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# Mechanisms Underlying Working Memory: Is an object the sum of its parts?

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#### Abstract

With life expectancy increasing worldwide, the number of people with dementia is estimated to reach 131 million by 2050<sup>1</sup>. Dementia is a neurodegenerative condition that affects working memory– the short-term storage and manipulation of sensory information lasting on the order of seconds– and is characterized by memory loss and cognitive impairment. Before we can develop new treatments, it is essential to improve our understanding of the cognitive component processes underlying short-term memory in health. Only after will we be able to fully comprehend which specific cognitive components are disrupted by the disease.

Working memory is a fundamental cognitive process, that can be decomposed into three components: encoding, maintenance and retrieval. Despite the fact that encoding and maintenance have been investigated intensively, we know very little about retrieval and how it affects memory quality. To address this question, sensitive cognitive tests were developed. Here, across three experiments, we have shown that the more information we have about an object the better we are able to remember it, irrespective of encoding. Since this only occurs when information exits working memory, this suggests retrieval might undergo a completely different process from encoding.

We began by examining whether manipulating the retrieval of information produces a greater effect on working memory recall than manipulating the process of information encoding in young healthy adults (n = 20, experiment 1). We evaluated two contrasting hypotheses by questioning if the increased complexity of memoranda (objects with additional features) enhances working memory or, conversely, impairs recall by demanding augmented cognitive processing in identifying and comparing items with similar characteristics (increased feature interference). This first experiment revealed an unbalanced contribution of features during encoding, possibly due to disproportionately weighing feature 'colour' as opposed to feature 'shape'. Therefore, the second experiment (experiment 2, n = 20) was conducted by presenting a cue before each trial to induce strategic encoding. We found no effect of manipulating encoding but a clear influence of the nature of retrieval on memory performance. We then asked how changing the amount of information of each item at retrieval– and the similarity between these memoranda– can affect the quality of mental representations (experiment 3, n = 21). The results suggest that more complex information at probing increases working memory performance. Increasing similarity between objects at retrieval also appears to enhance working memory personation.

The cognitive test we developed could potentially be administered online to a large number of people and used as a behavioural marker in different clinical populations to diagnose and differentiate problems with short-term memory.

Key words: working-memory, retrieval, complexity, competition.

<sup>&</sup>lt;sup>1</sup> World Alzheimer Report 2015: The global impact of dementia. An analysis of prevalence, incidence, costs and trends. London: Alzheimer's Disease International, 2015.

#### Resumo

O cérebro é um órgão de incomensurável complexidade e uma das suas múltiplas funções é a de apreender estímulos presentes no meio ambiente e extrair informações importantes do mundo visual, com o propósito de lembrar os elementos-chave. Este processo é influenciado pela natureza da informação sensorial, que é transitória, temporária e potencialmente colossal.

A memória é o rótulo atribuído às estruturas e processos envolvidos no armazenamento e posterior recuperação de informações. A *working memory* (memória funcional) é o meio pelo qual a informação é mantida e manipulada, na ordem dos segundos, estando a sua capacidade fortemente relacionada à faculdade intelectual e desempenho cognitivo.

Défices associados à memória funcional são um problema significativo em doentes com demência, independentemente da sua etiologia, sendo que, com o aumento da esperança de vida, prevêse que o número de pessoas com demência atinja globalmente 131 milhões em 2050<sup>2</sup>. A crescente prevalência de doenças neurodegenerativas tem sido frequentemente descrita como uma epidemia de rápido crescimento, não apenas com impacto económico (devido aos custos elevados associados a assistência médica), mas também com uma pesada carga social, e especialmente com um impacto profundo na vida dos doentes e das suas famílias.

Uma compreensão clara dos componentes cognitivos da *short-term memory* (memória a curto prazo), bem como os mecanismos subjacentes à memória funcional, poderão revelar-se inestimáveis no esforço para melhorar a qualidade de vida de doentes com demência. Antes de podermos desenvolver novos tratamentos para estas condições, é essencial compreender quais os processos cognitivos subjacentes à memória funcional, em indivíduos saudáveis. Só assim será possível compreender quais os componentes cognitivos que estão especificamente afetados na condição patológica.

O objetivo do presente estudo consistiu em contribuir para a compreensão dos mecanismos implícitos na memória funcional, através do estudo da natureza das representações de memória de curto prazo. Nesse sentido, foi desenvolvido um teste neuropsicológico capaz de testar a forma como recuperamos a informação, abordando questões que são fundamentais para interpretar temáticas como o esquecimento e a capacidade de armazenamento.

No presente trabalho de investigação, recorremos a três testes cognitivos com o intuito de examinar os efeitos de manipular *encoding* (codificação) e *retrieval* (recuperação) de informação na fidelidade da representação mental. Um objetivo adicional foi a exploração do efeito de manipulações de complexidade (número de características de um objeto) e competição (níveis de similaridade entre as características de um objeto) na robustez da memória funcional. A forma como os testes foram concebidos e implementados permitiu-nos explorar como as noções de identidade do objeto, localização e associações de objeto-localização são suscetíveis a manipulações de complexidade, competição e degradação ao longo do tempo.

<sup>&</sup>lt;sup>2</sup>World Alzheimer Report 2015: The global impact of dementia. An analysis of prevalence, incidence, costs and trends. London: Alzheimer's Disease International, 2015.

Os participantes foram testados com base em tarefas de memória visual de curto prazo sendo que os testes desenvolvidos para o presente estudo podem ser administrados *online*, a um grande número de pessoas. Estes testes têm ainda o potencial de ser introduzidos em contexto clínico com o propósito de auxiliarem na monitorização de doentes com défices cognitivos.

Na primeira experiência implementada, experiência 1, seis condições distintas foram apresentadas aos participantes. As três primeiras condições variam na forma como a codificação é manipulada, mantendo a recuperação constante; nas restantes, a codificação foi mantida constante enquanto a recuperação foi manipulada em termos de complexidade e competição. Com esta experiência, pretendíamos avaliar os efeitos que a manipulação da codificação e recuperação da informação produzem na fidelidade da representação mental, bem como a sua variação em função do tempo decorrido. Pretendíamos ainda explorar se a quantidade de informação exerce efeitos prejudiciais no ato de recuperação devido a uma potencial interferência crescente entre os recursos da memória funcional. Por fim, investigámos os efeitos da semelhança dos memorandos na modulação do desempenho. Colocámos a hipótese de que informação mais complexa na fase de recuperação é vantajosa, visto que o aumento da complexidade dos memorandos poderá levar a uma maior separação de padrões ao funcionar como pistas de recuperação. Propusemos ainda que memorandos menos semelhantes partilham menos características tornando-os menos competitivos e como tal previmos que poderiam potencializem a memória funcional graças ao seu menor grau de interferência.

Visto que na primeira experiência os resultados refletiram um efeito desproporcional da característica 'forma', no desempenho da memória, foi implementada uma segunda experiência. A experiência 2 teve como objetivo confirmar que os resultados obtidos na experiência 1 não foram corrompidos pelo facto dos participantes atribuírem mais peso à caraterística 'cor' em detrimento da característica 'forma', aquando da codificação da informação. Com a introdução de uma *cue* (pista) antes de cada codificação, impelimos que os participantes atribuíssem o mesmo peso a ambas as características.

Foi ainda desenvolvida uma terceira experiência, visto que nos testes anteriores foram utilizadas 'formas' demasiado complexas como parte dos estímulos de codificação e recuperação. Embora tais estímulos sejam mais difíceis de verbalizar, é-lhes associada uma desvantagem inerente para o propósito do presente trabalho de investigação: a sua complexidade não é comparável à complexidade da característica 'cor'. Por forma a ultrapassar este desequilíbrio entre estímulos visuais, nesta última experiência foram usados diferentes níveis de complexidade baseados na forma de um círculo. Na experiência 3 apenas a recuperação da memória funcional foi manipulada, mantendo-se a codificação constante. Quatro condições diferentes foram apresentadas a cada um dos participantes em blocos intermisturados. A primeira e terceira condições variaram em termos do número de características do objeto, enquanto que a segunda e quarta condições variaram em função da semelhança entre o alvo e o foil (objeto apresentado que não corresponde a nenhum dos objetos presentes no conjunto de codificação). Com este teste tencionámos avaliar se as informações visuais são armazenadas na memória funcional como características individuais ou como objetos integrados, formulando a hipótese de que o aumento da complexidade dos memorandos se traduz na alocação acrescida de recursos e subsequente melhoria de resolução. O papel da semelhança entre características na modulação do desempenho é igualmente explorado, ao conjeturar que uma maior semelhança entre recursos implica um maior grau de interferência, resultando numa perda de desempenho.

Com base nas experiências realizadas, concluímos que a complexidade na recuperação é o principal fator no mapeamento do desempenho, com alguma variabilidade devido ao tempo decorrido. Adicionalmente, demonstrámos que mais informações na fase de recuperação (memorandos de elevada complexidade) aumentam a qualidade das representações mentais. Propomos que isto esteja relacionado

com o facto de uma maior complexidade de um objeto estar associado a um maior número de características do mesmo. Estas características poderão corresponder a *retro-cues* (retro pistas) mais fidedignas, aumentando a acessibilidade às representações mentais e, consequentemente, melhorando a fidelidade da memória funcional.

Futuramente, pretendemos implementar a experiência 3 em grupos de idosos saudáveis, assim como doentes com Alzheimer, por forma a fazer um estudo comparativo. Tencionamos perceber se as conclusões tiradas com base numa população jovem são as mesmas comparativamente a uma população com um envelhecimento saudável e outra comprometida em termos cognitivos, e potencialmente encontrar um marcador comportamental que explique possíveis diferenças identificadas. Planeamos ainda testar grupos de jovens adultos utilizando ressonância magnética funcional (fMRI) para avaliar se existem diferentes regiões de ativação neuronal associados ao desempenho e precisão da identificação de memorandos. Além disso, permitir-nos-á avaliar diferentes ativações neurais associadas à codificação e recuperação e a sua inter-relação.

Palavras Chave: Memória funcional, memória de curto prazo, recuperação de informação, complexidade, similaridade.

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# List of Abbreviations

**AD:** Alzheimer's Disease

DS: Digit Span

MTL: Medial Temporal Lobe

LTM: Long Term Memory

**SD:** Standard Deviation

**SEM:** Standard Error of the Mean

**STM:** Short-Term Memory

**VSTM:** Visual Short-Term Memory

WM: Working Memory

## 1. Introduction

The brain's main role, if we are necessarily forced to apply a distinction of primary and secondary function to an organ of incommensurable intricacy, is to learn from the stimuli that are present in the environment by extracting important information from a dynamic multisensory world and remember key elements of it. This process is influenced by the nature of sensory information which is transient, temporary and potentially colossal in magnitude.

Memory is the label attributed to the structures and processes involved in the storage and subsequent retrieval of information. Short-term memory (STM) is one of the components of Working Memory (WM)<sup>3</sup>, the means by which information is retained and manipulated, lasting on the order of seconds (Baddeley, 2003) and its capacity is strongly related to cognitive ability and performance (Luck & Vogel, 2013). Deficits in WM are a significant problem in patients with dementia, regardless of aetiology (Yanhong, Chandra & Venkatesh, 2013). The increasing prevalence of neurodegenerative diseases has often been described as a fast-growing epidemic with not only an economic impact (high costs of medical care) but also with social burden. They are responsible for a progressive deterioration of memory, thinking, behaviour, and capacity to execute daily activities; bearing considerable negative implications, not only in patients' lives but also for their families.

Although we now know that short-term memory deficits occur in neurodegenerative diseases such as Alzheimer's disease (AD) (Baddeley, Bressi, Della Sala, Logie, & SpiInnler, 1991; Baddeley, Logie, Bressi, Sala, & Spinnler, 1986; Dorion et al., 2002; Liang et al., 2016; Perry, Watson, & Hodges, 2000; Simone & Baylis, 1997) it remains unclear which cognitive components are specifically affected: encoding, maintenance or retrieval (**Figure 1.1**). Understanding these elements, as well as the mechanisms underlying WM, would likely prove invaluable in the endeavour of enhancing the quality of life for dementia patients.



**Figure 1.1 Cognitive components of STM deficits.** STM is part of the mechanisms understood as WM and a crucial element in assisting everyday functioning. STM deficits are characteristic of neurodegenerative diseases and can be associated with different cognitive components. We still don't know which cognitive components are responsible for memory impairment and how they are affected by decay and interference.

<sup>&</sup>lt;sup>3</sup> The concepts of short-term memory and working memory are used interchangeably in this work. However, technically, short-term memory is just one component of working memory, the framework of structures and mechanisms used for the short storage and manipulation of information (Baddeley & Hitch, 1974; Baddeley & Logie, 1992). In short, WM is not solely maintenance or passive storage of information but is further involved in the manipulation of the contents of STM (Cowan, 2008).

Despite the fact that encoding and maintenance have been investigated intensively, we know very little about retrieval and how it affects memory recall. In this thesis, I intend to answer this key question by investigating whether the quality of memory is dependent upon the probe, i.e., if manipulating how information exits working memory has more of an effect on recall than manipulating the encoding of information.

Additionally, I will be investigating if increasing information interferes or assists at a probing phase and the role of feature similarity in modulating performance and misbinding rates. We posit that increased complexity of memoranda (higher number of features belonging to an object) will lead to more features among which the resource needs to be distributed, implicating a higher degree of mutual interference and increased decay over time. This hypothesis implies that the degree of mutual interference increases with the number of features of an object, but also with the similarity between them (levels of competition). Or if more information about an object corresponds to more faithful retro-cues (spatial cues that are shown after the retention interval of a visual working memory task, indicating which item will be tested) enhancing working memory representations.

Limitations in WM capacity and performance have been established in the literature through experiments that only manipulated encoding without taking retrieval into proper consideration. This neglect is explained by the fact that the processes underlying how information is forgotten is still a topic of debate. However, if forgetting is, in fact, interference-based, then the way information is retrieved could influence how we recall information. This warrants a review on how information is lost, whether through decay, interference or both. Additionally, the retro-cue literature strongly suggests that many of the limitations we observe in traditional tests emerge from the retrieval stage and that more information at the probing phase may improve recall by acting as a form of retro-cue. This reinforces our interest in exploring how manipulating retrieval modulates performance. For properly understanding limitations in performance, it is crucial to know if features are bound together as a whole or if the nature of information is fragmented. As such, I will briefly present some research pertaining binding information. If features are indeed bound together as a whole, then presenting half of that information at retrieval should be sufficient to facilitate recall. Even though our knowledge concerning retrieval is fairly constrained in the short-term, it has nonetheless been subject to more extensive inquiry in the long-term memory research. Thus, I will finish by briefly presenting some ideas from the LTM literature on pattern separation and pattern completion, as well as the role of hippocampus in binding information, with the latter providing a better understanding for the hypothesis that increased complexity of memoranda facilitates recall.

#### Working Memory Capacity: Slots or flexible Resources?

The most fundamental aspect of WM research has been focused on understanding its underlying architecture, as well as its limitations (Ji Ma, Husain, & Bays, 2014; Fallon, Zokaei, & Husain, 2016).

The amount of information than can be actively retained, known as working memory capacity, is very limited. An ongoing debate has been on the characterisation of its limitations. On the one hand, most studies usually assess WM using binary report measures and examine the quantity of information, i.e., number of items, that can be maintained. Thus, the classic view, formally illustrated in **Figure 1.2**, describes WM as limited in nature with a storage capacity of about three to four items (Cowan, 2001; Vogel, Woodman, & Luck, 2001; for a review on the classical view see Luck & Vogel, 2013). In this view, an

object either enters into a memory slot– and is, then, remembered accurately– or it is not, which translates into the non-recollection of an object (Luck & Vogel, 1997). Research also suggests that the limited nature of working memory, specifically as it pertains to our visual cognition and representation, is highly correlated with PPC (posterior parietal cortex) activity (Todd & Marois, 2004).



**Figure 1.2 Classic Model of WM.** A change detection task, aimed at providing an estimation of the capacity of VSTM, was implemented by varying the number of items to bear in mind. An inverse relationship between the probability of correctly recalling an object and the actual number of items to be remembered was observed. Furthermore, in an instance where the items outnumber the set of slots available, not all of the items are stored. Thus, the slot model predicts that errors due to misreporting an item are comprised of a mixture of high precision answers and random guesses (Luck & Vogel, 1997; Cowan, 2001).

On the other hand, many researchers have demonstrated the inadequacy of considering a hard limit on the number of items that can be stored, suggesting that WM might be better understood as a limited resource that can be distributed among retained items, with precision declining continuously as the number of items to be recalled increases (Wilken & Ma, 2004; for reviews see Fallon, Zokaei, & Husain, 2016; Ji Ma, Husain, & Bays, 2014) (Figure 1.3); contrary to the abrupt, steep decline (Figure 1.2) that would be expected by reaching a capacity limit of a fixed number of items (Luck & Vogel, 1997). Accordingly, in this model, precision is the fundamental metric of WM, not the number of objects to be remembered (Figure 1.3 d.). Therefore, the alternative view is that WM is limited, with no item limit: as memory load increases, the fidelity with which its visual feature is stored decreses (Palmer, 1990; Wilken & Ma, 2004; Bays & Husain, 2008; Bays, Catalao, & Husain, 2009).



Figure 1.3 Resource Model of WM. The conventional view of WM has been put to question by studies which require participants to reproduce features of an item (location, orientation and colour) from memory, using a continuous response space as opposed to a discrete measure. These delayed reproduction tasks have produced results that are consistent with the conception of a limited resource model, invalidating the idea that there is a capacity limit to the number of items held in memory (Wilken & Ma, 2004; Bays & Husain, 2008). (a) Experimental procedure of a location-judgment trial (left) and orientation judgement trial (right): Precision of recall task probed by altering the degree of change (delta) (Bays & Husain, 2008). (b) VSTM can be flexibly allocated among the items that are stored in memory, with no apparent limit to the number of items. Precision varied as a function of the number of items in the array, for both the location and orientation judgements precision decreased with increasing numbers of items stored (Bays & Husain, 2008). There is an interesting curve where the precision of the recall is a power function after 3 or 4 items. There is a significant drop between the first pair of items, but not between items 4 and 5. (c) Colour delayed-estimation task: Participants were asked to report the colour that matches a probed location by selecting from a colour wheel (Wilken & Ma, 2004). (d) Distribution of responses relative to the correct target colour: Responses to the colour delayed-estimation task depend on the number of items in the presented sample, with set size increases precipitating a decline in the precision of recall (Bays et al., 2009). (e) Precision (1/SD) begins to deteriorate as soon as sample size exceeds one item, but importantly there is no item limit (Bays & Husain, 2008). Note that SD is the measure of recall variability of error, which increases gradually with set size and saturates at items 3 and 4, with no capacity limit and a negative correlation between precision and N. In the slot model of WM, this function would be flat up to set size 4.

