercely debated (Altmann & Schunn, 2012; Waugh & Norman, 1965). As noted in our introductory paragraph, the axis of argument rests on the very nature of the confound in the Ally et al. study: does forgetting occur because of decay occurring as time is extended, or does it occur because of the disruptive influences of other events?

The present aim therefore is to manipulate time and events independently within a BPS task to arrive at a better understanding of the underlying factors affecting both pattern separation and pattern completion. This is critical for the effective application of the BPS within the neuroscience and psychological literatures more broadly, beyond accounting for the outcomes in the specific populations employed by Ally et al. (2013). We therefore recruited a young sample of adults of restricted age range, both to rule out extraneous age- and dementia-related factors (a younger sample is less likely to present with undetected neuropathology), and to allow for a more homogeneous group cognitively (older participants

become increasingly heterogeneous in this respect). Following Ally et al., stimulus pairs ('old' - 'old' and 'old' - 'similar' pairings) were separated by either 4 or 12 intervening items. In order to separately examine any effects of the retention interval itself, the memory retention interval between these stimulus pairs was manipulated. This necessitated the introduction of a third critical factor within memory research: the inter-item interval, which is the temporal interval between successively presented items within the continuous recognition task. We examined the effects of intervening items and inter-item interval using a continuous recognition task with the memoranda being a large and very diverse stimulus set of photographs of doors. Previously it has been suggested that the use of familiar visual stimuli can engage both verbal encoding of stimuli and activation of long term representations from stored memory (Liu, Gould, Coulson, Ward & Howard, 2016; Mckeown et al., 2014). Both are confounding variables when attempting to investigate temporal factors involved in short term memory as they may allow the participant both to access long-term associates and also to engage in sub-vocal rehearsal processes to maintain items in memory. The door stimuli were from a single stimulus category so that simple verbal labelling would be of minimal use in our task. Finally, we also report data where the memoranda were, as is more common in the pattern separation literature, pictures of a wide range of everyday objects (such as a car, rabbit or saucer).

Method

Participants

Thirty-five young adults (32 female), aged between 18 - 22 years ($M_{age} = 19.56$ years, $SD_{age} = .88$) were recruited from the School of Psychology at the University of Leeds. Participants were all native English speakers, with self-reported normal or corrected-to-normal vision. Using power analysis, a sample size of 28 was estimated to find a medium

effect size ($f=.25$) with $\alpha=.05$, $1-\beta=.80$ and a moderate correlation between repeated measures of $r=.50$. Our sample size comfortably exceeds this.

Materials

Visual stimuli were presented on a white background, on a Dell 1708FP monitor, with participants approximately 60cm away from the monitor. The experiment was run using E-Prime 2.0 software (Schneider, Eschman & Zuccolotto, 2002). Two types of stimuli were used: coloured photographs of a wide variety of doors (door stimuli) and very simple representations of common everyday objects (object stimuli). Our new set of door stimuli were designed to reduce the opportunity for category- or verbal-labelling within the task, which may be possible with varieties of simple pictures of everyday objects. The reason verbal labelling or verbal rehearsal may act as a possible confound in studies such as this, is that such memory codes involve long term verbal memory (McKeown et al., 2014) and the present concern is the short lived memory for visual stimulus features. By using a single item category of doors and a very great number of items within that category, we minimized both the possibility of similar labels of type of object, and of active verbal rehearsal of the individual items presented on every trial.

The door stimuli were taken from a larger image database, provided by Professor Alan Baddeley, University of York. The everyday object stimuli were by permission of Dr. Craig E. Stark, University of California. From both sets, 90 similar pairs and 270 individual images were used as 'new' and 'old' items (see below). Each image was adjusted to a height of 227 pixels and width of 178 pixels. Lacy, Yassa, Stark, Muftuler and Stark (2011) outline in detail the degree of similarity between the object stimuli used in the BPS task. Traditionally, the similar image pairs are two different objects that are matched in terms of their category label and perceptual similarity for example, two images of hammers that share similar visual features. In line with this, the new door similar image pairs were matched according to

categorical and perceptual similarity. The door stimuli were selected from a larger database of 400 images. This database consists of 100 groups of 4 images that are matched according to the following categorical features; function, age, colour, glazing, condition, shape, opening, details, surround and memorability. To obtain a set of similar image pairs that match both in terms of categorical features and perceptual similarity, two independent researchers generated every possible pairing within each door category group which was 600 image pairs. These image pairs were then rated in terms of their perceptual similarity using a 7-point Likert scale (1 = weak similarity and 7 = strong similarity). Based on the mode similarity rating, 90 similar image pairs were selected to be used in this study.

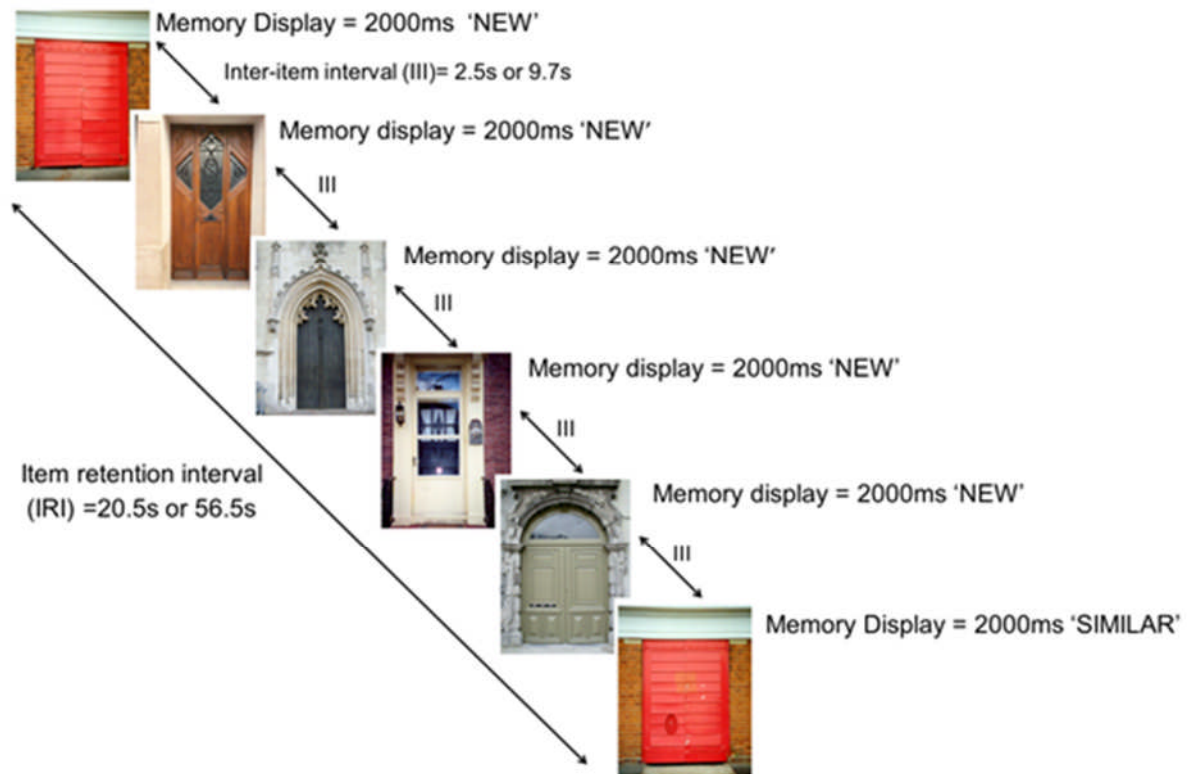


Figure 1. Example of the experimental procedure in the lag conditions: 4_short and 4_long.

