Cognitive and neural factors underlying the manipulation of visual memory representations

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I, Mara Golemme, hereby declare that this thesis and the work presented in it is entirely my own. Where I have consulted work of others, this is always clearly stated.

Signed: Date:

Statement on Collaborative or Shared Data Collection

The data collection for some of the Chapters of this thesis (5 and 6) was conducted collaboratively with other Goldsmiths and non-Goldsmiths based researcher for a project led by my first supervisor Dr Marinella Cappelletti.

The analyses and data collection of the remaining studies were conducted exclusively by myself.

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ABSTRACT

Goal-directed behaviour relies on the ability to store relevant information in visual short-term memory (VSTM) and to briefly maintain its representation for manipulations (Visual Working Memory, VWM). Crucial cognitive processes for this ability include perceptual encoding, maintenance and retrieval of task-relevant stimuli, as well as selectively suppress task-irrelevant information. Despite the relevance of these processes is known, their combined and individual contribution is less clear, as well as the specific role of the initial perceptual accuracy and individual variability in manipulating information held in memory.

This thesis addresses these issues by examining the cognitive and neural processes underlying the maintenance of memory representations for short intervals.

In the first part of this work, we used a novel behavioural paradigm to study the role of perceptual accuracy as well as of the combined and individual contribution of other cognitive factors underlying visual short-term memory. A second study extended the investigation to the maintenance period, providing task-based and endogenous electrophysiological correlates of successful maintenance.

The second part of this thesis used a retro-cue based WM paradigm to investigate the attentional and inhibitory mechanisms involve in the maintenance process, and required when manipulating stored information. Considering the vulnerability of these processes in healthy ageing, the investigation is also extended to an older sample.

This last part of the thesis provided cognitive and neural results that reconciled contrasting findings on the WM literature based on retro-cue. Specifically, a novel concept of cognitive flexibility and its electrophysiological predictors are proposed to underlie individual variability in manipulating memory representation.

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LIST OF ABBREVIATIONS

VSTM	Visual Short-Term Memory
VWM	Visual Working Memory
EEG	Electroencephalography
rsEEG	resting state electroencephalography
RCC	Retro-cue cost
RCE	Retro-cue effect
LRTC	Long Range Temporal Correlation
MVPA	Multivariate Pattern Analysis

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CHAPTER 1: INTRODUCTION

This chapter provides the theoretical framework underlying the investigation of a specific component of visual short-term memory (VSTM) and working memory (VWM): the ability to maintain and manipulate short-term memory representations.

Particular focus is dedicated to experimental proxies to investigate VSTM, namely perceptual encoding, stimulus complexity and attentional processes, as well as to the impact of age-related processes on this ability. For each of these aspects, evidence from electrophysiology (EEG) is presented, with a focus on the use of this technique to investigate and predict memory ability. This chapter represents the theoretical ground on which this thesis is built, which itself aims to examine the neural and cognitive predictors of the ability to manipulate visual short-term memory representations in the young and ageing brain.

1.1 SHORT-TERM & WORKING MEMORY

1.1.1 DEFINITIONS

Visual short-term memory (VSTM) is the ability to retrieve visual information representations after a short delay (Shimi, Nobre, Astle, & Scerif, 2014). This ability is not only useful for detecting changes between two scenes, but also for integrating visual information to provide a stable and unified view of surrounding scenes, as well as to guide movements (Brouwer & Knill, 2010; Henderson & Hollingworth, 1999; Théau, 2012). While we hold visual information, its manipulation relies on a more elaborate form of VSTM, known as Visual Working Memory (VWM)(Ma, Husain, & Bays, 2014). This corresponds to the ability to actively maintain visual information and it plays an important role in many aspects of cognition, such as intelligence, decision-making, and planning (Luck & Vogel, 1997). In this context, VSTM refers to the visual storage component of VWM (Alvarez & Cavanagh, 2004; Todd & Marois, 2004) and in this thesis these terms will be used interchangeably.

1.1.2 THEORETICAL ACCOUNTS

One of the most distinctive aspect of VSTM ability consists of its limited capacity, usually intended in terms of set size. Past studies have often investigated this aspect by manipulating the number of items presented in the initial stimuli array. For instance, Vogel and Luck (1997) used a delay-to-sample match task whereby participants were presented with an array of up to 12 coloured squares, followed by 1-second delay and then another array of squares including one that changed in colour relative to the initial display. Results showed that the number of items stored did not exceed four, regardless of whether the stimulus feature to remember was one or more (Cowan, 2001; Luck & Vogel, 1997). This was taken as evidence that items are represented in memory as object "slots", considered the unit of VSTM. Moreover, within this theoretical framework, known as "slot model", the probability to retrieve information after a brief interval simply depends on the probability that the information is encoded (Cowan, 2001; Luck & Vogel, 1997; Pashler, 1988). Based on this model, VSTM capacity is underpinned by the activity of the posterior parietal cortex, which increases with the increment of the stimuli set size (Todd & Marois, 2004). This model lies on the problematic assumption that visual stimuli are encoded in a binary fashion (present or not), therefore neglecting the role of distracters (or internal state) in probing false positive responses (Wilken & Ma, 2004).

Later studies suggested a more continuous processing of encoding. Rather than referring to a limit on the number of stimuli that can be encoded, these models explained capacity limits in terms of object complexity and internal noise, ultimately affecting the quality of the stimuli's representations (Alvarez & Cavanagh, 2004; Eckstein, Thomas, Palmer, & Shimozaki, 2000; Verghese, 2004; Wilken & Ma, 2004). This new framework, known as "continuous-resource models" (Bays & Husain, 2008b; Wilken & Ma, 2004), was further elaborated by suggesting that VSTM capacity is represented by a shared and flexible pool of resources which are distributed over the visual stimuli in different gradients, depending on the level of precision at the encoding level and decrease with set size (‘variable-precision model’) (van den Berg, Shin, Chou, George, & Ma, 2012). Therefore, rather than being restricted by “slots”, recent theories conceptualize the limited VSTM capacity in terms of the quality of stimulus encoding (Bays & Husain, 2008b; Wilken & Ma, 2004). Since this thesis focuses on the quality of VSTM processes from encoding to retrieval, it is based on the “Continuous Resource model” as the theoretical framework.

1.1.2. The role of attention in memory processes

Because of the limited amount of data that can be held in VSTM, attentional processes are crucial to select relevant information and suppress irrelevant information (Desimone, 1996). Attention modulates stimulus selection based on bottom-up factors such as visual salience (Desimone & Duncan, 1995) and top-down processes, and by flexibly identifying task-relevant stimuli (Corbetta & Shulman, 2002). Attention influences memory and *vice versa*, as one can determine or bias the content of the other (de Fockert, 2010; de Fockert, Rees, Frith, & Lavie, 2001), making their relationship bidirectional (Desimone, 1996). For instance, Kane and colleagues found that individual differences in performing tasks tackling control of attention towards task-relevant items correlated to WM capacity (Kane, Conway, Bleckley, & Engle, 2001), supporting the view that the ability to keep relevant information in an active and accessible form reflects the ability to control attention.

The experimental part of this thesis will address how bottom-up and top-down attentional processes can guide VSTM and VWM in the selection of task-relevant memory representations. Furthermore, I will investigate how memory representation can be prioritized by attentional goal-directed processes across the life span.

1.1.3 the effect of Load and Individual variability in VSTM

The ability to store and manipulate visual information varies substantially depending on stimulus load and across individuals (Cowan, 2010).

Stimulus-load depends on the increment in the number of stimuli to encode and remember, and greater load typically corresponds to a decrease in performance (longer response times and/or lower level of accuracy) (Baddeley, 2001; Hester & Garavan, 2005). Another source of load for memory capacity is stimulus complexity (Alvarez and Cavanagh, 2004). This has been established using experimental paradigms such as a match-to-sample task based on stimuli varying in complexity (letters, colours, Chinese characters, polygons and shaded cubes), whereby less complex stimuli (i.e. colours versus shaded cubes) corresponded to a significantly higher recall accuracy (Alvarez & Cavanagh, 2004). Subsequent studies further indicated that perceptual complexity stimuli modulates memory performance irrespective of the number of items presented (Eng et al., 2005).

Load can therefore be intended as *memory-* or *information-based*, depending on whether the number of items or the stimulus complexity is manipulated (Eng, Chen, & Jiang, 2005a). In this thesis, *information-based load* will be manipulated in some of the experimental paradigms used (see Chapters 3 and 4).

Another factor characterising the ability to hold information is that it varies between individuals, and such variability can predict individual differences in intellectual abilities as well as memory changes across the life span (Cowan, 2010). The reasons underlying such differences have been of great interest in the memory domain. An obvious contributing factor is the amount of information that can be stored, which becomes more challenging with each increment in span length (Cowan, Fristoe, Elliott, Brunner, & Saults, 2006; Cowan, Morey, Aubuchon, Zwilling, & Gilchrist, 2010). Other factors accounting for individual variability are linked to the strategies used to manipulate memory information effectively. For instance, some studies have shown that low-capacity participants hold more task-irrelevant information (Kane et al., 2001; Vogel, McCollough, & Machizawa, 2005). The second half of the experimental chapters aim to explain and predict different behavioural patterns emerging from the ability to maintain and manipulate memory representations.

1.1.4 VSTM MODULATING COGNITIVE FACTORS

In laboratory settings, VSTM is often investigated using change detection tasks (Phillips, 1974). Such tasks consist of the brief presentation of a visual stimulus array (including one or more targets), followed after a short interval by a similar array (probe). Participants' task is usually to compare the probe and its target, and to report any detected changes. Successful performance in this type of task depends on the success of a number of distinct cognitive processes: 1) perceptual encoding and the discrimination of the stimuli, 2) the creation and maintenance of their visual representation in memory, and 3) their retrieval by comparing the probe to the target stimulus (Jonides et al., 2008) . Successful performance is further challenged by task-irrelevant information (referred to as no-target stimuli hereafter) which may appear during any of these three processes.

Several studies investigated these cognitive processes, emphasizing the impact of one or another. For instance, studies on perceptual encoding and on visual stimuli discrimination showed that successful VSTM performance critically depends on the integrity of the perceptual encoding (Craik & Lockhart, 1972; (Eng et al., 2005a). In their study, Eng and colleagues, varied the duration of the stimulus array presentation to show that limited time at encoding prevents a more stable and elaborate perception of a stimulus (i.e. perceptual grouping of similar items only occurs at longer stimuli presentation) (Eng et al., 2005a).

Therefore, depending on the depth/stage of the perceptual analysis, the memory trace may be characterized by richer or more sparse sensory representations, ultimately affecting the performance in change detection tasks (Craik & Lockhart, 1972b; Galli, 2014; Rodrigues, Sauzéon, Langevin, Raboutet, & N'Kaoua, 2010; Treisman, 1998).

In a recent VSTM review, Jonides and colleagues (2008) indicated some reasons why lack of explicit assessment of perceptual processes may generate misleading interpretation of results. One such reason is based on the assumption that stimuli presented within the established fixed-limit capacity fall within the attention focus, allowing memory representations to be effectively encoded and retrieved (Garavan, 1998; McElree, 2006). However, perceptual encoding is not limited to the focus of attention and participants could have control over this process, for instance by ignoring incoming stimuli. Indeed, supporting evidence from neuroimaging studies shows that the presentation of distracting stimuli, relative to the conditions where no distracting stimuli were presented, is associated with increased activity in the dorsolateral prefrontal cortex, selectively modulating more posterior perceptual areas and their processing of incoming visual stimuli (Postle, 2006).

However, when the mechanism of ignoring incoming stimuli fails, distracting stimuli are processed, which can have a detrimental effect on VSTM performance. Similarly, another point reported in Jonides and colleagues's (2008) review is the possibility that encoding and the memory representation may be disrupted by a new stimulus entering the focus of attention, either a distractor or a probe. These have the potential to overwrite features of the initial target stimuli, ultimately affecting the quality of their early representation. Altogether, these points reveal how relevant it is to assess the quality of perceptual stimuli encoding for a deep understanding of VSTM performance.

Following perceptual encoding, stimulus representations are maintained in memory (Hollingworth, 2003), a process that activates the same brain circuits involved in primitive attentive processes such as perceptual encoding (Miller, 2000). This represents further evidence that memory and perceptual processes provide a combined contribution to performance, which motivates investigating their joint contribution.

The final VSTM stage involved in change detection tasks corresponds to stimuli retrieval or recognition, depending on task instruction (Smith & Nielsen, 1970). The retrieval or recognition of task-relevant (target) information is substantially influenced by the degree of similarity between a target and a probe (Awh et al., 2007; Eng et al., 2005; Jonides & Nee, 2006), with a strong involvement of lateral and anterior prefrontal cortex (Johnson et al., 2008). Additionally, if participants have no *a priori* knowledge of the target stimulus among the presented visual stimuli, successful performance also requires disregarding the memory representations which do not correspond to the target (no-target stimulus) (Shin & Ma, 2017).

In this case, it is crucial to understand to what extent successful VSTM performance reflects the quality of the initial encoding, the suppression of distracting stimuli, and/or the unsuccessful discrimination of the stimuli. Moreover, this approach is based on the idea that memory processes result from the contribution of different factors, which should be jointly considered and explicitly tested. Chapters 3 and 4 aim at addressing these questions by using a novel VSTM paradigm that allows us to assess the combined and the individual contribution of perceptual, memory and inhibitory factors on change detection performance, while directly controlling for perceptual discrimination accuracy.

1.1.5 MAINTENANCE IN VISUAL SHORT-TERM MEMORY (VSTM)

How we maintain information in memory has been a pressing question in the domain of STM and different explanations have been proposed (Jonides et al., 2008). One of these concerns the encoding of visual stimuli in VSTM in relation to each other, and more specifically that in simultaneous presentations stimulus encoding influences the subsequent memory representation. This is usually termed "relational processing" (Jiang, Olson, & Chun, 2000). Stimulus representations can be related to each other in two ways: via semantic mechanisms, when a stimulus matches a semantic context stored in long-term memory (for example, it is relatively easy to identify and remember a fridge in a kitchen, as it is a probable object to be found in that specific context); or via perceptual grouping, when many stimuli are grouped based on a salient feature (Jiang et al., 2000). This perceptual relational processing approach is adopted in this thesis (Chapters 3 and 4), whereby two sinusoidal gratings (Gabor patches) with no explicit semantic value could have the same or different gradients of similarity in terms of degrees of orientation. Perceptual grouping is expected to occur when the two Gabor patches have the same degree of orientation.

Stimulus maintenance could be also assessed by investigating the effect of memory capacity during the delay interval (Vogel & Machizawa, 2004), for instance by providing visuo-spatial attention cues ('retrospective-cue') which re-orient attention towards cued items held in memory (Awh et al., 2007; Kuo, Stokes, & Nobre, 2012; Postle, 2006) (see section 1.1.4 for further discussion), or by varying the length of the retention interval (Magnussen & Greenlee, 1992; Magnussen, Greenlee, Asplund, & Dyrnes, 1990). The former method also corresponds to the expedient implemented in this thesis (Chapters 4 and 5) to investigate the role of selective attention processes during stimulus maintenance.

1.1.5.1 Neural correlates of maintenance in VSTM

Neuroimaging studies have shown that stimulus maintenance is associated with activity in a set of fronto-parietal areas (Postle, 2015). Specifically, these areas allow keeping the representations coming from sensory-posterior regions, and prevent their disruptions by new incoming stimuli (Pasternak & Greenlee, 2005; Postle, 2006; Ranganath, 2006). The involvement of posterior regions has been linked to the attentional process of rehearsal, which activates the same brain circuits involved in low level attentive processes such as perceptual encoding (Jonides, Lacey, & Nee, 2005; Wheeler et al., 2006), enabling us to maintain a stimulus image with a certain degree of fidelity (Svein Magnussen, 2000).

Posterior activation has also been successfully used to decode which information will subsequently be remembered (Emrich, Riggall, LaRocque, & Postle, 2013; Harrison & Tong, 2009; Riggall & Postle, 2012) using Multivariate Pattern Analysis (MVPA, described in section 2.6). For instance, the accurate retention of motion was decoded by the activity of brain areas involved in motion discrimination like the lateral extrastriate and medial calcarine cortex (Emrich, Riggall, LaRocque, et al., 2013; Riggall & Postle, 2012). Additional studies reported the possibility to decode information on the retention of complex artificial visual stimuli from parietal and occipital neural activity, typically involved in early stimulus processing (Christophel, Hebart, & Haynes, 2012). This evidence further supported the relationship between perceptual processes and the subsequent memory stages, maintenance and retrieval.

Studying the quality of perceptual processes in the context of memory would allow us to disentangle and better understand the nature and importance of these processes for successful retrieval as indicated by theories emphasizing the role of "deep" (versus "shallow") perceptual encoding (Craik & Lockhart, 1972a; Galli, 2014). Recent reports on the potential role of perceptual confidence (assessed with subjective confidence rating scales) facilitating tasks involving cognitive control, such as working memory, have shown that perceptual accuracy but not its confidence rate has an effect on memory performance (Koizumi, Maniscalco, & Lau, 2015; Samaha, Barrett, Sheldon, LaRocque, & Postle, 2016).

In this thesis, in order to investigate the influence of perceptual encoding quality on memory performance, a VSTM task requiring an explicit perceptual discrimination judgement was used (Chapters 3 and 4), and its effect in terms of oscillatory activity was assessed during maintenance (Chapter 4). Brain oscillations or rhythmic brain activity was the index of choice to address our experimental question. This is because oscillations can successfully be used to can reveal the different frequencies involved during stimulus maintenance (Burgess & Gruzelier, 1997; Düzel, Penny, & Burgess, 2010; Roux & Uhlhaas, 2014), and have previously been used to provide distinct neural markers for memory accuracy as well as memory representation load (for a review, Martini, Furtner, Maran, & Sachse, 2015). For instance, neural oscillatory activity in the theta band (4-7 Hz) shows enhanced magnitude at frontal sites in the case of successful memory performance (Klimesch, Doppelmayr, Pachinger, & Ripper, 1997; Rutishauser, Ross, Mamelak, & Schuman, 2010) and also of increased load and consequently task difficulty (Gevins, Smith, McEvoy, & Yu, 1997; Meltzer et al., 2008).