The resource is limited and can be flexibly allocated so some items are prioritised and represented with greater fidelity, but this comes at a cost with other items in WM being recalled less precisely (Bays et al., 2009, 2011; Bays & Husain, 2008; Gorgoraptis, Catalao, Bays, & Husain, 2011). Also, by biasing memory resources to a specific item in memory, researchers have shown that its representation can be recalled with the same fidelity as if there was a single item in WM (Pertzov, Manohar, & Husain, 2016).

Remarkably, these studies based all their claims on manipulation of complexity at **encoding**. They assumed that retrieval was an accurate, uncorrupted "read off" of stored information, i.e., that the way in which information is **retrieved** has no effect on our ability to recall information.

One of the reasons why retrieval has been neglected is because there has been a debate about how information is forgotten. Some investigators posit it is only delay, some say interference is important. If forgetting is interference based, then how it is retrieved could influence recall. Thus, we are going to review the literature from different fields about what could be going on at retrieval.

#### More information at retrieval: help or hindrance?

#### Working Memory Degradation: Decay or Interference?

How information is forgotten is important. If information is forgotten through interference-based processes, then changing the way information is retrieved could induce a change in memory performance. In the literature, the mechanisms underlying information loss over the short-term have been largely discussed. Understanding what causes rapid forgetting would be a major step towards understanding the role of retrieval in working memory, by using a delayed estimation task to combine manipulations of complexity at **retrieval** during different retention periods.

Some researchers argue that forgetfulness is caused because information decays over time, with longer periods of retention leading to poorer recall because time plays an important role in the degradation process of the fidelity of mental representation (Brown, 1958; Baddeley et al., 1986; Towse, Hitch, & Hutton, 2000; Barrouillet, Bernardin, & Camos, 2004; Barrouillet, De Paepe, & Langerock, 2012). Other investigators believe that forgetting is due to the interference between items in WM and processing of distractors (Saito & Miyake, 2004; Lewandowsky, Geiger, & Oberauer, 2008; Oberauer & Lewandowsky, 2008; Berman, Jonides, & Lewis, 2009; Lewandowsky & Oberauer, 2009; Lewandowsky, Geiger, Morrell, & Oberauer, 2010; Oberauer, Lewandowsky, Farrell, Jarrold, & Greaves, 2012). Accordingly, interference-based models assume that processing involves encoding of distractor representations in WM and time is used to process the removal of distractors, since it introduces irrelevant information into memory which interferes with memoranda (Saito & Miyake, 2004; Oberauer & Kliegl, 2006; Oberauer et al., 2012). However, although interference predicts negative effects on memory performance, retro-cues<sup>4</sup>, which are a form of positive interference, may provide a different window into WM representations due to their beneficial effects on later recollection (Griffin & Nobre, 2003; Kuo, Stokes, & Nobre, 2012).

Some investigators have even provided evidence for the influence of both factors in healthy people (Pertzov et al., 2016). By examining how interaction among items in memory contributes to rapid forgetting, over different durations, and how forgetting is influenced by directing attention towards a single representation in memory (**Figure 1.4**), they revealed that forgetting implicates an interaction between time and the number of items kept in memory, with an accelerated deterioration of object's representations due to competition between stored elements.

However, combined manipulation of complexity at **retrieval** and during retention has not been assessed for visual objects using a delayed estimation method. To provide compelling evidence of limitation in **retrieval** rather than encoding it would be decisive to show that these capacity limitations increase with retention duration. Here, in Experiments 1 and Experiment 2 we attempt to overcome this by addressing how information is maintained, or indeed forgotten over different time intervals by manipulating both encoding and retrieval.

<sup>&</sup>lt;sup>4</sup> Informative cues presented during the maintenance of visual information, after encoding, indicating what items are going to be probed.



**Figure 1.4 Forgetting over different durations as a function of items in memory. (a)** Experimental design used by Pertzov et. al.. Different orientations of 1, 2, 3, 4, 6 colored items were presented for 5s. A probed item with the color of one of the items previously seen was presented after different delayed periods. Participants were then asked to adjust the orientation of the probe to match the remembered orientation of the item with the same color. (b) Mean error of recall for increasing delays and set sizes. Results showed that a single item can be remembered with high fidelity over the short-term. However, when further items are added, they ultimately compete with each other, degrading representations as time passes (Pertzov et al., 2016).

#### *Retro-cueing: a benefit to memory*

Other ideas of WM can lead to predict what happens to WM performance, using retro-cues to provide protection from interference and attention to preserve it from decay. Some WM theories assume that maintaining a set of objects within the focus of central executive processes requires a broad focus of attention, assumed to hold up to four independent chunks (Cowan, 2010), or executive attention (Kane & Engle, 2002). Other researchers are doubtful of the dependency that sustained focal attention introduces on the capacity to maintain information in a privileged state<sup>5</sup> (Rerko, Souza, & Oberauer, 2014), associating the latter with other processes responsible for selectively improving accessibility of one object within a set, in response to a retro-cue. Thus, one of the approaches on the mechanisms of attentional selection in WM has been the retro-cue paradigm (Griffin & Nobre, 2003; Landman, Spekreijse, & Lamme, 2003; for a review see Souza & Oberauer, 2016). In the retro-cue paradigm, a spatial cue (called retro-cue, due to its retroactive effect) is shown after the retention interval of a VWM task, indicating which item will be tested. Interestingly, presenting participants with a cue, after encoding information, guides attention to a specific representation in WM, enhancing its relevance and improving recall, often over and above that seen for remembering an item for a similar period of time. Thus, preceding research has shown that retro-cues are proficient in producing strong benefits for the cued item on later recollection (Griffin & Nobre, 2003; Kuo et al., 2012), triggering a withdrawal of memory resources from the uncued items to attain a sustained maintenance of the cued memoranda (Pertzov, Bays, Joseph, & Husain, 2013). This data stands in alignment with the assumption of voluntary control over maintenance (Marshall & Bays, 2013).

Different- but not mutually exclusive- hypotheses have been presented to explain the retro-cue effect (**Figure 1.5**). One of these propositions is based in the idea that the focus of attention may be responsible for strengthening the binding between the content (e.g., dimension of colour or shape) and the context (e.g., location) of a cued representation by improving its accessibility at retrieval (**Figure 1.5** (a))

<sup>&</sup>lt;sup>5</sup> WM items can be in different states (Oberauer, 2002). There is information that is temporarily peripheral to the current mental manipulations but is stored for later use and there is information that is within the focus of central executive processes and therefore is active.

(Loaiza & McCabe, 2012; Rerko & Oberauer, 2013; Rerko et al., 2014). An alternative idea put forth that the benefits derived from retro-cueing were not a consequence of changes in the cued representation but a product of the removal of irrelevant (non-cued) information (**Figure 1.5 (b**)), with the augmented WM capacity leading to reduced competition, interference and, as a result, improved retrieval of the target representation (Williams, Hong, Kang, Carlisle, & Woodman, 2013; Rerko et al., 2014; Van Moorselaar, Olivers, Theeuwes, Lamme, & Sligte, 2015). Another suggested hypothesis, the retrieval head start hypothesis, implies that the retro-cue offers the opportunity to retrieve the representation of the cued object before using this information to decide. By assuming that retrieval is the gradual accumulation of information about the target's features in the focus of attention (**Figure 1.5 (f**)), it follows that delaying the memory test impels the accumulation of more information over time, predicting an increase in performance (Purcell et al., 2010; Souza & Oberauer, 2016).



Figure 1.5 Different retro-cues hypothesis. (a) The refreshing hypothesis states that reinforcing the binding between the item and its context is rendered viable through focused attention, materializing in improved retrieval. It predicts that cued items increase memory accessibility, whereas non-cued items remain unchanged in WM. (b) The removal hypothesis assumes that the retro-cue removes the uncued items from the memory array, freeing WM capacity. The larger the number of uncued items removed, the greater the magnitude of performance improvement. Note that it is impossible to eliminate the effect of memory load on accuracy in its entirety, despite enhancements in performance. (c) This hypothesis supports the notion that focused attention protects visual stimuli from contaminating memory representations, predicting that retro-cueing an item will protect it from interference and preserve its integrity, making it more robust to interference (Matsukura, Luck, & Vecera, 2007). (d) The hypothesis that retro-cues protect memoranda from decay assumes that the strength of memoranda representations deteriorates over time, submitting that when a retro-cue is presented, attention attends to the retro-cue item instead of being distributed among all items, protecting it from further forgetting (Pertzov, Bays, et al., 2013). (e) The prioritization for comparison hypothesis proposes that memory is searched sequentially and that when an item is retro-cued it receives priority over the rest of the memoranda array (Astle, Summerfield, Griffin, & Nobre, 2012; Pertzov, Bays, et al., 2013). (f) The retrieval head start hypothesis assumes that the retro-cue introduces a temporal separation between retrieval and decision processes, resulting in the accumulation of more target information in the focus of attention and subsequent reduction in the influence of irrelevant information on the decision process. (Figure adapted from Souza & Oberauer, 2016)

In the WM literature, it has usually been accepted that performance is a direct function of the limitations of encoding and storage. The retro-cue effect, however, shows that this is not the case because many of the limitations we observe in traditional tests transpire at the **retrieval** stage. It also shows that information presented after encoding can affect the probability of retrieval, but the actual event of that probe can be a retro-cue itself. This reinforces our interest in exploring how manipulating **retrieval** modulates performance. More specifically, this suggests that rather than acting as a form of interference and impairing memory, more information at **retrieval** can improve recall by serving as a more faithful retro-cue.

So far, we have only looked at WM for whole objects. However, another recent trend in WM research is to look at the fragmentary, incomplete, retrieval of information in WM. We will now proceed to discuss this.

#### Binding

The potentially fragmented nature of encoding and retrieval is still a matter of debate. Crucially, the nature of fragmentation may be key to answer whether increased complexity of memoranda facilitates recall. If features are bound together as a whole (Luck & Vogel, 1997), presenting half of that information at retrieval should be sufficient to facilitate recall. Thus, the union of complex information and the mechanisms that maintain these bindings within WM are fundamental for properly understanding limitations in performance. It is not yet clear whether VWM represents objects as bound units, with each slot storing an object together with all the features that belong to it (colour, size, orientation) by bounding together both the object and its properties in a slot (**Figure 1.6**) (Treisman & Gelade, 1980; Ceraso, 1985; Irwin, 1991; Luck & Vogel, 1997; Vogel et al., 2001; Oberauer & Lin, 2017), or if items collapse into individual components as soon as attention<sup>6</sup> is removed (Horowitz & Wolfe, 1998; Wolfe, 1999).



**Figure 1.6 Feature Binding in a Slot.** Memory performance plotted as a function of set size (number of objects) and mean accuracy for the features associated with each object (colour, size, orientation, gap and conjunction). Luck and Vogel (1997) showed increasing recall errors ensuing increases in the number of objects in a memory array. Conversely, they found that variations in the number of features failed to produce any distinguished effect. Here, accuracy in the conjunction condition was similar to single-feature performance for colour, size, orientation and gap. This was interpreted as evidence for "whole object" representation in VWM (Vogel et al., 2001).

<sup>&</sup>lt;sup>6</sup> Act of selective concentration on a particular aspect of the stimulus input.

Wheeler and Treisman (Wheeler & Treisman, 2002) failed to support a memory advantage of grouping features into objects. Their findings suggest that error rates were instead determined by the *total number of features* that needed to be remembered within each feature dimension. They posited that, alternatively to a single memory store maintaining integrated object representation, features from the same dimension compete for capacity, whereas features from different dimension may be stored in parallel, with focused attention being necessary in creating and maintaining the binding between features over time (*attention maintenance hypothesis*), given the vulnerability of this integrated information to interference. Nonetheless, Wheeler and Treisman's (Wheeler & Treisman, 2002) design of Experiments 4A and 4B (**Figure 1.7**), did not manipulate attention in a way where the binding deficits can be conclusively attributed to the withdrawal of attention from the items in VSTM.



**Figure 1.7 Stimuli used in the binary Experiment 4A and 4B of Wheeler and Treisman** (Wheeler & Treisman, 2002). Three different conditions at test: whole-array test condition (with changed trials and no-changed trials) and single-item probe condition. (a) In the whole-array test condition, on changed trials, the position of each item was altered along with the color/shape of two of the items. (b) In the whole-array test condition, on no-changed trials, the pairing of color and shape remained the same and only the position of the items was changed. (c) In the single-item probe condition, a single item was presented in the center of the screen. This item could be either identical to one of the items on the encoded array or have the color of one of the items presented in the sample array. (Figure adapted from Johnson, Hollingworth, & Luck, 2008)

In order to test the hypothesis that sustained attention is necessary to maintain bindings in VSTM, Luck et al. (Johnson, Hollingworth, & Luck, 2008) controlled the attentional demands during maintenance and found that binding memory and feature memory were equally impaired by the search task (the attention requiring search task did not expressively alter performance, though changes in binding memory were noted to a greater degree).

Previous research has shown that attention is biased towards items that match the current content of working memory (memory-driven attentional capture) (Olivers, Meijer, & Theeuwes, 2006). It remains unclear if this effect is automatic or under voluntary control and a consensus on the role of attention in maintaining feature bindings has not yet been reached.

This suggests retrieval might undergo a completely different process from encoding. However, previous investigations could not directly address whether binding failures increase with more information at retrieval since, to the best of our knowledge, short-term literature has not yet addressed this topic.

### Pattern separation and pattern completion

Retrieval is more often studied in long-term memory, which is separate from working memory, as mentioned earlier in the introduction. Retrieving memories through incomplete or degraded cues and storing them as single representations are some of the components that the hippocampus is involved in (Yassa & Stark, 2011). Hence, we can advance a division of labour in the main tasks that the hippocampus is purported to perform: pattern completion (**Figure 1.8**) which consists in assembling a total representation grounded on the previously detailed incomplete or partial retrieval cues (Bakker, Kirwan, Miller, & Stark, 2008) and pattern separation (**Figure 1.8**), key in the storage process of sensory inputs with large similarities; preventing proactive memory interferences and maintaining unique, orthogonal representations for comparable patterns of activation. (Yassa & Stark, 2011).



**Figure 1.8 The pattern completion and pattern separation processes**. <u>Pattern completion:</u> (A) A group of input patterns is introduced by experimental design and projected onto the hippocampal formation, activating a unique set of synapses and storing these experiences as an index. (B) Index activation is susceptible to the introduction of a subset of the original neocortical pattern. (C) Following index activation, the material from the hippocampal formation is projected back to the neocortex to spur the complete pattern. <u>Pattern separation</u>: The hippocampal formation promotes the creation of distinct indices to interchangeable neocortical patterns (separate representational units are derived from ABCD and CDEF). The hippocampus serves as a corrective mechanism, mitigating the inherent difficulty of the neocortex in distinguishing and adequately separating different patterns. (Figure adapted from Rudy, 2009)

Behavioural human studies propose that pattern completion results on hippocampal integration of newly captured information with previously stored representations (Hunsaker & Kesner, 2013; Yassa & Stark, 2011). Therefore, when manipulating complexity at retrieval, pattern completion suggests that retrieval of memoranda will be done irrespective of the number of features that belong to it. Whereas pattern separation predicts easier access to an object's mental representation, i.e., a more complex object has more features to remember thus more retrieval cues to rely on. Accordingly, pattern completion and separation

act as balancing counterparts dynamically at odds with one another. (Yassa et al., 2010; Yassa & Stark, 2011; Hunsaker & Kesner, 2013). Here, throughout different experiments, by varying complexity at encoding vs retrieval we are able to manipulate retrieval independently of encoding. When varying the complexity of memoranda at retrieval we will be inducing high pattern completion in order to assess if this will manifest in enhanced recall, suggesting that retrieval is improved by more information.

#### Methodology of probing Working Memory

Surprisingly, no previous study of object-location memory has looked at the effect of manipulating retrieval on short-term memory and how these effects influence the distribution of spatial errors. The way we probe working memory is crucial in understanding its underlying mechanisms, i.e., its capacity limitations and its relationship with degradation and attention. Most of the previous studies have focused on how much information can be retained over the short term by asking participants on whether an item was remembered or not, solely quantifying the information that can be retained over short periods by using binary reports (Luck & Vogel, 1997; Miller, 1956). More recently, a new approach has been to probe the fidelity with which an item is stored. By asking participants to reproduce the exact location of the remembered item, researchers are able to investigate the resolution (fidelity) which items are retained by using continuous, parametric report designs (Pertzov et al., 2012; Ma et al., 2014; Fallon et al., 2016). By evaluating working memory in a qualitative, analogue way and not in a binary, quantitative manner, this new approach opens the possibility to analyse the causes and consequences of how these representations are corrupted by deconstructing working memory pattern of recall error in three components (Palmer, 1990; Wilken & Ma, 2004; Bays & Husain, 2008; Bays et al., 2009, 2011; Gorgoraptis et al., 2011; Ji Ma et al., 2014). These components are precision, which is the faithfulness with which an item location is reproduced (Figure 2.3 (c)); misbinding, which refers to the probability of misreporting features of non-probed items (features belonging to the other items in the memory array) (Figure 2.3 (d), Misbinding) and random guessing, which quantifies the proportion of times an item is completely forgotten (Figure 2.3 (d), Chance).

In order to address all of the questions we laid down previously, here, in three experiments, we investigate how the effects of manipulating the amount of information at retrieval affects recall; by allowing participants to localise objects with different number of features and different levels of features similarities using a touch screen. This enabled us to analyse errors in respect not only to the original object location (**Figure 2.3 (a**)), but also to the location of other objects presented in the array (**Figure 2.3 (d**)).