Design and Procedure

Participants completed two versions of the continuous recognition task, one with the door stimuli and one with the everyday object stimuli. The task was adapted from Ally et al. (2013) and arranged into 60-trial blocks, consisting of 20 single 'new' items, 10 'old' item pairs (an item presented and later presented again), and 10 'similar' item pairs (an item presented and a very similar item presented later). Throughout we use the words new, old and similar to refer both to our stimuli and to the response to those stimuli. This avoids what we consider as the confusion of a plethora of terms within the literature; in the present context it is evident where a word refers to a stimulus or to a response.

Participants completed nine experimental blocks for doors and nine for objects in counterbalanced order. As shown in Figure 1, each item was presented on the screen for 2 s,

followed by an inter-item interval (III) of either 2.5 s or 9.7 s. Old and similar pairs were separated by 4 or 12 intervening items so that, taking into account item duration and III, the old and similar pairs were separated by an item retention interval (IRI) of either 20.5 s (4 intervening items) or 56.5 s (12 intervening items). This produced 3 item x interval conditions: 4_long (4 intervening items with a 9.7 s III), 12_short (12 intervening items with a 2.5 s III), and 4_short (4 intervening items with a 2.5 s III). Importantly, in two of the conditions, 4_long and 12_short, the IRI was equal. In a sequence of images participants reported by button press whether it was new (first time presented), old (the image had been previously presented) or similar (image shared similar visual features, but was not identical to, an image previously presented). Following 12 practice trials at the start of each session, participants completed three blocks for each condition (a total of 180 trials). Blocks were either 11.7 min (4_long) or 4.5 min in duration (4_short and 12_short), but test sessions were maintained at approximately equal duration (participants completed either one of the longer blocks or two of the shorter blocks in a daily session). Each item lag condition was completed in a separate experimental block. Participants completed four sessions with the order counterbalanced, as was the order of condition within a session. There was a 10-minute break between blocks. Visual images were not repeated across experimental blocks and participants were informed that images were not repeated from earlier blocks or sessions and as such their judgments of old, new and similar should be based on the current experimental block.

Consistent with previous research (Lacy et al., 2011) a measure of perceptual similarity for the new door stimuli was calculated for each similar pair. Twenty-nine young adults ($M_{age}=18.97$, $SD_{age}=2.04$), who did not participate in the continuous recognition task, viewed 90 door image pairs, and were asked to rate their perceptual similarity on a 7-point Likert scale (1=weak similarity to 7=strong similarity). The ratings revealed no significant

difference in perceptual similarity between pairs used across our experimental conditions ($\chi^2(12, N = 90) = 9.5, p = .66$).

Results

Overview of Measures

For each type of stimulus (door and everyday object), the mean proportion of responses was calculated for lag (4_long, 12_short, 4_short). Three outcome measures were calculated: the recognition accuracy score (RAS), the behavioural pattern separation (BPS), and the behavioural pattern completion (BPC). These derived measures were based on hits and false alarms across the stimulus and response possibilities in the task (see Table 1) following Stark et al. (2013), but using signal detection methods, our measures used a normalized score as a bias free index of sensitivity (d' , Bi, 2002). The 'raw' proportions are shown for each stimulus condition in Table 2 ($N = 34$: one participant identified as an outlier was excluded as their 'new' responses exceeded 60 % new responses for old and similar items). The RAS equalled the mean normalized proportion of old items correctly identified as 'old' minus the mean normalized proportion of new items incorrectly identified as 'old'. The BPS equalled the mean normalized proportion of similar items identified as 'similar' minus the mean normalized proportion of new items incorrectly identified as 'similar'. The BPC equalled the mean normalized proportion of similar items incorrectly identified as 'old' minus the mean normalized proportion of new items incorrectly identified as 'old'. Analyses below are based on these derived measures. Analyses of the raw proportions uncorrected for observer bias are reported but did not uncover contrasting patterns of performance.

Table 1

Definitions of the response possibilities for the new, old and similar stimuli; and formulae used for the main derived measures

Stimulus	Response		
	New	Old	Similar
New	Correct Rejection Rate	False Alarm Rate	Similar Bias Rate
Old	Miss Rate	Hit Rate	Incorrect
Similar	Incorrect	Pattern Completion Rate	Pattern Separation Rate

Recognition accuracy score (RAS) = $Z(\text{hit rate}) - Z(\text{false alarm rate})$

Behavioural pattern separation (BPS) = $Z(\text{pattern separation rate}) - Z(\text{similar bias rate})$

Behavioural pattern completion (BPC) = $Z(\text{pattern completion rate}) - Z(\text{false alarm rate})$

Door Stimuli: Recognition Accuracy Score

To investigate whether lag affected participants' ability to correctly identify repeated items (correct 'old' responses), the mean proportions of hits and false alarms was calculated at each lag. For the hit rate, a one way repeated ANOVA with factor of lag (4_long, 12_short, 4_short) was significant, $F(2, 66) = 15.30, p < .001, \eta_p^2 = .32$. We then performed paired sample t-tests to separately test for effects of IRI and for number of intervening items. The hit rate was significantly higher for 4_long than for 12_short, $t(33) = 5.24, p < .001, d = .76$; and 4_short, $t(33) = 3.10, p = .004, d = .41$. Hit rate for 4_short was significantly higher than

12_short, $t(33) = -2.67, p = .012, d = .34$. There was no significant main effect of lag for false alarm rates, $F(2, 66) = 2.14, p = .125$.

The outcomes for the RAS measure are shown in Figure 2. For RAS, a one way repeated ANOVA with factor of lag (4_long, 12_short, 4_short) was significant $F(2, 66) = 19.2, p < .001, \eta_p^2 = .37$. We then performed paired sample t-tests to separately test for effects of IRI and for number of intervening items. This confirmed higher performance at 4_long ($M = 2.64, SD = .78$) than for 12_short ($M = 1.93, SD = .74$), $t(33) = 5.55, p < .001, d = .94$ and 4_short ($M = 2.28, SD = .64$); $t(33) = 3.57, p = .001, d = .52$. RAS for 4_short was higher than for 12_short, $t(33) = 3.08, p = .004, d = .51$.