In this thesis (Chapter 4), the investigation of theta oscillation will be extended by studying memory representations in terms of load and accuracy at the perceptual level.

1.2 ATTENTIONAL AND INHIBITORY PROCESSES DURING MAINTENANCE IN VISUAL WORKING MEMORY (VWM)

In a delayed-to-match task where information about a target item is provided during maintenance, attentional control over memory representation comes into play, converting a VSTM into a working memory (WM) task (Baddeley, 2001). More specifically, selective attention within a WM task allows us to prioritise task-relevant information while ignoring irrelevant information (Desimone & Duncan, 1995). This ability can be assessed by investigating attention shifts within memory representations, using cues which share one or more features with the visual stimuli in an array. For instance, in the current research coloured arrows displayed in different orientations were cued using colour information. Cues could be presented either before the memory array presentation (stimuli encoding) or during the consolidation stage of WM (Griffin & Nobre, 2003). Most commonly, cues have been provided before encoding which usually results in a more advantageous retrieval or recollection of the cued item (Cheal & Gregory, 1997; Posner, 1980; Schmidt, Vogel, Woodman, & Luck, 2002). However, attention can also be redirected by displaying a cue between the offset of the memory array and the onset of the probe, during their maintenance (retrospective-cue or retro-cue). Retro-cues require a greater amount of WM flexibility as they need re-directing attention towards the encoded memory array to select the item that shares the same feature as the retro-cue from others (Bays, Catalao, & Husain, 2009; Griffin & Nobre, 2003). Retro-cue can be manipulated in terms of how relevant/informative they are in relation to the probed items in different experimental conditions (valid, invalid and neutral retro-cue). Retro-cue studies reported consistent advantages for trials in which the retro-cue corresponds to the memory probe for the selected feature (*valid* retro-cue) compared to *neutral* conditions, whereby no information about the to-be-probed item is provided. This beneficial effect has been named as retro-cue effect (RCE) (Gozenman, Tanoue, Metoyer, & Berryhill, 2014; Rerko, Souza, & Oberauer, 2014; Zokaei, Manohar, Husain, & Feredoes, 2014).

Different theories have been proposed to explain this effect. One theoretical account, the *Protection Hypothesis* assumes that after a retro-cue presentation, allocating attention is advantageous for the cued item, while non-cued items go through to decay and interference (Makovski, Sussman, & Jiang, 2008; Matsukura, Luck, & Vecera, 2007; Pertzov, Bays, Joseph, & Husain, 2013). Alternatively, after cueing a specific memory representation, the non-cued items could be actively removed from the central WM store (*Removal Hypothesis*), because they are perceived as no longer relevant (Kuo et al., 2012; Rerko et al., 2014; Williams, Hong, Kang, Carlisle, & Woodman, 2013). An additional theoretical framework (*Prioritization during maintenance Hypothesis*) proposes a redistribution of resources after retro-cue presentation, which privileges the cued item leaving fewer resources for non-cued items, consequently remembered less accurately (Myers, Chekroud, Stokes, & Nobre, 2018; Myers, Stokes, & Nobre, 2017; Myers, Stokes, Walther, & Nobre, 2014). This more recent framework the 'Representational reformatting' (Myers et al., 2017) is in line with a more dynamic WM architecture that has been proposed (Christophel, Klink, Spitzer, Roelfsema, & Haynes, 2017), which suggests the existence of multiple states of prioritization. Specifically, once the retro-cue is processed, the prioritization and reformatting of one of the available memory representations are then completed. Attention could then be directed to another memory representation without affecting the retro-cue benefit (Hollingworth & Maxcey-Richard, 2013; Makovski & Pertzov, 2015; Rerko et al., 2014).

These theories have focused on valid retro-cued and the fate of the non-cued items, but an extra level of complexity is added when invalid retro-cues are used. This is because they prompt an item that does not match the one subsequently probed. Invalid retro-cues are cognitively more resourceful and challenging as participants are required to compute a double shift of attention. One would back to the initial memory array display, discarding the invalidly cued item and the other one would be directed towards the probed item (Gressmann & Janczyk, 2016). This is expected to induce a cost in performance, known as retro-cue cost (RCC), and differently explained by the above theoretical frameworks. For instance, based on the Protection and the Removal accounts, the retro-cue cost is because most cognitive resources are allocated to the cued item which turns out to be incorrect at the probe presentation (Souza, Rerko, & Oberauer, 2014). Thus, the probed item refers to an uncued item which had been either disregarded because considered task-irrelevant, or is still maintained but in a less accessible way.

Alternatively, based on the Prioritization hypothesis, the retro-cue cost is minimal or possibly undetectable as its representation is still available, but subject to a response conflict. This is because the response to the probe is different from the one initially prepared for the uncued item (Gozenman et al., 2014). Accordingly, based on the New Representation Reformatting account, the retro-cue cost is likely to be related to task switch in response to a cognitive conflict (due to a probed and cued item mismatch), rather than to the inaccessibility to non-cued representations (Myers et al., 2017). This explains why some studies have observed invalid cue costs only in reaction times and not in accuracy (Astle, Summerfield, Griffin, &

Nobre, 2012; Gozenman et al., 2014; Rerko et al., 2014; Van Moorselaar, Olivers, Theeuwes, Lamme, & Sligte, 2015).

A number of factors can significantly modulate benefit and cost effects of retro-cue (Gozenman et al., 2014). One of these factors is the reliability of the cue, namely the ratio in which valid and invalid retro-cues are presented (Astle et al., 2012). In a recent study Gunseli et al., 2015 manipulated the probability of the valid cue trials (80% valid vs 50% valid) replicating a reduced invalid retro-cue cost when the cue-reliability was around or at the chance-level (50 % valid in Landman, Spekreijse, & Lamme, 2003 and Lepsien & Nobre, 2007; 66% valid in Rerko & Oberauer, 2013). Thus, when a cue has low reliability (low valid-to-invalid trials ratio), participants maintain the un-cued stimuli in case of invalid retro-cue trials (Gunseli et al., 2015; Myers et al., 2017; Shimi et al., 2014), or alternatively they pay more attention at the encoding level, trying to ignore the cue information (Berryhill, Richmond, Shay, & Olson, 2012). Accordingly, "trusting" a cued item regardless of its value leads to detrimental effect on behaviour and eventually to "mistrust" the cues, also resulting in reduced benefit (Gozenman et al., 2014).

Far from a unified model that accommodates findings on retro-cue effect, recent "Hybrid models" suggest the possibility to switch between theoretical approaches (Gozenman et al., 2014) and the existence of multiple memory representational states (Myers et al., 2017) which may explain successful performance in invalid retro-cue trials.

Individual variability in attentional states and flexibility also plays a crucial role, resulting in participants using different strategies when processing invalid retro-cue trials (Berryhill et al., 2012; Lim, Wöstmann, Geweke, & Obleser, 2018). Indeed, participants can either ignore, suppress or be vulnerable to cue information, preventing a clear effect to emerge, at the group level. Individual differences have been recently reported for the valid retro-cue benefit in the context of a syllable-pitch discrimination task (Lim et al., 2018). In this study, after encoding two, four or six auditory syllables, participants were asked to judge whether a probe syllable had higher or lower pitch compared to the same category syllable heard during the encoding. During retention, a valid or neutral visual retro-cue was presented. Participants showed no change in memory precision at the group level after valid cue presentation relative to neutral. However, further analyses showed that cue benefit was modulated by memory load (length of syllables sequence to encode), such that some participants showed a benefit from the valid cue associated to higher memory load, whereas others showed the opposite pattern (valid cue benefit for lower memory load). Supported by additional neuropsychological tests, such inter-individual variability was interpreted in terms of variability of the cognitive resources available, in the context of the "Continuous Resource Model" (Bays & Husain, 2008a; Wilken & Ma, 2004).

In this thesis, the RCC and RCE effects are investigated in combination. Starting from the contradicting findings around the presence of a behavioural cost associated to invalid retro-cue, our working hypothesis is that the lack or reduced RCC related to the invalid retro-cue (namely an inverted RCC effect) may positively correlate to the benefit related to the valid retro-cue (RCE effect). This would suggest that the both the prioritization of task-relevant and the suppression of task-irrelevant information are present. In other words, this scenario may suggest a common ability modulating the RCC and RCE effects, which we here refer to as *working memory flexibility*. Alternatively, the inverted RRC effect could reflect the mere suppression of information presented during maintenance, leading to reduced cost but at the same time also reduced benefit, depending on whether invalid or valid retro-cue trials are processed[1]. Chapter 5 will investigate these hypotheses, also by assessing electrophysiological patterns recorded at rest.

1.2.1. NEURAL CORRELATES OF MAINTENANCE IN VWM

At the neural level, re-directing attention in VWM engages a network of top-down attentional processes distributed over a number of brain regions (Babiloni et al., 2004; Gazzaley, Cooney, McEvoy, Knight, & D'Esposito, 2005; J. M. Palva, Monto, Kulashekhar, & Palva, 2010).

The majority of previous neurophysiological studies exploited the contralateral organization of our visual system, and presented cues or retro-cues during the retention period. This oriented participants' attention to either the left or the right hemifield and modulated the amplitude of an event-related brain potential (ERP) on lateral posterior electrodes ipsilateral and contralateral to the memorized side of the stimulus array (Vogel & Machizawa, 2004). This brain signal, known as the Controlateral Delay Activity (CDA), is linked to the number of representations held in visual working memory (Ikkai, McCollough, & Vogel, 2010). When using retro-cues, selective attention is retrospectively directed to information held in memory, possibly influencing the number of items held in memory (Kuo et al., 2012; Nobre, 2008). Accordingly, the CDA can accurately detect changes in attention orientation within WM

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[1] Other possibilities could be considered as we cannot exclude that: 1) RCC and REC may be mediated by other factors; or that 2) they are indeed independent.

representations. For instance, Williams and Woodman (2012) investigated the event-related correlates of items that participants either remembered or forgot in relation to retro-cues. Both retro-cue conditions (of remembered and forgotten items) showed a CDA component, however the CDA associated to the remembered items had earlier onset and larger amplitude, most likely resulting from orienting of attention towards some specific items representations (Williams & Woodman, 2012).

Recent investigations of the oscillatory correlates of retro-cues focused on the alpha frequency range (8-12 Hz). This is because this frequency is known for its functional inhibitory role, which implies an active involvement in tasks relying on top-down attentional processes by regulating the engagement of sensory regions based on task-relevance (Haegens & Zion Golumbic, 2018; Jensen & Mazaheri, 2010; Klimesch, Sauseng, & Hanslmayr, 2007). The inhibitory role of alpha is further supported by several studies highlighting a close relationship between CDA and increased contralateral alpha power in perceptual tasks (Capilla, Schoffelen, Paterson, Thut, & Gross, 2014; Sauseng et al., 2009; Siegel, Donner, Oostenveld, Fries, & Engel, 2008).

A first study to test alpha power sensitivity for attentional shifts within WM was conducted by Poch, Campo and Barnes (2014) using magnetoencephalograhy (MEG) recordings in a spatial retro-cue paradigm with valid or neutral condition only. The neurophysiological analyses revealed a significant retro-cue related increase in occipital alpha power ipsilateral to the attended hemifield, and a significant decrease in the contralateral hemisphere. This supports the suppressive role of alpha for task-irrelevant regions as a consequence of information prioritization, an effect confirmed by subsequent studies in young (Ciavarro et al., 2013; Myers, Walther, Wallis, Stokes, & Nobre, 2015; D. Schneider, Mertes, & Wascher, 2016) as well as in older adults adults (Mok, Myers, Wallis, & Nobre, 2016).

In this thesis VWM oscillatory correlates – rather than VWM task-related brain activity guided the selection of frequency bands used as predictor of the effective manipulation of memory representations (see section 1.2.3).

1.2.2 VWM MAINTENANCE IN AGEING

As discussed above, the ability to effectively manipulate memory representations relies on selective attention processes and on flexibility. In particular, these abilities require the selection and maintenance of task-relevant information and the suppression of the interference deriving from competing, task-irrelevant information.

A growing body of research has shown that these abilities tend to decline with age (Gazzaley & D'Esposito, 2007; Zanto & Gazzaley, 2009). To understand the nature of this impairment, previous studies analysed age-related changes in general WM processing. The *Processing Speed Theory* posits a general decline in processing speed that affects a number of cognitive abilities including memory. For instance, the amount of information that can be maintained in memory typically declines with age (Bopp & Verhaeghen, 2009; Parra, Abrahams, Logie, & Sala, 2009; Sander, Werkle-Bergner, & Lindenberger, 2011). More specifically, age-related decline is known to affect the ability to bind visual features (i.e. location and colour) into an object representation (Peich, Husain, & Bays, 2013). This is reflected in binding errors, consisting of swapping stimulus features. For example, participants may correctly identify a target stimulus on the basis of a feature, for instance colour, but wrongly associate it to a feature of a no-target stimulus, for instance its location, an effect that increases with memory load (Peich et al., 2013).

Despite this decline, more recent findings have observed comparable performance between younger and older adults especially if increased presentation time is provided (Sander et al., 2011).

When continuous rather than binary (correct/incorrect) performance measures were implemented, results differed. These measures, inspired by "continuous-resource models", provide an estimate of how precisely information is remembered and sources of errors such as the probability to recall the target and the no-target stimuli, instead of simply measuring whether or not stimuli are remembered (Bays et al., 2009; Wilken & Ma, 2004). Memory accuracy or precision is typically obtained by comparing participants' estimation of a memorised feature with the veridical one. By using a dual-feature recall VSTM task, Peich and colleagues (2013) found an age-related decline in memory precision and also in colour-orientation binding. A subsequent study reported a non-significant decrease in object-location binding, therefore suggesting that the potential increase in misbinding errors with age could be explained in terms of errors in target identification, rather in binding visual features (Pertzov, Heider, Liang, & Husain, 2015), adding further inconsistencies to the binding effect in ageing (Mitchell & Cusack, 2018; Rhodes, Parra, Cowan, & Logie, 2017).

The ability to bind information can also be investigated by means of retro-cue. As discussed in the previous section (1.1.3), the use of the retro-cue during maintenance triggers the distribution of attentional resources more towards the cued stimulus and less on the un-cued ones (Griffin & Nobre, 2003; Matsukura et al., 2007; Rerko et al., 2014). Older adults typically show a difference in performing the informative (valid) and the neutral retro-cue conditions, implying flexible selective attention within memory representations in ageing (Borghini et al, 2018; Duarte et al., 2013; Mok et al., 2016; Newsome et al., 2015).

At the neural level, the retro-cue benefit is characterized by the parametric increment in magnitude of alpha power corresponding to the amount of benefit, and of beta (13-30 Hz) lateralization (Mok et al., 2016). The neurophysiological effect of alpha was observed in concurrent retro-cue benefit in a younger sample, whereas the beta modulation, was shown to be distinctive of RCE for the older adults sample, likely to correspond to compensatory strategies employed by the ageing brain (Cabeza, Anderson, Locantore, & McIntosh, 2002; Park & Reuter-Lorenz, 2009).

Crucially, when invalid retro-cues are used, additional effort has to be made in order to suppress the invalidly cued stimulus information. A recent study specifically investigated the effect of invalid retro-cues in an older adult sample and observed decreased memory precision in comparison to a younger sample. Specifically, older adults were less likely to respond to a target stimulus and showed increased mis-binding errors relative to a younger sample and to valid retro-cues (Borghini et al., 2018). These results were interpreted in the framework of the 'Inhibition deficiency theory', suggesting an age-related decline in the mechanisms underlying the inhibition of task-irrelevant information, ultimately leading to decline in selective attention during stimulus encoding, maintenance or retrieval (Hasher & Zacks, 1988; Kane, Hasher, Stoltzfus, Zacks, & Connelly, 1994; Wais & Gazzaley, 2014; Zanto & Gazzaley, 2009; Ziegler, Janowich, & Gazzaley, 2018).

Interestingly, Borghini and colleagues (2018) used alpha bilateral parietal-transcranial alternating current stimulation (tACS) to test the causal link between alpha oscillations and inhibitory abilities. Alpha-tACS improved older participants' ability to respond to the target stimuli to a level comparable to younger adults. Besides supporting the causal link between alpha oscillations and top-down attention abilities, these results suggest that possibility to temporary improve these abilities, usually impoverished by age.

Starting from these results, Chapter 6 will test whether suppressing task-irrelevant information may correlate with stimuli prioritization in older adults' and will also investigate predictive neural correlates of flexible VWM. This is in line with the view of a beneficial approach for ageing cognition, which instead of merely searching for overall differences across the life-span, supports the identification of abilities resilient or malleable by age-related processes (Perfect & Maylor, 2000).