The aim of the present study is to contribute to the understanding of the underlying mechanisms of WM by providing a deeper insight into the nature of STM representations. In order to do that, a sensitive cognitive test was developed to test how we retrieve information, by addressing questions that are central to interpretations of forgetting and memory capacity. Accordingly, in our first 2 experiments we examine the effect of manipulating encoding and retrieval on the fidelity of mental representation and how this varies as a function of delay. To investigate whether increased complexity of memoranda will set increased pattern separation, leading to less decay over time, potentially making WM more robust, experiment 1 and 3 incorporated memoranda with different levels of complexity and similarity. In addition to this, we also assess whether visual information is stored in WM as individual features or as integrated objects, by hypothesizing that increased complexity of memoranda will lead to the allocation of more resources and consequent gain of resolution (experiment 3). Throughout these experiments, we also study the role of feature similarity in

modulating performance and their misbinding rates by conjecturing that increased similarity between features implicates a higher degree of interference, resulting in worse performance and higher misbinding rates.

For this research project, I contributed by designing and programing a computer based memory task for experiment 3 using analytical tools such as *JSON Editor Online* and *MATLAB®* (note that I was also involved in some programming aspects of experiment 1 and experiment 2). I tested 61 young volunteers by using the *Oxford Psychology Research Participant Recruitment Scheme* on the SONA system and obtained data thought experimental research, Oxford memory Tests, using an interactive touch-sensitive screen of an iPad. I processed, extracted and analysed the collected data using *MATLAB®* and *IBM SPSS Statisticss*.

#### 2. Experiment 1: Manipulation of encoding and retrieval on memory recall

#### 2.1. Introduction

To the best of our knowledge, limitations in working memory performance have always been established through experiments that only manipulated encoding, without taking into consideration retrieval (Ceraso, 1985; Irwin, 1991; Wheeler & Treisman, 2002; Zhang & Luck, 2008; Luck & Vogel, 2013). An alternative way to explore the limits of VWM is to consider not only the precision with which an item is stored (Bays & Husain, 2008), but also the resolution of its retrieval. Additionally, combining manipulation of complexity at retrieval and retention period has not yet been assessed for visual objects using a delayed estimation method. In this experiment, we presented six different conditions to each participant in inter-mixed blocks of trials. The first three conditions varied in the way we manipulated encoding, keeping retrieval constant. On the other four conditions, encoding was kept constant while retrieval was being manipulated in terms of complexity (number of features) and competition (level of similarity between features).

Here, we assess the effects of manipulating encoding and retrieval on the fidelity of mental representation and how this varies as a function of delay. We want to evaluate different hypotheses about the effects of varying complexity at encoding and retrieval have on the various components of recall (accuracy, precision, misbinding). Whether more information at retrieval helps improve memory performance by hypothesising that increased complexity of memoranda will set increased pattern separation, possibly working as retrieval cues. Or if more information will have a hindering effect on recall by potentially increasing interference between features in WM. We also want to study the role of feature similarity in modulating performance and their misbinding rates, by hypothesising that less competitive memoranda may result in lower misbinding rates due to a lower degree of interference between features, potentially enhancing working memory.

# 2.2. Methods

#### 2.2.1.Participants

**Digit Span Backwards** 

**Digit Span Total** 

20 young adults (mean age = 24, SD = 4.18, 9 males, 11 females) were recruited to take part in the study. Demographics are displayed in **Table 2.1**. Participants gave written informed consent and the study was approved by the local ethics committee. Only participants with normal or corrected-to-normal vision and no history of neurological or neuropsychiatric illness were eligible to take part.

on)			
Metric	Mean	SD	Min-Max
Age (years old)	24	4.18	19-34
Digit Span <sup>7</sup> Forward	12.20	2.07	8-15

7

19.20

2.29

3.58

4-12

12-25

Table 2.1 Participant Demographics for Experiment 1. The amount of variation of the data set is quantified by SD (standard

<sup>7</sup> The Digit Span (DS) in the standardized version of the Wechsler Adult Intelligence Scale-Revised was used in the present
study. Digit-span task is a cognitive test used to measure WM's numbers storage capacity. It was presented beginning with a
length of 3 in forward or 2 in backward. The Digit Span Forward consists in remembering the numbers in the same order of
the heard sequence whereas the Digit Span Backwards consists in giving it back to the researcher in backwards order. Two
trials were presented at each length, with increasingly longer sequences being tested in each trial until two sequences of a
particular length were recalled incorrectly.

#### 2.2.2. Stimuli, Design and Procedure

Participants sat in front of an interactive touch-sensitive screen (iPad version 9.3.5(13G36), model MGTX2B/A) with 1536x2048 pixel matrix. They were 30cm away from the screen and the stimuli subtended an angle of approximately 2.3°. The stimulus set was presented as three compound object set, either circles with different colour, identical shapes with different colours or different shapes with different colours and each shape was presented in a randomly generated location.

The ability to remember the identity of objects and their location was assessed using a paradigm that provides a measure of recall performance on a continuous, analogue scale.

The experiment involved a computer-based memory task with 6 conditions within 1 block of 24 trials by 2 delays (48 trials per condition) (**Figure 2.1** and **Figure 2.2**).

Each intermixed trial began with the presentation of three objects, simultaneously presented in pseudo-random locations on a grey background for 2 seconds. They had to encode the shape, colour and spatial position of memoranda. Following a short delay (1 second) or a long delay (4 seconds)<sup>8</sup> a twoalternative forced choice between one of the matching displayed objects and a (novel) foil was presented. At the end of each trial, in the probe phase, participants were required to identify these memoranda and 'drag' these items to their remembered, original location on the screen. Depending on the Condition participants were being probed on, they had to match colour, shape or colour and shape. After placing the object in its desired location, participants had to press the word "Done" to confirm their response and the next experimental trial started right after. They were not given feedback on their performance.

The task (**Figure 2.1** and **Figure 2.2**) featured 6 conditions in which we manipulated the complexity at encoding or retrieval. We also manipulated the retention period/delay.

#### Variations of encoding:

In these 3 conditions, we varied the manner in which stimuli had to be encoded keeping retrieval constant.

**1. [Circle: Colour]** Participants had to **encode three circles with different colours** and they were asked to identify the colour of the item. This condition allowed us to manipulate dimensional complexity at encoding (number of dimensions at encoding was low).

2. [Same Shapes with Different Colours: Colour] Presented three identical shapes with different colours, and participants had to match the colour of the item presented in the array. This condition also manipulated dimensional complexity at encoding (number of dimensions at encoding was high).

<sup>&</sup>lt;sup>8</sup> Information that is attended to, arrives in a temporary store called short-term memory. Peterson and Peterson aimed to investigate the duration of STM and provide empirical evidence for the multi-store model (Peterson & Peterson, 1959). They asked participants to recall a trigram (meaningless three-consonant syllables) after intervals of 3, 6, 9, 12, 15 or 18 seconds. To prevent rehearsal, participants were asked to count backwards in threes or fours, from a specific random number, until a red light was displayed (a procedure known as the Brown-Peterson technique). They concluded that STM has a limited duration when rehearsal is prevented and that items fade within seconds 18 seconds. The results of this study also showed that STM is different from LTM in terms of duration, supporting the multi-store model of memory (Baddeley et al., 1975; Baddeley, 1986).

**3.** [Different Colour Shapes: Colour]: Subjects had to encode three different shapes with different colours and they were expected to choose the matching colour. Here we manipulated dimensional complexity at encoding (number of dimensions at encoding was high) and at retrieval (number of dimensions at retrieval was high) but in this case, there is no features similarities.



**Figure 2.1 Schematic representation of the stimuli and procedure of Experiment 1 for manipulations of encoding:** Six conditions were used in the working memory paradigm, three of these consisted in manipulations of encoding, keeping retrieval constant: Circle: Colour (encoded different colour circles, probed by colour), SSDC: Colour (encoded same shapes with different colour shapes, probed by colour). Participants had to encode the shape, colour and spatial position of the memoranda, identify these memoranda at a probe phase and drag these items to their remembered location. In this experiment participants saw three shapes, each with a different colour and spatial position, for 2 s. After a blank display, a probe item with the colour, shape or colour & shape and a novel item were presented after a variable delay (1 or 4 s). Subjects had to identify the memoranda and drag it to its remembered location. This allowed us to probe by identification accuracy and obtain a fine-grained representation of the quality of remembered items. We varied the manner in which stimuli had to be encoded by asking participants to encode three circles with different colour (Circle: Colour), three identical shapes with different colours (SSDC: Colour) and three different shapes with different colour (DCS: Colour).

#### Variations of retrieval:

In these 4 conditions, we varied the manner in which stimuli had to be retrieved keeping encoding constant. Note that condition *DCS: Colour* is the same for variations of encoding and variations of retrieval.

3. [Different Colour Shapes: Colour]: Subjects had to encode three different shapes with different colours and they were expected to choose the matching colour. Here we manipulated

dimensional complexity at encoding (number of dimensions at encoding was high) and at retrieval (number of dimensions at retrieval was high) but in this case, there is no features similarities.

**4.** [Different Colour Shapes: Shape]: Keeping complexity at encoding constant participants had to encode three different shapes with different colours and they were asked to match the shape of the remembered memoranda. This condition allowed us to manipulate dimensional complexity at retrieval (number of dimensions at retrieval was high).

**5.** [Different Colour Shapes: Different Colours]: Participants had to encode three different shapes with different colours and they were asked to identify both **shape and colour**. In this condition, the shapes that were probed had different colours. This condition enabled us to manipulate levels of competition at retrieval (features similarities was low).

6. [Different Colour Shapes: Single Colour]: Presented three different shapes with different colours, probed by **shape and colour**. In this last condition, the shapes that were probed had the same colour, here we manipulated levels of competition (features similarities were high).



**Figure 2.2 Schematic representation of the stimuli and procedure of Experiment 1 for manipulations of retrieval:** Six conditions were used in the working memory paradigm, three of these consisted in manipulations of retrieval, keeping encoding constant (note that condition *DCS: Colour* is the same for variations of encoding and variations of retrieval): DCS: Colour (encoded different colour shapes, probed by colour), DCS: Shape (encoded different colour shapes, probed by shape), DCS: DC (encoded different colour shapes, probed by 2 colours) and DCS: SC (encoded by different colour shapes, probed by 1 colour). Participants had to encode the shape, colour and spatial position of the memoranda, identify these memoranda at a probe phase and drag these items to their remembered location. In this experiment participants saw three shapes, each with a different colour and spatial position, for 2 s. After a blank display, a probe item with the colour, shape or colour & shape and a novel item were presented after a variable delay (1 or 4 s). Subjects had to identify the memoranda and drag it to its remembered location. This allowed us to probe by identification accuracy and obtain a fine-grained representation of the quality of remembered items. We varied the manner in which stimuli had to manipulated at retrieval by probing by dimensional complexity: low number of dimensions (DCS: Colour) and high number of dimensions (DCS: Shape) and levels of competition: low feature similarity (DCS: DC) and high feature similarity (DCS: SC).

#### 2.2.3.Recall Analysis

This study used a delayed reproduction tasks allowing us to assess the fidelity of working memory representations by measuring precision of recall (pattern of recall errors), which provided information on the quality of memory representations and enabled us to analyse the sources of errors contributing to the pattern of performance (Palmer, 1990; Wilken & Ma, 2004; Bays & Husain, 2008; Bays et al., 2009, 2011; Gorgoraptis et al., 2011; Ji Ma et al., 2014). Errors occurred as a result of different factors:

• Precision, which is the quality with which an item location is reproduced (**Figure 2.3** (c)). This metric (**Equation 2.1**) was only considered on trials where an object was correctly identified and was calculated by the Euclidian distance between the centre of the reported location and the centre of the original location of the probed item.

**Equation 2.1: Precision, P** is calculated by the Euclidian distance between points **p** (the center of the true location of the target) and **p**' (center of the location reported by the subject) is the length of the line segment connecting  $\mathbf{p} = (x,y)$  and  $\mathbf{p}' = (x',y')$ ,  $d(\mathbf{p},\mathbf{p}') = d(\mathbf{p}',\mathbf{p}) = (\overline{\mathbf{pp}'})$ , given by the Pythagorean formula.

$$P = (pp') = \sqrt{(x - x')^2 + (y - y')^2}$$
(2.1)

• Misbinding, which refers to the probability of misreporting features of non-probed items (features belonging to the other items in the memory array) (**Figure 2.3 (d), Misbinding**). This was calculated (**Equation 2.2**) by counting the frequency with which targets are localized within a circumference (circular radius, calculated for each participant, taking into account their overall mean precision) from the location of other objects presented in the original memory array.

**Equation 2.2: Misbinding,**  $\beta$  is the probability of swapping the location of an item, **p** with that of another item in the array, **f**. Note that this was calculated by counting the frequency with which targets are localized within a circular radius r (the radius is the mean precision of each participant performance), from the location of other objects presented in the original memory array.

$$\beta = \left(\overline{pf}\right) \le r, r = \frac{\sum_{i=1}^{N} P_i}{N}$$
(2.2)

• Random guessing, which quantifies the proportion of times an item is completely forgotten (Figure 2.3 (d), Chance). This corresponds to the proportion of responding randomly to the target location (Equation 2.3).

**Equation 2.3: Guessing,**  $\gamma$  corresponds to the proportion of responding to one of the locations that is not the target location. Note that  $\beta$  is the probability of responding to non-targets and P is precision.

$$P = 1 - \gamma - \beta \iff \gamma = 1 - P - \beta \tag{2.3}$$

# 2.2.4. Statistical Analysis

Accuracy or identification performance (proportion with which participants touched the correct object in the identification phase) and precision (distance between the reported location and the true location of the target) were our main metrics of recall. Data were analysed in MATLAB<sup>®</sup> (R2016b) and SPSS 22.0 (IBM Corp.). Two repeated measures ANOVA were used to examine the effect of varying the manner in which stimuli had to be encoded (Circle: Colour, SSDC: Colour and DCS: Colour) and retrieved (DCS: Colour, DCS: Shape, DCS: DC, DCS: SC) and the retention period (1s and 4s delay) as within subject factors. Significant interactions were followed by pairwise comparisons but no corrections for multiple comparisons, nor post-hoc tests were applied.



**Figure 2.3 Working Memory tasks' measurements of recall. (a) Identification performance:** Frequency with which participants touch the correct shape (target) in the two alternatives forced choice. (b) **Reaction Time:** Length of time taken by participants to touch the correct shape, in the two-alternative choice. (c) **Precision:** Euclidian distance between the center of reported location and the true, original location of an object. I was only measured on trials where an object was correctly identified. (d) **Sources of errors:** To understand if the error of misreporting the location of an item results from a degraded memory of an object's location or if a participant localized the target at the location of another object they had seen in the original memory array, two types of errors can be extracted. Errors due to **Chance. Misbinding** is calculated by counting the frequency with which targets are localized within a circumference (circular radius) from the location of other objects presented in the original memory array. Errors within this perimeter are called 'swap errors' because they arise from swapping the location of an object with that of another item in the array.

# 2.3. Results

#### 2.3.1.Identification Accuracy

First, we analysed accuracy or identification performance, i.e., the proportion with which participants touched the correct shape in the identification phase (**Figure 2.4**).



**Figure 2.4 Accuracy for Experiment 1:** Identification performance for different encoding and different retrieval, for Short (1s) and Long Delays (4s). Six conditions used in the working memory paradigm: Circle: Colour (encoded circle, probed by colour), SSDC: Colour (encoded same shapes with different colours, probed by colour), DCS: Colour (encoded different colour shapes, probed by colour), DCS: DC (encoded different colour shapes, probed by 2 colours) and DCS: SC (encoded by different colour shapes, probed by 1 colour). At retrieval, manipulation of complexity and competition by probing by colour (low complexity), shape (high complexity), dual colour (low competition) and single colour (high competition).

A Paired sample *t* test was applied, \* p-values < .05 and \*\* p-values < .01. Error bars reflect standard error of the mean (SEM)..

A repeated measures ANOVA was conducted that examined the effect varying the manner in which stimuli had to be encoded (Circle: Colour, SSDC: Colour and DCS: Colour) and delay (1s or 4s) had on accuracy levels. We manipulated the encoding type by presenting different levels of dimensional complexity, encoding by single feature of colour (Circle: Colour), by dual features of shape and colour (SSDC: Colour) and by dual features of different shape and colour (DCS: Colour).

There was no significant effect of **encoding type** (F(2, 38) = .295, p = .746) or effect of **delay** F(1, 19) = 3.332, p = .084) or **interaction** between encoding type and delay (F(2, 38) = 1.107, p = .324). Thus, encoding type did not seem to be a strong modulator of identification performance. Nor did the retention interval differentially affect performance on these trials.

We then looked at how varying the **retrieval type** affected accuracy, we used a repeated measures ANOVA with the complexity of the information presented at retrieval (DCS: Colour, DCS: Shape, DCS: DC, DCS: SC) and delay (1s or 4s) as within subject factors.

There was a main effect of retrieval type on recognition accuracy (F(3, 57) = 111.760, p < .001). To decompose this effect, we split our analysis into dimensional complexity and competition.

Though matched for putative levels of **dimensional complexity** (number of dimensions), accuracy when retrieving by the single feature of shape (DCS: Shape) was reduced compared to retrieval by single feature of colour (DCS: Colour) (t(19) = 15.233, p < .001). Accuracy retrieval by dual feature of colour and shape (DCS: DC) and dual feature of shape and single colour (DCS:SC) was also reduced compared to retrieval by colour (DCS: Colour) ((t(19) = 18.343, p < .001), (t(19) = 14.145, p < .001) respectively). This means that participants were generally less accurate when presented with more information at retrieval, but retrieval of shape information seems to exert a disproportionate cost on recall.

By looking, not just at the amount of information that needs to be utilised for retrieval but the **levels of competition** (feature similarity) between the two items at probe (DCS: DC, DCS:SC) we were able to evaluate how the difficulty of discrimination at probe interfered with accuracy. There was no significant difference between trials where participants were probed by low competition (DCS: DC) compared to high competition (DCS:SC) (t(19) = 1.707, p = .104). Nor was there a significant difference between trials with high complexity (DCS: Shape) and high competition (DCS:SC) (t(19) = .171, p = .866). This suggests that more competition between memoranda leads to less accuracy.

**Delay** exerted a cost on recognition accuracy, participants were more accurate for shorter delays (1s) compared to longer (4s) retention periods (F(1, 19) = 47.778, p < .001). In contrast to the effects in encoding, delay modulated the **effect of retrieval type on accuracy** (F(3, 57) = 6.189, p = .004). Accuracy was significantly higher for shorter trials compared to longer trials, in conditions where participants had to retrieve by shape (DCS: Shape) (t(19) = 3.800, p = .001), by dual colour (DCS: DC) (t(19) = 4.921, p < .001) and single colour (DCS: DC) (t(19) = 3.441, p = .003). However, in trials where participants had to retrieve by colour (DCS: Colour) delay did not exert an effect (t(19) = .567, p = .577). Thus, the effect of retention period on accuracy varied according to the nature of retrieval.