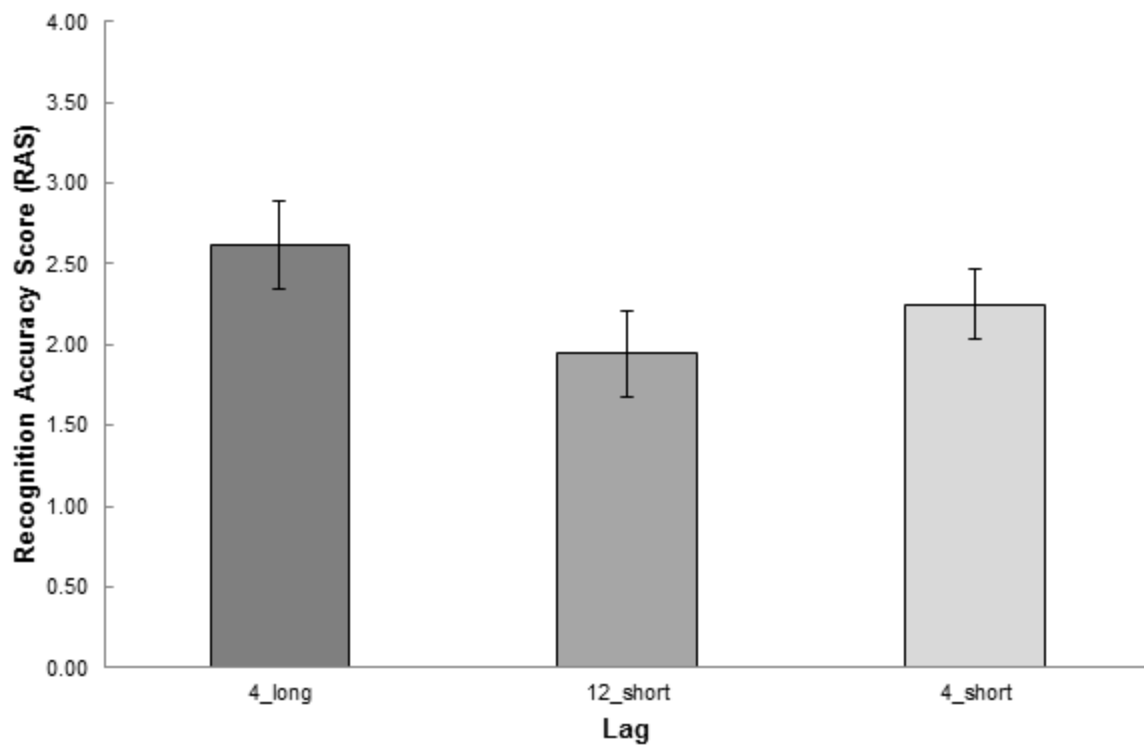


Figure 2. Mean recognition accuracy score (RAS) as a function lag (4_long, 12_short, 4_short) for the door stimuli. Error bars are shown as 95% confidence intervals.

Door Stimuli: Behavioural Pattern Separation

To investigate whether lag affected participants' ability to correctly identify similar items (correct 'similar' responses), the mean proportions of pattern separation rate and similar bias rate was calculated at each lag. As shown in Table 1, these two rates were used to calculate the derived measure of behavioural pattern separation (BPS). The outcomes for the BPS measure are shown in Figure 3. A one way repeated ANOVA with factor of lag (4_long, 12_short, 4_short) was significant, $F(2, 62) = 8.51, p < .001, \eta_p^2 = .22$. We then performed paired sample t-tests to separately test for effects of IRI and for number of intervening items. Performance was significantly higher for 4_long ($M = .76, SD = .55$) than for 12-short ($M = .46, SD = .41$); $t(32) = 3.34, p = .002, d = .64$; and 4_short ($M = .6, SD = .49$); $t(31) = 2.15, p = .04, d = .31$. BPS for 4_short was significantly higher than for 12_short, $t(32) = 2.21, p = .034, d = -.32$.

A one way repeated ANOVA with factor of lag (4_long, 12_short, 4_short) was not significant for pattern separation rate, $F(2, 66) = 2.91, p = .06, \eta_p^2 = .08$. However, it was found that the average pattern separation rate was significantly higher for 4_long than for 12_short, $t(33) = 2.52, p = .02, d = .39$. There was no significant main effect of item lag for similar bias rate, $F(2, 66) = 1.39, p = .255, \eta_p^2 = .04$.

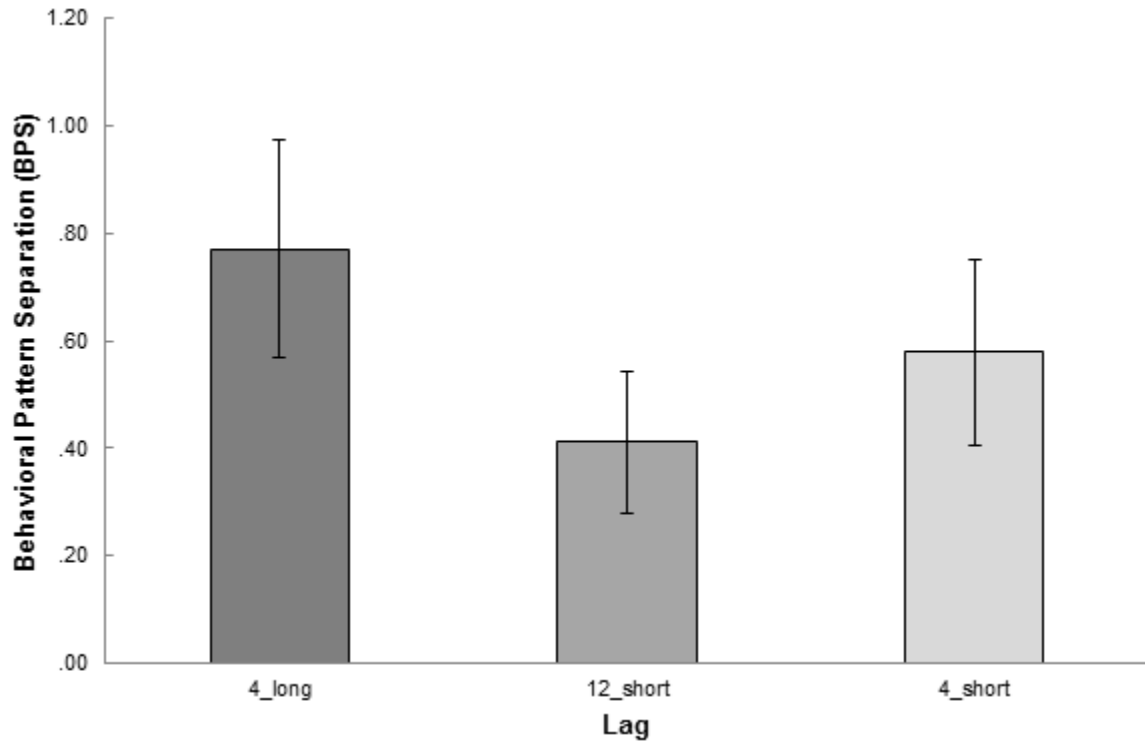


Figure 3. Mean behavioural pattern separation (BPS) as a function of lag (4_long, 12_short, 4_short) for the door stimuli. Error bars are shown as 95% confidence intervals.

Door Stimuli: Behavioural Pattern Completion

The outcomes for the BPC measure are shown in Figure 4. For BPC a one-way repeated ANOVA with factor of lag (4_long, 12_short, 4_short) revealed a significant main effect, $F(2, 66) = 9.23, p < .001, \eta_p^2 = .22$. We then performed paired sample t-tests to separately test for effects of IRI and for number of intervening items. Performance was higher for 4_long ($M = 1.48, SD = .34$) than for 12_short ($M = 1.21, SD = .5$); $t(33) = 2.92, p = .006, d = .65$; and 4_short ($M = 1.15, SD = .41$); $t(33) = 5, p < .001, d = .89$. No other pairwise comparison was significant.