1.2.3 ENDOGENOUS CORRELATES OF VWM MAINTENANCE

In the last decades, there has been an increased interest in linking spontaneous (endogenous) brain oscillations to behavioural patterns in clinical and in healthy populations (Deco, Jirsa, & McIntosh, 2011; Rosazza & Minati, 2011). Such interest has found its rationale in the notion that task-related neural recordings strongly depend on the prior default brain dynamics, which have an effect on performance and its neural signatures (Buzsáki, 2009; Buzsáki & Draguhn, 2004). Activity recorded at rest, prior to performing a cognitive task, is usually reflected in the activation of the 'Default Mode Network' (DMN), a node of regions usually deactivated during goal-oriented tasks (Knyazev, Slobodskoj-Plusnin, Bocharov, & Pylkova, 2011; Scheeringa et al., 2008). The DMN has been mainly investigated using neuroimaging techniques such as functional magnetic resonance imaging (fMRI) and positron emission tomography (PET), and only recently EEG (Hlinka, Alexakis, Diukova, Liddle, & Auer, 2010). In terms of brain oscillations, there is an overlap between alpha frequency band and DMN activity both in resting state and during task execution (Knyazev et al., 2011), leading to the suggestion that alpha frequency band represents the closest EEG measure of the DMN.

Crucially, alpha frequency band is the most prominent oscillatory activity at rest and its power and temporal dynamics are functionally relevant for cognitive task performance (Mahjoory, Cesnaite, Hohlefeld, Villringer, & Nikulin, 2019). Indeed, the spontaneous status of the brain before an event is presented determines the direction of event-related brain activity (Doppelmayr, Klimesch, Pachinger, & Ripper, 1998; Klimesch, Vogt, & Doppelmayr, 1999).

Thus, for instance, task demands usually associated to alpha power (8-12 Hz) suppression, may be preceded by alpha power increase at rest (Doppelmayr et al., 1998). This is considered a predictor of successful memory performance specifically in terms of capacity (Klimesch, Doppelmayr, Schwaiger, Auinger, & Winkler, 1999). More recently, alpha power has been found to positively correlate also with tasks requiring sustained attention during encoding and maintenance of information (Mahjoory et al., 2019). The inverted pattern between task performance and rest condition is only one of the effects related to alpha oscillations. According to the *Inhibition-timing hypothesis* (Klimesch et al., 2007), alpha-band power amplitude increases (event-related synchronizations, ERS) when inhibiting task-irrelevant information or when brain regions compete with task demand. On the other hand, a decrease in alpha amplitude, referred to as 'event-related desynchronization' (ERD) is usually present in task-relevant brain areas, reflecting the release from inhibition (Klimesch et al., 2007; Pfurtscheller, 1992; Pfurtscheller, Stancák, & Neuper, 1996). During periods of increased alpha activity, action potentials generation is also inhibited and signal-to-noise ratio increased, ultimately facilitating information processing (Haegens, Luther, & Jensen, 2012; Klimesch, 2012). Therefore, based on the inhibition-timing hypothesis, ERS at rest can desynchronize more easily during task execution and information is accessed more effectively, with possible beneficial effects on task performance (Klimesch, 2012). Evidence of the relationship between WM capacity and alpha oscillations is supported by the observation that alpha peak at rest significantly predicts performance in the reverse digit span (Clark et al., 2004). For instance, 1-Hz increase in frequency is associated with a 0.21 increase in reverse digit span score (Clark et al., 2004). In a more recent study, this relationship was extended to a larger set of standardized neuropsychological tests testing memory and attention (Oswald et al., 2017).

Other factors underlying the correlations between memory performance and activity at rest correspond to measures of attentional state and arousal (Heister et al., 2013; Laufs et al., 2006; MacLean, Arnell, & Cote, 2012). A recent study into the phenomenon of attentional blink suggested that high attentional investment may be characterized by increased alpha at rest, accompanied by increased beta (13-30 Hz) and decreased theta (4-7 Hz) oscillations (MacLean et al., 2012). Indeed, evidence of a relationship between electrophysiological activity recorded during rest, resting EEG (rsEEG), and WM processes was also found for theta oscillations, suggesting network interactions that are mainly driven by pyramidal cells in the hippocampus and which then extend to the prefrontal cortex (Miller, 1989; Preston & Eichenbaum, 2013). Furthermore, a negative correlation between theta band and the activity of DMN at rest suggests that theta-ERD at rest is linked to the relative increase during task and correlates with higher performance (Klimesch, 1999; Klimesch, Doppelmayr, Schimke, & Ripper, 1997). Indeed, despite observed increased power in theta during a wide range of tasks (i.e. error detections, working memory, mental arithmetic) (Gevins et al., 1997; Jensen & Tesche, 2002; Onton, Delorme, & Makeig, 2005), the opposite pattern has been observed at rest (Klimesch, Vogt, et al., 1999). This inverse pattern has been found for older adults (Finnigan & Robertson, 2011) likely to be due to the increase in theta typically observed with age progression (Cummins & Finnigan, 2007).

Taken together, these findings led research in the direction of exploit spontaneous, task-independent fluctuations in neural activity to obtain predictive information of behavioural patterns in a faster way than recording task-related brain activity.

In this thesis, the investigation of spontaneous brain oscillations prior to task execution will be used for characterizing and explaining individual differences in VWM flexibility in the young and older adults brain (Chapter 5 and 6, respectively) as well as VSTM accuracy and load (Chapter 4).

1.3 OUTLINE AND AIMS OF THE THESIS

This thesis consists of two main parts, the first examining the cognitive and neural correlates of VSTM performance, focusing on the role of perceptual discrimination, and the second investigating the role of individual variability across age, in terms of the flexible manipulation of VWM representations.

The thesis' primary aims were to:

1 Investigate the role of perceptual processing in memory performance using a novel VSTM paradigm. This will be done by (a) directly assessing the quality of perceptual discrimination and (b) manipulating the degree of similarity ('load') between probe, target and non-target stimuli (Chapter 3);

2 Assess the functional significance of perceptual processing during the maintenance of memory representations. This will be achieved by studying electrophysiological recordings of brain activity during and prior to task execution (Chapter 4). Specifically, event-related and spontaneous oscillatory activity will be analysed in accurate trials in both perceptual and memory tasks.

3 Test whether individual differences in the flexibility of memory representations may be predicted by spontaneous oscillatory activity recorded at rest (Chapter 5). For this, power and long-range temporal correlation analyses will be performed on oscillatory activity. These two measures will be implemented with multivariate pattern analysis to discriminate and predict whether different neural profiles may be associated to different patterns of memory performance.

4 Assess whether the flexible manipulation of memory representations is modulated by age and investigate whether this ability could be associated to electrophysiological spontaneous activity recorded at rest (Chapter 6). This will be achieved by performing power and long-range temporal correlations analyses on oscillatory activity.

CHAPTER 2: METHODS

This chapter provides a brief overview of the behavioural and electrophysiological (EEG) methods implemented in this thesis, including power spectral density (PSD), time-frequency (TFR) and long-range temporal correlations (LRTC). Each method is discussed in terms of its rationale and specific methodological choices implemented for the studies reported in this thesis. These methods jointly contributed to characterize at the neural level different patterns of performance emerging in the manipulation of memory representations. Specific emphasis is placed on multivariate pattern analysis (MVPA), a decoding technique used to classify participants from the multivariate patterns of neural activity.

2.1 VISUAL SHORT-TERM AND WORKING MEMORY EXPERIMENTAL PARADIGMS

In this thesis two experimental paradigms have been used.

In Chapter 3 and 4, a novel paradigm was implemented which deconstructs the main steps involved in VSTM: encoding, probe comparison with target and no-target load. The task involved similarity judgments based on orientation degrees (for the encoding phase) and comparison in terms of orientation as well as location (right or left to the fixation point) for subsequent memory judgment.

Stimuli consisted of sinusoidal gratings (Gabor patches), whose level of perceptual similarity was individually adjusted for each participant before task execution. This was obtained by asking participants to complete a psychophysical staircase indicating the individual threshold (for details see method section of chapter 4).

In chapter 5 and 6, we used a paradigm allowing us to measure the quality of memory performance in terms of accuracy (precision), as well as the source of errors (Borghini et al., 2018), based on the continuous resource allocation WM model (Bays et al., 2009) (for details see methods section of chapter 5).

2.2 ELECTROENCEPHALOGRAPHY AND THE ORIGIN OF ITS SIGNAL

In Chapters 4, 5 and 6 of this thesis electroencephalography (EEG) was used to investigate the neural correlates and predictors of visual short-term and working memory.

EEG is a method used to record the electrical activity originated from the brain via electrodes placed on the scalp. Neural electrical activity is associated to two main sources: post-synaptic potentials (PSP) and action potentials. However, considering the timing and physical arrangement of axons generating action potentials, they are not thought to contribute largely to EEG activity (Nunez, 1974). Conversely, PSP corresponding to either excitatory or inhibitory changes in the membrane resting potential (about -70 mV), are longer in duration (tens or hundreds of milliseconds versus the 1 millisecond for action potentials) and originate from the dendrites of neurons. When they occur simultaneously, they largely contribute to the activity recorded from EEG scalp electrodes.

The main characteristic of EEG is its high-temporal resolution measure of neural activity, despite the low spatial resolution, as the signal at each electrode corresponds to the summation of unknown and variable number of neural sources (Luck, 2012).

2.2.1 EEG RECORDING

For the studies reported in this thesis, a Biosemi ActiveTwo amplifier from 64 Ag-AgCl electrodes was used. Electrodes were placed accordingly to the international 10-20 system. The signal obtained from each electrode is the difference in voltage between each electrode and an electrode (or combination) used as reference, which could be either the mastoids, a single electrode (usually Cz) or the earlobes. For our recordings, the average of the two electrodes placed on the earlobes was used. Additional electrodes for vertical and horizontal electrooculogram detection and two more were placed on the participants' earlobes and used as reference electrodes.

2.2.2 EEG PRE-PROCESSING

Before conducting any analyses, EEG data were pre-processed using the EEGlab toolbox (Delorme & Makeig, 2004) implemented in Matlab® (The MathWorks Inc., Natick, Massachusetts). Although data were recorded at a higher sampling rate of 1024 Hz (resulting in improved temporal resolutions), a standard down-sampling to 512 Hz was then applied in order to speed up computation time needed for future analyses.

In order to reduce the influence of noise sources, filtering is usually applied (Luck, 2012). Noise can be characterized by oscillations at a particular frequency (for instance, 50 Hz induced by the alternating current) (Luck, 2012). For this reason, researchers usually filter out frequencies falling beyond the range of interest, by applying a low-pass filter. For the EEG data in Chapter 5, a low pass filter of 50 Hz was used (also known as 'notch filter'). For the EEG data reported in Chapters 4, 6, 7 no low-pass filter was applied as high frequency neural oscillations in the gamma band (35-115 Hz) were used in order to normalize the signal.

Another filter commonly applied to remove frequencies below approximately 1 Hz is the 'high pass' filter. This is because relatively slow changes in the potentials measured at the scalp (below 1 Hz) are thought to reflect changes in conductance from sweating rather than neural activity.

In the experiments reported here, we used either continuous or epoched data (see below). This choice depended on the purpose of our investigation and whether the EEG recording was task-free (Chapter 5 and 6) or task related (Chapter 4). For the latter one, the continuous EEG signal underwent *epoching,* which corresponds to the division of the continuous data into intervals time-locked to the event of our interest (condition A). The resulting epochs are then averaged together and could be used in comparison to another averaged condition (B). Epoch length for time frequency analysis (Chapter 4) depended on the event of interest (specifically the probe onset).

Sources of artefacts as eye-movements (blinks and saccade) as well as rapid (no-task related) movements cause distinctive profile of activity in the EEG signal, especially in the frontal and temporal sites, ultimately affecting the results. These types of activity do inevitably affect most of the EEG data sets (Luck, 2012), although participants are clearly instructed to minimize eye and head movements during the recording. For these reasons, continuous and epoched EEG data was corrected by using different artefact correction methods, and specifically *Visual inspection, Independent Component Analysis (ICA)* and *artefact rejection.*

Visual inspection was applied to remove segments of data clearly not corresponding to neural activity or eye movements. This is usually done by the same researcher to maintain consistency, whereas the Independent Component Analysis (ICA) is used to increase the sensitivity of eye movements source detection.

The ICA method is a spatial filter used to decompose the EEG signal into a number of constituent maximally independent subcomponents, or theoretical sources. Considering their large impact, some of these components will represent the signal to be caused by eye-movements and blinks. Components generated by ocular activity are distinct due to their frontal distribution and smoothly decreasing frequency responses. Ocular artefacts can be "corrected" by re-computing the EEG signal excluding the components identified as eye-movement and blink related. The primary advantage of the artefact correction is to recover data that would otherwise be rejected. In the experiments reported here ICA was used mainly to correct for eye-movement and blink artefacts. In order to improve the identification of eye-movements, additional electrodes are placed on the outer canthi of the eyes, and for blinks above and below the left eye. It is important to note that in case of particularly noisy or missing electrodes, these were marked and excluded from the ICA (as they would have explained most of the noise variance) and after ICA correction, *interpolation* was applied to them, based on neighbouring electrodes activity.

In the case of epoched data, a further semi-automated artefact rejections method was used. This pre-processing option excludes trials that contain voltage exceeding ± 100 μV, therefore not generated from neural sources and most likely corresponding to momentary loss of adequate connection, from movement artefacts, or intermittently faulty electrodes.

2.3 POWER SPECTRAL DENSITY (PSD)

The EEG signal contains rhythmic activity reflecting fluctuations in the excitability of large populations of neurons. When large ensembles of neurons are synchronously active, the sum of the neurons electrical fields become large enough to be recorded from the scalp sensors.

The rhythmic signal obtained from the scalp sensors (raw data) contains multiple different frequencies simultaneously, which can be decomposed into a sum of sinusoids using signal processing techniques. There are two main way in which spectral analysis could be computed: Fast Fourier Transform (FFT) or a Power Spectral Density (PSD). The first one is computed when data contains no random noise and effects, whereas the second one is recommended when random effects could be present (for instance in a task-free recording), however both consist of the conversion of the signal from the time to the frequency domain and allow us to analyse the power of individual frequency bands (Martin, 2001).

For the analysis of the spontaneous neural activity, that is resting state, spectral power density (from 2 to 115 Hz) was obtained from the pre-processed continuous EEG data by using the EEGlab function *spectopo*, which implements the Welch's periodogram method with a Hamming window and 50% overlap.

Power values were normalized into decibels (dB) using the log-transformation and as baseline the average power spectral density within a frequency range of no interest (Herrojo Ruiz, Brücke, Nikulin, Schneider, & Kühn, 2014). The frequency range used as baseline corresponded to the combination of two intervals free of artefacts (by visual inspection): 81-95 and 105-115 Hz. This normalization step was done in order to compensate inter-individual differences in the absolute spectral power density, arising from differences in signal-to-noise ratio or morphological factors of the head (such as thickness of the skull or the volume of cerebrospinal fluid) (Kounios et al., 2008). Excluding ranges corresponding to line noise (50Hz), power values were extracted for the frequency range of interest: delta (1-3 Hz), theta (4-7Hz), alpha (8-12 Hz), beta (13-30Hz) and low gamma (30-45 Hz).

2.4 TIME-FREQUENCY TRANSFORMATION (TFR)

The frequency estimation of EEG time series data could be obtained in numerous ways, which mainly rely on the mathematical procedure of *convolution*, whereby one signal is weighted by another signal that slides along the first signal in time. Over time, what the first and second signal have in common is computed in the frequency content. This is obtained by repeatedly applying a time-series limited sinusoidal wave (known as a wavelet) to reveal approximately when the EEG signal contains data similar to the frequency limited wavelet, ultimately isolating frequency-band-specific activity over time (for a detailed discussion of the procedure (Cohen, 2014).

Irrespective of the type of analysis used for time-frequency decomposition, all methods balance a compromise in temporal and frequency resolution, as these methods usually rely on estimating the spectral content at a given time point. This means that the larger the 'window' used to estimate the frequency content at a given time point, the greater the frequency resolution but the poorer the temporal resolution. The method of time-frequency decomposition used in this thesis is known as complex Morlet wavelet analysis, which uses wavelets consisting of multiple sinusoidal waves with Gaussian tapers. This is one of the most common methods of time-frequency decomposition and is known to be well suited to localising frequency information in time for EEG data (Cohen, 2014).

The number of cycles used in the analyses represents the trade-off in precision of time and frequency resolution. Large number of cycles provides a better frequency precision, whereas a small number better temporal resolution. In this thesis, we aimed to study low and high frequency bands, and therefore the number of wavelet cycles used linearly increased from 3 to 10 (Roach & Mathalon, 2008). We were interested in detecting dynamics of cells assembly because they play a crucial role in a wide range of memory processes such as maintenance. We therefore used time-frequency rather than time domain average (ERP analysis) since this method tends to not capture information that is not phase-locked with the stimulus (Bastiaansen & Hagoort, 2003).

2.4.1. NON-PARAMETRIC ANALYSES: CLUSTER-BASED PERMUTATION TEST

This approach to the analyses of multidimensional neuroimaging data extracts spatiotemporal regions showing significant differences between conditions or groups without any a priori assumptions of spatial regions or time windows. It therefore identifies effects that are robust within a cluster of electrodes/time points, rather than highly significant on one dimension (i.e. a single electrode and/or time point). The method is robust against Type I error as this is intrinsically controlled for by evaluating only the maximum cluster-level statistics under the null hypothesis.

The following steps were taken to identify significant clusters: 1) paired samples t-statistics comparing two conditions were obtained for each of the samples in the multidimensional data structure; 2) T-statistics above a *p*-value threshold ($p<.05$) were then calculated and neighbouring data points exceeding it were identified; 3) The t-statistics were added up to calculate the cluster level statistic; 4) The maximum cluster statistic under its permutation distribution (shuffled data) was evaluated, based on the test statistics obtained from the dependent samples t-tests based on 1000 random permutations. The cluster-level significance threshold was set at the two-tailed level of 0.025 and a minimum of 3 electrodes was considered in order to obtain a cluster. Finally, dependent samples t-tests were run on the frequency of interest power values at cluster electrodes/time points comparing different experimental conditions.