# 2.3.2. Precision

Next, we analysed the distance (cm) between the reported location and the original location of the target shape (**Figure 2.5**). Trials with incorrect identifications were excluded from further analysis.



**Figure 2.5 Precision for Experiment 1:** Error distance (cm) for different encoding and different retrieval, for Short (1s) and Long Delays (4s). Six conditions used in the working memory paradigm: Circle: Colour (encoded circle, probed by colour), SSDC: Colour (encoded same shapes with different colours, probed by colour), DCS: Colour (encoded different colour shapes, probed by colour), DCS: DC (encoded different colour shapes, probed by 2 colours) and DCS: SC (encoded by different colour shapes, probed by 1 colour).

At retrieval, manipulation of complexity and competition by probing by colour (low complexity), shape (high complexity), dual colour (low competition) and single colour (high competition).

A Paired sample *t* test was applied, \* *p*-values < .05 and \*\* *p*-values < .01. Error bars reflect SEM.

Similar to identification performance, we used a repeated measures ANOVA with encoding type (Circle: Colour, SSDC: Colour and DCS: Colour) and delay (1s or 4s) as within-subject factors to analyse localisation performance. **Encoding type** significantly influenced the fidelity of working memory in young adults (F(2,38) = 4.619, p = .017). The representation of dual features of different shapes and colour during encoding (DCS: Colour) lead to significant worse precision compared to encoding single feature of colour (Circle: Colour) (t(19) = 2.692, p = .014) and encoding dual feature of colour and shape (SSDC: Colour) (t(19) = 2.855, p = .010).

On top of this, precision was significantly affected by **delay** with shorter delays being associated with improved precision (F(1,19) = 11.395, p = .003). There was no **interaction** between encoding type and delay (F(2,38) = 1.130, p = .331). Therefore, type of encoding affected precision, specifically trials with more features were associated with impaired precision.

Keeping complexity at encoding constant, we then looked at how varying the **nature of retrieval** affected precision, using repeated measures ANOVA with retrieval type (DCS: Colour, DCS: Shape, DCS: DC, DCS: SC) and delay (1s or 4s) as within-subject factors. Again, we decomposed this effect by splitting our analysis into dimensional complexity and competition.

Precision was significantly affected by retrieval type (F(3,57) = 60.364, p < .001). Although matched on **dimensional complexity** (DCS: Colour and DCS: Shape), presenting feature of shape (DCS: Shape) at retrieval lead to reduced precision compared to single feature of colour (DCS: Colour) (t(19) = 10.077, p < .001). Participant's precision on trials where probed by dual feature of colour and shape (DCS: DC) and dual feature of shape and single colour (DCS:SC) was also reduced compared to retrieval by colour (DCS: Colour) ((t(19) = 10.039, p < .001), (t(19) = 2.641, p = .016) respectively). This indicates that participants were less precise when dimensional complexity was high compared when it was low.

By examining the levels of similarity in the features of the items that had to be retrieved, participants were significantly more precise when retrieving high **competition** information (DCS: SC) compared to low (DCS: DC) (t(19) = 5.164, p < .001). When comparing trials where participants were probed with single feature of shape (DCS: Shape) to trials where participants had to retrieve dual features of shape and colour (DCS: SC) **Figure 2.5** suggests that the presence of an extra feature to be remembered lead to a smaller error distance, as was confirmed by the statistical difference (t(19) = 8.857, p < .001). Thus, extra information at retrieval lead to improved precision.

Additionally, for trials with different retrieval, the **delay** exerted a cost on precision with shorter delays being associated with improved precision (F(1,19) = 74.419, p < .001).

In contrast with trials where we manipulated the nature of encoding, **interaction between delay and retrieval type** significantly affected precision (F(3,57) = 13.601, p < .001), with shorter delays leading to a significant enhancement of precision when participants were asked to retrieve by shape, (DCS: Shape) (t(19) = 5.029, p < .001), by dual colour (DCS:DC) (t(19) = 5.004, p < .001) and by single colour (DCS:SC) (t(19) = 4.702, p < .001). However, delay did not exert an effect on trials where participants had to retrieve by colour (t(19) = .725, p = .477). Thus, as was the case for accuracy, the effect of retention period on precision varied according to the nature of retrieval.

#### 2.3.3. Proportion of Errors due to Misbinding

Lastly, we looked at errors due to misbinding (**Figure 2.6**), also referred to as 'swap errors' since they result from swapping the location of a target with that of another item in the array.

The proportion of misbinding was calculated by counting the frequency with which targets were localised within a circumference from the location of other objects presented in the original memory array.



**Figure 2.6 Proportion of Misbinding for Experiment 1**: Proportion of errors due to misbinding, for different encoding and different retrieval, for Short (1s) and Long Delays (4s). Six conditions used in the working memory paradigm: Circle: Colour (encoded circle, probed by colour), SSDC: Colour (encoded same shapes with different colours, probed by colour), DCS: Colour (encoded different colour shapes, probed by colour), DCS: Shape (encoded different colour shapes, probed by 2 colours) and DCS: SC (encoded by different colour shapes, probed by 2 colours) and DCS: SC (encoded by different colour shapes, probed by 1 colour). At retrieval, manipulation of complexity and competition by probing by colour (low complexity), shape (high complexity), dual colour (low competition) and single colour (high competition).

A Paired sample *t* test was applied, \* *p*-values < .05 and \*\* *p*-values < .01. Error bars reflect SEM.
Following the same statistical procedure employed in identification and localization performance, we examined how misbinding varied according to encoding type and whether the probability of misbinding was greater for short delays or long delays. A repeated measures ANOVA was applied with encoding type (Circle: Colour, SSDC: Colour and DCS: Colour) and delay (1s or 4s) as within-subject factors.

There was no significant effect of **encoding type** (F(2, 38) = 3.225, p = .063) or effect of **delay** (F(1, 19) = .671 p = .423) or **interaction** between encoding type and delay (F(2, 38) = 3.157, p = .054). Therefore, manipulating complexity of encoding or the retention interval did not produce a significant effect on the proportion of swap errors.

Second, we examined misbinding rates in repeated measures ANOVA with retrieval type (DCS: Colour, DCS: Shape, DCS: DC, DCS: SC) and delay (1s or 4s) as within-subject factors. There was a significant main effect of **retrieval type** (F(3, 57) = 77.786, p < .001). This effect was once again decomposed enabling us to analyse dimensional complexity and competition separately.

In congruence with previous observations with reference to accuracy and precision, although matched on dimensional complexity, retrieval by single feature of shape (DCS: Shape) impacted the proportion of errors due to misbinding. Thus, misbinding when retrieving by single feature of shape (DCS: Shape) increased in respect to retrieval by single feature of colour (DCS: Colour) (t(19) = 16.015, p < .001).

Furthermore, retrieval by dual feature of colour and shape (DCS: DC) and dual feature of shape and single colour (DCS: SC) resulted in greater proportions of misbinding errors when compared to solely retrieval by colour (DCS: Colour) (t(19) = 2.169, p = .043; (t(19) = 2.107, p = .049, respectively). We also identified more pronounced effect on misbinding on trials where participants were asked to retrieve by single feature of shape (DCS: Shape), compared to high competition trials (DCS: SC), impose on misbinding (t(19) = 11.784, p < .001). These results compel us to further reinforce and reiterate the disproportionate cost that retrieval of shape appears to bear on recall.

However, when examining the levels of resemblance in the features of the items that had to be retrieved, we did not find any significant difference between high **competition** trials (DCS:SC) and low (DCS: DC) (t(19) = .236, p = .816). This illustrates that errors in WM recall are primarily driven by an overload of the number of dimensions in memory (levels of dimensional complexity) instead of irrelevant items which share similar features (levels of competition).

A trend was observed for shorter **delays** leading to less errors due to misbinding (F(1, 19) = 4.321 p = .051). **Interaction between delay and retrieval type** significantly affected misbinding (F(3, 57) = 5.159, p = .012), with shorter delays leading to significant less misbinding when participants were asked to retrieve by shape, (DCS: Shape) (t(19) = 3.199, p = .005), and by single colour (DCS:SC) (t(19) = 2.450, p = .024). However, delay did not exert an effect on trials where participants had to retrieve by colour (t(19) = 1.719, p = .102) or by shapes with different colours (t(19) = .444, p = .662). Thus, as was the case for accuracy and precision, the effect of retention period on misbinding varied according to the nature of retrieval.

# 2.4. Discussion

Working memory is a fundamental cognitive process. If we cannot remember something, whether or not it may be related to retrieval (due to the corruption of information from storage) has yet to be investigated. Therefore, understanding retrieval and how its manipulations may affect WM is essential.

The classical model of WM, also known as the slot model (Miller, 1956; Pashler, 1988; Luck & Vogel, 1997, 2013; Cowan, 2001), proposes a limitation due to the total number of items which can be encoded since the capacity of VSTM itself is limited (Pashler, 1988; Luck & Vogel, 1997, 2013; Cowan, 2001). In the literature, inferences on the limit of performance have always been based on manipulations of encoding, without taking into consideration retrieval (Ceraso, 1985; Irwin, 1991; Wheeler & Treisman, 2002; Zhang & Luck, 2008; Luck & Vogel, 2013). The present study addressed this matter for the first time, by manipulating both encoding and retrieval as a function of the complexity of the objects to be encoded and retrieved. Thus, in this experiment, we investigated whether the effect of manipulating encoding is similar to the effect of manipulating retrieval on the fidelity of mental representation.

The results of this experiment strongly suggest that it is the complexity at retrieval that determines performance (with some variability induced by delay).

Firstly, we looked at the differences of the shared figures between target and foil (if the target and foil shared the same feature affected retrieval). Retrieving similar items in working memory was found to induce greater resolution (**Figure 2.5, DCS: SC Condition**) supporting the theory of a memory-driven attentional capture where attention is biased towards items that match the current content of working memory (Olivers et al., 2006) increasing the accessibility of its retrieval.

Then, we examined how manipulating the number of features that the probe item had affected retrieval. Overall recall was better for trials were participants had less information to be retrieved (**Figure 2.4, DCS: Colour Condition**). Conversely, trials where participants were presented with more information were found to induce a disproportionately detrimental effect on WM performance (**Figure 2.4 and Figure 2.5, DCS: Shape Condition**) leading to greater rates of errors due to misbinding (**Figure 2.6, DCS: Shape**). This may have been driven by the asymmetry in the difficulty by retrieving by shape as opposed to colour. However, another consideration is the possibility that people were strategically focusing on the colours and not the shape information, i.e., that colour was more weighted at encoding leading to better retrieval in trials where participants were probed by colour.

This was assessed by means of a second experiment, Experiment 2.

### 3. Experiment 2: Cueing information before manipulating encoding and retrieval

#### 3.1. Introduction

In the previous experiment, participants may have been weighting more feature colour, to the detriment of feature shape during encoding. This would explain the disproportionate effect of feature shape compared to feature colour in memory performance. By cueing participants before each trial, we intend to assess whether results from Experiment 1 are due to an unbalanced contribution of features or if retrieving items in working memory actually induces greater identification problems in trials where participants are presented with more information.

Here, we hypothesise that more complex memoranda will result in additional features to be remembered (or features with a higher dimensional level of representation), leading to the allocation of more resources and ensuing loss of precision.

### 3.2. Methods

#### 3.2.1.Participants

20 young adults (mean age = 24, SD = 3.10, 8 males, 12 females) were recruited to take part in the study. Demographics are displayed in **Table 3.1**.

Participants gave written informed consent and the study was approved by the local ethics committee. Only participants with normal to corrected-to-normal vision and no history of neurological or neuropsychiatric illness were eligible to take part. Moreover, participants could not have taken part in the RIVERHEAD task (Experiment1).

 Table 3.1. Participant Demographics for Experiment 2. The amount of variation of the data set is quantified by SD (standard deviation)

Metric	Mean	SD	Min-Max
Age (years old)	23.5	3.10	18-29
Digit Span <sup>9</sup> Forward	11.95	2.76	6-16
Digit Span Backwards	7.75	2.45	4-14
Digit Span Total	19.70	4.65	10-29

#### 3.2.2. Stimuli, Design and Procedure

The method adopted was the same as in Experiment1, except for the fact that before each trial participants were cued, for 2 seconds, based on the manner in which they would be probed, in order to make sure colour and shape were equally weighted at encoding.

The experiment involved a computer-based memory task with 6 conditions within 1 block of 24 trials in which we manipulated the delay (short delays = 1s and long delays = 4s) as well as the complexity at encoding or retrieval (**Figure 3.1**). Thus, each participant performed 48 trials per condition.

- 1. [Circle: Colour]: Circle probed by colour. Cued by colour.
- 2. [SSDC: Colour]: Same shapes with different colours probed by colour. Cued by colour.
- 3. [DCS: Colour]: Different colour shapes probed by shape. Cued by shape.

<sup>&</sup>lt;sup>9</sup> The Digit Span (DS) in the standardized version of the *Wechsler Adult Intelligence Scale-Revised* was used in the present study.

- 4. [DCS: Shape]: Different colour shapes probed by colour. Cued by colour and shape.
- 5. [DCS: DC]: Different colour shapes probed by dual colour. Cued by colour and shape.
- 6. [DCS: SC]: Different colour shapes probed by single colour. Cued by colour and shape.

# 3.2.3. Recall Analysis and Statistical Analysis

The procedure of Experiment 2 was exactly the same as that of Experiment 1.



**Figure 3.1 Experiment 2:** Participants were cued for 2 sec. The cue differed on how they would be probed (in this example, 'Colour'). They were then presented with 3 shapes for 2 sec. Depending on the condition, they had either to encode 3 circles with different colours (Circle: Colour), or 3 identical shapes with different colours (SSDC: Colour) or, as shown in this example, 3 different colour shapes (DCS: Colour, DCS: Shape, DCS: DC, DCS: SC). After a variable delay period of 1 or 4 seconds, they were presented with a dual choice between a novel item or a matching object from the sample array (in this case they would have to choose the green colour to match the green shape presented at encoding). Just like Experiment1, participants were probed either by Colour (Circle: Colour, SSDC: Colour, DCS: Colour), by Shape (DCS: Shape), by Shapes with different colours (DCS: DC) or by Shapes with the same colour (DCS: SC). After identifying the memoranda subjects had to drag these to their remembered location.

# 3.3. Results

The data pertaining Experiment 2, for identification performance (**Figure 7.3**)<sup>10</sup>, precision (**Figure 7.4**)<sup>11</sup> and proportion of misbinding (**Figure 7.5**)<sup>12</sup> was analysed while operating within the same methodological framework of Experiment 1. Results were substantially the same as Riverhead, see **Table 7.3**, **Table 7.4** and **Table 7.5** in APPENDIX for a summary.

### 3.4. Discussion

In this experiment, we examined the possibility that WM performance in **Experiment 1** was reflecting an unbalanced contribution of features during encoding. To make sure participants were weighting colour in the same way as shape during encoding, we conducted **Experiment 2** in which the memory requirements were the same as in the original experiment but this time we cued the participants before each trial in order to induce strategic encoding. By encouraging participants to strategically focus on certain elements we were able to assess if there were any changes on the results of the previous study.

The results indicate that – even when participants are explicitly cued on what features they need to encode, the effects observed in **Experiment 1** are still found: there was no effect of manipulating encoding but a clear consequence of manipulating the nature of retrieval. Moreover, retrieving items in working memory was found to induce greater identification problems in trials where participants were presented with more information (**Figure 7.3**).

# All dimensions are equal, but some dimensions are more equal than others.

In this memory paradigm two dimensions of complexity could be distinguished: (a) the number of features associated with an object (single representations and double representations); (b) feature's dimensional level of representation. Consistent with the results of Wheeler and Treisman (Wheeler & Treisman, 2002, Experiment 4A) and Jonhson, Hollingworth and Luck (Johnson et al., 2008, Experiment 3), overall recall was highest in the single colour condition (Figure 7.3, DCS: Colour Condition) and worst in the dual colour and shape condition (Figure 7.3, DCS: DC Condition). This may suggest that the basic features and the binding of information into a whole object, are remembered through different mechanisms and that binding features requires additional memory capacity.

The cost of binding features together in memory may not be constant for all feature dimensions. For example, shape retrieval had a disproportionately detrimental effect on WM performance (**Figure 7.4, DCS: Shape Condition**) compared to dual feature trials (**Figure 7.4, DCS: DC Condition**, suggesting that memory for the whole object information may be constrained by memory capacity for the more difficult feature (Wheeler & Treisman, 2002, Experiment 3B). WM identification accuracy was lower in both the shape (**Figure 7.3, DCS: Shape Condition**) and dual shape and colour condition (**Figure 7.3, DCS: DC Condition**) than in the single colour condition (**Figure 7.3, DCS: Colour Condition**). This suggests that the two features compete for the same storage capacity and are neither

<sup>&</sup>lt;sup>10</sup> See APPENDIX (Experiment 2, **Identification Accuracy**) for a more detailed description of the statistical analysis.

<sup>&</sup>lt;sup>11</sup> See APPENDIX (Experiment 2, **Precision**) for a more detailed explanation of the statistical analysis.

<sup>&</sup>lt;sup>12</sup> Please go to APPENDIX (Experiment 2, **Proportion of Errors due to Misbinding**) for a more detailed explanation.

stored in parallel as Wheeler and Treisman suggested (Wheeler & Treisman, 2002, Experiment 3A) nor automatically bound in one unit (Treisman & Gelade, 1980; Ceraso, 1985; Irwin, 1991; Luck & Vogel, 1997; Vogel et al., 2001; Oberauer & Lin, 2017).

Precision however, in the dual colour and shape condition (**Figure 7.4, DCS: DC Condition**) was practically the same as in the single colour condition (**Figure 7.4, DCS: Colour Condition**). This proposes that participants may maintain different information in the features condition (single representation of colour, single representation of shape) than in the binding condition (binding together features into a whole object). Different feature representations (colour, shape) may need the allocation of different amounts of memory resources which would explain why colour is easier to retrieve than shape. It may also be the case that there is a memory mechanism characterised by different levels of feature's representations in parallel (Wheeler & Treisman, 2002), each with their own memory capacity and with different levels of accessibility. This possibility provides additional support for the idea that memory resources are not distributed evenly, they can be shifted flexibly between objects, with allocation biased by selective attention (Bays & Husain, 2008). This is also consistent with the idea that bindings between different features of an object may be maintained through a mechanism that relies on a limited flexible resource such as attention (Horowitz & Wolfe, 1998; Wolfe, 1999).