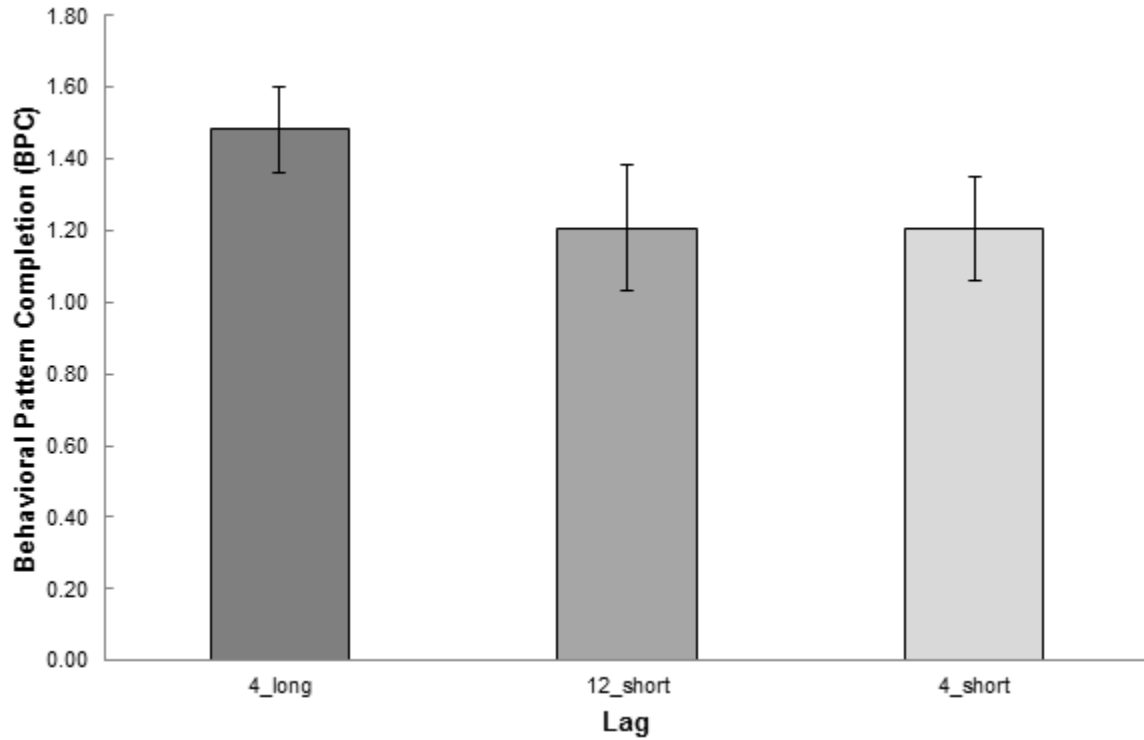


Figure 4. Mean behavioural pattern completion (BPC) as a function of lag (4_long, 12_short, 4_short) for the door stimuli. Error bars are shown as 95% confidence intervals.

Everyday Object Stimuli

Performance on the continuous recognition task was higher overall for everyday object stimuli than for door stimuli. Separate 2 (stimulus type: door, object) x 3 (lag: 4_long, 12_short, 4_short) ANOVAs revealed significant main effect of stimuli for BPS, $F(1, 29) = 232.03, p < .001, \eta_p^2 = .89$, RAS, $F(1, 32) = 90.19, p < .001, \eta^2 = .74$ and BPC, $F(1, 33) = 31.48, p < .001, \eta_p^2 = .49$.

One way repeated measures ANOVAs showed no significant effect of lag on the BPS measure, $F(2, 58) = .22, p = .806$ or for the RAS measure, $F(2, 56) = 2.6, p < .082$. However, given the trends in the means in the three RAS conditions, further t-tests were performed between them: a t-test showed that for RAS performance for 4_long ($M = 3.28, SD = .71$) was higher than for 4_short ($M = 2.91, SD = .87$); $t(32) = 2.15, p = .039, d = .45$. No

other pairwise comparisons were significant. There was no significant effect of lag for the BPC measure, $F(2, 66) = 1.26, p = .29, \eta_p^2 = .04$. Overall, therefore pattern of performance at least for the RAS measure was therefore broadly similar to the door stimuli.

Table 2

Mean proportions (p) for each response possibility (New, Old, and Similar) across lag for door and object stimuli. Standard deviation is given in parentheses.

		Door			Object		
		4_long	12_short	4_short	4_long	12_short	4_short
New	p(new)	.82	.78	.79	.96	.96	.96
		(.12)	(.14)	(.16)	(.04)	(.06)	(.06)
	p(old)	.07	.09	.07	.02	.02	.02
		(.06)	(.08)	(.05)	(.03)	(.03)	(.04)
	p(similar)	.12	.13	.14	.02	.02	.02
		(.10)	(.11)	(.13)	(.03)	(.04)	(.03)
Old	p(new)	.13	.24	.16	.07	.11	.19
		(.13)	(.19)	(.18)	(.09)	(.10)	(.26)
	p(old)	.79	.64	.71	.85	.81	.74
		(.17)	(.22)	(.21)	(.11)	(.11)	(.26)
	p(similar)	.08	.12	.09	.08	.08	.07
		(.08)	(.10)	(.11)	(.08)	(.07)	(.08)
Similar	p(new)	.29	.39	.41	.11	.15	.16
		(.18)	(.20)	(.21)	(.12)	(.14)	(.13)
	p(old)	.44	.39	.34	.41	.43	.38
		(.15)	(.19)	(.16)	(.16)	(.17)	(.16)
	p(similar)	.27	.22	.25	.49	.43	.46
		(.14)	(.13)	(.15)	(.20)	(.19)	(.19)

Discussion

Using a continuous recognition task with a large stimulus set of single-category memoranda, the present experiment aimed to examine the effect of intervening items separate from an increasing retention interval. By manipulating the inter-item interval, we were able to maintain a fixed item retention interval between old and similar pairs, while increasing the level of interference created by additional intervening items. As noted, for the everyday object stimuli, our manipulation of intervening item and inter-item interval did not significantly affect performance, except for a marginal benefit for the 4_long over the 4_short condition by our recognition accuracy score (based on accuracy in identifying previously presented images). However, the high performance overall we have suggested may be accounted for by the availability of verbal labelling of the objects in this stimulus set. The use of verbal labels can be an effective strategy to improve visual recognition memory, as categorising memoranda forms a less noisy representation (Lupyan, 2008). For mixed-category visual stimuli, verbal labels can facilitate memory recall (Lupyan, 2008; Richler, Palmeri & Gauthier, 2013) and over short time intervals, protect it from decay and interference through active rehearsal (Berman, Jonides & Lewis, 2009). When investigating visual memory often verbal rehearsal is eliminated by introducing articulatory suppression during each inter-item interval (Lewandowsky & Oberauer, 2015). However, Sense, Morey, Prince, Heathcote and Morey (2016) highlights that there is an assumption in that the availability of verbal label will always lead to participants adopting a verbal strategy, regardless of the type of visual stimuli and the nature of the task. For within-category stimuli such as the door stimuli, the use of verbal labels can be detrimental to memory performance (Lupyan, 2008). Feedback from our participants both after the practice trials and the study, suggests they did not employ a verbal strategy to perform the task with the door stimuli as they believed it would not facilitate their new, old and similar judgements.