2.5 LONG-RANGE TEMPORAL CORRELATION (LRTC)

An increasing number of studies have revealed that brain activity exhibits scale-free properties across different levels of spatial or temporal organisation (Bak & Bak, 2013). This means that, although characteristic scales do not dominate brain dynamics, their underlying processes can be revealed by quantifying fluctuations of parameters such as "self-organized criticality" (Bak & Bak, 2013). Based on this phenomenon, brain dynamics show the tendency to evolve to a critical state, characterized by long-range spatio-temporal correlations. Therefore, by measuring correlations across different temporal scales from milliseconds to seconds, it is possible to infer information of how adaptively brain networks shift to new states and situations (Tateishi-Karimata & Sugimoto, 2012). These correlations between amplitude fluctuations over time are known as long-range temporal correlations (LRTC)(Tateishi-Karimata & Sugimoto, 2012). In the case of non-stationary time series, as in the case of EEG signals, LRTC properties can be assessed using *detrended fluctuation analysis (DFA)* (Lux & Marchesi, 1999; Nikulin & Brismar, 2004; Palva, Zhigalov, Hirvonen, Korhonen, & Linkenkaer-Hansen, 2013). DFA provides a scaling exponent, also known as 'self-similarity parameter' (Lux & Marchesi, 1999; Tateishi-Karimata & Sugimoto, 2012), ranging from 0 to 1, with 0 reflecting random temporal correlations, and values from 0.5 to 1 indicating long-range temporal correlations in the time series.

A positive correlation between higher LRTC values and faster responses has been found in attentional tasks, flexible decision making, and reduced cost in task-switching (Colosio, Shestakova, Nikulin, Blagovechtchenski, & Klucharev, 2017; Irrmischer, Poil, Mansvelder, Intra, & Linkenkaer-Hansen, 2018; Mahjoory et al., 2019). In this thesis, we investigated the link between resting-state LRTC and the ability to retrospectively select memory representations based on their task-relevance (Chapters 5 and 6).

2.5.1 Method

In order to evaluate such relationship for the frequency bands of interest (alpha, theta, delta), following previous studies (Herrojo Ruiz et al., 2014), the raw continuous signal was band-filtered around the frequency of interest using the function *eegfilt.m* implemented in the EEGlab toolbox (Delorme & Makeig, 2004). The Hilbert transformation was applied to the data to extract the alpha-band amplitude envelope (Figure 2.1 A and B). The DFA analysis was then applied to amplitude of alpha oscillations with the following steps.

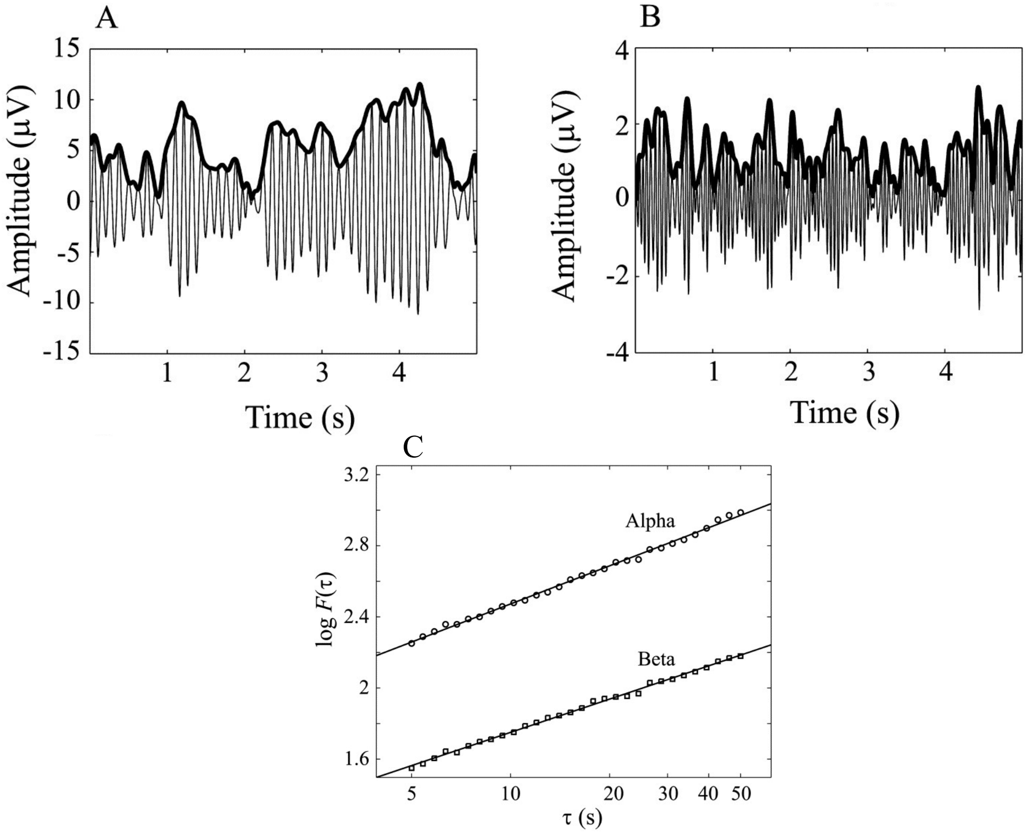

Figure 2.1 Long-range temporal correlation. α and β frequency band oscillations (A and B respectively). The black thin line corresponds to the amplitude envelope of the oscillations after Hilbert transformation. (C) The slope of the line associating $\log F(\tau)$ and τ corresponds to Detrended Fluctuation Analysis (DFA) exponent for α and β oscillations, quantifying the autocorrelation degree. (Adapted from (Nikulin & Brismar, 2005).

We calculated a cumulative sum (integral) of the signal shifted by the mean. These data were then binned on a logarithmic axis in 20 non-overlapping windows of different sizes, allowing as maximal scale 1/10 of the total length.

In each window, the signal was locally fit using the least-squares method to obtain a linear function. This linear function was subtracted from the signal in that window, thus effectively detrending the signal by removing the local linear trend. The mean-squared residual (fluctuation) function F was extracted. Across different time scales, the corresponding fluctuation function F was estimated (see details in, Herrojo Ruiz et al., 2014) was evaluated.

By plotting in a double log-log representation the fluctuation functions versus window sizes, a linear relationship can be observed, corresponding with power-law scale-free behaviour. The slope of the linear fit, which corresponds to the scaling exponent (DFA coefficient) (Figure 2.1C) was extracted for each channel, for each subject.

2.6 MULTIVARIATE PATTERN ANALYSIS (MVPA)

Traditional univariate analysis techniques applied to neuroimaging data were recently complemented by a methodological approach known as multivariate pattern analysis. The characteristic feature of this approach is that it takes into account the existing relationship between multiple variables (in the case of EEG, electrodes) to provide information which is otherwise not detected by averaging signals (Grootswagers, Wardle, & Carlson, 2017). This approach has the advantage of accessing brain state information in a way as close as possible to how information is actually encoded and transmitted at the neural level, namely by patterns of brain activity, rather than single feature (Haxby, Connolly, & Guntupalli, 2014). Thus, MVPA allows us to differentiate which patterns of neural activity are associated to a specific cognitive state. This is achievable by using machine learning algorithms that learn data patterns and classify them. The MPVA classification involves splitting the data into different datasets: a training and a test set. The former corresponds to the portion of data on which decision rules on pattern classification are derived, whereas the latter set is used to test the validity of the classifier. An initial step involves selecting the pattern classifier of our interest (for instance, frequency band) and converting each EEG data point into a vector that reflects the pattern of activity across sensors at that frequency band. Then, the pattern classifier is trained in order to distinguish between two classes of stimuli or, as in this study, behavioural patterns: inverted RCC/RCC effect. This process is conducted on the training set and successively applied on an independent set of data (test set). How well the pattern classifier generalizes to a new test set is assessed using cross-validation. In this specific step, the data are divided into k-folds (subsets), which contain a balanced amount of data from each class of stimuli/conditions. The classifier is then trained using all-but-one folds from the training set and successively used to predict these classes from a new set (test set). This process is repeated for all k-folds and it results in a percentage value for each k-fold, corresponding to the proportion of classifier's accuracy. Based on the number of k-folds in which the data is split into and on which information (pattern feature) is included as classifier, the classification accuracy values can be compared and the most suitable classification for a specific cognitive state identified (see Figure 2.2).

The objective of the decoding analysis is to test whether we can predict a specific cognitive state and therefore a performance from the participants' patterns of brain activity. Specifically, for this study we reasoned that if the behavioural patterns of RCC/inverted RCC effect could be successfully classified from patterns of brain activity at rest, we could then conclude that some information linked to that specific performance is already present in the spontaneous brain activity, prior to task execution.

2.6.1 METHOD

For this analysis, we used normalised spectral power and LRTC coefficients in the alpha band from single subjects and the 64 EEG channels as features. The computations were performed with MATlab and a standard library for Support-Vector Machine (SVM) (Chang & Lin, 2011; Fowler, 2000). We trained a classifier on a subset of participants to distinguish between those who exhibited a retro-cue cost, RCC effect (class A) or a retro-cue benefit, inverted RCC effect (class B). To validate our predictions, we used a two-fold leave-one-out cross-validation procedure. The classification accuracy was averaged across the leave-one-out cross-validations to obtain a population decoding accuracy. We statistically assessed whether cross-participants classification accuracy was significantly above chance by estimating the chance level using permutation tests. Note that the theoretical chance level of 50% for a two-class (group) classification is often violated in the case of small sample size. However, permutation tests can overcome this issue by estimating the appropriate chance level from the data (Herrojo Ruiz et al., 2014).

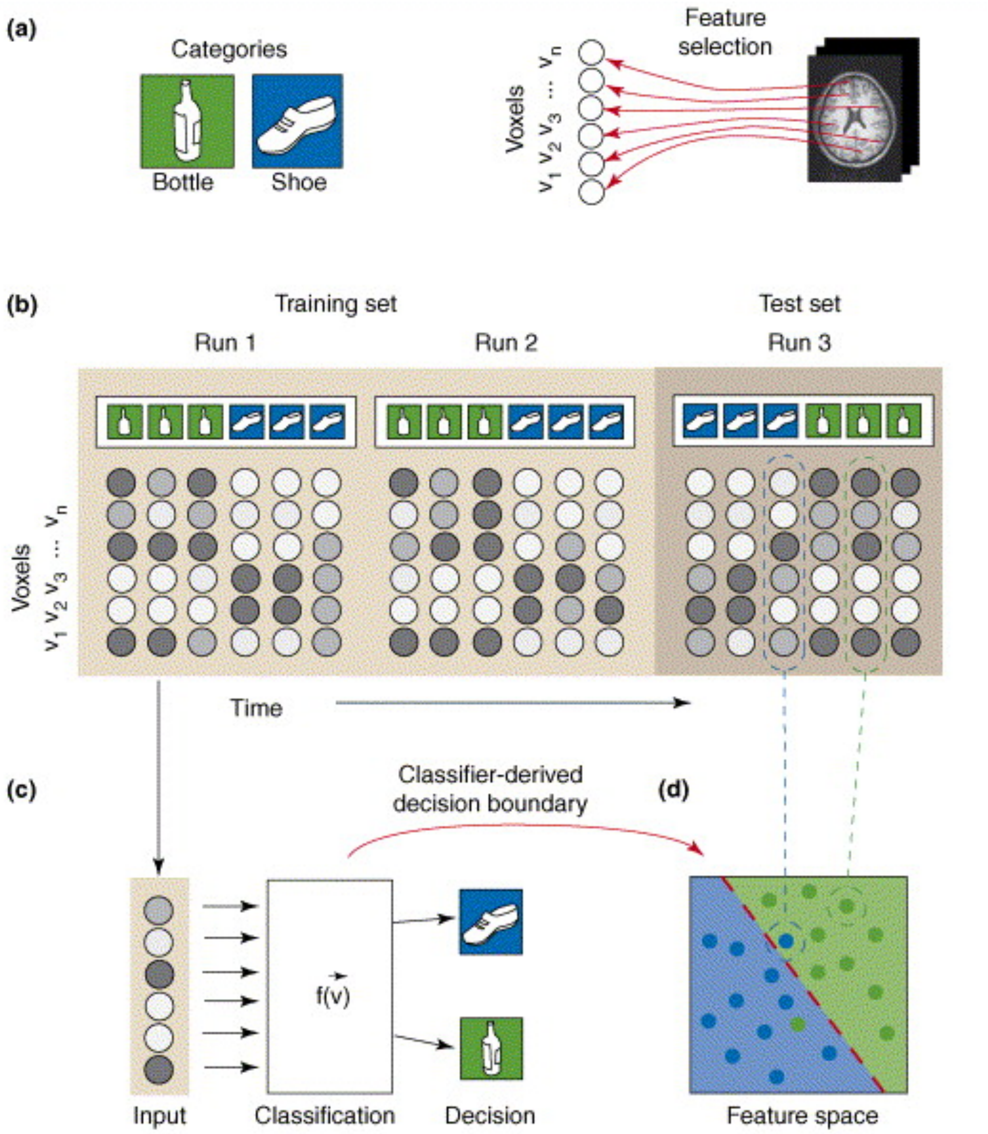

Figure 2.2 Multivariate pattern analysis. An hypothetical experiment in which MPVA is applied; for illustrative purposes, the example is based on functional imaging (fMRI). **(a)** Two objects are shown to participants (bottle and shoe). Some features (voxels) are selected for the classification analysis. **(b)** fMRI times series are decomposed in patterns of activity corresponding to two conditions (bottle and shoe) and divided into: training and testing set. **(c)** Training set patterns train a classifier function which determines brain patterns for each of the experimental conditions **(d)** A decision boundary (red dashed line) is defined by the trained classifier function in the feature space (voxels, in this case). Each dot represents a pattern and its colour defines its category. The trained classifier predicts the membership of the patterns from the test set (in this example two possible accuracy scenarios are shown: one in which the classifier accurately identifies the bottle pattern (green dot) and one in which misidentifies the shoe pattern as a bottle (blue dot). (Figure from Norman et al., 2006).

CHAPTER 3: THE EFFECT OF COGNITIVE FACTORS ON VISUAL SHORT-TERM MEMORY

Visual short-term memory (VSTM) is often unreliable, but which cognitive process(es) may account for its unpredictable success is an open question. Recent VSTM theories have suggested that successful performance may depend on bottom up factors and on the quality of memory processes. In this chapter, we manipulated orientation similarity (load) between target, no-target distracting stimuli and an initial stimuli array to test three possible contributing factors: the perception and the memory of a target stimulus itself, and the retrospective inhibition of distractors. To minimize the possibility that any memory failure resulted from 'shallow' encoding, we requested participants an explicit perceptual discrimination judgment after stimuli presentation; this was followed by a recognition task whereby participants matched a delayed stimulus to one initially presented in the context of a no-target stimulus.

Taken independently, both correct perceptual discrimination as well as no-target load explained successful VSTM performance, although memory load most strongly accounted for successful memory, especially in combination with perceptual and inhibitory load.

Collectively, these results highlight the importance of considering the independent and combined contribution of distinct cognitive factors for a better understanding of VSTM performance.

3.1 INTRODUCTION

The ability to retrieve goal-relevant visual stimuli after a short delay (visual short-term memory, VSTM) is critical for many everyday activities (Shimi et al., 2014). However, remembering information can be challenging, and failures are very common (Cowan, 2001; Marois & Ivanoff, 2005), which is why it is important to understand which processes underpin successful performance.

Existing models of VSTM have explained its limitations in terms of exceeding fixed capacity for storing information ('slot models') (Fukuda, Awh, & Vogel, 2010; G. Miller, 2000). A more recent theoretical account has proposed that the retrieval performance may depend on the variability on available top-down resources or on bottom-up factors ('variable precision model') (Fougnie, Suchow, & Alvarez, 2012; Van den Berg, Shin, Chou, George, & Ma, 2012). Based on this account, even within the capacity set-size, VSTM can still be challenged, for instance, by noisy recall, random guessing, swap errors (reporting a no-target item from the initial memory array), depending on the stability of the stored information and the complexity of the stimuli to be remembered (Bays & Husain, 2008a; Ma et al., 2014).

In a typical VSTM paradigm a visual target is briefly presented among distractors and then matched to a stimulus or probe. Participants' response is likely to reflect the joint contribution of processes such as perception, memory and inhibition (Beck & Kastner, 2009; Shapiro & Miller, 2011). Perceptual processes may affect the precision of a retrieved memory trace depending on the depth/stage of the stimuli's perceptual encoding (Craik & Lockhart, 1972b; Galli, 2014; Rodrigues et al., 2010; Treisman, 1998). Evidence from neuroimaging studies showed that individual differences at the level of the visual cortex during the encoding stage correlate with and predict the precision of subsequent recall (Emrich, Riggall, Larocque, & Postle, 2013; Ester, Anderson, Serences, & Awh, 2013; Postle, 2015). However, previous VSTM studies often inferred perceptual encoding by manipulating the stimuli's perceptual complexity (Konstantinou & Lavie, 2013; Lavie, 2010) or by investigating the neural correlates of perceptual discrimination (Cruz, Miyakoshi, Makeig, Kilborn, & Evans, 2016; Zizlsperger, Sauvigny, Händel, & Haarmeier, 2014), rather than by explicitly assessing perceptual accuracy. Here, using a novel behavioural paradigm based on orientation discrimination, we tested the contribution of perceptual processing by directly assessing the quality of the initial stimuli discrimination, as well as by manipulating the degree of similarity between stimuli (here intended as load). Therefore, rather than the typical manipulation of load in terms of number of items, stimuli complexity was changed by varying the orientation degree between the stimuli. Specifically, this was between the two stimuli in the initial array (perceptual load), the target stimulus and the memory probe (memory load), and the no-target stimulus and the memory probe (inhibitory load). Load was based on using three conditions (low, medium, high), respectively corresponding to identical (no discrepancy), large and small discrepancy. The comparison between target stimulus and memory probe (memory factor) was based on the conjunction of two features (degrees of orientation and location) which requires features-binding, an automatic process in VSTM (Allen, Baddeley, & Hitch, 2006). VSTM retrieval also implies inhibitory processes to protect a target visual representation from task-irrelevant interference in the form of no-target stimuli (Corbetta, Kincade, Ollinger, McAvoy, & Shulman, 2000; Desimone & Ducan, 1995). Because participants did not have any prior knowledge on the identity of the target and no-target stimulus, we expected the latter stimulus to have a retrospective distracting effect (inhibitory factor).