Given these asymmetries in binding colour and shape, we cannot make any strong conclusions about complexity effects on retrieval. For this reason, we carried out **Experiment 3** to tests whether more complex information at retrieval, i.e., more information at probe, would enhance WM performance.

# 4. Experiment 3: Manipulation of complexity and competition at retrieval

# 4.1. Introduction

In the previous experiments, we used very complex shapes as part of the retrieval stimuli. While such stimuli might be harder to verbalise, they have an inherent disadvantage for the purpose of this study because their complexity does not have a comparable term. In order to decrease this unbalanced level of complexity between visual stimuli, we used different levels of complexity within the shape of a circle.

In this experiment, only retrieval was manipulated, keeping encoding constant. Four different conditions were presented to each participant in inter-mixed blocks of trials. The first and third conditions varied in the way we manipulated the number of features at probe and the second and fourth conditions varied with level of similarity between target and foil.

Here, we want to investigate whether more information interferes or helps at a probing phase. We posited that increased complexity of memoranda (higher number of representations in WM) will lead to more features among which the resource needs to be distributed, implicating a higher degree of mutual interference and increased decay over time. This hypothesis implies that the degree of mutual interference increases with the number of features of an object, but also with the similarity between them (levels of competition). Or if more information load corresponds to more faithful retro-cues enhancing working memory representations.

Thus, we examined how information about object identity, location and object-location associations are susceptible to manipulations of complexity, competition and degradation over time.

### 4.2. Methods

### 4.2.1. Participants

21 young adults aged between 18 and 30 years old (mean age = 23.33, SD = 3.68, 15 males, 6 females; see demographics displayed in **Table 4.1**) were recruited to take part in the study.

Participants were recruited from the Oxford Psychology Research Participant Recruitment Scheme on SONA. They had no history of neurological or psychiatric disease and good vision. Permission for this study was obtained from the local ethics committee and all subjects gave written informed consent.

 Table 4.1 Participant Demographics for Experiment 3. The amount of variation of the data set is quantified by SD (standard deviation)

Metric	Mean	SD	Min-Max
Age (years old)	23.33	3.68	18-30
Digit Span <sup>13</sup> Forward	12.33	2.63	6-16
Digit Span Backwards	8.43	2.67	4-14
Digit Span Total	20.29	5.32	10-29

<sup>13</sup> The Digit Span (DS) in the standardized version of the *Wechsler Adult Intelligence Scale-Revised* was used in the present study.

### 4.2.2. Stimuli, Design and Procedure

The task used in this study required participants to encode the identity and location of a pair of objects. After a delay, they were assessed in a continuous, parametric scale, by being asked to drag it to its original location.

Participants sat in front of an interactive touch-sensitive screen (iPad version 9.3.5(13G36), model MGTX2B/A) with 1536x2048 pixel matrix. Stimuli were presented on a grey background and were drawn from a library of 42 foils, randomly selected without repetitions for every trial. Six colours were used (yellow, pink, cyan, red, green, blue) and were randomly selected for each display with the constrain that no repetition of colour be within an object. The stimuli were presented at a viewing distance of approximately 30 cm and subtended an angle of approximately 2.3°. The task featured four experimental conditions randomly presented, within 1 Block of 48 trials (24 trials for 1 second delay maintenance and 24 trials for 4 seconds delay maintenance) (**Figure 4.1**):

- 1. Low complexity and low competition at retrieval
- 2. Low complexity and high competition at retrieval
- 3. High complexity and low competition at retrieval
- 4. High complexity and high competition at retrieval



**Figure 4.1 Experimental Design of Experiment 3:** Participants were required to remember two coloured circles (presented for 2000ms in all conditions) and the location they appeared in. After a short delay of 1s or a long delay of 4s participants were asked to identify the shape they saw previously and drag its original location. A key manipulation was to vary complexity and competition at retrieval and the retention period. The various conditions were randomly intermixed and complexity at encoding was kept constant. Participants were instructed to match the memoranda presented at retrieval with the memoranda presented at encoding. In the first condition on the left, participants were probed with two half circles with different colours. One of the matched the memoranda presented at encoding and the other was a novel, never seen foil. In contrast, in the second condition on the left, participants were probed with a mirror shape of the one they were expected to match. They had to remember the matching half-circle and discard the distractor. In the third condition on the left, participants were probed with a pair of circles with different colours, one was a perfect match to the one they saw at encoding and the other one was a novel foil. The first condition on the right was very similar to the single distractor condition, once again, we manipulated the feature similarity between the matching item and the irrelevant item, but this time we presented the participant with more information at retrieval.

In all conditions participants had to encode differently coloured circles for 2 seconds, randomly presented on the screen. After a maintenance period of 1 second or 4 seconds, they were presented with a dual choice. Depending on the Condition participants were being probed on, they had to match the whole coloured circle or just half of the coloured circle, and drag it to its original location. After placing the object in its desired location, participants had to press the word "Done" to confirm their response. They were not given feedback on their performance.

Low Complexity and Low Competition condition: A pair of circles were presented for 2 seconds during encoding. After a delay of 1 or 4 seconds, a pair of half circles was presented during retrieval. One was a novel (unseen foil) and the other matched half of the information presented during encoding. Participants had to choose the half matching piece of the circle and reproduce its original location.

Low Complexity and High Competition condition: Participants were presented with two circles randomly presented on the screen. After a blank screen delay (of 1 or 4 seconds), came the probe phase. In the probe phase, two half-circles were presented. However, in this condition, one of these shapes was a distractor since it had the same colour feature as the matching memoranda but did not matched for shape, i.e. was a flip image of the original shape.

**High Complexity and Low Competition condition:** Just like the two previous conditions we did not manipulate encoding but once again we manipulated retrieval. In this condition, we probed high complexity shapes, full circles, after a 1 or 4 second maintenance period. At the probing phase, one of the circles matched perfectly one of the encoded memoranda and the other was a novel, unseen foil.

**High Complexity and High Competition condition:** Keeping complexity at encoding constant participants were probed with high complexity shapes (circles with two colours). In this condition, they were probed with a dual choice: a distractor, mirrored/flipped image of the matching shape and a shape that perfectly matched the target.

#### 4.2.3. Recall Analysis and Statistical Analysis

The procedure was the same as that of Experiment 1 and Experiment 2, with the following exception. Identification accuracy, precision, proportion of misbinding, reaction time and proportion of errors due to chance were analysed by a 2x4 repeated measures ANOVA with delay (1 vs 4 seconds), complexity (high and low) and competition (high and low).

#### 4.3. Results

#### 4.3.1.Identification Accuracy

We first tested whether the amount of information (dimensional complexity), level similarity between the features of the items retrieved (levels of competition) and the retention period affected the ability to identify the correct item. Accordingly, a repeated measures ANOVA was conducted that examined the effect of complexity (high and low) competition (high and low) and delay (1s or 4s) on accuracy level (proportion correct).

Across the four conditions (**Figure 4.2**) there was no main effect of delay on how frequently participants selected the correct memoranda (F(1, 20) = 2.149, p = .158).

The amount of information that had to be retrieved (**complexity**) exerted a cost on recognition accuracy (F(1, 20) = 6.252, p = .021), i.e., overall, participants had higher accuracy when retrieving high complexity shapes (all the information) compared to low complexity shapes (half of the information). There was also a main effect of **competition** between two items (F(1, 20) = 48.178, p < .001) with low competition trials leading to significantly more accurate responses for high complexity compared to low complexity (t(20) = 4.038, p = .001). However, these two factors were found to significantly **interact** (F(1, 20) = 16.616, p = .001). On low competition trials, participants were significantly *more* accurate when retrieving by high complexity compared to low (t(20) = 4.038, p = .001), but on high competition trials there was no such difference (t(20) = 1.127, p = .273). Moreover, on low complexity trials, participants were less accurate when probed with high competitive memoranda compared to low, on high complexity trials (t(20) = 4.758, p = .0001). Additionally participants were also less accurate when presented with high competitive memoranda compared to low, on high complexity trials (t(20) = 9.171, p < .001). None of the other interactions were significant (p > .138).

In summary, complexity of memoranda as well as competition between probed items affected identification accuracy. Thus, more information with less resemblances at retrieval enhanced recognition accuracy.



**Figure 4.2 Accuracy for Experiment 3:** Identification rates for each experimental condition with low or high complexity and low or high competition at retrieval. A Paired sample *t* test was applied, \* *p*-*values* < .05 and \*\* *p*-*values* < .01. Error bars reflect SEM.

#### 4.3.2. Precision

Following participants' accuracy performance, we examined the distance between the reported location and the actual, original location of the target shape. A repeated measures ANOVA was conducted that examined the effect of complexity (high and low) competition (high and low) and delay (1s or 4s) on precision. Again, as with the previous experiments, only trials where participants correctly identified the target shape were included in this analysis.

Here, on this metric, delay exerted a cost on precision with participants being significantly less precise for the longer delay period (F(1, 20) = 47.940, p < .001). A significant **interaction between delay and competition** (F(1, 20) = 4.972, p = .037), revealed that the effect competition was significantly higher for longer delays compared to shorter delays (**Figure 4.3**), i.e., participants performed significantly worse on trials where we manipulated competition for long delays (t(20) = 4.845, p = .000098) but not for short delays (t(20) = 1.159, p = .260).

There was a main effect of complexity on precision (F(1,20) = 50.317, p < .001). Error distance was significantly higher for low **complexity** trials compared to high complexity trials (t(20) = 11.681, p < .001). Thus, participants were less precise when presented with less information at retrieval (**Figure 4.4**).

By looking, not just at the amount of information that needs to be appropriated at retrieval, but also the level of **competition** (Figure 4.4), we observed that participants were significantly less precise when presented with low competition trials (t(20) = 4.561, p = .00019).

**Interaction between complexity and competition** significantly affected precision (F(1, 20) = 12.910, p = .002). Particularly in the low complexity trials, participants made significantly more mistakes when competition was low compared to when it was high (t(20) = 4.561, p = .00019). However, presenting high complexity trials with high competition, compared to high complexity with low competition, did not have a significant effect on precision (t(20) = 1.403, p = .176). Additionally, the presentation of low competition information resulted in a significant decreased on precision for low complexity trials compared to high complexity trials (t(20) = 11.681, p < .001). This significant impairment on precision was not observed when presenting high complexity with low competition memoranda, compared to high complexity with high competition (t(20) = .612, p = .547) (**Figure 4.4**).

None of the other interactions were significant (p > .101). Thus, being presented with more information with higher levels of similarity at probe enhances working memory precision.



**Figure 4.3 Precision performance for Experiment 3: (a)** Error distance (cm) for short delays (1s). **(b)** Error distance (cm) for long delays (4s). A Paired sample *t* test was applied, \* *p*-values < .05 and \*\* *p*-values < .01. Error bars reflect SEM.



**Figure 4.4 Precision performance across delay for Experiment 3:** A Paired sample *t* test was applied, \* *p*-values < .05 and \*\* *p*-values < .01. Error bars reflect SEM.

#### 4.3.3. Proportion of Errors due to Misbinding

A repeated measures ANOVA was performed that examined the effect of complexity (high and low) competition (high and low) and delay (1s or 4s) on the proportion of misbinding (**Figure 4.5**). Delay did not significantly impact the number of errors due to misbinding (F(1, 20) = .020, p = .890). Misbinding errors were significantly more likely in low **complexity** trials compared to high complexity trials (F(1, 20) = 72.151, p < .001). Thus, the presence of less information at retrieval increased the probability of responding to a non-target location. Misbinding was also more likely to occur in low **competition** trials compared to high competition trials (F(1, 20) = 20.926, p = .000184).

The **interaction effect** between complexity and competition significantly affected misbinding levels (F(1, 20) = 5.210, p = .034). Unpacking this interaction, revealed that there was a disproportionate effect of competition in low complexity trials compared to high, i.e., the effect of competition in low complex trials (t(20) = 3.861, p = .001) was higher compared to higher complexity trials (t(20) = 2.492, p = .022). Significant effects of complexity were observed for both low (t(20) = 8.916, p < .001) and high competition trials (t(20) = 3.861, p = .001).

None of the other interactions were significant (p > .148).



**Figure 4.5 Proportion of Misbinding for Experiment 3:** Misbinding occur when there is an incorrect bind (error that results from swapping the location of a target with that of another probed item). A Paired sample t test was applied, \* p-values < .05 and \*\* p-values < .01. Error bars reflect SEM.

### 4.4. Discussion

The purpose of this experiment was to assess complexity and competition effects on retrieval. In contrast with the previous experiments (**Experiment 1 and Experiment 2**), the present paradigm avoided the comparison of memoranda in conditions where they are different in nature, by presenting features with the same levels of attentional demands.

Overall, results support the notion that the ways in which retrieval of information can influence WM are associated not only with the amount of information available at probe, with more memory load increasing WM performance (**Figure 4.4, High Complexity Condition**), but also with the levels of similarity between objects at retrieval, with increasing similarity leading to higher WM resolution (**Figure 4.4, High Competition Condition**).

Primarily, we assessed how manipulating the amount of information at the probe phase affected recall. The results from **Experiment 3** showed that accuracy affected the identification of the item (**Figure 4.2**) whereas precision affected binding in space (**Figure 4.4**). These dissociable effects on recognition and binding of information support several other studies that have demonstrated that different neuroanatomical regions match for unified objects and for spatial binding (Colby & Goldberg, 1999; Corbetta, Miezin, Shulman, & Petersen, 1993; Corbetta, Shulman, & Miezin, 1995; Friedman-Hill, Robertson, & Treisman, 1995; Haxby et al., 1991; Mishkin, Ungerleider, & Macko, 1983; Ward, Danziger, Owen, & Rafal, 2002).

A consistent finding, irrespective of the WM model, has been that recall decreases with more information (higher WM load), either because there are insufficient slots (Luck & Vogel, 1997)) or the flexible resource is spread too thinly (Bays & Husain, 2008). On one hand, the slot model describes WM as limited in capacity with a storage capacity of about three to four items (Cowan, 2001; Vogel, Woodman, & Luck, 2001; for a review on the classical view see Luck & Vogel, 2013). In the other, the resource model advocates that WM is limited but no quantal with no item limit (Palmer, 1990; Wilken & Ma, 2004; Bays & Husain, 2008; Bays, Catalao, & Husain, 2009, Wilken & Ma, 2004; for reviews see Fallon, Zokaei, & Husain, 2016; Ji Ma, Husain, & Bays, 2014). The resource is continuous and can be flexibly shifted amount items , with a decrese on the fidelity of mental representation as memory load increases (Bays et al., 2009, 2011; Bays & Husain, 2008; Gorgoraptis et al., 2011). Our findings indicate that none of the aforementioned models are able to completely explain our data, by revealing that more information at probe enhances working memory precision (**Figure 4.4, High Complexity Condition**).

The slot model is not able to explain this effect since it is based on the premise that either an object is remembered or it is not, with each object being stored in one of a fixed number of memory slots with high resolution (Luck & Vogel, 1997; Pashler, 1988). Luck and Vogel have also reported a series of experiments where they provide evidence that items stored in VSTM are encoded as a whole, and not as a composition of their elementary features (Luck & Vogel, 1997). Thus, we would expect accuracy to be the same across both low and high complexity conditions (**Figure 4.2**) since as long as an item is not considered to be new, the fragment of information presented at probe should be sufficient for recall.

The results are also hard to reconcile with the resource model (Wilken & Ma, 2004; Bays & Husain, 2008), which argues that more information leads to the allocation of more resources causing a decrease on the fidelity of mental representation. Thus, under this model, a higher number of features should require more features to maintain and recall. However, here we found that more features enhance memory performance (**Figure 4.4, High Complexity Condition**). One explanation for this is that the

higher number of features may correspond to more faithful retro-cues, i.e., higher number of pathways able to selectively access an object's characteristics.

Despite the fact that WM models do not fully explain this effect, ideas from LTM on pattern separation and the role of the hippocampus (in binding information) could potentially provide a better model for these effects. These ideas are discussed in greater detail in the general discussion.

Our analysis also revealed that more memory load was also found to be responsible for decreasing the probability of responding to a non-target location (**Figure 4.5, High Complexity Condition**), supporting previous findings that spatial location has a central role in feature binding (Treisman & Zhang, 2006).

Next, we assessed if similarity between target and foil affected the resolution of WM. Only when we presented half of the information (low complexity), did we observe effects of competition (**Figure 4.3** and **Figure 4.4**). This may have been due to the fact that presenting half of the information at retrieval disrupted the internal object binding. In addition, less information with less resemblances at retrieval enhanced the likelihood of misreporting an item, i.e., increased misbinding (**Figure 4.5**, **Low Competition and Low Complexity Condition**). This result is incongruent with the notion that memory performance is limited by interference, which can arise from multiple sources (Saito & Miyake, 2004; Lewandowsky, Geiger, & Oberauer, 2008; Oberauer & Lewandowsky, 2008; Berman, Jonides, & Lewis, 2009; Lewandowsky & Oberauer, 2009; Lewandowsky, Geiger, Morrell, & Oberauer, 2010; Oberauer, Lewandowsky, Farrell, Jarrold, & Greaves, 2012). One being the superposition of overlapping memory representations, blurring each other; the other being the increased of confusion between target and foil since they are bound to similar characteristics (Oberauer, Farrell, Jarrold, Pasiecznik, & Greaves, 2012). However, we may infer that less information at retrieval with less similarities between each other may correspond to less faithful retro-cues enhancing swap errors. Thus, we need further work to be able to make any conclusions related to complexity at retrieval, in WM.

### 5. General Discussion and Conclusion

Mild cognitive impairment and dementia are affected by changes in mental capacity and resolution (Ally, Hussey, Ko, & Molitor, 2013; Pertzov et al., 2013; Stark, Yassa, Lacy, & Stark, 2013; Kensinger, Shearer, Locascio, Growdon, & Corkin, 2003; Liang et al., 2016), entailing a significant deterioration in patients' quality of life. By understanding the mechanisms underlying working memory in a healthy population, we may be able to infer the STM cognitive components that are disrupted in neurodegenerative diseases. This may facilitate early detection and the development of improved treatment.

The aim of this study was to examine the effect of manipulating encoding and retrieval on the fidelity on mental representation. A specific focus of this research was to investigate whether manipulations of complexity and competition between memoranda influence WM robustness, in order to do that we developed three tablet based memory tasks (**Experiments 1, 2 and 3**).