The more interesting data here are the measures for the new door stimuli which resist verbal labelling or category-like labelling. Participants' ability to identify similar and old items was strongly affected by the manipulation of the retention interval. Inter-item interference undoubtedly played a role too: in conditions where item retention intervals were equal, performance *decreased* as the number of intervening items increased. Importantly, however, our BPS (thought to reflect a form of 'pattern separation' in memory) and RAS (thought to reflect broadly the fidelity of the memory trace) measures showed declining performance as the inter-item interval was reduced from 9.7s and 2.5s. In the 4_short and 4_long conditions, where the number of intervening items was equal, performance *improved* with increasing inter-item intervals. Our confidence in the major contrasts between 4_short, 4_long and 12_short is perhaps most clearly justified by the convergence of statistical support revealed by all three of the reported measures.

Implications for Behavioural Measures of Pattern Separation

Theoretical developments of the role of the hippocampal system in episodic memory are progressing rapidly, arising within the neurosciences from studies of the effects of lesions to hippocampal circuits, of spatial learning in animals, and of behavioural studies in humans in the sorts of continuous stimulus recognition task described here. The influential suggestion (Rolls, 2013) is that a form of auto associative network is realized by hippocampal CA3 neurons to permit pattern completion based on partial cues. The sparse connectivity of mossy fibres to CA3 has a randomizing effect on the representations within that network so that the patterns stored are as different from one another and from other patterns as is possible to allow pattern separation. The randomizing of patterns within CA3 will mean that interference between similar pattern memories is minimized. Our data reveal that both pattern completion and pattern separation (captured by our reported measures) rely on the opportunity within an

extended temporal interval to encode and maintain representations of objects within immediate memory.

It has already been suggested that our understanding of the proposed hippocampal pattern completion and pattern separation processes based on human behavioural discrimination learning and retrieval must be cautiously welcomed (Hunsaker and Kesner, 2013). The comparisons of older adults, individuals with aMCI and with AD in the study of Ally et al. (2013), which formed the basis for the present investigation, appeared to uncover a form of rapid interference-based forgetting. Individuals with aMCI and AD showed decreased pattern separation scores (BPS) with increasing 'lag'. However, unlike the current study, Ally et al.'s manipulation of lag was created by increasing the number of intervening items to extend the time elapsing between pairs of items. Using a cognitively homogeneous young sample, however, we have here shown that the likely cause of the poorer performance in the aMCI and AD participants in that study was not due to failures of pattern completion or pattern separation as suggested by these authors, but rather to difficulties in encoding the items fully into immediate memory. The problem, in other words, may have been one of memory consolidation (Wixted, 2004). Such a conclusion is fully in line with the recent observation by Molitor et al. (2014), using an eye-tracking measure to assess false alarms in a continuous recognition task like that used here: apparently errors in the task of reporting 'old' to similar items were associated with decreased fixations during the earlier presentations of those items. In a temporally densely packed sequence of items, the problem presumably was one of insufficient encoding of images into memory. A natural assumption therefore might be that one form of impairment within aMCI and early AD is encoding or consolidation time for items within a continuous recognition task, rather than failures in pattern completion and pattern separation per se.

Recent evidence points to rate of learning as a key feature of aMCI and early onset dementia (Hanseeuw et al., 2011; Walsh et al., 2014); whilst Wang, Li, Li and Zhang (2013) have identified a key variable under conditions using massed trials in aMCI: the impairment in encoding into memory of successive items. Alternatively, it may be acknowledged that memory precision gets worse with age. Studies in the working memory literature using continuous reproduction tasks have shown that even to retain a single item in memory (e.g., a single colour patch), older adults show lower precision (Peich, Husain, & Bays, 2013; Pertzov, Heider, Liang, & Husain, 2015; Souza, 2016; Zokaei, Burnett Heyes, Gorgoraptis, Budhdeo & Husain, 2015). Therefore, it is possible to view the BPS as a measure of memory precision of an item (how precisely do I remember the item I saw before) so as to be able to tell that a subsequent similar item is “just” similar and not exactly the same. In this sense we note that the data of Toner et al (2009) show that older adults reported similar objects more often “old” than “similar”, whereas young adults showed the reverse pattern. This is congruent with a lower precision for the stored information within memory.

A Role for Temporal Distinctiveness?

We have identified a critical variable, time following item presentation, within this behavioural task thought to index *both* the efficient separable encoding of items into memory and their later retrieval. To address why an increasing inter-item interval leads to such marked improvements, we look to current accounts of time-based forgetting in visual short term memory. One account of such time-based influences appeals to the temporal distinctiveness of items within their spatial and temporal context (Brown, Neath & Chater, 2007; Ecker, Brown and Lewandowsky, 2015). It is possible that increasing the inter-item interval reduces the confusion between memory items on a trial by trial basis (Ecker, Tay & Brown, 2015; Mercer, 2014). In comparison to the consolidation account, temporal distinctiveness states that successful memory retrieval is determined by the ratio between the

inter-item intervals between successive to be remembered items and the retention interval between initial encoding and subsequent retrieval (Ecker, Tay, et al., 2015; Souza & Oberauer, 2014). It has been argued that this ratio is critical for successful memory recall because when memory traces are maintained longer in short term memory they are compressed in psychological space (Grange & Cross, 2015) and by reducing the inter-item interval, it produces confusion between those items within their spatial and temporal context (Ecker, Brown, et al., 2015; Ecker & Lewandowsky, 2012).

One of the strengths of the temporal distinctiveness account is that specific predictions may be made for a given forgetting function based on relative time. A recent study by Souza and Oberauer (2014) manipulated the ratio between inter trial interval (ITI) and memory retention interval (RI), to investigate the effect of temporal distinctiveness separate from simple decay. In their continuous colour recall task (Zhang & Luck, 2008), participants were presented with a visual item consisting of six coloured circles. Following a brief delay of 1000ms or 3000ms, a colour wheel was presented with a cue to the location of one of the coloured circles. Participants were required to recall the colour of the cued item. Each trial was separated by an ITI of 7500ms or 1000ms. Based on the RI and ITI, Souza and Oberauer were able to estimate the distinctiveness of each memory display. Using these calculations, they found that performance did not vary when the RI was increased while the distinctiveness was maintained between items. However, it should be noted that evidence against temporal distinctiveness has been found in other memory paradigms using longer RIs of 1-12s, similar to the time intervals used in the present study (Ricker & Cowan, 2014; Ricker, Spiegel & Cowan, 2014).

Yet, with an emphasis on interference created by prior memory traces, distinctiveness accounts should at least partially explain the positive influence of increased inter-item interval in the sorts of task we have used. For example, when the number of intervening items

is equal, increasing the inter-item interval from 2.5s to 9.7s in our task would be expected to make each image more temporally isolated. As such the amount of proactive interference should be reduced. Various distinctiveness accounts have been proposed since Murdoch (1960) but most rely on identifying the source of proactive interference local to an item. Thus, Souza and Oberauer (2014) apply a familiar simple ratio of retention interval (current trial between memory display and probe) and the time that has elapsed since the presentation of the memory display on the previous trial. It is of course possible for us to calculate a similar distinctiveness ratio, where the retention interval is between the first presentation of an item and its subsequent 'repeat' or 'similar' image probe; and the time elapsed since the previous trial is simply our inter-item interval. However, in our continuous recognition task where 'the memory judgement' is compared with items earlier in the sequence such a straightforward ratio of time intervals is probably over-simplistic as it ignores intervening items. So, despite the growing body of evidence in support of the temporal distinctiveness account (Ecker, Brown, et al., 2015; Ecker, Tay, et al., 2015), we are as yet unsure how it would predict our current findings.