By decomposing the cognitive processes and their interaction behind successful memory recognition, we aimed to investigate the role of successful perceptual discrimination. We predicted that successful perceptual discrimination may facilitate the formation of memory representations resistant to the detrimental effect of perceptual and inhibitory load. Alternatively, perceptual facilitation may not prevent memory traces from being challenged by no-target stimuli or by memory load itself (Bays & Husain, 2008a). This may be because memory and/or inhibitory load may affect more strongly the consolidation and manipulation of visual representations rather than their initial perceptual discrimination (Neokleous, Shimi, & Avraamides, 2016). In this case, we aimed to characterize the precise level of perceptual, memory and inhibition load accounting for unsuccessful memory recognition.

We expected a decrease in recognition performance corresponding to the increase in the stimuli similarity (homogeneity/low load) at the perceptual and retrieval stages (Shapiro & Miller, 2011). This would be in line with the 'Biased Competition Theory' account (Beck & Kastner, 2009; Desimone & Ducan, 1995) which predicts higher level of accuracy when stimuli do not differ in terms of perceptual representations. We also predicted higher recognition performance in the case of large perceptual similarity (or 'medium' load condition) between probe and no-target stimulus (inhibitory factor), compared to small perceptual similarity (or 'high' load condition). This is based on models of visual search reporting increased difficulty when the similarity between probe and no-target decreases (Duncan & Humphreys, 1989). For the remaining conditions (high and low load), two scenarios were expected based on previous research: 1) No discrepancy between the probe and the no-target stimulus ('low' load) may facilitate perceptual representation grouping based on orientation; 2) discrepancy in terms of location, namely the fact that target and probe stimuli may appear in different locations (right and left of the fixation dot) could still interfere with performance (Emrich & Ferber, 2012). The small difference in orientation between probe and no-target stimuli ('high' load) may also increase swap errors (mis-binding), as differences are less distinguishable, as suggested by previous research (Schneegans & Bays, 2016).

3.2 METHODS

3.2.1 PARTICIPANTS

Thirty right-handed students from Goldsmiths, University of London (7 males, mean age: 26; SD: ± 5.2) provided written informed consent to volunteer to the study, which was approved by the Ethics Committee of the Department of Psychology at Goldsmiths. An initial questionnaire established that their vision was normal or corrected to normal.

3.2.2 STIMULI AND TASK

The experimental task comprised two explicit judgements: perceptual discrimination and recognition (see Figure 3.1). To avoid individual differences being driven by semantic valence or familiarity with the stimuli (Kafkas & Montaldi, 2012, 2014), we opted for a paradigm which implemented a purely stimulus-driven memorability with the use of spatial frequency gratings (Gabor patches). Black and white Gabor patches (4 cycles/degree, contrast 100%, 4.50° eccentricity) were displayed on the horizontal meridian to the left and right (37% and 63% of the screen width, respectively) of a white fixation point (visual angle 0.6°), centered on a grey background. Stimuli were generated using MATLAB 2012a and presented using Psychophysics Toolbox Version 3.0.8 (Brainard, 1997).

Each trial began with the perceptual discrimination judgement, in which a 250 ms central fixation point was followed by two Gabor patches simultaneously presented for 500 ms to the left and the right of the fixation. Key presses during this time window were not allowed in order to reduce the occurrence of anticipatory responses that could have hampered the processing of both spatial location (left/right) and degree of orientation of the stimuli (Fig 3.1 A&B).

The patches' presentation was followed by a 2000 ms question mark, during which participants judged for maximum of 900 ms whether the two patches had the same or different degrees of orientation, by pressing "S" or "D" on the keyboard, respectively. The recognition task started immediately after, with the presentation of the probe which corresponded to a single grating. Using the same keyboard keys ("S" or "D"), participants judged whether the orientation of the probe was the same or not relative to the stimulus in the same position during the initial stimulus presentation (target), Figure 3.1A. The probe was equally presented either to the left or right of the fixation point. Participants could not anticipate the position of the probe until its appearance, which encouraged the maintenance of both stimuli representations, in line with previous studies (Andrade, Kemps, Werniers, Jon, & Szmalec, 2002).

Load was varied for both judgements (perceptual and memory) and the no-target stimulus. The latter provided a measure of inhibitory ability towards task-irrelevant memory representations as it did not correspond to the memory probed stimulus (Figure 3.1B). Load modulation was obtained by manipulating the orientation similarity between: the visual stimuli at the initial presentation (perceptual load), the target and the probe (memory load), the target and the no-target (inhibitory/distractor load), with three levels of difficulty. Specifically, for all three investigated factors (perceptual, memory, inhibitory), the Gabor patches had same ('low' load, 0° difference), between 27° and 9° ('medium' load) or between 20° and 5° difference ('high' load) in orientation (see also 'Thresholding' below). A number of features were implemented to avoid adaptation to spatial local position and orientation discrimination: first, in the recognition task the two stimuli were presented equally often to the left or the right of the fixation in random order; the rotation of the Gabor patches was both clockwise and counter-clockwise; third, the stimuli appeared in equal number in three different degrees of orientation (5°, 30°, 60°) across trials. There were 144 trials for each gradient of difficulty (load) and each judgment (i.e. 144 for perceptual and 144 for memory judgment), with 48 trials for each possible combination between loads for perceptual and memory as well as inhibition and memory factors, resulting in a total of 432 trials for the whole experimental session divided in 4 blocks.

When these perception, memory and inhibition were considered in combination, the design was unavoidably unbalanced because of the intrinsic nature of the task. For instance, if the condition in which both perceptual discrimination and recognition had low load (namely, no difference in orientation degrees), the no-target could only have a low load, preventing other possible load combinations between these factors to occur. This resulted in testing 15 out of 27 potential combinations between the three factors (the implications of this design on the analyses are discussed on the Data Analysis section below).

The experiment lasted about 45 minutes, with breaks between the self-initiated blocks.

3.2.3 EXPERIMENTAL PROCEDURE

Participants were seated in a darkened room at about 57 cm from the computer monitor, and were asked to fixate at the centre of the monitor in order to better discriminate the orientation of the two stimuli. Following previous studies (Huang, Kahana, & Sekuler, 2009), a long presentation time for the perceptual judgement was intended to encourage a more detailed perceptual processing of the stimuli orientation and spatial location, which were essential for recognition (Figure 3.1).

3.2.4 THRESHOLDING

Prior to administering the task, the individual orientation discrimination level was measured. Following previous studies (Bartolucci & Smith, 2011), the tested levels were chosen *a priori*, assuming that by decreasing the difference between the stimuli orientation, the discrimination difficulty will increase. Across three orientation ranges (5°, 30°, 60°), four staircase steps were established with the following differences in degrees between the two stimuli for large and small discrepancies, respectively: 20°/27° (staircase step 1), 15°/21° (staircase step 2), 10°/15° (staircase step 3), 5°/9° (staircase step 4). The cut-offs for the difficult categories were determined in an adaptive way using a staircase procedure based on Palamedes toolbox (http://www.palamedestoolbox.org). The method is based on each participant's orientation discrimination ('same' or 'different' response with keys 'S' or 'D') of two Gabor patches presented for 250ms. A step towards a more difficult level was made if four consecutive perceptual discriminations were made correctly. After one incorrect response, the difficulty level was reduced by one step. This ensured that perceptual discrimination was above chance, while allowing for adequate error rates for analysis. Upon completion of 45 trials, the participant's discrimination level was defined and a difficulty level of one step higher was assigned to ensure the appropriate level of challenge in the experiment.

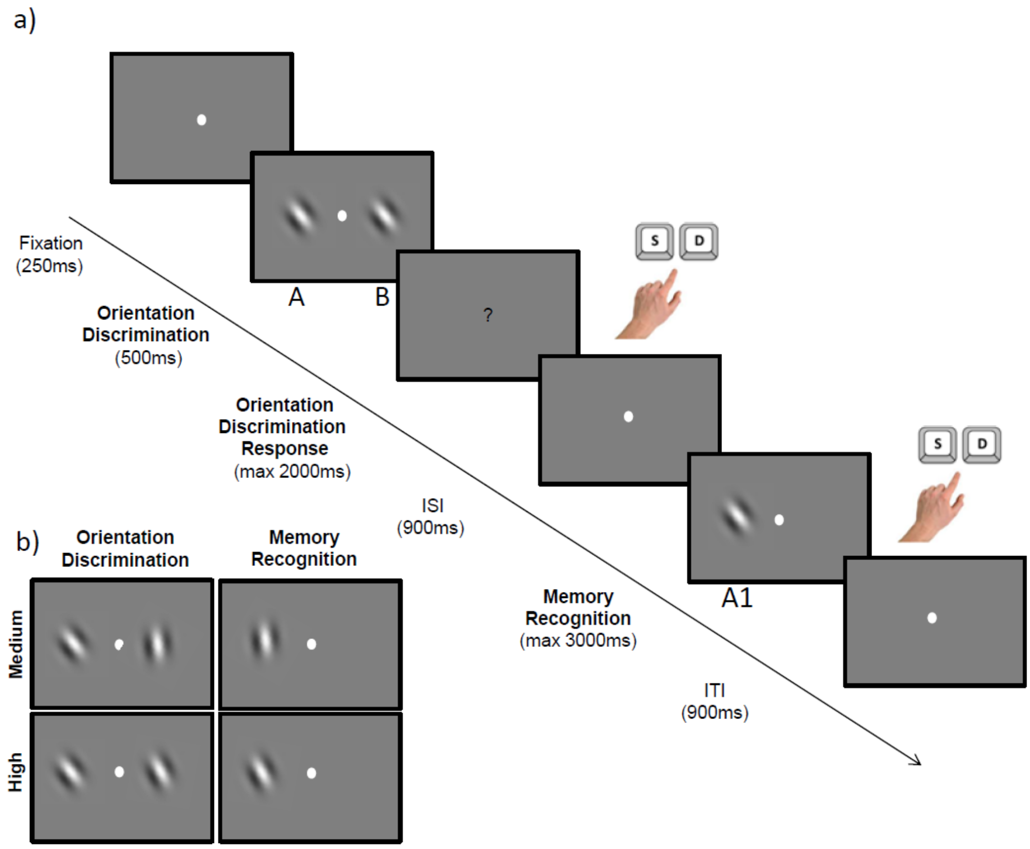

Figure 3.1 The experimental task and design: (a) After 250 ms of a fixation dot, two Gabor patches whose orientation may or may not differ are presented for 500 ms on each side of the fixation dot. Their perceptual orientation judgement is made after the appearance of the probe '?', by using the 'S' (for 'same') and 'D' (for 'different') keys on the keyboard. After a 900ms interval, only one Gabor patch is presented to the left or the right or the fixation point, in equal amount. During the stimulus presentation (max 3000 ms) participants judge whether the orientation of this single patch (A1) is same or different relative to the patch previously presented in the same position (A or B). The no-target stimulus (here B) is expected to have an interfering effect depending on its gradient of similarity to the memory target. For display purposes, here the stimulus is presented only in one spatial location and with same orientation (i.e. no difference condition). (b) Example of the stimuli in the high and medium load conditions (the 'low' condition is described in section (a)). Participants provided answers by using their index finger of their dominant hand.

3.2.5 DATA ANALYSIS

The perceptual discrimination and memory recognition judgements were analysed separately. This was due to differences in the data extraction, preventing direct comparison (see Method).

For the perceptual judgment, measures of sensitivity (d') and response criterion (C) were used. These two measures are applied by the signal detection theory when stimuli should be discriminated, accounting for noise (response bias).

The d' measure was calculated by subtracting the Z-score of the proportion of false alarms (FA) from hits (H); the C measure was obtained by averaging the Z-scores corresponding to FA and H, measuring the deviations from the neutral point in standard deviation units. When C has a value of 0, response bias (noise) and sensitivity overlap, indicating that no response bias is present (neutral point).

Using this method, Stanislaw & Todorov, (1999) compared low vs medium load trials; negative values of C indicated a bias towards responding *same* to signal detection, whereas positive values of C signified a bias towards the *different* response, with criterion lying to the left or to the right of the neutral point respectively for negative and positive values (Stanislaw & Todorov, 1999). T-test against 0 were then performed in order to assess whether the C value was significantly different from the neutral point.

These measures were preferred over accuracy proportion because they allowed us to assess any bias towards one of the two-alternative forced choice options (i.e., "same" or "different"). As there were three load conditions, d' and C were calculated separately for low versus medium, and low versus high load. For the comparisons between high and medium load conditions, hit rates were used instead of sensitivity measures. This was done because false alarm and miss values would be the same for both conditions (based on the low load trials). Therefore, hit rates and d' would be functionally equivalent.

For the memory recognition judgment, accuracy was measured for each load condition (low, medium and high); this corresponded to the proportion of correct responses based on the total amount of trials per condition or combination of conditions. Information about the effect of the no-target stimulus was extracted from recognition performance and reflected the ability to perform the recognition task under the interfering influence of a task-irrelevant stimulus (B1 in Figure 3.1).

Levene's test assessed the homogeneity of variance in the data and the Greenhouse-Geisser correction (in case of significant Mauchley's test) was applied in a repeated-measures Analysis of Variance (ANOVA), with difficulty as a within-subject factor, and accuracy of the perceptual judgment as a between-subject factor, where relevant. Both analyses were followed by Bonferroni corrected t-tests.

Next, generalized linear mixed-effect models were used to investigate the degree to which load in both the perceptual and inhibition factors influenced recognition. The dichotomous dependent variable was whether memory recognition was successful or not in a given trial, with a Bernouilli distribution assumed for this variable. In the model, we treated 'condition' as a single categorical predictor with 15 levels (the combinations of the three load variables that occurred in the experiment), and used a dummy coded contrast to enter this in the model as fixed effect. Random intercepts were included to account for the repeated-measures structure of the data. The model is effectively a logistic regression model with random intercepts and fixed slopes for the dummy coded predictors (see the Experimental Design and Stimuli section for details). To address the factorial nature of combinations of the three load manipulations, we used the model estimates in a planned-comparisons contrast analysis, applying a Bonferroni correction to keep the family-wise error rate smaller than $\alpha = 0.05$. To estimate the model, we used the lme4 package (Bates, 2007) for the R statistical computing environment (R

Development Core Team, 2008), while the planned-comparisons were performed with the “multcomp” package.

3.3 RESULTS

3.3.1 PERCEPTUAL JUDGMENT

Perceptual accuracy was modulated by stimuli load [$F_{(2, 87)}=5.77, p=.004, \eta_p^2=.11$], with a significant higher accuracy for the low relative to high ($t_{(29)} = 6.86$ $p< .001$), and medium relative to high load condition ($t_{(29)} = 2.95$ $p< .006$)[2].

Sensitivity analyses (Table 3.1) highlighted no response bias when low and medium load were compared, as the Criterion (bias) was not significantly different against zero ($t_{(27)} = -1.57$ $p = .126$). However, response bias towards the answer “same” was found when low load sensitivity was calculated in relation to high load condition ($t_{(26)} = -3.06$ $p = .005$) (Table 3.2).

This significant effect of bias response may be due to the unbalanced number of trials for “same”/“different” answers (‘same’ restricted to low and ‘different’ for both medium and high load). Alternatively, this may be the result of load differences between conditions, which was further supported by the post-hoc t-test analysis reported above.

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[2] Mean proportion of for each load and type of response are reported in the appendix for perceptual and memory judgment.

Table 3.1 Means and Standard deviations of hit, false alarm, missed and correct rejection for Low versus Medium perceptual load conditions. Sensitivity and Criterion values with standard deviation (in brackets).

Hits	False Alarms	Misses	Correct rejection	Sensitivity (d')	Criterion (C)
.82 (.13)	.23 (.20)	.17 (.13)	.76 (.20)	1.87(1.10)	-.13(.46)

Table 3.2 Means and Standard deviations of hit, false alarm, missed and correct rejection for Low versus Medium perceptual load conditions. Sensitivity and Criterion values with standard deviation (in brackets).

Hits	False Alarms	Misses	Correct rejection	Sensitivity (d')	Criterion (C)
.82 (.13)	.32(.20)	.17(.13)	.67 (.20)	1.54(.86)	-.25(.42)

Considering the significant response bias towards the 'same' response in low and high load conditions, we assessed to what extent this could have influenced memory performance. A partial correlation was run between memory and perceptual judgment accuracy (merging load conditions) while controlling for the response bias (criterion) between load and high perceptual load. There was a moderate, positive, statistically significant partial correlation between memory and perceptual accuracy ($r_{(25)} = .46$, N=30, $p = .015$). However, zero-order correlation between memory recognition and perceptual accuracy, without controlling for response bias, showed that there was a statistically significant, moderate, positive correlation between the two variables ($r_{(26)} = .54$, N=30, $p = .003$), indicating that response bias had very little influence in controlling for the relationship between perceptual and memory accuracy.