The literature to date contains conflicting conclusions concerning capacity limitations in working memory. The slot model or item limit model, describes working memory as a small set of high-precision representations, with the inability of retaining more information than the number of 3 to 4 fixed available slots (Pashler, 1988; Luck & Vogel, 1997). A more recent version of this theory has been that visual working memory is composed of a fixed number of slots each represented with a fixed discrete resolution (Zhang & Luck, 2008). Whereas the resource model advocates that there is no fixed limit on the number of objects that can be stored in VWM but a fixed resource, instead. This resource is claimed to be flexibly allocated to either a small number of items with high resolution or a larger number of items with lower precision (Bays & Husain, 2008; Wilken & Ma, 2004). An alternative way to explore the limits of visual working memory would be to consider, not only the precision with which an item is stored (Bays & Husain, 2008) but also the resolution of its retrieval.

Unlike the vast majority of studies in the literature of working memory, we investigated the effect of manipulating both encoding and retrieval as a function of the load and similarity between the objects to be encoded and retrieved. Thus, we were able to investigate whether the effect of manipulating encoding was similar to the effect of manipulating retrieval on the fidelity of WM.

The data presented in **Experiment 1** and **Experiment 2** strongly suggest that it is the complexity at retrieval that determines performance, with some variability induced by delay; whereas manipulating complexity at encoding did not produce any effect on the quality of mental representation. The task used in the first two experiments, however, did not allow us to clearly isolate manipulation of complexity and competition. In order to study the role of complexity and competition between memoranda in modulating performance, we designed and established a tablet-based continuous recognition paradigm, **Experiment 3**.

Firstly, we investigated how increasing the number of features at retrieval (complexity of memoranda) affected mental representations (**Experiment 3**). We showed that there are dissociable effects on recognition and binding of information, with accuracy affecting the identification of the item (**Figure 4.2**) and precision affecting binding in space (**Figure 4.4**). These results accord well with several other studies postulating that the unified object and spatial binding are associated with different neuroanatomical regions (Colby & Goldberg, 1999; Corbetta, Miezin, Shulman, & Petersen, 1993; Corbetta, Shulman, & Miezin, 1995; Friedman-Hill, Robertson, & Treisman, 1995; Haxby et al., 1991;

Mishkin, Ungerleider, & Macko, 1983; Ward, Danziger, Owen, & Rafal, 2002). Thus, a next interesting layer of investigation would be to use functional magnetic resonance imaging (fMRI) to access if there are different neuronal activation regions for identification performance and precision. In addition, we would be able to assess different neural activations associated with encoding and retrieval and their inter-relationship.

We also studied the role of feature similarity (**Experiment 3**) by asking participants to retrieve high competitive memoranda (Erro! A origem da referência não foi encontrada., **third condition on the left**) and low competitive memoranda (Erro! A origem da referência não foi encontrada., **first condition on the right**). Effects of competition on precision were only observed when participants were presented with less information (**Figure 4.4**) suggesting that a bigger amount of information at retrieval may enhance the internal object binding.

On top of that, misbinding rates were disproportionally larger for trials with less information and less resemblances at retrieval (**Figure 4.5, Low Competition and Low Complexity Condition**). These results suggest that less information with less resemblances may correspond to less accurate retrocues (cues presented after encoding, that suggest what items are going to be presented at retrieval). Although a plausible account of our data, this view is inconsistent with several other sources of data that support the idea that misbinding rates are usually found to increase with increasing load (Gorgoraptis et al., 2011) and that memory performance is limited by interference (Saito & Miyake, 2004; Berman, Jonides, & Lewis, 2009; Lewandowsky & Oberauer, 2009; Lewandowsky, Geiger, Morrell, & Oberauer, 2010; Oberauer, Lewandowsky, Farrell, Jarrold, & Greaves, 2012) because of the overlap of similar memory characteristics, thus weakening their representations in memory or by causing confusion (Oberauer, Farrell, et al., 2012).

A concern is that the effect of complexity and competition on misbinding may have occurred due to attentional mechanisms. Whether attention is necessary to bind features together has been a topic of debate in object perception research (Horowitz & Wolfe, 1998; Treisman & Gelade, 1980; Vogel et al., 2001). Some investigators support the theory that objects are stored as unified objects and memory capacity is not affected by the number of features of an object (Luck & Vogel, 1997). Others consider that objects breakdown to their individual features as soon as attention is removed (Wheeler & Treisman, 2002). In order to address whether attention is necessary to maintain the correct binding between features as less information at retrieval dramatically increased misbinding (Figure 4.5, Low Competition and Low Complexity Condition), future studies will need to be conducted. Implementing Experiment 3 with the paradigm that Fallon et al. developed to test the differential roles of attention and feature binding (Fallon, Mattiesing, Dolfen, Manohar, Husain, submitted) may be a pertinent way to look at this.

Overall, we found evidence for significantly enhanced short-term memory performance in trials where participants were presented with more information (**Figure 4.4**). Even though WM capacity models do not fully explain these results given that they have not been orientated to understanding retrieval (Pashler, 1988; Luck & Vogel, 1997; Bays & Husain, 2008; Wilken & Ma, 2004), ideas from the LTM literature on pattern separation and pattern completion - and the role of the hippocampus (Bakker et al., 2008; Squire, Stark, & Clark, 2004) - could possibly provide a better explanation of the results.

The ability to store and retrieve memoranda is intimately associated to the medial temporal lobe (MTL) (Squire et al., 2004) with dysfunctions in the MTL being a dominant factor in age-related

cognitive decline (Petersen et al., 1999; Stark et al., 2013). Critically, the role of the hippocampus<sup>14</sup>, is thought to be essential in binding information together (Pertzov et al., 2013; Libby, Hannula, & Ranganath, 2014; Fallon, Zokaei, & Husain, 2016; Liang et al., 2016) with VSTM conjunctive binding deficits recently suggested among the earliest cognitive changes indicative of the clinical state of Alzheimer's Disease (Dubois et al., 2016).

Our findings provide evidence for the existence of a pattern separation process at the time of encoding, making the stored features more distinct from each other, and pattern completion at the time of retrieval, enabling the repossession of the whole stored object from a retrieval cue (O'Reilly & McClelland, 1994). It is unclear how pattern separation and completion are related to the retro-cue hypothesis, yet they are not competing explanations.

The different mechanisms for pattern separation and pattern completion are considered in the context of hippocampal function theories (O'Reilly & McClelland, 1994; Squire et al., 2004; Norman & O'Reilly, 2003; Yassa & Stark, 2011). Pattern separation refers to the process of transforming similar inputs into distinct, independent memory representations in a way where memories can be stored quickly without inducing large amounts of interference (Bakker et al., 2008; Mcclelland, Mcnaughton, & O'Reilly, 1995; Norman & O'Reilly, 2003; Stark et al., 2013). Whereas the process of pattern completion enables the recovery of a complete stored representation based on a partial, degraded, or noisy retrieval cue (Ally et al., 2013; Bakker et al., 2008; O'Reilly & McClelland, 1994). Higher recall rates on trials where we lowered the border of pattern completion by presenting information with low similarity (**Experiment 3, Figure 4.2**) is in line with this theory, as well as participants ability to do better in high complexity trials compared to low complexity trials (**Experiment 3, Figure 4.4**).

Thus, we suggest that retrieving information according to levels of complexity taxes pattern completion (**Experiment 3, Figure 4.2 and Figure 4.4**) whereas pattern separation did not seem to have the same effect when manipulating encoding (**Experiment 1 and Experiment 2**) leading us to consider that perhaps, it is not much of a role of pattern separation to determine the pattern of recall.

In summary, we tested participants using new visual-short-term memory tasks with a continuous measure of report, allowing us to investigate the nature of WM deficits rather than only their frequency. We examined whether recall accuracy is affected by how information is retrieved from short-term memory in healthy people. The findings of the current study clearly showed that the nature of retrieval can significantly affect memory reports and that complexity at retrieval is what determines performance, with some variability by delay. We also propose that more information at retrieval (high complex memoranda) enhances the quality of mental representation. This suggests that an object is remembered as the sum of its parts, not as a whole: if an object was remembered as a whole, presenting half of the information would have the same exact effect on memory recall as presenting the entirety of the features of an object.

The novel tablet devices tasks implemented throughout this research project were developed thanks to different engineering contributions:

- defining research problems identified when reviewing published works;

<sup>&</sup>lt;sup>14</sup> The most significant component of the MTL.

- finding and analysing **solutions** while considering the limitations imposed by practicality and objectives;
- **designing** an experimental task that considered different constraints in order to develop a test that is simple enough to control for different variables, easy to use and with the right time length to be able to collect high quality data without frustrating the user;
- **conducting research** in more than 60 participants using *Oxford Psychology Research Participant Recruitment Scheme* on the SONA and **analysing** the data;
- applying different **techniques** and **computer tools**, such as *JSON Editor Online*, *MATLAB*® and *IBM SPSS Statistics* to produce and examine a technological solution that translates science into an application that fulfils to medical needs.

Thus, this research project proposes a solution that can be further developed and potentially introduced in clinics to assist in monitoring memory responses in different clinical populations.

# 6. 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 amnestic mild cognitive impairment. *Hippocampus*, 23(12), 1246–1258.
- Astle, D. E., Summerfield, J., Griffin, I., & Nobre, A. C. (2012). Orienting attention to locations in mental representations. *Attention, Perception, & Psychophysics*, 74(1), 146–162.
- Baddeley, A. (2003). Working memory and language: an overview. *Journal of Communication Disorders*, (36), 189–208.
- Baddeley, A., Bressi, S., Della Sala, S., Logie, R., & SpiInnler, H. (1991). The Decline Of Working Memory In Alzheimer's Disease. *Brain*, 114(6), 2521–2542.
- Baddeley, A., & Hitch, G. (1974). Working Memory. *Psychology of Learning and Motivation*, 8, 47–89.
- Baddeley, A., Logie, R., Bressi, S., Sala, S. Della, & Spinnler, H. (1986). Dementia and working memory. *The Quarterly Journal of Experimental Psychology Section A*, *38*(4), 603–618.
- Baddeley, A., & Logie, R. H. (1992). Auditory imagery and working memory. *Lawrence Erlbaum* Associates, 179–197.
- Bakker, A., Kirwan, C. B., Miller, M., & Stark, C. E. L. (2008). Pattern Separation in the Human Hippocampal CA3 and Dentate Gyrus. *Science*, *319*(5870), 1640–1642.
- 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.
- Barrouillet, P., De Paepe, A., & Langerock, N. (2012). Time causes forgetting from working memory. *Psychonomic Bulletin & Review*, *19*(1), 87–92.
- Bays, P. M., Catalao, R. F. G., Husain, M., J., D., C., K., & M., H. (2009). The precision of visual working memory is set by allocation of a shared resource. *Journal of Vision*, 9(10), 7–7.
- Bays, P. M., Gorgoraptis, N., Wee, N., Marshall, L., Husain, M., & S., K. J. (2011). Temporal dynamics of encoding, storage, and reallocation of visual working memory. *Journal of Vision*, 11(10), 6–6.
- Bays, P. M., & Husain, M. (2008). Dynamic shifts of limited working memory resources in human vision. *Science*, 321(5890), 851–4.
- 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.
- Brown, J. (1958). Some tests of the decay theory of immediate memory. *Quarterly Journal of Experimental Psychology*, 10(1), 12–21.
- Ceraso, J. (1985). Unit Formation in Perception and Memory. *Psychology of Learning and Motivation*, 19, 179–210.
- Colby, C. L., & Goldberg, M. E. (1999). Space And Attention In Parietal Cortex. Annual Review of Neuroscience, 22(1), 319–349.
- Corbetta, M., Miezin, F., Shulman, G., & Petersen, S. (1993). A PET study of visuospatial attention. *Journal of Neuroscience*, 13(3), 1202–1226.
- Corbetta, M., Shulman, G. L., & Miezin, F. M. (1995). Superior Parietal Cortex Activation During Spatial Attention Shifts and Visual Feature. *Petersen Source: Science, New Series*, 270(5237), 802–805.
- Cowan, N. (2001). Metatheory of storage capacity limits. *Behavioral and Brain Sciences.*, 24(1), 154–176.
- Cowan, N. (2010). The Magical Mystery Four. Current Directions in Psychological Science, 19(1), 51-

- Cowan, N. (2008). What are the differences between long-term, short-term, and working memory? *Progress in Brain Research*, *169*, 323–38.
- Dorion, A., Sarazin, M., Hasboun, D., Hahn-Barma, V., Dubois, B., Zouaoui, A., ... Duyme, M. (2002). Relationship between attentional performance and corpus callosum morphometry in patients with Alzheimer's disease. *Neuropsychologia*, 40(7), 946–956.
- Dubois, B., Hampel, H., Feldman, H. H., Scheltens, P., Aisen, P., Andrieu, S., ... Jack, C. R. (2016). Preclinical Alzheimer's disease: Definition, natural history, and diagnostic criteria. *Alzheimer's & Dementia*, 12(3), 292–323.
- Fallon, S. J., Zokaei, N., & Husain, M. (2016). Causes and consequences of limitations in visual working memory. *Ann. N.Y. Acad. Sci*, *1369*, 40–54.
- Friedman-Hill, S. R., Robertson, L. C., & Treisman, A. (1995). Parietal Contributions to Visual Feature Binding: Evidence from a Patient with Bilateral. *Science, New Series*, *269*(5225), 853–855.
- Gorgoraptis, N., Catalao, R. F. G., Bays, P. M., & Husain, M. (2011). Dynamic Updating of Working Memory Resources for Visual Objects. *Journal of Neuroscience*, *31*(23), 8502–8511.
- Griffin, I. C., & Nobre, A. C. (2003). Orienting Attention to Locations in Internal Representations. Journal of Cognitive Neuroscience, 15(8), 1176–1194.
- Haxby, J. V, Grady, C. L., Horwitz, B., Ungerleider, L. G., Mishkin, M., Carson, R. E., ... Rapoport, S. I. (1991). Dissociation of object and spatial visual processing pathways in human extrastriate cortex (regional cerebral blood flow/positron emission tomography). *Neurobiology*, 88, 1621–1625.
- Horowitz, T. S., & Wolfe, J. M. (1998). Visual search has no memory. Nature, 394(6693), 575-577.
- Hunsaker, M., & Kesner, R. (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.
- Irwin, D. E. (1991). Information Integration across Saccadic Eye Movements. *Cognitive Psychology*, 23, 42–456.
- Ji Ma, W., Husain, M., & Bays, P. M. (2014). Changing concepts of working memory. *Nature Neuroscience*, *17*(3), 347–356.
- Johnson, J. S., Hollingworth, A., & Luck, S. J. (2008). The role of attention in the maintenance of feature bindings in visual short-term memory. *Journal of Experimental Psychology. Human Perception* and Performance, 34(1), 41–55.
- Kane, M. J., & Engle, R. W. (2002). The role of prefrontal cortex in working-memory capacity, executive attention, and general fluid intelligence: An individual-differences perspective. *Psychonomic Bulletin & Review*, 9(4), 637–671.
- Kensinger, E. A., Shearer, D. K., Locascio, J. J., Growdon, J. H., & Corkin, S. (2003). Working memory in mild Alzheimer's disease and early Parkinson's disease. *Neuropsychology*, *17*(2), 230–239.
- Kuo, B.-C., Stokes, M. G., & Nobre, A. C. (2012). Attention Modulates Maintenance of Representations in Visual Short-term Memory. *Journal of Cognitive Neuroscience*, 24(1), 51–60.
- Landman, R., Spekreijse, H., & Lamme, V. A. F. (2003). Large capacity storage of integrated objects before change blindness. *Vision Research*, *43*(2), 149–164.
- Lewandowsky, S., Geiger, S. M., Morrell, D. B., & Oberauer, K. (2010). Turning simple span into complex span: Time for decay or interference from distractors? *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 36(4), 958–978.
- Lewandowsky, S., Geiger, S. M., & Oberauer, K. (2008). Interference-based forgetting in verbal short-

term memory. Journal of Memory and Language, 59(2), 200-222.

- Lewandowsky, S., & Oberauer, K. (2009). No evidence for temporal decay in working memory. *Journal* of Experimental Psychology: Learning, Memory, and Cognition, 35(6), 1545–1551.
- Liang, Y., Pertzov, Y., Nicholas, J. M., Henley, S. M. D., Crutch, S., Woodward, F., Husain, M. (2016). Visual short-term memory binding deficit in familial Alzheimer's disease. *Cortex*, 78, 150–164.
- Libby, L. A., Hannula, D. E., & Ranganath, C. (2014). Medial temporal lobe coding of item and spatial information during relational binding in working memory. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *34*(43), 14233–42.
- Loaiza, V. M., & McCabe, D. P. (2012). Temporal–contextual processing in working memory: Evidence from delayed cued recall and delayed free recall tests. *Memory & Cognition*, 40(2), 191–203.
- Luck, S. J., & Vogel, E. K. (1997). The capacity of visual working memory for features and conjunctions. *Nature*, 390, 279–81.
- Luck, S. J., & Vogel, E. K. (2013). Visual working memory capacity: from psychophysics and neurobiology to individual differences. *Trends in Cognitive Sciences*, *17*(8), 391–400.
- Marshall, L., & Bays, P. M. (2013). Obligatory encoding of task-irrelevant features depletes working memory resources. *Journal of Vision*, 13(2), 21–21.
- Matsukura, M., Luck, S. J., & Vecera, S. P. (2007). Attention effects during visual short-term memory maintenance: protection or prioritization? *Perception & Psychophysics*, 69(8), 1422–34.
- 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.
- Miller, G. A. (1956). The magical number seven, plus or minus two: Some limits on our capacity for processing information. *Psychological Review*, *101*(2), 343–352.
- Mishkin, M., Ungerleider, L. G., & Macko, K. A. (1983). Object vision and spatial vision: two cortical pathways. *Trends in Neurosciences*, *6*, 414–417.
- Norman, K. A., & O'Reilly, R. C. (2003). Modeling hippocampal and neocortical contributions to recognition memory: A complementary-learning-systems approach. *Psychological Review*, *110*(4), 611–646.
- O'Reilly, R. C., & McClelland, J. L. (1994). Hippocampal conjunctive encoding, storage, and recall: Avoiding a trade-off. *Hippocampus*, 4(6), 661–682.
- Oberauer, K. (2002). Access to Information in Working Memory: Exploring the Focus of Attention. *Journal of Experimental Psychology*, 28(3), 411–421.
- Oberauer, K., Farrell, S., Jarrold, C., Pasiecznik, K., & Greaves, M. (2012). Interference between maintenance and processing in working memory: The effect of item-distractor similarity in complex span. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 38*(3), 665–685.
- Oberauer, K., & Kliegl, R. (2006). A formal model of capacity limits in working memory. *Journal of Memory and Language*, 55(4), 601–626.
- Oberauer, K., & Lewandowsky, S. (2008). Forgetting in immediate serial recall: Decay, temporal distinctiveness, or interference? *Psychological Review*, *115*(3), 544–576.
- Oberauer, K., Lewandowsky, S., Farrell, S., Jarrold, C., & Greaves, M. (2012). Modeling working memory: An interference model of complex span. *Psychonomic Bulletin & Review*, 19(5), 779–819.
- Oberauer, K., & Lin, H.-Y. (2017). An interference model of visual working memory. *Psychological Review*, *124*(1), 21–59.