Time for Consolidation?

A somewhat different account of time-based memory improvements is the well-rehearsed idea that 'time for consolidation' enhances short-term memory (Bayliss, Bogdanovs & Jarrold, 2015; Jolicœur & Dell'Acqua, 1998). During an unfilled time interval, memory consolidation can be defined as an active process that works to strengthen a new memory trace so that it can be successfully retrieved at a later point in time (Dewar, Alber, Cowan & Della Sala, 2014; Mercer, 2015). Arguably, visual memoranda suffer from rapid time based decay if there is reduced opportunity for engaging in a consolidation process (Knöchel et al., 2015); as a result, the memory trace is more vulnerable to interference or overwriting from succeeding items (Nieuwenstein & Wyble, 2014, offer a recent test of so-called short-term

consolidation). One influential champion of memory consolidation has been Wixted (2004). As this author points out, the concept is hardly new and may be traced to a forgetting law of Jost at the end of the 19th century captured by the insight that, with elapsing time, old encoded items within memory become less vulnerable to the disruptive effects of subsequent events: in other words, they show an ever-slowing proportional memory decay function. This temporal gradient of retroactive interference, whereby allowing a temporal interval free of interfering material post encoding strengthens the memory trace, has intuitive appeal and empirical support. Thus, using visual characters (unfamiliar written items) as memoranda and varying time between items, Ricker & Cowan (2014) observed that limiting post-encoding consolidation time using brief inter-stimulus intervals, impaired memory recall. They concluded that “whether or not time-based forgetting will be observed in a working memory task is largely determined by the amount of time allowed for consolidation of working memory” (p. 427). Similarly, Bayliss et al., (2015) varied post-encoding time for lists of consonants by introducing a demanding processing activity either immediately or following a delay (whilst equating retention interval across conditions); they interpreted the impaired performance in the immediate condition as consistent with a consolidation process. Unfortunately, as a careful reading of a recent review (Ricker, 2015) of consolidation in short-term memory makes clear, there is a surprising lack of clarity as to the time-course of short-term consolidation or indeed whether and how it might differ from the more familiar 'encoding time' of the memory trace. While a solely interference account is insufficient for our own findings, further research is urgently needed to develop a clearly defined account of consolidation in visual short term memory.

Conclusion

Recent research on pattern separation and pattern completion using the BPS task is extensive, yet we have only just begun to examine not only the validity of this task but the underlying forgetting mechanisms underpinning these processes. Whilst we have shown the critical influence of inter-item interval in this behavioural task, we have also demonstrated that it is more than of secondary theoretical interest for forgetting itself but rather temporal variables underlie the efficiency of pattern separation and pattern completion mechanisms themselves. Although our own primary focus has been on the window of opportunity for the encoding of information into memory (and hence pattern separation), naturally the continuous recognition task is one where the processes underlying retrieval (and hence pattern completion) are similarly implicated as participants make their old, new, and similar responses on each trial. In other research (e.g. McKeown & Mercer, 2012; Mercer & McKeown, 2014) we have suggested that, in elaborating the mechanisms underlying encoding and retrieval of non-verbal memory it may be necessary to extend the 'short' in short-term memory. Naturally, we might consider whether our participants relied on some form of long-term storage of the entire set of stimuli accumulating throughout an experimental session. We do not favour such a view for two reasons. First, the continuous recognition situation does not demand the sorts of capacity-limited recall of sets of stimuli seen in typical working memory recall tasks; and secondly, if performance was capacity-limited we would expect severe penalties when we extend the number of intervening items beyond 3 or 4 (Cowan, 2011; Hardman & Cowan, 2015), which we do not observe. Nevertheless, in the present task we remain undecided as to whether our temporal manipulations are uncovering predominantly short-term memory processes or more long-term mechanisms of retrieval, and look forward to future developments.

In summary, whether through time for memory consolidation of items (Wixted, 2004) or through enhanced temporal distinctiveness (Brown et al., 2007), the inter-item interval in continuous recognition tasks indexing pattern completion and pattern separation is a vital controlling variable. For our cognitively unimpaired young sample of participants, in which age and dementia related factors have been carefully controlled, inter-item interval appeared to be the critical variable governing encoding/retrieval of brief image memory. Therefore, we conclude that future work using this continuous recognition task to interrogate pattern completion and pattern separation, with both normal and cognitively impaired populations, must carefully control for inter-item spacing; and more broadly, we advocate a closer attention within the psychological study of human pattern memory across the lifespan, and in the amnesias, of how stimulus items are separated from one another in time.

Acknowledgements

We thank the editor, Dr Maire Poiter and Reviewers, Dr Timothy Ricker and Dr Alessandra Souza for their valuable comments on an earlier version of this manuscript. Special thanks goes to Emma Almond, Tom Kelly Sarah Wilding, Michelle Ames and Kinga Bugajska for their invaluable help with part of the data collection.

References

- Ally, B. A., Hussey, E. P., Ko, P. C., & Molitor, R. J. (2013). Pattern separation and pattern completion in Alzheimer's disease: Evidence of rapid forgetting in amnesic mild cognitive impairment. *Hippocampus*, 23(12), 1246-1258. doi:10.1002/hipo.22162
- Altmann, E. M., & Gray, W. D. (2002). Forgetting to remember: The functional relationship of decay and interference. *Psychological Science*, 13(1), 27-33. doi:10.1111/1467-9280.00405
- Altmann, E. M., & Schunn, C. D. (2012). Decay versus interference: a new look at an old interaction. *Psychological Science*, 23(11), 1435-1437. doi:10.1177/0956797612446027
- Barrouillet, P., Bernardin, S., & Camos, V. (2004). Time constraints and resource sharing in adults' working memory spans. *Journal of Experimental Psychology: General*, 133(1), 83-100. doi:10.1037/0096-3445.133.1.83
- Barrouillet, P., Bernardin, S., Portrat, S., Vergauwe, E., & Camos, V. (2007). Time and cognitive load in working memory. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 33(3), 570-585. doi:10.1037/0278-7393.33.3.570
- Barrouillet, P., & Camos, V. (2014). On the proper reading of the TBRS model: reply to Oberauer and Lewandowsky (2014). *Frontiers in Psychology*, 5 (1331), 1-3. doi:10.3389/fpsyg.2014.01331

- Bayliss, D. M., Bogdanovs, J., & Jarrold, C. (2015). Consolidating working memory: Distinguishing the effects of consolidation, rehearsal and attentional refreshing in a working memory span task. *Journal of Memory and Language*, 81, 34-50. doi:10.1016/j.jml.2014.12.004
- Berman, M. G., Jonides, J., & Lewis, R. L. (2009). In search of decay in verbal short-term memory. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 35(2), 317-333. doi: 10.1037/a0014873
- Bi, J. (2002). Variance of d' for the same-different method. *Behavior Research Methods, Instruments, & Computers*, 34(1), 37-45. doi:10.3758/BF03195421
- Brown, G. D., Neath, I., & Chater, N. (2007). A temporal ratio model of memory. *Psychological Review*, 114(3), 539-576. doi:10.1037/0033-295X.114.3.539
- Carr, V. A., Castel, A. D., & Knowlton, B. J. (2015). Age-related differences in memory after attending to distinctiveness or similarity during learning. *Aging, Neuropsychology, and Cognition*, 22(2), 1-15. doi:10.1080/13825585.2014.898735
- Cowan, N. (2011). The focus of attention as observed in visual working memory tasks: Making sense of competing claims. *Neuropsychologia*, 49(6), 1401-1406. doi: 10.1016/j.neuropsychologia.2011.01.035
- Deuker, L., Doeller, C. F., Fell, J., & Axmacher, N. (2014). Human neuroimaging studies on the hippocampal CA3 region—integrating evidence for pattern separation and

completion. *Frontiers in Cellular Neuroscience*, 8(64), 1-9.