3.3.2 RECOGNITION JUDGMENT

On average, successful recognition was nearly at chance level (M = .56 SE = .01), with a significant impact of the stimuli load on accuracy, which decreased in a linear fashion ($p < .001$) with the increase of stimuli similarity (load) [$F_{(1.30,\ 32.78)} = 160.67$, $p < .001$, $\eta_p^2 = .84$]. Post-hoc t-test showed significant differences in all the comparisons between the three conditions (Bonferroni corrected).

Since performance was modulated by stimuli load (Table 3.3), we can conclude that low accuracy was not merely the result of guessing.

Table.3.3 Means and Standard deviations of accuracy for each memory load with standard deviation (in brackets).

Memory load	Accuracy
Low	.87 (.04)
Medium	.47 (.16)
High	.38 (.16)

3.3.3 INFLUENCE OF PERCEPTUAL ACCURACY AND LOAD ON RECOGNITION

We tested to what extent successful recognition was modulated by perceptual accuracy and load by running a 2x3x3 ANOVA. Included factors were: perceptual accuracy (correct and incorrect) and load, both for the perceptual and the memory stimuli, (low, medium, high). Perceptual accuracy and memory load significantly modulated recognition performance ($F_{(1,\ 7)} = 13.25$, $p = .008$, $\eta_p^2 = .65$ and $F_{(1.21,\ 8.54)} = 48.47$, $p < .001$, $\eta_p^2 = .65$ respectively), whereas a marginal effect was found for perceptual load ($F_{(1.17,\ 8.19)} = 3.665$, $p = .052$, $\eta_p^2 = .34$). Overall, accuracy was higher in trials preceded by accurate perceptual judgment (M=.37, SE: .04) relative to inaccurate (M:.17, SE: .01). Post-hoc t-tests applied to memory load effect highlighted significantly ($p \leq .001$) higher level of accuracy for the low load conditions compared to medium and high. A significant interaction between memory load and perceptual accuracy ($F_{(2,14)}$ = 8.90, p=.003, η_p^2=.56), showed that in the case of accurate perceptual judgment only, recognition accuracy was higher in stimuli with medium relative to high load.

An additional significant interaction between perceptual and memory load emerged ($F_{(4, 28)}$ = 7.80, p<.001, η_p^2 =.52) because within high perceptual load, accuracy was higher in trials with high memory load compared to those with medium load (Figure 3.2).

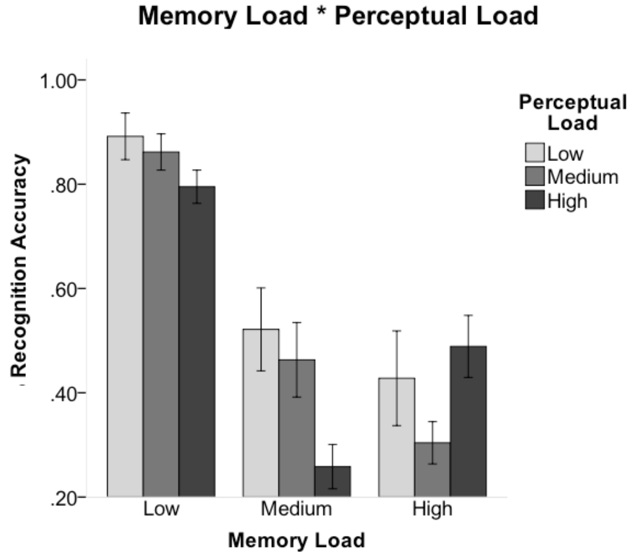

Figure 3.2 The interaction between memory and perceptual load factors. All the comparisons within each memory load factor are significantly different (p<.001). Error bars represent +/- 2 S.E.M.

These results suggest that both perceptual discrimination and perceptual load characterize recognition performance. Our next analyses explored to what extent the no-target (distractor) stimulus contributed to successful and unsuccessful recognition.

3.3.4 Influence of the no-target stimulus load on recognition

We repeated the above analyses by including the no-target stimulus load instead of perceptual load. The main effect of load for the perceptual and memory factors was confirmed, although no main effect of no-target load was found ($p>.05$).

Despite this, load in the no-target stimulus significantly modulated the memory load [significant interaction: $F_{(1.63,\ 13.06)} = 37.09$, $p<.001$, $\eta_p^2=.82$], specifically under high no-target load, recognition performance was lower for medium relative to high memory load (mean difference=-.24, $p>.001$), compared to the other no-target load conditions. The effect of no-target load on memory performance was also modulated by perceptual accuracy (three-way interaction: $F_{(1.83,\ 14.67)} = 4.28$, $p=.007$, $\eta_p^2=.34$), because performance differed significantly in trials preceded by accurate vs inaccurate perceptual judgment (Figure 3.3). When preceded by incorrect perceptual judgment, recognition performance only was lower, with load differences less pronounced.

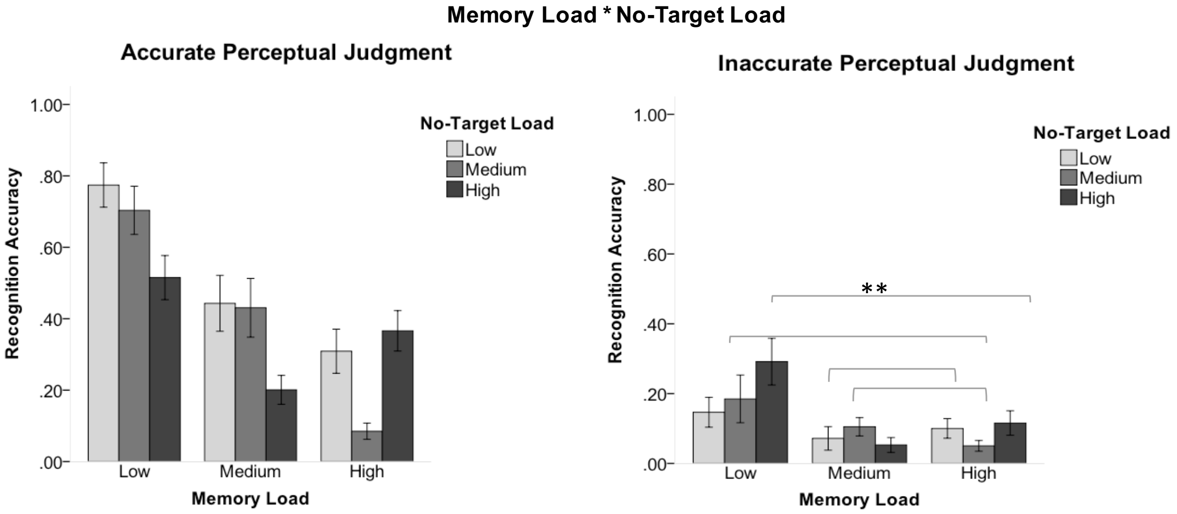

Figure 3.3. Interaction between memory and no-target load during accurate (left panel) and inaccurate (right panel) perceptual judgment. For accurate perceptual judgment, all the comparisons within each memory load factor were significantly different (Bonferroni corrected $p<.001$). For inaccurate perceptual judgment, significant differences between conditions are marked (**$p<.001$). Error bars represent +/- 2 S.E.M.

3.3.5 SUMMARY

When independently investigated, perceptual and inhibitory load contributed differently to the recall of VSTM representations**.** An initial correct perceptual discrimination of the stimuli was beneficial for recognition performance, and it also made memory representations more resistant to the high load conditions, both in the perceptual and distracting factor. Furthermore, perceptual accuracy modulated the effect of no-target stimulus load on memory recognition. Perception and inhibition considered together may further account for recognition performance; next, we investigated the combined influence of these factors.

3.3.6 COMBINED INFLUENCE OF PERCEPTUAL AND INHIBITORY LOAD ON MEMORY RECOGNITION

To analyse whether high load of perception, memory and inhibition had an influence on recognition performance jointly, also accounting for individual variability, we used a combination of generalized linear mixed-effects modelling and planned contrasts. We defined two contrasts for each of the three factors (perception, memory, inhibition load). In the high load contrast (hereafter defined as contrast number '1'), we compared performance at the high load level to average performance in the remaining load levels ('medium' and 'low' load). To determine the separate contribution of these two averaged levels, in the low load contrast (hereafter defined as contrast number '2'), we compared the low load level to the medium load level. To assess whether these contrasts for a specific factor (e.g., memory load) were moderated by another factor (e.g., perceptual load), we also defined contrasts for all pairwise interactions between factors. Table 3.2 shows the results of each contrast for each factor, as well as their two-way interactions (respectively Perception*Memory, Perception*Inhibition, Memory*Inhibition).

Table 3.4

Results of the planned contrasts for the generalized linear mixed-effects model, including all trials regardless of perceptual accuracy. For each **contrast, its** estimate relative standard error, z-value and Bonferroni-corrected *p*-value are reported.

	Factors' Contrast	Estimate	S.E.	z-value	*p*-value
Main Effects	**Perception1:** High vs. Low & Medium load	-21.77	4.65	-4.6	<.001
	Perception2: Low vs. Medium load	6.68	1.63	4.08	<.001
	Memory1: High vs. Low & Medium load	-69.54	3.92	-17.7	<.001
	Memory2: Low vs. Medium load	39.70	2.64	15.02	<.001
	Inhibition1: High vs. Low & Medium load	6.06	4.16	1.45	1.00
	Inhibition2: Low vs. Medium load	-11.81	2.59	-4.54	<.001
Interactions	**Perception1 * Memory1**	0.13	0.15	0.87	1.00
	Perception2 * Memory1	-0.02	0.17	-0.11	1.00
	Perception1 * Memory2	0.85	0.22	3.87	.001
	Perception2 * Memory2	1.11	0.18	6.06	<.001
	Perception1 * Inhibition1	1.40	0.16	8.65	<.001
	Perception2 * Inhibition1	-1.52	0.19	-8.03	<.001
	Perception1 * Inhibition2	-0.09	0.21	-0.43	1.00
	Perception2 * Inhibition2	4.22	0.18	22.97	<.001
	Memory1 * Inhibition1	-0.37	0.15	-2.49	0.27
	Memory2 * Inhibition1	0.30	0.21	1.44	1.00
	Memory1 * Inhibition2	1.97	0.20	9.70	<.001
	Memory2 * Inhibition2	-0.22	0.25	-0.86	1.00

As expected, high perceptual and memory load, as main effects, negatively affected accuracy in recognition compared to medium and low load (*p*<.001). Medium load also negatively affected recognition compared to low load (*p*<.001). Low load of the no-target stimulus (inhibition) resulted in reduced memory performance relative to medium load (*p*<.001). These results replicate the linear effect of memory and perception load found in the ANOVAs reported earlier, with the highest recognition accuracy in the context of low load. In addition to our univariate analyses, this model highlighted the main effect of no-target load. The condition of low compared to medium load negatively impact recognition performance (*p*<.001).

We then considered the effect on recognition performance of the following combined contrasts: memory*perception, memory*distractor and perception*distractor. We were specifically interested in whether and how the effect of high memory load (compared to low and medium load, i.e. the high memory load contrast) was moderated by the other load factors. The detrimental effect of high memory load on recognition was significantly reduced when the inhibition/distractor load was low as compared to medium (Significant interaction of Memory1 and Inhibition2; estimate: 1.97 (SE 0.20), z= 9.70]. The effect of high memory load was not moderated by other factors.

The beneficial effect of low memory load on recognition increased when perceptual load was high compared to low or medium [significant interaction of Perception1 and Memory2; estimate: 1.40 (SE 0.16), z= 8.65]. This effect also increased when perceptual load contrast was between low and medium [significant interaction of Perception2 and Memory2; estimate: 1.11 (SE 0.18), z= 6.06].

The effect of distractor load was also moderated by perceptual load. The detrimental effect of low distractor load (as compared to medium distractor load) was reduced when perceptual load was low compared to medium [significant interaction of Perception2 and

Inhibition2; estimate: 4.22 (SE 0.18), z= 22.97]. Moreover, high distractor load (compared to medium and low load) had a more beneficial effect when perceptual load was high compared to medium or low [significant interaction of Perception1 and Inhibition1; estimate: 1.40 (SE:0.16), z= 8.65], but had a larger negative effect when perceptual load was low compared to medium [significant interaction of Perception2 and Inhibition1; estimate: -1.52 (SE 0.19), z= -8.03] (see Table 3.2).

These analyses show that recognition was mainly modulated by the load of the memory stimuli, but also that perceptual and inhibitory factors, individually or in combination, had an impact on recognition performance (Table 3.2). Equivalent results were obtained when only trials preceded by correct perceptual discrimination were analysed (Table 3.3), although the main effect of low vs medium load was no longer significant for perceptual and distractor factors.

This pattern of results was also reflected in the factors' interactions. In successfully discriminated trials, the high similarity of perceptual and memory stimuli in combination attenuated their detrimental effect on recognition performance [estimate: -1.29 (SE 0.13), z= -9.47]. This is in line with previous results showing that successful perceptual discrimination makes performance less vulnerable to the detrimental effect of load, an effect that extended to high load contrast for both perceptual and memory factors.

Table 3.5

Linear Mixed Model output, including only trials preceded by correct perceptual discrimination. For each of the contrast estimate and its relative standard error (SE), z-values and Bonferroni-corrected *p*-values are reported.

	Factors' Contrast	**Estimate**	**S.E.**	**z-value**	***p*-value**
Main Effects	**Perception1:** High vs. Low & Medium load	-25.08	5.88	-4.26	<.001
	Perception2: Low vs. Medium load	12.91	4.99	2.58	0.17
	Memory1: High vs. Low & Medium load	-73.37	5.16	-14.20	<.001
	Memory2: Low vs. Medium load	10.66	2.05	5.18	<.001
	Inhibition1: High vs. Low & Medium load	9.63	6.09	1.58	1.00
	Inhibition 2: Low vs. Medium load	-0.23	2.63	-0.08	1.00
Interactions	**Perception1 * Memory1**	-1.29	0.13	-9.47	<.001
	Perception2 * Memory1	-0.06	0.23	-0.27	1.00
	Perception1 * Memory2	0.46	0.26	1.72	1.00
	Perception2 * Memory2	1.34	0.24	5.44	<.001
	Perception1 * Inhibition 1	1.26	0.14	8.94	<.001
	Perception2 * Inhibition 1	-1.89	0.28	-6.58	<.001
	Perception1 * Inhibition 2	0.06	0.25	-0.26	1.00
	Perception2 * Inhibition 2	4.28	0.21	19.49	<.001
	Memory1 * Inhibition 1	-0.47	0.22	-2.14	0.27
	Memory2 * Inhibition 1	0.18	0.30	0.60	1.00
	Memory1 * Inhibition 2	2.08	0.25	8.26	<.001
	Memory2 * Inhibition 2	-0.17	0.29	-0.59	1.00

3.4 DISCUSSION

This study was aimed at understanding the independent and combined contribution of three cognitive factors known to influence VSTM performance: perceptual discrimination and memory of a target stimulus as well as the inhibition of a no-target stimulus (Beck & Kastner, 2009; Montaser-Kouhsari & Carrasco, 2009; Shapiro & Miller, 2011). We designed a paradigm requiring an explicit perceptual judgement and parametrically manipulated the high, medium and low load levels of the stimuli to be encoded (perceptual factor), remembered (comparing probe to target, memory factor) and ignored (suppressing the influence coming from the representation of no-target item, inhibitory factor).

In accordance with visual attention theories (Beck & Kastner, 2009; Shapiro & Miller, 2011), we expected recognition accuracy, decreasing proportionally to the increase of both perceptual and memory load. Results stemming from univariate analysis confirmed both these predictions. In addition, as expected, higher recognition performance was explained by successful perceptual discrimination, indicating that correct perceptual discrimination supports the consolidation of memory representations, ultimately making them more resistant to distractors and to the interference of perceptual similarity between target and probe (Bettencourt & Xu, 2016; Galli, 2014; Vogel, Woodman, & Luck, 2006). This result supported our methodological decision to manipulate the perceptual load and include an explicit perceptual discrimination.

The inhibitory factor was strongly influenced by perceptual accuracy, and in turn affected memory load, by reducing the difference between load conditions. This in accordance with previous visual search studies that tightly relate the influence on no-target stimuli to the representation of the target stimuli (Rosenholtz, 2001).

In order to explain the factors' combined contribution and the individual variability in recognition, mixed model analysis revealed that memory's high load mostly accounted for unsuccessful recognition, by having the highest detrimental effect on recognition performance. Additionally, mixed model analyses highlighted the detrimental effect on recognition performance of low load of the no-target stimulus, independent from other factors. This is in line with the view that the homogeneity between no-target and probe may harm performance, possibly by increasing swap errors in terms of stimulus location (Emrich & Ferber, 2012).

An additional reduced performance in recognition emerged when high memory load was combined with high perceptual load and low inhibition load. Lowest recognition therefore corresponded to high memory load associated with increased distractor processing, which represents a further evidence of an interaction between these factors (Rosenholtz, 2001).

When mixed model analysis was restricted to trials preceded by accurate perceptual discrimination, recognition remained vulnerable to perceptual load and even more strongly to memory load. When the memory factor was considered in combination with others, the load of the no-target stimuli (inhibitory factor) had an additional detrimental effect. Therefore, despite being relevant for successful discrimination, the challenge associated with high memory load was such that recognition remained unsuccessful (Shapiro & Miller, 2011; Vogel et al., 2006). Although successful and within capacity resources of encoding, demanding probe-target comparisons may have reduced the ability to preserve memory representations because they exceeded executive control resources, ultimately affecting the VSTM performance (Scalf, Dux, & Marois, 2011; Todd & Marois, 2004). This further supports the resource allocation models, in which VSTM success is promoted by the quality of memory representation and its stability against load and task-irrelevant information (Bays & Husain, 2008b; Wilken & Ma, 2004).