- Olivers, C. N. L., Meijer, F., & Theeuwes, J. (2006). Feature-Based Memory-Driven Attentional Capture: Visual Working Memory Content Affects Visual Attention. *Journal of Experimental Psychology*, *32*(5), 1243–1265.
- Palmer, J. (1990). Attentional limits on the perception and memory of visual information. *Journal of Experimental Psychology: Human Perception and Performance*, *16*(2), 332–350.
- Pashler, H. (1988). Familiarity and visual change detection. *Perception & Psychophysics*, 44(4), 369–378.
- Perry, R. J., Watson, P., & Hodges, J. R. (2000). The nature and staging of attention dysfunction in early (minimal and mild) Alzheimer's disease: relationship to episodic and semantic memory impairment. *Neuropsychologia*, *38*(3), 252–271.
- Pertzov, Y., Bays, P. M., Joseph, S., & Husain, M. (2013). Rapid Forgetting Prevented by Retrospective Attention Cues. *Journal of Experimental Psychology*, *39*(5), 1224–1231.
- Pertzov, Y., Dong, M. Y., Peich, M.-C., Husain, M., & Schumacher, E. (2012). Forgetting What Was Where: The Fragility of Object-Location Binding. *PLoS ONE*, 7(10), e48214.
- Pertzov, Y., Manohar, S., & Husain, M. (2016). Rapid forgetting results from competition over time between items in visual working memory. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 43(4), 528–536.
- Pertzov, Y., Miller, T. D., Gorgoraptis, N., Caine, D., Schott, J. M., Butler, C., & Husain, M. (2013). Binding deficits in memory following medial temporal lobe damage in patients with voltage-gated potassium channel complex antibody-associated limbic encephalitis. *Brain*, 136(8), 2474–2485.
- Petersen, R. C., Smith, G. E., Waring, S. C., Ivnik, R. J., Tangalos, E. G., & Kokmen, E. (1999). Mild Cognitive Impairment. *Archives of Neurology*, *56*(3), 303.
- Purcell, B. A., Heitz, R. P., Cohen, J. Y., Schall, J. D., Logan, G. D., & Palmeri, T. J. (2010). Neurally constrained modeling of perceptual decision making. *Psychological Review*, 117(4), 1113–43.
- Rerko, L., & Oberauer, K. (2013). Focused, Unfocused, and Defocused Information in Working Memory Discrete-Capacity Theories. *Journal of Experimental Psychology*, 39(4), 1075–1096.
- Rerko, L., Souza, A. S., & Oberauer, K. (2014). Retro-cue benefits in working memory without sustained focal attention. *Memory & Cognition*, 42(5), 712–728.
- Rudy, J. W. (2009). Context representations, context functions, and the parahippocampal-hippocampal system. *Learning & Memory*, *16*(10), 573–85.
- Saito, S., & Miyake, A. (2004). On the nature of forgetting and the processing–storage relationship in reading span performance. *Journal of Memory and Language*, 50(4), 425–443.
- Simone, P. M., & Baylis, G. C. (1997). Selective attention in a reaching task: Effect of normal aging and alzheimer's disease. *Journal of Experimental Psychology: Human Perception and Performance*, 23(3), 595–608.
- Souza, A. S., & Oberauer, K. (2016). In search of the focus of attention in working memory: 13 years of the retro-cue effect. *Attention, Perception, & Psychophysics*, 78(7), 1839–1860.
- Squire, L. R., Stark, C. E. L., & Clark, R. E. (2004). The Medial Temporal Lobe. Annual Review of Neuroscience, 27(1), 279–306.
- Stark, S. M., Yassa, M. A., Lacy, J. W., & Stark, C. E. L. (2013). A task to assess behavioral pattern separation (BPS) in humans: Data from healthy aging and mild cognitive impairment. *Neuropsychologia*, *51*(12), 2442–2449.
- Todd, J. J., & Marois, R. (2004). Capacity limit of visual short-term memory in human posterior parietal cortex. *Nature*, 428(6984), 751–754.
- Towse, J. N., Hitch, G. J., & Hutton, U. (2000). On the interpretation of working memory span in adults. *Memory & Cognition*, 28(3), 341–348.

- Treisman, A. M., & Gelade, G. (1980). A Feature-Integration Theory of Attention. *Cognitive Psychology*, *12*, 97–136.
- Treisman, A., & Zhang, W. (2006). Location and binding in visual working memory. *Memory & Cognition*, 34(8), 1704–1719.
- van Moorselaar, D., Olivers, C. N. L., Theeuwes, J., Lamme, V. A. F., & Sligte, I. G. (2015). Forgotten but not gone: Retro-cue costs and benefits in a double-cueing paradigm suggest multiple states in visual short-term memory. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 41(6), 1755–1763.
- Vogel, E. K., Woodman, G. F., & Luck, S. J. (2001). Storage of features, conjunctions, and objects in visual working memory. *Journal of Experimental Psychology: Human Perception and Performance*, 27(1), 92–114.
- Ward, R., Danziger, S., Owen, V., & Rafal, R. (2002). Deficits in spatial coding and feature binding following damage to spatiotopic maps in the human pulvinar. *Nature Neuroscience*, 5(2), 99–100.
- Wheeler, M. E., & Treisman, A. M. (2002). Binding in Short-Term Visual Memory. *Smith & Jonides*, 131, 48–64.
- Wilken, P., & Ma, W. J. (2004). A detection theory account of change detection. *Journal of Vision*, 4(12), 1120–1135.
- Williams, M., Hong, S. W., Kang, M.-S., Carlisle, N. B., & Woodman, G. F. (2013). The benefit of forgetting. *Psychonomic Bulletin & Review*, 20(2), 348–355.
- Wolfe, J. M. (1999). Inattentional Amnesia, In V. Coltheart (Ed.), Fleeting Memories, 71-94.
- Yanhong, O., Chandra, M., & Venkatesh, D. (2013). Mild cognitive impairment in adult: A neuropsychological review. Annals of Indian Academy of Neurology, 16(3), 310–8.
- Yassa, M. A., & Stark, C. E. L. (2011). Pattern separation in the hippocampus. *Trends in Neurosciences*, 34(10), 515–525.
- Zhang, W., & Luck, S. J. (2008). Discrete fixed-resolution representations in visual working memory. *Nature*, 453(7192), 233–236.

# 7. APPENDIX

# 7.1. Experiment 1: Manipulation of encoding and retrieval on memory recall

# 7.1.1.Reaction Time

Reaction time is the length of time taken by participants to touch the correct shape, in the twoalternative choice (**Figure 7.1**). Note that trials with incorrect identifications were excluded from further analysis.



**Figure 7.1 Reaction Time (s) for Experiment 1:** Reaction Time for different encoding and different retrieval, for Short (1s) and Long Delays (4s). At retrieval, manipulation of complexity and competition by probing by colour (low complexity), shape (high complexity), dual colour (low competition) and single colour (high competition). A Paired sample *t test* was applied, \* *p-values < .*05 and \*\* *p-values < .*01. Error bars reflect SEM.

A repeated measures ANOVA was conducted that examined the effect varying the manner in which stimuli had to be encoded (Circle: Colour, SSDC: Colour and DCS: Colour) and delay (1s or 4s) had on reaction time.

There was no significant effect of **encoding type** (F(2, 38) = .547, p = .561) or effect of **delay** (F(1, 19) = 3.077, p = .096) or **interaction effect** between encoding type and delay (F(2, 38) = 4.976, p = .016).

Next, we looked how varying the **stimuli retrieved** affected reaction time. We used ANOVA with repeated measures on retrieval type (DCS: Colour, DCS: Shape, DCS: DC, DCS: SC) and delay (1s or 4s). There was a main effect of **retrieval type** (F(3, 57) = 30.492, p < .001), **delay** (F(1, 19) = 29.427, p < .001) and an **interaction effect** between delay and retrieval type (F(3, 57) = 11.108, p < .001).

**Table 7.1 Summary of Paired sample** *t-test* **for Reaction Time on different retrieval trials**. \* *p-values* < .05 and \*\* *p-values* < .01.

Paired Conditions	SD	t	df	р
DCS: Colour - DCS: Shape (Short Delay)	835.9	5.699	19	<.001**
DCS: Colour - DCS: DC (Short Delay)	492.3	-6.320	19	<.001**
DCS: Colour - DCS: SC (Short Delay)	527.5	-7.153	19	<.001**
DCS: Shape - DCS: DC (Short Delay)	523.8	3.156	19	.005*
DCS: Shape - DCS:SC (Short Delay)	602.6	1.644	19	.1166
DCS: DC - DCS: SC (Short Delay)	449.5	-1.473	19	.1571
DCS: Colour - DCS: Shape (Long Delay)	1041	5.490	19	<.001**
DCS: Colour - DCS: DC (Long Delay)	813.4	-7.794	19	<.001**
DCS: Colour - DCS:SC (Long Delay)	668.6	-7.402	19	<.001**
DCS: Shape - DCS: DC (Long Delay)	778.7	801	19	<.001**
DCS: Shape - DCS: SC (Long Delay)	614.4	1.248	19	.2273
DCS: SC – DCS: DC (Long Delay)	593.3	2.344	19	.0301*
DCS: Colour (Short Delay) – DCS: Colour (Long Delay)	244.9	.5070	19	.6180
DCS: Shape (Short Delay) – DCS: Shape (Long Delay)	421.65	-1.962	19	.065
DCS: DC (Short Delay) – DCS: DC (Long Delay)	466.1	-6.660	19	<.001**
DCS:SC (Short Delay) – DCS: SC (Long Delay)	494.2	-2.128	19	.04667*

# 7.1.2. Chance

Chance, also denoted random guessing, is the probability of making a guess response in which there is no correspondence between a response and any of the placements participants were shown during that trial (**Figure 7.2**).

Note that trials with incorrect identifications were excluded from further analysis.



**Figure 7.2 Proportion of Errors due to Chance for Experiment 1:** Errors due to chance for different encoding and different retrieval, for Short (1s) and Long Delays (4s). At retrieval, manipulation of complexity and competition by probing by colour (low complexity), shape (high complexity), dual colour (low competition) and single colour (high competition). A Paired sample *t test* was applied, \* *p*-values < .05 and \*\* *p*-values < .01. Error bars reflect SEM.

A repeated measures ANOVA was conducted that examined the effect varying the manner in which stimuli had to be encoded (Circle: Colour, SSDC: Colour and DCS: Colour) and delay (1s or 4s) had on proportion of errors due to chance.

There was no significant effect of **encoding type** (F(2, 38) = 2.586, p = .094) or effect of **delay** (F(1, 19) = .350, p = .561) or **interaction effect** between encoding type and delay (F(2, 38) = .779, p = .453).

Next, we looked how varying the **stimuli retrieved** affected reaction time. We used ANOVA with repeated measures on retrieval type (DCS: Colour, DCS: Shape, DCS: DC, DCS: SC) and delay (1s or 4s). There was a main effect of **retrieval type** (F(3, 57) = .598, p = .001), **delay** (F(1, 19) = 9.160, p = .007) but no **interaction effect** between delay and retrieval type (F(3, 57) = 1.772, p = .177).

Paired Conditions	SD	t	df	р
DCS: Colour - DCS: Shape (Short Delay)	.2825	-3.230	19	.004**
DCS: Colour - DCS: DC (Short Delay)	.2083	-2.453	19	.024*
DCS: Colour - DCS: SC (Short Delay)	.1932	-1.053	19	.306
DCS: Shape - DCS: DC (Short Delay)	.2618	1533	19	.142
DCS: Shape - DCS:SC (Short Delay)	.3596	1.972	19	.063
DCS: DC - DCS: SC (Short Delay)	.3040	1.011	19	.325
DCS: Colour - DCS: Shape (Long Delay)	.4068	-2.968	19	.008**
DCS: Colour - DCS: DC (Long Delay)	.2189	1154	19	.909
DCS: Colour - DCS:SC (Long Delay)	.3738	-1.993	19	.061
DCS: Shape - DCS: DC (Long Delay)	.4720	2.504	19	.022*
DCS: Shape - DCS: SC (Long Delay)	.3274	1.413	19	.174
DCS: SC – DCS: DC (Long Delay)	.3784	-1.902	19	.072
DCS: Colour (Short Delay) – DCS: Colour (Long Delay)	.2200	-1.431	19	.169
DCS: Shape (Short Delay) – DCS: Shape (Long Delay)	.3918	-1.556	19	.136
DCS: DC (Short Delay) – DCS: DC (Long Delay)	.2895	.5901	19	.562
DCS:SC (Short Delay) – DCS: SC (Long Delay)	.3397	-2.521	19	.021*

# 7.2. Experiment 2: Cueing information before manipulating encoding and retrieval

### 7.2.1.Identification Accuracy

We started our analysis by looking at the proportion with which participants touched the correct shape in the identification phase (**Figure 7.3**).

Our main interest in this study was to examine how identification performance varied depending on the experiment (experiment1 or experiment2). As a consequence, we began by analysing the data as a between-subject design, given the presence of different participants in each experiment and therefore dealing with two independent samples, being "experiment" (experiment1 or experiment 2) the betweensubjects factor. There was no statistically significant difference between experiments for accuracy when manipulating both encoding (F(1, 38) = .673, p = .417) and retrieval (F(1, 38) = .432, p = .515).



**Figure 7.3** Accuracy for Experiment 2: The proportion with which participants touched the correct shape in the identification phase for different encoding and different retrieval, for Short (1s) and Long Delays (4s). A Paired sample *t* test was applied, \* p-values < .05 and \*\* p-values < .01. Error bars reflect SEM. Six conditions used in the working memory paradigm: Circle: Colour (encoded circle, probed by colour), SSDC: Colour (encoded same shapes with different colours, probed by colour), DCS: Colour (encoded different colour shapes, probed by colour), DCS: Shape (encoded different colour shapes, probed by 2 colours) and DCS: SC (encoded by different colour shapes, probed by 1 colour).

The data pertaining Experiment 2 (**Figure 7.3**) was analysed while operating within the same methodological framework of Experiment 1. Results were substantially the same as Riverhead, see **Table 7.3**.

**Table 7.3 Analysis of variance (ANOVA) of Experiment 2 on Accuracy.** In blue are reported the results of a repeated measures ANOVA that examined the effect varying the manner in which stimuli had to be encoded (Circle: Colour, SSDC: Colour and DCS: Colour) and delay (1s or 4s) had on accuracy levels. In red are reported the results of a repeated measures ANOVA with the complexity of the information presented at retrieval (DCS: Colour, DCS: Shape, DCS: DC, DCS: SC) and delay (1s or 4s) as within subject factors.

ANOVA on Identification Accuracy	df	F	p-value	MSE
Encoding type	2	2.704	.098	.021
Delay	1	.045	.834	.022
Interaction between encoding type and delay	2	1.495	.239	.019
Retrieval type	3	88.437	< .001	.095
Delay	1	34.803	< .001	.047
Interaction between retrieval type and delay	3	6.22	.006	.067

Trailing the conclusions from Experiment 1, there was no o main effect of **encoding type** (F(2, 38) = 2.704, p = .098), or effect of **delay** (F(1, 19) = .045, p = .834) or **interaction** between encoding type and delay (F(1, 19) = 1.495, p = .239) on accuracy.

Also in concordance with the previous enquiry, a substantial influence of **retrieval type** was found (F(3, 57) = 88.437, p < .001). We then proceeded with our investigation through the customary disjunction between dimensional complexity and competition.

Looking at trial where we manipulated **complexity**, although matched on dimensional complexity participants were inaccurate to a much greater extent when they were asked to retrieve by shape (DCS: Shape) compared to colour (DCS: Colour) (t(19) = 16.419, p < .001). They also demonstrated better accuracy results when probed by colour (DCS: Colour) compared to different colour shapes (DCS: DC) (t(19) = 10.167, p < .001). Additionally, the proportion with which participants touched the correct shape in the identification phase, by contrasting with retrieval by single feature of colour (DCS: Colour), deteriorated when they were probed by shapes with a single colour (DCS: SC) (t(19) = 13.303, p < .001). Hence, we continued verifying the trend that increases in the number of features while probing, particularly in trials where participants were required to retrieve information by shape, demanded inexorable losses of performance.

Even though participants were generally less accurate when presented with different shapes with a single colour (DCS: SC) compared to different shapes with different colours (DCS: DC), there was no significant distinction when the level of **competition** was manipulated at retrieval (t(19) = 1.173, p = .255).

Shorter retentions periods were associated with significantly smaller recall errors (F(1, 19) = 34.803, p < .001).

**Interaction** effect between retrieval type and delay was significant (F(3, 57) = 6.22, p = .006).

This effect varied according to the nature of retrieval, as well. Participants were significantly less accurate for long delays (4s) compared to short (1s), on trials where they had to retrieve by shape (DCS: Shape) (t(19) = 3.163, p = .005), dual colour (DCS:DC) (t(19) = 3.183, p = .005) and single colour (DCS: SC) (t(19) = 4.669, p = .0002). However, in trials where they were probed by colour (DCS: Colour), delay did not exert any considerable effect (t(19) = .809, p = .428).

### 7.2.2. Precision

We proceeded with the analysis by examine the distance (cm) between the reported location and the original location of the target shape (**Figure 7.4**). Trials with incorrect identifications were precluded from further analysis.

To determine whether precision varied depending on the experiment (experiment1 or experiment2), and to provide a dependable estimate of its extent, the data was analysed as a between-subject design, with 'experiment' as a between-subjects factor (experiment 1 or experiment 2).