doi:10.3389/fncel.2014.00064

Dewar M, Alber J, Cowan N, & Della Sala, S. (2014) Boosting long-term memory via wakeful rest: intentional rehearsal is not necessary, consolidation is sufficient. *PLoS ONE* 9(10), e109542. doi:10.1371/journal.pone.0109542

Ecker, U. K., Brown, G. D., & Lewandowsky, S. (2015). Memory without consolidation: Temporal distinctiveness explains retroactive interference. *Cognitive science*, 39(7), 1570-1593. doi: 10.1111/cogs.12214

Ecker, U. K., & Lewandowsky, S. (2012). Computational constraints in cognitive theories of forgetting. *Frontiers in Psychology*, 3(400), 1-5. doi:10.3389/fpsyg.2012.00400

Ecker, U. K., Tay, J. X., & Brown, G. D. (2015). Effects of prestudy and poststudy rest on memory: Support for temporal interference accounts of forgetting. *Psychonomic Bulletin & Review*, 22(3), 772-778. doi:10.3758/s13423-014-0737-8

Grange, J. A., & Cross, E. (2015). Can time-based decay explain temporal distinctiveness effects in task switching? *The Quarterly Journal of Experimental Psychology*, 68(1), 19-45. doi:10.1080/17470218.2014.934696

Hanseeuw, B., Dricot, L., Kavec, M., Grandin, C., Seron, X. & Ivanoiu, A. (2011).

Associative encoding deficits in amnesic mild cognitive impairment: a volumetric and functional MRI study. *Neuroimage*, 56(3), 1743- 1748.

doi:10.1016/j.neuroimage.2011.030.34

Hardman, K. O., & Cowan, N. (2015). Remembering complex objects in visual working

memory: Do capacity limits restrict objects or features? *Journal of Experimental*

Psychology: Learning, Memory, and Cognition, 41(2), 325. doi: 10.1037/xlm0000031

Hardt, O., Nader, K., & Nadel, L. (2013). Decay happens: the role of active forgetting in memory. *Trends in Cognitive Sciences*, 17(3), 111-120.

doi:10.1016/j.tics.2013.01.001

Henderson, J. M., & Hollingworth, A. (2003). Eye movements and visual memory: Detecting changes to saccade targets in scenes. *Perception & Psychophysics*, 65(1), 58-71.

doi:10.3758/BF03194783

Holden, H. M., Toner, C., Pirogovsky, E., Kirwan, C. B., & Gilbert, P. E. (2013). Visual object pattern separation varies in older adults. *Learning & memory*, 20(7), 358-362.

doi:10.1101/lm.030171.112

Hunsaker, M. R., & Kesner, R. P. (2013). The operation of pattern separation and pattern completion processes associated with different attributes or domains of memory.

Neuroscience & Biobehavioral Reviews, 37(1), 36-58.

doi:10.1016/j.neubiorev.2012.09.014

Jolicœur, P., & Dell'Acqua, R. (1998). The demonstration of short-term consolidation.

Cognitive Psychology, 36(2), 138-202. doi:10.1006/cogp.1998.0684

Kirwan, C. B., & Stark, C. E. (2007). Overcoming interference: An fMRI investigation of pattern separation in the medial temporal lobe. *Learning & Memory*, 14(9), 625-633.

doi:10.1101/lm.663507

Knöchel, C., Oertel-Knöchel, V., Bittner, R., Stäblein, M., Heselhaus, V., Prvulovic, D., ... &

Linden, D. E. (2015). Consolidation time affects performance and neural activity during visual working memory. *Psychiatry Research: Neuroimaging*, 231(1), 33-41.

doi:10.1016/j.psychresns.2014.10.025

Koutstaal, W., & Schacter, D. L. (1997). Gist-based false recognition of pictures in older and younger adults. *Journal of Memory and Language*, 37(4), 555-583.

doi:10.1006/jmla.1997.2529

Lacy, J. W., Yassa, M. A., Stark, S. M., Muftuler, L. T., & Stark, C. E. (2011). Distinct pattern separation related transfer functions in human CA3/dentate and CA1 revealed using high-resolution fMRI and variable mnemonic similarity. *Learning & Memory*,

18(1), 15-18. doi:10.1101/lm.1971111

Lewandowsky, S., & Oberauer, K. (2015). Rehearsal in serial recall: An unworkable solution to the nonexistent problem of decay. *Psychological review*, 122(4), 674-699. doi:

10.1037/a0039684

Lewandowsky, S., Oberauer, K., & Brown, G. D. (2009). No temporal decay in verbal short-term memory. *Trends in Cognitive Sciences*, 13(3), 120-126.

doi:10.1016/j.tics.2008.12.003

Liu, K. Y., Gould, R. L., Coulson, M. C., Ward, E. V., & Howard, R. J. (2016). Tests of pattern separation and pattern completion in humans—A systematic review.

Hippocampus. 26(6), 705-717. doi:10.1002/hipo.22561

Lupyan, G. (2008). From chair to "chair": a representational shift account of object labelling effects on memory. *Journal of Experimental Psychology: General*, 137(2), 348-369.

doi: 10.1037/0096-3445.137.2.348

McClelland, J. L., McNaughton, B. L., & O'Reilly, R. C. (1995). Why there are complementary learning systems in the hippocampus and neocortex: insights from the successes and failures of connectionist models of learning and memory. *Psychological Review*, 102(3), 419-457. doi:10.1037/0033-295X.102.3.419

McKeown, D., Holt, J., Delvenne, J. F., Smith, A., & Griffiths, B. (2014). Active versus passive maintenance of visual nonverbal memory. *Psychonomic Bulletin & Review*,

21(4), 1-7. doi:10.3758/s13423-013-0574-1

McKeown, D., & Mercer, T. (2012). Short term forgetting without interference. *Journal of Experimental Psychology: Learning, Memory and Cognition*, 38(4), 1057-1068.

doi:10.1037/a0027749

- Mercer, T. (2014). The loss of short-term visual representations over time: Decay or temporal distinctiveness? *Journal of Experimental Psychology: Human Perception and Performance*, 40(6), 2281-2288. doi:10.1037/a0038141
- Mercer, T. (2015). Wakeful rest alleviates interference-based forgetting. *Memory*, 23(2), 127-137. doi:10.1080/09658211.2013.872279
- Mercer, T., & Duffy, P. (2015). The loss of residual visual memories over the passage of time. *The Quarterly Journal of Experimental Psychology*, 68(2), 242-248. doi:10.1080/17470218.2014.975256
- Mercer, T., & McKeown, D. (2014). Decay uncovered in nonverbal short-term memory. *Psychonomic Bulletin & Review*, 21(1), 128-135. doi:10.3758/s13423-013-0472-6
- Molitor, R. J., Ko, P. C., Hussey, E. P., & Ally, B. A. (2014). Memory-related eye movements challenge behavioral measures of pattern completion and pattern separation. *Hippocampus*, 24(6), 666-672. doi:10.1002/hipo.22256
- Nieuwenstein, M., & Wyble, B. (2014). Beyond a mask and against the bottleneck: Retroactive dual-task interference during working memory consolidation of a masked visual target. *Journal of Experimental Psychology: General*, 143(3), 1409-1427. doi:10.1037/a0035257