It is important to note that although differences between load conditions were present, the very low level of accuracy for the medium and high load may not be attributed to intrinsic task difficulty but it may have been the result of a perceptual grouping effect, likely to occur for the low load condition. Indeed, in this particular load condition stimuli identical in orientation may be grouped in one memory representation, effectively reducing the memory load (in terms of number of items) to one item (Eng et al., 2005). This effect may have contributed to generate a significantly higher number of errors for high and medium relative to low load conditions.

Overall, this study provides insights into the understanding of the cognitive factors underlying successful VSTM. Successful perceptual discrimination encouraged by an explicit perceptual judgment at stimulus encoding supported excluding the possibility that recognition errors were merely the result of weak perceptual discrimination. Moreover, perceptual, memory and inhibitory load allowed identifying the factors most strongly accounting for recognition performance. High load of the stimuli to be remembered, especially if combined with high load of the stimuli to be perceptually discriminated and low load of the stimuli to be ignored, accounted most strongly for unsuccessful recognition and showed that perception is necessary but not sufficient to protect VSTM. Besides these interactions, high memory load played a predominant role over the other factors in determining successful recognition.

By emphasizing the close relationship between perceptual, memory and inhibitory factors in VSTM performance within set-size capacity, this study provides further support to the role of quality and of memory precision as well as defining the “weight” of contributing VSTM factors.

Following up on these findings, future studies may investigate whether high memory load representations are maintained differently from other load conditions, during the delay interval. This would elucidate whether these results mainly reflect a challenging comparison between probe and target or whether the fidelity by which we maintain memory representations affects subsequent comparisons, regardless of their difficulty. Viable ways to test this would be by directly assessing representation maintenance or by investigating potential difference in the neural correlates in different perceptual load conditions, before probe appearance. This, together with our proposed decomposition of steps and factors involved in VSTM, would lead to a deeper and more comprehensive understanding of how and why we do not always successfully remember information.

CHAPTER 4: THE ROLE OF PERCEPTUAL LOAD AND ACCURACY DURING VSTM MAINTENANCE: AN ELECTROPHYSIOLOGICAL INVESTIGATION OF TASK-RELATED AND ENDOGENOUS NEURAL ACTIVITY.

In the previous chapter, we investigated whether successful recognition in a VSTM task depends on the following factors: quality of the stimulus encoding; difficulty in the comparison of the encoded memory representation with a probe stimulus; suppression of task-irrelevant information. We showed that all the considered factors played an important role, but the similarity between the probe and target stimulus remained the most crucial one.

However, the previous study did not focus on another stage in the VSTM process known as maintenance, corresponding to the retention of memory representations (Hollingworth, 2003). In this chapter, maintenance was investigated using electrophysiological measures of brain activity prior (at rest) and during task execution. We aimed to further our understanding of how oscillatory neural activity contributes to mechanisms of VSTM and whether it may be used as a predictor of these processes.

4.1 THEORETICAL BACKGROUND

The cognitive stages defining memory processing are typically divided into encoding, maintenance and retrieval (Baddeley, 2001). The study described in the previous chapter provided a direct measure of the encoding and retrieval processes, by including load and an explicit judgment for both processes. However, it is possible that even in the case of successful perceptual encoding failures in the comparison between target and probe may be due to a loss or overwriting of information during retention (Shapiro, Arnell, & Raymond, 1997), which could make memory representations more vulnerable at the retrieval stage (Galli, 2014; Park, Min, & Lee, 2010; Théau, 2012).

Therefore, this study aimed at specifically investigating the maintenance period, with the purpose of elucidating the role of accurate perceptual discrimination on recognition, obtained by comparing the electrophysiological correlates when maintaining memory representations differing in stimulus complexity (load).

Maintenance involves distributed neural regions primarily in the frontal and parietal lobes, and is thought to result from the synchronization of neuronal assembles across a number of different frequencies (Gevins et al., 1997; Jensen & Tesche, 2002; Raghavachari et al., 2001). Previous studies have demonstrated the involvement of theta (4-7Hz), alpha (8-12 Hz), beta (13-30 Hz) and gamma (above 30 Hz) during the maintenance of memory representations (Herrmann, Munk, & Engel, 2004; Jensen & Colgin, 2007; Raghavachari et al., 2001; Tallon-Baudry, Mandon, Freiwald, & Kreiter, 2004).

Specifically 'load' – which is usually described as the number of stimuli in the initial sample array – is typically associated with theta power, although the direction of this relationship in terms of polarity has been controversial (Jensen & Tesche, 2002; Onton et al., 2005; Raghavachari et al., 2001). Indeed, some studies have reported higher theta power for increased load, in accordance with the view that higher frontal theta reflects enhanced attention (Bruneau, Roux, Guérin, Garreau, & Lelord, 1993; Deiber et al., 2007; Gevins et al., 1997). Conversely, other studies have found a decrease of theta power with memory load increase (Babiloni et al., 2004; Bastiaansen, Posthuma, Groot, & De Geus, 2002; Pan, Tan, Gao, Li, & Wang, 2018). Increased alpha and decreased beta activity also reflect increased short-term memory load (Jensen, Gelfand, Kounios, & Lisman, 2002; Pesonen, Hämäläinen, & Krause, 2007).

Non-human primate studies showed that the association between maintenance and subsequent performance accuracy corresponds to increased synchronization in the beta range during memory maintenance for correct but not for incorrect trials (Tallon-Baudry et al., 2004).

Human studies, on the other hand, report a detectable difference in the power of gamma oscillations related to the number of hits versus misses in the encoding phases of a memory task (Park et al., 2010).

Although these studies identified the neural features of successful short-term memory task performance by investigating the maintenance period, their focus has been on the memory judgement, neglecting the role of accurate perceptual discrimination and its potential effect on load processing following encoding.

In order to address this question, this study used the same task as in Chapter 3, differing only in the level of load (two instead of three levels). Participants were still required to retain binding information (location and orientation) of briefly presented visual stimuli in the form of Gabor patches, to explicitly discriminate them and then compare them to a probe, after a short interval.

This study had three aims: 1) replicate the results reported in Chapter 3; 2) investigate the neural signatures of the load effect during the maintenance of successfully encoded and subsequently retrieved stimuli; 3) if present, assess whether these could be predicted from resting state neural activity prior the task execution. In the context of past electrophysiological studies, a theta increment associated with load was observed when stimuli were presented sequentially (mostly using the Sternberg task whereby participants decide whether a probe item belongs to a sequence of previously presented stimuli) (Sternberg, 1966) and/or when exploring episodic memory (Jensen & Tesche, 2002; Klimesch, Doppelmayr, Pachinger, et al., 1997; Onton et al., 2005; Raghavachari et al., 2001). Conversely, a recent study using a delayed match-to-sample task and manipulating the length of the delay period, showed a decrease of theta power with the increase of time length (Pan et al., 2018). This novel finding was interpreted as the effect of items being encoded and maintained spatially rather than temporally, which is known to affect theta increase with the increment of the memorized items (Bastiaansen et al., 2002; S. Palva, Kulashekhar, Hamalainen, & Palva, 2011; Roberts, Hsieh, & Ranganath, 2013)

In light of this, we reasoned that maintenance could be characterized by a decrement of theta power as the stimuli here were presented simultaneously and with a constant set size. Alternatively, if high load corresponded to the most challenging condition at the behavioural level, then theta power may increase following past observations that this corresponds to an increment of attentional effort (Bruneau et al., 1993; Deiber et al., 2007; Klimesch, Vogt, et al., 1999).

To investigate the extent to which the neural processes underlying maintenance also promote successful memory performance, we investigated the association between theta frequency recorded at rest (prior to task execution) and subsequent performance.

4.2 METHODS

4.2.1 PARTICIPANTS

Thirty-two right-handed students from Goldsmiths, University of London (8 males, mean age: 26.4 ±4.3) with normal or corrected to normal vision provided written informed consent to volunteer to the study, which was approved by the Ethics Committee of the Department of Psychology at Goldsmiths.

Three participants were excluded due to technical issues during EEG data recording, therefore the final sample was of 29 participants (7: males, mean age: 26.5 ±4.6).

4.2.2 Stimuli and Task

The stimuli and experimental task were identical to the one used in Chapter 3 except for the use of only two rather than three load levels, high and low. Therefore, for each of three investigated factors, the similarity between stimuli in terms of degrees of orientation, was either the same ('low' load) or slightly differing ('high load') (see section 3.2.2 p.48 for similar approach). We did not include a third load level as we wanted to focus on the load conditions that proved to be the most challenging in our previous study.

There were 144 trials for each gradient of difficulty and each judgment, with 72 trials for each possible combination, resulting in a total of 288 for the entire experimental session, divided in 4 blocks.

4.2.3 Experimental Procedure

Participants were seated in a dark room at approximately 57 cm from the computer monitor, and were asked to fixate at the centre of the monitor in order to better discriminate the orientation of the two stimuli.

In contrast to the previous study (Chapter 3), participants completed a practice block of 20 trials, where feedback was provided for both the perceptual and memory judgments. After the practice session, participants were instructed to initiate the experiment which took about 45 minutes, with breaks between the self-timed blocks.

Electrophysiological activity was recorded for five minutes prior to task execution and during the whole task.

4.2.4 THRESHOLDING

The same thresholding procedure used in Chapter 3 was used for this study.

4.2.5 BEHAVIOURAL DATA ANALYSIS

The same approach for behavioural data analysis used in Chapter 3 was also applied here, except that no generalized mixed model was used. This is because only two contrasts (high and low) were available for this study, which is below the minimum requirement for mixed models.

4.2.6 ELECTROPHYSIOLOGICAL DATA ANALYSIS

A time-frequency transformation was computed to examine whether there was any systematic variation in energy at different frequencies in the EEG signal during the maintenance interval (900 ms before probe presentation). As our main interest was restricted to this interval, time frequency representations of individual trials were calculated using Morlet wavelet analysis with a wavelet number of cycles that linearly increased from 3 to 8 depending on the frequency range, time-locked to the memory probe presentation.

Trials were then averaged for each perceptual load condition and normalised to the entire trial epoch as baseline period (-3500ms to 1000ms). We reasoned that since the physical characteristics of the visual stimuli (the fixation dot during the maintenance interval and the Gabor patch during the probe presentation) were identical to those during the remainder of the trial, the main neural difference between these periods are likely to correspond to memory maintenance. For the statistical analyses, non-parametric cluster permutation was used (Maris & Oostenveld, 2007) (for details on this method, see Chapter 2).

4.3 BEHAVIOURAL RESULTS

4.3.1 PERCEPTUAL SENSITIVITY

For the perceptual judgement, paired-samples t-tests showed no significant effect of load on the perceptual factor (p>.05). Participants discriminated the orientation of the initial stimuli with no significant difference between high and low load. Moreover, sensitivity analysis showed no response bias towards any of the two response options (same or different), as criterion (response bias) did not significantly differ from zero ($t_{(28)}$ = -.24 p=.808) (see Table 4.1).

Table 4.1 **Mean (and standard deviation) of hit, false alarm, missed and correct rejection for each perceptual load condition (low or high). Sensitivity and criterion values with standard deviations. As the task was a two-Alternative Forced-Choice (2AFC) same-different judgement, the sensitivity and criterion scores reflects the combination of the two types of load (high vs low load).**

Type of response	**Perceptual load**	Hit	False alarm	Misses	Correct rejection	**Sensitivity (d')**	**Criterion (C)**
Same	Low	.83(.12)	.20(.14)	.17(12)	.79(.14)	2.25(.78)	-.02(.49)
Different	High	.79(.14)	.17(12)	.20(.14)	.83(.12)		

4.3.2 INFLUENCE OF THE PERCEPTUAL ACCURACY AND LOAD ON MEMORY

On average, memory recognition performance was above chance (M = .66 SD = .08), with a significant impact of memory load on accuracy, such that low load resulted in higher accuracy than high load ($t_{(28)}$ = 6.17 p< .001) (see Table 4.2).

Next, we tested to what extent successful memory recognition was modulated by perceptual performance by repeating the previous analyses with the inclusion of perceptual accuracy (correct vs incorrect) and load ('low' and 'high' conditions) in the memory and perceptual factor as within-subject factor.

Perceptual accuracy, perceptual load and memory load all significantly influenced recognition performance [main effects: perceptual accuracy ($F_{(1, 19)} = 303, 63$, $p<.001$, $\eta_p^2 = .94$); perceptual load ($F_{(1, 19)} = 16, 84$, $p=.001$, $\eta_p^2 = .47$), memory load ($F_{(1, 19)} = 14, 20$, $p=.001$, $\eta_p^2 = .42$)]. There was a significant higher ($p< .001$) proportion of correct recognition answers after accurate relative to inaccurate perceptual discrimination. Recognition performance significantly decreased ($p< .001$) with the increase of load, both for the perceptual and memory factor. Furthermore, the interaction between memory load and perceptual accuracy ($F_{(1, 25)} = 9.37$, $p=.006$, $\eta_p^2 =.33$) was driven by higher memory performance in trials preceded by accurate perceptual discrimination compared to inaccurate, with a stronger difference between high and low load conditions ($p<.001$) (see Table 4).

Table 4.2 Mean (and standard deviation) memory accuracy for each memory load condition (low or high), according to perceptual judgement (accurate or inaccurate) and perceptual load (low or high).

Type of response	Memory load		**Perceptual judgement**			
			Accurate		Inaccurate	
			Perceptual load			
			Low	**High**	**Low**	**High**
Same	**Low**	.80(.12)	.35(.08)	.31(.09)	.06(.04)	.09(.05)
Different	**High**	.51(.17)	.23(.08)	.19(.09)	.05(.05)	.03(.02)

Altogether the three factors (perceptual accuracy, memory and perceptual load) modulated recognition performance [three-way interaction of perceptual accuracy*perceptual load*memory load: ($F_{(1, 23)} = 6.58$, $p=.019$, $\eta_p^2 = .25$)]; despite the lack of interaction between perceptual and memory load, and between perceptual accuracy and load ($p>.05$),

Post-hoc analyses showed that memory load was significantly ($p< .001$) modulated by perceptual load in the expected direction (higher recognition accuracy for low than high) in accurately but not in inaccurately discriminated trials. This specific effect should be taken with caution, considering the small number of trials preceded by inaccurate perceptual discrimination.

Overall, these results provide further evidence of the relevance of accurate perceptual discrimination and of the effect of perceptual load, specifically for perceptually accurate trials. This confirms that recognition is more likely to be successful when it is preceded by correct perceptual discriminations and is characterized by a linear effect of difficulty both at the perceptual and memory level.

In the following section, we explored the role of the no-target (distractor) stimulus in determining successful recognition.

4.3.3 INFLUENCE OF NO-TARGET STIMULUS LOAD ON MEMORY RECOGNITION

Recognition accuracy as a function of the similarity between the target and no-target stimulus reflected the ability to inhibit memory representations no longer relevant for recognition. As in Chapter 3, the different levels of load in the no-target stimulus, did not impact on performance ($F_{(1,\ 25)} = .734$, $p = .399$, $\eta_p^2 = .025$). Next, we tested whether the lack of perceptual load effect was due to incorrect perceptual discrimination and whether the no-target load modulation may change once we account for perceptual accuracy (as reported in Chapter 3). This is based on the assumption that if the two initial stimuli are not successfully discriminated after probe presentation, then the no-target stimulus may not have a distracting effect simply because it was not properly processed. To test this hypothesis, the previous analysis was repeated including perceptual discrimination accuracy, keeping no-target and memory load as factors.

Perceptual accuracy and memory load significant modulated performance [($F_{(1,\ 19)} = 264.37$, $p < .001$, $\eta_p^2 = .93$), ($F_{(1,\ 19)} = 15.92$, $p = .001$, $\eta_p^2 = .45$), respectively], with lower recognition performance in trials preceded by inaccurate perceptual discrimination relative to accurate (mean difference = -.21, p<.001) as well as in high memory load compared to low (mean difference = -.06, p=.001).

The no-target stimulus load did not overall modulate performance (p<.05), but it interacted with perceptual accuracy ($F_{(1,\ 19)}$ = 15.84, p=.001, η_p^2 = .45), such that lower performance for low no-target load relative to high (mean difference= .-02, p<.001) emerged only in trials preceded by perceptual inaccuracy. Crucially, no-target load also significantly modulated memory load ($F_{(1,\ 19)}$ = 10.25, p=.005, η_p^2 = .35) because low no-target load significantly increased the memory load effect (mean difference between low and high memory load: .08, p<.001), see Figure 4.2.

The three-way interaction of perceptual accuracy*no-target load* memory load did not reach significance (p>.05).

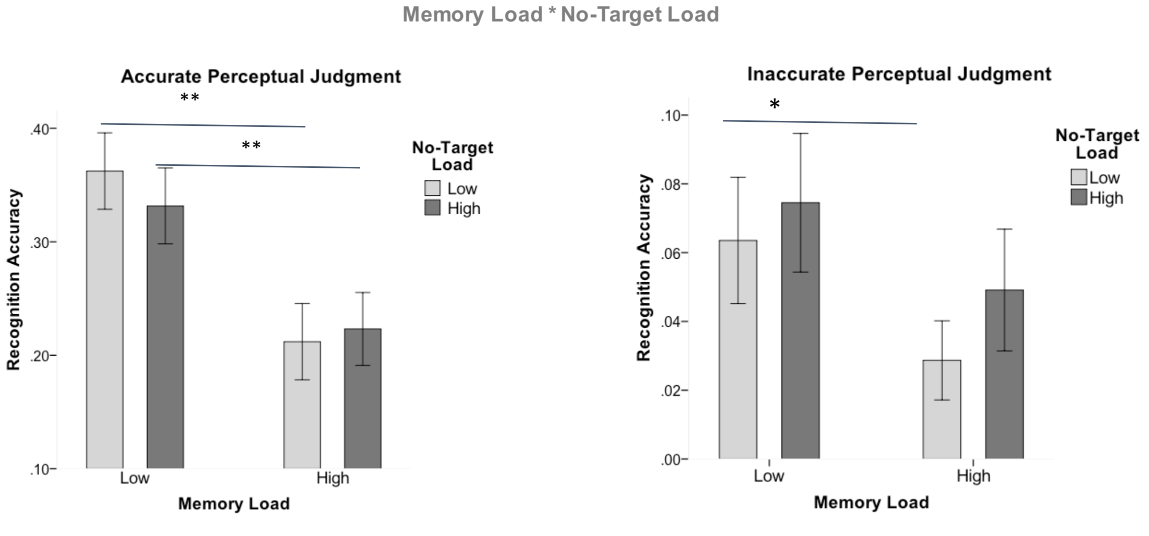

Figure 4.1 The interaction between no-target and memory load, under the condition of accurate and inaccurate perceptual judgment. Error bars correspond to standard errors and asterisks indicate significant differences between conditions (*p<.05, **p<.01,). Note that two different scales have been used.