There was no significant difference between experiments for precision as a function of encoding (F(1, 38) = .622, p = .435) or retrieval (F(1, 38) = .061, p = .807).



**Figure 7.4 Precision for Experiment 2**: Error distance (cm) for different encoding and different retrieval, for Short (1s) and Long Delays (4s). A Paired sample *t* test was applied, \* p-values < .05 and \*\* p-values < .01. Error bars reflect SEM. Six conditions used in the working memory paradigm: Circle: Colour (encoded circle, probed by colour), SSDC: Colour (encoded same shapes with different colours, probed by colour), DCS: Colour (encoded different colour shapes, probed by colour), DCS: Shape (encoded different colour shapes, probed by shape), DCS: DC (encoded different colour shapes, probed by 2 colours) and DCS: SC (encoded by different colour shapes, probed by 1 colour).

Evaluating the localisation performance of Experiment 2 (**Figure 7.4**) was achieved by implementing the same statistical approach as in Experiment 1. Those results are presented in **Table 7.4** which are largely the same as in Experiment 1.

**Table 7.4 Analysis of variance (ANOVA) of Experiment 2 on Precision.** Results of a repeated measures ANOVA that examined the effect varying the manner in which stimuli had to be encoded (Circle: Colour, SSDC: Colour and DCS: Colour) and delay (1s or 4s) had on precision are presented in blue. In red are reported the results of a repeated measures ANOVA with the complexity of the information presented at retrieval (DCS: Colour, DCS: Shape, DCS: DC, DCS: SC) and delay (1s or 4s) as within subject factors.

ANOVA on Precision	df	F	p-value	MSE
Encoding type	2	1.216	.302	602.137
Delay	1	30.176	< .001	228.951
Interaction between encoding type and delay	2	.861	.419	614.814
Retrieval type	3	58.605	< .001	1933.106
Delay	1	67.717	< .001	754.545
Interaction between retrieval type and delay	3	7.639	.002	952.808

Similar to identification performance, we used a repeated measures ANOVA with encoding type (Circle: Colour, SSDC: Colour and DCS: Colour) and delay (1s or 4s) as within-subject factors to analyse localization performance. **Encoding type** significantly influenced the fidelity of working memory in young adults (F(2,38) = 4.619, p = .017). The representation of dual features of different shapes and colour during encoding (DCS: Colour) lead to significant worse precision compared to encoding single feature of colour (Circle: Colour) (t(19) = 2.692, p = .014) and encoding dual feature of colour and shape (SSDC: Colour) (t(19) = 2.855, p = .010).

On top of this, precision was significantly affected by **delay** with shorter delays being associated with improved precision (F(1,19) = 11.395, p = .003). There was no **interaction** between encoding type and delay (F(2,38) = 1.130, p = .331). Therefore, type of encoding affected precision, specifically trials with more features were associated with impaired precision.

Keeping complexity at encoding constant, we then looked at how varying the **nature of retrieval** affected precision, using repeated measures ANOVA with retrieval type (DCS: Colour, DCS: Shape, DCS: DC, DCS: SC) and delay (1s or 4s) as within-subject factors. Again, we decomposed this effect by splitting our analysis into dimensional complexity and competition.

Precision was significantly affected by retrieval type (F(3,57) = 60.364, p < .001).

Precision was significantly affected by retrieval type (F(3,57) = 60.364, p < .001). Although matched on **dimensional complexity** (DCS: Colour and DCS: Shape), presenting feature of shape (DCS: Shape) at retrieval lead to reduced precision compared to single feature of colour (DCS: Colour) (t(19) = 11.737, p < .001). Participant's precision on trials where probed by dual feature of colour and shape (DCS: DC) and dual feature of shape and single colour (DCS:SC) was also reduced compared to retrieval by colour (DCS: Colour) ((t(19) = 6.478, p < .001), (t(19) = 3.013, p = .007) respectively). This indicates that participants were less precise when dimensional complexity was high compared when it was low.

By examining the levels of similarity in the features of the items that had to be retrieved, participants were significantly more precise when retrieving high **competition** information (DCS: SC) compared to low (DCS: DC) (t(19) = 5.164, p < .001). When comparing trials where participants were probed with single feature of shape (DCS: Shape) to trials where participants had to retrieve dual features of shape and colour (DCS: SC) *Figure 1.4* suggests that the presence of an extra feature to be

remembered lead to a smaller error distance, as was confirmed by the statistical difference (t(19) = 8.857, p < .001). Thus, extra information at retrieval lead to improved precision.

Additionally, for trials with different retrieval, the **delay** exerted a cost on precision with shorter delays being associated with improved precision (F(1,19) = 74.419, p < .001).

In contrast with trials where we manipulated the nature of encoding, **interaction between delay** and retrieval type significantly affected precision (F(3,57) = 13.601, p < .001), with shorter delays leading to a significant enhancement on precision when participants were asked to retrieve by shape, (DCS: Shape) (t(19) = 5.029, p < .001), by dual colour (DCS:DC) (t(19) = 5.004, p < .001) and by single colour (DCS:SC) (t(19) = 4.702, p < .001). However, delay did not exert an effect on trials where participants had to retrieve by colour (t(19) = .725, p = .477). Thus, as was the case for accuracy, the effect of retention period on precision varied according to the nature of retrieval.

### 7.2.3. Proportion of Errors due to Misbinding

A misbinding event results from recalling the correct object but dragging it to the location of another item presented in the memory array (**Figure 7.5**).

To assess how the proportion of errors due do misbinding fluctuated, the method applied to both variables previously scrutinized was replicated, with 'experiment' (experiment 1 or experiment2) as a between-subjects factor (**Table 7.5**).

There was not a statistically significant deviation between experiments regarding the proportion of swap errors when manipulating both encoding (F(1, 38) = .028, p = .868) and retrieval (F(1, 38) = .698, p = .409).



**Figure 7.5 Proportion of Misbinding for Experiment 2**: Proportion of "swap errors" for different encoding and different retrieval, for Short (1s) and Long Delays (4s). A Paired sample *t* test was applied, \* p-values < .05 and \*\* p-values < .01. Error bars reflect SEM. Six conditions used in the working memory paradigm: Circle: Colour (encoded circle, probed by colour), SSDC: Colour (encoded same shapes with different colours, probed by colour), DCS: Colour (encoded different colour shapes, probed by colour), DCS: Shape (encoded different colour shapes, probed by shape), DCS: DC (encoded different colour shapes, probed by 2 colours) and DCS: SC (encoded by different colour shapes, probed by 1 colour).

**Table 7.5 Analysis of variance (ANOVA) of Experiment 2 on errors due do misbinding.** In blue are presented the results of a repeated measures ANOVA that examined the effect of manipulating information during encoding and delay had on the proportion of errors due to misbinding. In red are described the results of a repeated measures ANOVA with the complexity of the information presented at retrieval and delay as within subject factors. Note that, contrary to the previous experiment, Experiment1, **encoding type** seems to be a strong modulator of the proportion of errors due to misbinding (F(2, 38) = 9.374, p = .00049).

ANOVA on proportion of errors due misbinding		F	p-value	MSE
Encoding type	2	9.374	.00049	.050
Delay	1	3.269	.086	.045
Interaction between encoding type and delay	2	1.081	.349	.058
Retrieval type	3	49.163	< .001	.083
Delay	1	4.513	.047	.054
Interaction between retrieval type and delay	3	1.067	.369	.059

Contrary to the previous experiment, Experiment1, **encoding type** seems to be a strong modulator of the proportion of errors due to misbinding (F(2, 38) = 9.374, p = .00049). Having to encode different colour shapes (DCS: Colour) enhanced misbinding in comparison to both encoding same shapes with different colours (SSDC: Colour) (t(19) = 2.644, p = .016) and circles (Circle: Colour) (t(19) = 4.290, p = .00396). Thus, misbinding appears to be greater when participants were required to encode more elaborated, complex information.

Both retention period duration (F(1, 19) = 3.269, p = .086) and interaction effect between encoding type and delay were not influential movers of swap errors (F(2, 38) = 1.081, p = .349).

We subsequently directed our focus to examine the effect that variations of the **retrieval type** inflicted on the proportion of misbinding. A main effect of task when keeping complexity at encoding constant was observed (F(3, 57) = 49.163, p < .001). This effect was scrutinized by parting the data into levels of complexity and levels of similarity.

The proportion of errors due to misbinding was significantly impacted by dimensional **complexity**. Although matched for putative levels of complexity, misbinding when retrieving by single feature of shape (DCS: Shape) was considerably increased with respect to retrieval by single feature of colour (DCS: Colour) (t(19)=11.3, p < .001). Additionally, binding information seems to be important in order to make less misbinding, since participants made significantly more misbindings when probed just by shape (DCS: Shape) compared both to when they were probed by shapes with different colours (DCS: DC) (t(19) = 8.771, p < .001) and shapes with the same colour (DCS: SC) (t(19) = 9.040, p < .001).

When looking at trials where **competition** was manipulated, misbinding did not increase when participants were asked to retrieve more similar objects (DCS: SC) in comparison to probing more distinctive ones (DCS: DC) (t(19) = .273, p = .788).

The likelihood of reporting the location of a non-target item varied with the duration of the **retention period**, with longer delays leading to higher proportion of errors due to misbinding (F(1, 19) = 4.513, p = .047).

There was no interaction effect between delay and retrieval type (F(3, 57) = 1.067, p = .369).
## 7.2.4. Reaction Time

Reaction time (s) was significantly shorter for experiment 2 (**Figure 7.6**) compared to experiment 1, both when manipulating encoding (F(1, 38) = 111.389, p < .001) and retrieval (F(1, 38) = 51.878, p < .001).



**Figure 7.6 Reaction Time (s) for Experiment 2**: Length of time taken to touch the correct shape for different encoding and different retrieval, for Short (1s) and Long Delays (4s). A Paired sample *t test* was applied, *\* p-values < .05* and *\*\* p-values < .01*. Six conditions used in the working memory paradigm: Circle: Colour (encoded circle, probed by colour), SSDC: Colour (encoded same shapes with different colours, probed by colour), DCS: Colour (encoded different colour shapes, probed by colour), DCS: Shape (encoded different colour shapes, probed by shape), DCS: DC (encoded different colour shapes, probed by 2 colour). Error bars reflect SEM.

The data was analysed in the same way as in Experiment 1.

There was a significant main effect of **encoding type** (F(2, 38) = 4.362, p = .040) with participants being significantly quicker to respond to the target when asked to encoded single feature colour (Circle: Colour) compared to when they had to encode dual feature different shape and colour (DCS: Colour) (t(19) = 2.222, p = .039). Participants were also faster to respond to target when they had to encode dual feature same shapes and different colour (SSDC: Colour) compared to dual feature different colour shapes (DCS: Colour) (t(19) = 2.094, p = .050). Thus, manipulating encoding exerted a significant effect on reaction time.

There was no main effect of **delay** (F(1, 19) = .469 p = .502) nor **interaction** between encoding type and delay (F(2, 38) = 1.065, p = .322).

Next, we looked how varying the stimuli retrieved affected reaction time. Once again, we decomposed this effect in order to analyse dimensional complexity and competition separately.

There was a main effect of **retrieval type** (F(3, 57) = 23.386, p < .001).

Reaction time was significantly affected by retrieval type (F(3,57) = 60.364, p < .001). Although matched on **dimensional complexity** (DCS: Colour and DCS: Shape), presenting feature of shape (DCS: Shape) at retrieval lead to reduced precision compared to single feature of colour (DCS: Colour) (t(19) = 5.192, p < .001)Participant's precision on trials where probed by dual feature of colour and shape (DCS: DC) and dual feature of shape and single colour (DCS:SC) was also reduced compared to retrieval by colour (DCS: Colour) ((t(19) = 6.293, p < .001), (t(19) = 6.277, p < .001) respectively). This indicates that reaction times were significantly higher when dimensional complexity was high compared when it was low.

Even though participants were slower to respond when presented with high competition trials (DCS: SC) compared to trials where they had to retrieve features with less similarities (DCS: DC) this difference wasn't significant (t(19) = .597, p = .557).

**Delay** also exerted a cost on reaction time, with longer delays being associated with longer reaction times ( $F(1, 19) = 32.814 \ p < .001$ ).

Finally, there was no interaction effect between delay and task (F(3, 57) = 2.281, p = .110).

# 7.2.5. Chance

When manipulating encoding, the proportion of errors due to chance was significantly higher experiment 2 (**Figure 7.7**) compared to experiment 1 (F(1, 38) = 4.246, p = .046). However, this was not the case when manipulating retrieval (F(1, 38) = .647, p = .426).



**Figure 7.7 Proportion of Errors due to Chance (s) for Experiment 2**: Proportion of random guessing for different encoding and different retrieval, for Short (1s) and Long Delays (4s). A Paired sample *t test* was applied, \* *p-values* < .05 and \*\* *p-values* <.01. Six conditions used in the working memory paradigm: Circle: Colour (encoded circle, probed by colour), SSDC: Colour (encoded same shapes with different colours, probed by colour), DCS: Colour (encoded different colour shapes, probed by colour), DCS: Shape (encoded different colour shapes, probed by shape), DCS: DC (encoded different colour shapes, probed by 2 colours) and DCS: SC (encoded by different colour shapes, probed by 1 colour). Error bars reflect SEM.

The data was analysed in the same way as in Experiment 1.

There was a significant main effect of **encoding type** (F(2, 38) = 6.923, p = .004) with trials where participants had to encode dual feature same shapes with different colours (SSDC: Colour) leading to significant more chance compare to trials where they had to encode single feature colour (Circle: Colour) (t(19)=3.655, p = .002).

There was also a main effect of **delay** with longer retentions periods leading significantly more errors due to chance compared to shorter delays (F(1,19) = 4.576 p = .046).

There was no interaction effect between delay and task (F(2, 38) = 5.134, p = .017).

Then, we looked how varying the stimuli retrieved affected the proportion of errors due to chance. Once again, we decomposed this effect in order to analyse dimensional complexity and competition separately.

There was a main effect of **retrieval type** (F(3, 57) = 5.709, p = .003).

Considering trials where we manipulated the complexity at retrieval, although matched on **dimensional complexity** participants made significantly more errors due to chance when asked to retrieve by shape (DCS: Shape) compared to colour (DCS: Colour) (t(19) = 3.309, p = .004). Participant's chance errors on trials where probed by dual feature of colour and shape (DCS: DC) and dual feature of shape and single colour (DCS:SC) was also reduced compared to retrieval by colour (DCS: Colour) ((t(19) = 3.008, p = .007), (t(19) = 1.099, p = .286) respectively). This indicates that errors due to chance were significantly lower when dimensional complexity was low compared when it was high.

Looking at trials where we manipulated **competition** there was no significant difference on chance when probing features with similarity (DCS: SC) compared to low similarity (DCS: DC) (t(19) = 1.818, p = .085). However, when comparing trials where they had to retrieve by single feature shape (DCS: Shape) and dual feature shape and same colour (DCS: SC) participants made significantly more errors due to chance when they only had to retrieve by single feature (t(19) = 2.567, p = .019).

**Delay** also exerted a cost on reaction time, with longer delays being associated with longer reaction times ( $F(1, 19) = 17.974 \ p = .0004$ ).

Lastly, there was no **interaction** effect between delay and retrieval type (F(3, 57) = 2.492, p = .077)

### 7.3. Experiment 3: Manipulation of complexity and competition at retrieval

#### 7.3.1.Reaction Time

A repeated measures ANOVA was conducted that examined the effect of complexity (high and low), competition (high and low) and delay (1s or 4s) on reaction time (**Figure 7.8**).

There was a main effect of **delay** (F(1, 20) = 12.811, p = .002).

There was a main effect of **complexity**, reaction time is significantly higher for low complexity trials compared to high complexity trials (F(1, 20) = 39.766, p < .001).

Reaction time was not significantly affected by **competition** (F(1, 20) = .333, p = .570).

There was an **interaction effect** between complexity and competition (F(1,20) = 6.475, p = .019). On trials high complexity trials, reaction time is significantly higher for low competition memoranda compared to high (t(20) = 2.126, p = .046). Additionally, on trials where we presented low competition memoranda, participants were significantly slower to respond to the target when presented with low complexity shapes compared to high (t(20) = 6.103, p < .001). On top of that, on trials where we presented low competition memoranda, they took significantly longer to respond when presented with low complexity trials compared to high (t(20) = 3.839, p = .001). However, manipulating competition on low complexity trials did not lead to any significant difference on reaction time (t(20) = .718, p = .481).

None of the other interactions were significant (p > .417).



**Figure 7.8 Reaction time (ms) for Experiment 3:** Time taken to touch the correct shape for low complexity trials and high complexity trials with manipulation of competition (low and high). A Paired sample *t test* was applied, \* *p*-values < .05 and \*\* *p*-value <.01. Error bars reflect SEM.

## 7.3.2. Chance

A repeated measures ANOVA was conducted that examined the effect of complexity (high and low) competition (high and low) and delay (1s or 4s) on proportion of errors due to chance (**Figure 7.9**).

There was a main effect of **delay** with participants being significantly more likely to make a error due to chance on trials with a longer maintenance (F(1, 20) = 8.290, p = .009).

The presence of more information decreased the probability of making a guess response (**Figure 7.9**), consequently making a chance error is more likely for low **complexity** trials compared to high complexity trials (F(1, 20) = 20.518, p = .000204).

Additionally, chance errors are significantly higher for low **competition** trials compared to high competition trials (F(1, 20) = 4.821, p = .040077).

The **interaction effect** between complexity and competition is significantly affecting the proportion of errors due to chance (F(1, 20) = 16.100, p = .000683). The proportion of errors due to chance were significantly diminished in the high complexity trials compared to the low complexity trials only on trials where we presented low competition memoranda (t(20)= 6.884, p < .001), not when presented with high competition memoranda (t(20)= .877, p = .391). Furthermore the proportion of errors due to chance were significantly diminished in the high competition trials compared to the low competition trials when participants were presented with less information (low complexity) (t(20) = 3.556, p = .002) but this difference was not significant when participants had to retrieve more information (high complexity) (t(20) = .308, p = .761).



None of the other interactions were significant (p > .159).

**Figure 7.9 Proportion of errors due to chance for Experiment 3**: Proportion of random guessing for low complexity trials and high complexity trials with manipulation of competition (low and high). A Paired sample *t test* was applied, \* *p*-values < .05 and \*\* *p*-values. Error bars reflect SEM.