- Norman, K. A., & Schacter, D. L. (1997). False recognition in younger and older adults: Exploring the characteristics of illusory memories. *Memory & Cognition*, 25(6), 838-848. doi:10.3758/BF03211328
- Oberauer, K., & Kliegl, R. (2006). A formal model of capacity limits in working memory. *Journal of Memory and Language*, 55(4), 601-626. doi:10.1016/j.jml.2006.08.009
- 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. doi: 10.1037/a0033236
- Pertsov, Y., Heider, M., Liang, Y., & 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. doi: 10.1037/a0038396
- Richler, J. J., Palmeri, T. J., & Gauthier, I. (2013). How does using object names influence visual recognition memory? *Journal of Memory and Language*, 68(1), 10-25. doi: 10.1016/j.jml.2012.09.001
- Ricker, T. J. (2015). The role of short-term consolidation in memory persistence. *AIMS Neuroscience*, 2 (4), 259-279. doi:10.3934/Neuroscience.2015.4.259

Ricker, T. J., & Cowan, N. (2014). Differences between presentation methods in working memory procedures: A matter of working memory consolidation. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 40(2), 417-428.

doi:10.1037/a0034301

Ricker, T. J., Spiegel, L. R., & Cowan, N. (2014). Time-based loss in visual short-term memory is from trace decay, not temporal distinctiveness. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 40(6), 1510-1523.

doi:10.1037/xlm0000018

Rolls, E. T. (2007). An attractor network in the hippocampus: theory and neurophysiology. *Learning & Memory*, 14(11), 714-731. doi:10.1101/lm.631207

Rolls, E. T. (2013). The mechanisms for pattern completion and pattern separation in the hippocampus. *Frontiers in Systems Neuroscience*, 7(74), 1-21.

doi:10.3389/fnsys.2013.00074.

Schneider, W., Eschman, A., & Zuccolotto, A. (2002) E-Prime User's Guide. Pittsburgh:

Psychology Software Tools Inc. Retrieved from <http://www.pstnet.com/eprime.cfm>

Sense, F., Morey, C. C., Prince, M., Heathcote, A., & Morey, R. D. (2016). Opportunity for verbalization does not improve visual change detection performance: A state-trace analysis. *Behavior Research Methods*. Advance online publication. doi:

10.3758/s13428-016-0741-1

- Souza, A. S. (2016). No Age Deficits in the Ability to Use Attention to Improve Visual Working Memory. *Psychology and Aging*. Advance online publication. doi: 10.1037/pag0000107
- Souza, A. S., & Oberauer, K. (2014). Time-based forgetting in visual working memory reflects temporal distinctiveness, not decay. *Psychonomic Bulletin & Review*, 22(1), 156-162. doi:10.3758/s13423-014-0652-z
- Stark, S. M., Yassa, M. A., Lacy, J. W., & Stark, C. E. (2013). A task to assess behavioral pattern separation (BPS) in humans: Data from healthy aging and mild cognitive impairment. *Neuropsychologia*, 51(12), 2442-2449. doi:10.1016/j.neuropsychologia.2012.12.014
- Toner, C. K., Pirogovsky, E., Kirwan, C. B., & Gilbert, P. E. (2009). Visual object pattern separation deficits in nondemented older adults. *Learning & Memory*, 16(5), 338-342. doi:10.1101/lm.1315109
- Vergauwe, E., Dewaele, N., Langerock, N., & Barrouillet, P. (2012). Evidence for a central pool of general resources in working memory. *Journal of Cognitive Psychology*, 24(3), 359-366. doi: 10.1080/20445911.2011.640625
- Vergauwe, E., Hartstra, E., Barrouillet, P., & Brass, M. (2015). Domain-general involvement of the posterior frontolateral cortex in time-based resource-sharing in working memory: An fMRI study. *NeuroImage*, 115, 104-116. doi: 10.1016/j.neuroimage.2015.04.059

Walsh, C. M., Wilkins, S., Bettcher, B. M., Butler, C. R., Miller, B. L., & Kramer, J. H.

(2014). Memory consolidation in aging and MCI after 1 week. *Neuropsychology*, 28(2), 273-280. doi:10.1037/neu0000013

Wang, P., Li, J., Li, H., & Zhang, S. (2013). Differences in learning rates for item and

associative memories between amnesic mild cognitive impairment and healthy

controls. *Behavioral and Brain Functions*, 9(1), 29-40. doi:10.1186/1744-9081-9-29

Waugh, N. C., & Norman, D. A. (1965). Primary memory. *Psychological review*, 72(2), 89.

doi:10.1037/h0021797

Wilson, I. A., Gallagher, M., Eichenbaum, H., & Tanila, H. (2006). Neurocognitive aging:

prior memories hinder new hippocampal encoding. *Trends in Neurosciences*, 29(12),

662-670. doi:10.1016/j.tins.2006.10.002

Wixted, J. T. (2004). The psychology and neuroscience of forgetting. *Annual Review of*

Psychology, 55, 235-269. doi:10.1146/annurev.psych.55.090902.141555

Yassa, M. A., Lacy, J. W., Stark, S. M., Albert, M. S., Gallagher, M., & Stark, C. E. (2011).

Pattern separation deficits associated with increased hippocampal CA3 and dentate

gyrus activity in nondemented older adults. *Hippocampus*, 21(9), 968-979.

doi:10.1002/hipo.20808

Yassa, M. A., & Stark, C. E. (2008). Multiple signals of recognition memory in the medial

temporal lobe. *Hippocampus*, 18(9), 945-954. doi:10.1002/hipo.20452

- Yassa, M. A., & Stark, C. E. (2011). Pattern separation in the hippocampus. *Trends in Neurosciences*, 34(10), 515-525. doi:10.1016/j.tins.2011.06.006
- Yassa, M. A., Stark, S. M., Bakker, A., Albert, M. S., Gallagher, M., & Stark, C. E. (2010). High-resolution structural and functional MRI of hippocampal CA3 and dentate gyrus in patients with amnesic Mild Cognitive Impairment. *Neuroimage*, 51(3), 1242-1252. doi:10.1016/j.neuroimage.2010.03.040
- Yeung, L. K., Ryan, J. D., Cowell, R. A., & Barense, M. D. (2013). Recognition memory impairments caused by false recognition of novel objects. *Journal of Experimental Psychology: General*, 142(4), 1384-1397. doi:10.1037/a0034021
- Zhang, W., & Luck, S. J. (2008). Discrete fixed-resolution representations in visual working memory. *Nature*, 453(7192), 233-235. doi:10.1038/nature06860
- Zhang, W., & Luck, S. J. (2009). Sudden death and gradual decay in visual working memory. *Psychological Science*, 20(4), 423-428. doi:10.1111/j.1467-9280.2009.02322.x
- Zokaei, N., Burnett Heyes, S., Gorgoraptis, N., Budhdeo, S., & Husain, M. (2015). Working memory recall precision is a more sensitive index than span. *Journal of neuropsychology*, 9(2), 319-329. doi: 10.1111/jnp.12052