To sum up, both perceptual accuracy and memory load revealed the influence of the no-target factor. A higher level of recognition accuracy was found in trials preceded by correct perceptual discrimination, whereas the effect of the no-target load emerged only in inaccurately discriminated trials, where low load was associated with lower performance than high load. Accordingly, under the condition of high no-target load, the effect of memory load emerged more strongly. This provides evidence for an interaction between these factors. However, given the low number of trials inaccurately discriminated, these results should be considered with caution.

4.3.4 SUMMARY

Replicating the findings from Chapter 3, recognition was modulated by perceptual accuracy and by no-target load. More specifically, an initial correct perceptual discrimination of the stimuli was beneficial for recognition and also revealed the effect of memory load in the expected direction (low being less challenging than high load).

Additionally, there was a significant effect of perceptual load because performance was better for low relative to high load conditions; note that this effect was only marginally significant in the study reported in Chapter 3 (section 3.3.3).

The no-target load modulated recognition when perceptual accuracy was taken into account, such that the most challenging condition was when the probe and no-target were identical, confirming the mixed model results in Chapter 3. This impact of the no-target load was also reflected on memory load, whose effect was enhanced in the least challenging no-target condition (high load).

To sum up, these results partly replicate our initial findings of an interaction between perceptual, inhibitory (no-target) and memory load on recognition performance. Crucially, these findings further support our methodological decision to explicitly test perceptual accuracy in a recognition task.

4.4 ELECTROPHYSIOLOGICAL RESULTS

4.4.1 TIME-FREQUENCY ANALYSES DURING MAINTENANCE

In this study, participants were asked to maintain stimuli information (both location and orientation) for 900ms, between the perceptual discrimination judgment and the probe onset. We were particularly interested in the effect of perceptual load during this interval, and in the case where trials were accurate both at the perceptual and memory recognition level.

By comparing trials grouped according to perceptual load, we observed an increase in theta synchronization for low compared to high perceptual load. This was in two different time windows: from -.900 to -.700 ms and -.600 to -.300 ms prior the probe presentation. As Figure 4.3b shows, these effects were observed first over a central-parietal cluster (p =.007), and subsequently over frontal regions (p<.001). Paired sample t-tests comparing the averaged theta (4-7 Hz) power across cluster electrodes/time points for low and high load conditions showed higher theta power (p<.001) both for the first and second time window (mean difference: -.170 (SE: .037) and -. 138 (SE:.20) (Figure 4.3c).

None of the other frequency band activity studied (alpha, beta and gamma) showed any reliable differences between low and high perceptual load during the maintenance interval at any electrode site.

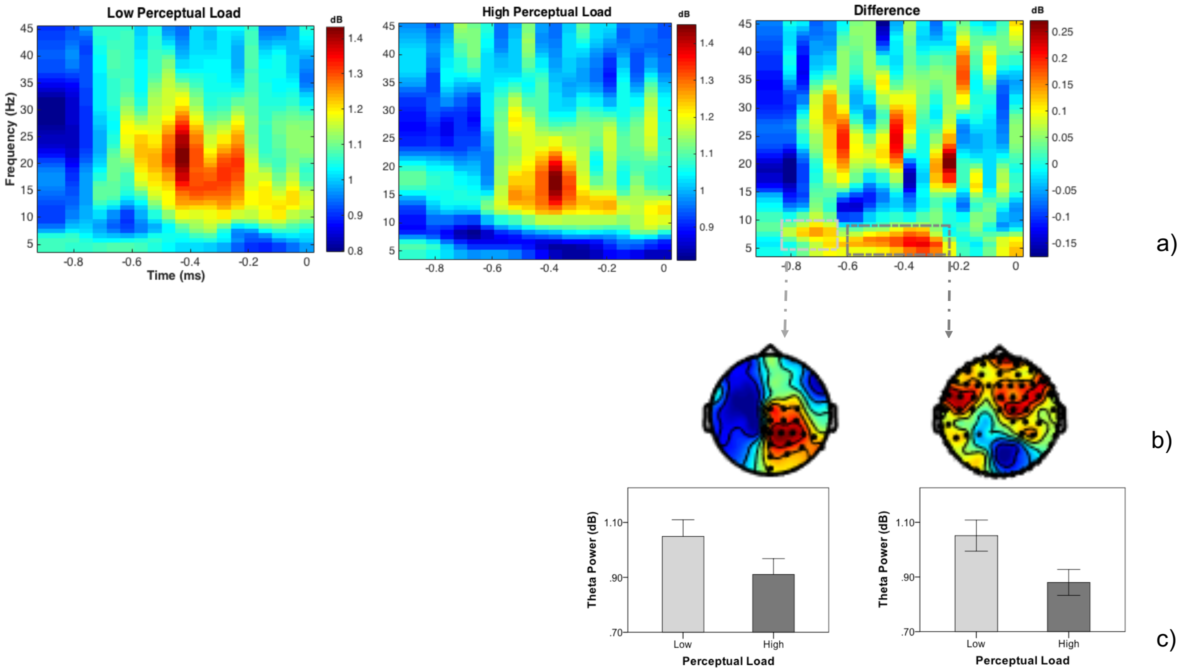

Figure 4.2. Grand averaged probe-locked power in the theta band (4-7Hz). a) Time-frequency plots at a representative electrode (FCz) locked to stimulus onset (0). b) Scalp maps of theta power at significant time points (-.900 to -.700ms, on the left and -.600 to -.300 on the right) where significant cluster electrodes are highlighted. c) The bar graphs show the averaged power at significant cluster electrode sites, and time points for low (light grey) and high (dark grey) perceptual load conditions. Error bars show +/- SEM.

4.4.2 POWER SPECTRAL DENSITY ANALYSES AT REST

To test whether theta oscillations at rest could be associated with subsequent recognition performance, the mean power spectral density in the theta band (4-7 Hz) during a rest period prior to the task was correlated with accuracy in trials with both correct perceptual and memory judgements.

Resting state theta power values were extracted from the frontal electrodes identified by the cluster permutation analysis of the maintenance interval. Spearman correlation (theta power * accuracy proportion) highlighted a significant negative association such that higher recognition performance corresponded to lower power in the theta band ($r_{s(27)}$ = -.47, p=.02), see Figure 4.4.

This correlation was only present for trials in which both a correct perceptual and memory judgment was made. Indeed, theta power at rest extracted from the cluster electrodes, did not correlate with performance when both perceptual and memory judgements were incorrect, or when only one of the two judgements was correct.

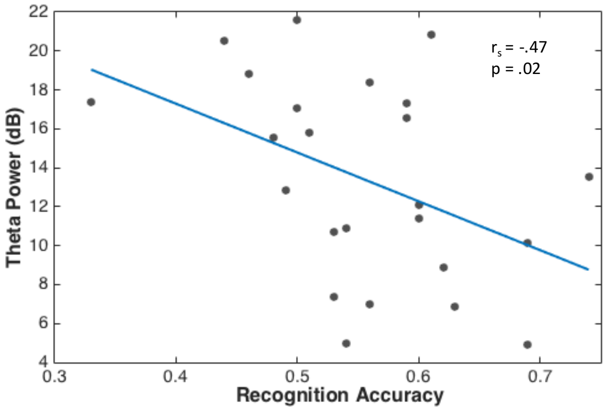

Figure 4.3 A negative correlation between recognition accuracy and theta values extracted **during rest and prior task execution** from clusters electrode sites differing in the low and high perceptual load during maintenance.

4.5 DISCUSSION

In the present study, we replicated the load effect on recognition of the three selected cognitive factors: perception, memory and inhibition. Moreover, we investigated the EEG oscillatory activity corresponding to the maintenance of the representation of the two stimuli correctly discriminated, before a successful probe-target comparison. This was assessed by manipulating the level of similarity (high versus low load) between the two initial Gabor stimuli. Successful perceptual and recognition judgments were accompanied by increased theta power initially over posterior regions, and subsequently over bilateral frontal areas during the maintenance interval, in low versus high stimuli load. We also observed that theta activity recorded at rest was negatively correlated with memory performance, specifically in the electrodes discriminating perceptual load in the maintenance interval.

4.5.1 THE EFFECT OF THE THREE COGNITIVE FACTORS ON MEMORY RECOGNITION PERFORMANCE

Our behavioural data partially replicated the results from Chapter 3 by showing a significant modulation of the orientation similarity (load) between target, no-target and initial stimuli array and their effect on recognition performance. Overall, memory recognition performance was higher than that reported in Chapter 3.

A number of methodological differences between the two studies may explain the difference in recognition accuracy: the lack of response bias at the perceptual level, the presence of a practice session (not included in the analysis) and a balanced proportion of trials for the answer “same” and “different”.

Despite this, memory recognition performance for the high load condition was still at chance level. This may be due to intrinsic difficulties of the task, such as dual judgment as well as the possibility of interaction between load intended as stimulus complexity as well as number of items to remember discussed in the Paragraph 3.4.

Since our main goal was to investigate the maintenance period, only two load conditions were present in this study, therefore no mixed model contrast analysis was conducted, and no regression coefficients for each of the factors investigated were therefore extracted.

4.5.2 THETA DECREASES WITH THE INCREASE OF MEMORY REPRESENTATIONS' LOAD

Although the involvement of theta (4-7 Hz) in memory processes is well-established, its specific role during maintenance has been overlooked after controlling for perceptual accuracy.

Our results showed that a decrease in theta was associated with holding binding information (location and orientation) from two correctly discriminated visual stimuli over a brief delay. These results challenges an influential view that theta increases with load increment, although intended as number of items (Gevins et al., 1997; Klimesch, Doppelmayr, Schimke, et al., 1997; Onton et al., 2005).

However, this inverted pattern in theta oscillatory activity has been reported in other visuospatial memory tasks, where stimuli were presented simultaneously and when the number of items was not manipulated (Babiloni et al., 2004; Bastiaansen et al., 2002; Pan et al., 2018). As the increase in theta has been associated with activation of the cortico-hippocampal circuit involved in attentional effort and memory (Preston & Eichenbaum, 2013; Ritchey, Libby, & Ranganath, 2015; Treves & Rolls, 1994), the present decrement in power could reflect the inhibition of information processing throughout these loops (Babiloni et al., 2004).

Our topography across time is in accordance with previous data showing significant changes in theta-band activity across the visual and prefrontal cortex during the maintenance of memory representations (Liebe, Hoerzer, Logothetis, & Rainer, 2012). Posterior regions activity has been related to the reactivation of information representation (Sarnthein, Petsche, Rappelsberger, Shaw, & von Stein, 1998), and the more anterior to their maintenance (Siegel, Warden, & Miller, 2009; Tsujimoto, Shimazu, Isomura, & Sasaki, 2009).

Beyond oscillatory power, investigating the interaction between frequency bands (cross-frequency coupling) may help to explain how these spectrally distributed oscillations interplay with each other. Indeed recent evidence suggests that a hierarchy of interacting oscillations may be a candidate mechanism for integrating information processing across multiple spatial and temporal scales (Axmacher et al., 2010; Colgin, 2015; Liebe et al., 2012). For example, depending on the phase of theta oscillations, the power of both beta and gamma oscillations can systematically vary. This may be particularly relevant here considering the intrinsic binding nature of our stimuli. Indeed, although no significant association emerged with frequencies different from theta, a visual inspection of the time-frequency representation of the maintenance interval showed an increase in beta oscillatory activity specifically for the low load condition. Enhanced beta in the delay period of delayed-matching-to-sample tasks (Tallon-Baudry et al., 2004) is known to parametrically increase with load (Leiberg, Lutzenberger, & Kaiser, 2006), and is also related to assemble task-relevant stimulus features (Tallon-Baudry, Kreiter, & Bertrand, 1999; Varela, Lachaux, Rodriguez, & Martinerie, 2001).

Further exploration of intra- and cross-spectral synchrony could better delineate the interactive role of these oscillatory activities in memory processing, controlling for accurate perceptual processes. To note, comparisons with perceptually incorrect trials were not possible because there were too few trials available after artefact rejection; we cannot therefore rule out the possibility that high theta difference might reflect the difference in performance between the two memory conditions. By selecting trials correct at both perceptual and recognition level, we provided novel evidence of the neural signature of holding information that has been successfully discriminated for perceptual features and subsequently recognized.

4.5.3 THETA AT REST PREDICTS ACCURATE PERCEPTUAL AND MEMORY RECOGNITION PERFORMANCE

Having established that theta oscillations characterized load manipulation in trials correctly discriminated and remembered, we used EEG task-related results to lead the analysis of resting state activity. Specifically, theta power spectral density (PSD) at rest was extracted for those electrodes showing significant load differences during task execution. These clusters negatively correlated with memory recognition performance, specifically only trials that were correct at the perceptual and memory level.

This result is in accordance with the established theory that successful memory performance is associated with decreased theta power at rest relative to task-related activity (Klimesch, Doppelmayr, Schimke, et al., 1997; Klimesch, Vogt, et al., 1999). Such "inverse-pattern" has also led to the hypothesis that the Default Mode Network (DMN), dominant in resting conditions and comprising regions implicated in higher order cognition, is negatively operating in theta range (Scheeringa et al., 2008). In our study, we extended these findings and showed a relationship between theta oscillations and accurate memory recognition performance, aligned to theta activity during the maintenance interval.

4.6 CONCLUSION

Taken together, our results suggest that a decrease in theta oscillations during maintenance is associated with the load of memory representations. Furthermore, theta power at rest also predicted accurate memory performance, only in items successfully discriminated at the perceptual level.

CHAPTER 5: ENDOGENOUS NEURAL ACTIVITY CORRELATIONS WITH FLEXIBLE MANIPULATION OF VISUAL WORKING MEMORY REPRESENTATIONS

In this chapter, we focused on individual variability in the flexible manipulation of memory representations to investigate the role of retrospective-cues in memory, and to clarify past inconsistencies in the literature. WM performance and resting state EEG (rsEEG) were collected in healthy young participants subdivided into those showing different level of flexibility in performance associated with retro-cues cost, associated the invalid retro-cue condition. rsEEG features in the alpha band (8-12 Hz), power spectral density and long-range temporal correlations recorded at rest identified participants who effectively used the retro-cue information. This emerged in a small cost for invalid cues and at the same time a benefit for valid cues, therefore suggesting stronger cognitive flexibility. Additional cognitive tasks indicated that this neural characterization was not attributable to more general-domain cognitive differences between subgroups. These results provide the first characterization of individual differences in response to invalid retro-cues measured at rest, reconciling a debate in the working memory literature.

5.1 INTRODUCTION

A crucial component of working memory (WM) is the ability to flexibly manipulate memory representations, by directing attention towards goal-relevant stimuli and inhibiting the task-irrelevant ones (Nobre et al., 2004; Zanto & Gazzaley, 2009). Flexible manipulation of the memory representations and inhibitory abilities can be assessed via experimental paradigms based on retrospective-cues (retro-cues) which are presented during the maintenance period, between the offset of a memory array and the onset of a probe (Bays et al., 2009; Griffin & Nobre, 2003). Retro-cue studies report consistent findings of improved memory recall in trials with retro-cues corresponding to a memory probe for a selected feature (*valid retro-cue*) compared to neutral conditions, in which no information about the to-be-probed item is provided (Pertzov et al., 2013; Rerko et al., 2014; Zokaei et al., 2014). This advantage is known as retro-cue effect/benefit (RCE) (Gözenman, Tanoue, Metoyer, & Berryhill, 2014). Findings are, however, less consistent when using *invalid retro-cues,* which reinforce an item not subsequently probed. Indeed, invalid retro-cues are sometimes, but not consistently, associated to a cost in memory recall (retro-cue cost, RCC), namely worse performance for invalid relative to neutral conditions (Astle et al., 2012; Gözenman et al., 2014; Griffin & Nobre, 2003; Pertzov et al., 2013). The detrimental effect of invalid retro-cues is explained by three distinct but not mutually exclusive accounts: (i) the *protection* hypothesis (uncued items tend to decay), (ii) the *removal* hypotheses (uncued items are removed from the central WM store) (Kuo & Astle, 2014; Matsukura et al., 2007; Pertzov et al., 2013; Souza, Rerko, & Oberauer, 2016), and (iii) the *prioritization* hypothesis (cognitive resources are redistributed following the presentation of a retro-cue, leaving fewer for the uncued ones) (Myers et al., 2014). In a revised version of the latter hypothesis, the 'Representational reformatting' account, the retro-cue cost is related to task preparation as well as to the inaccessibility of the uncued stimulus, each contributing to the precision of memory, misbinding errors (when a feature of an item is incorrectly associated to the probe) and also response speed (Gressmann & Janczyk, 2016; Gunseli et al., 2015; Myers et al., 2017; Shepherdson, Oberauer, & Souza, 2018).

These views may collectively account for the inconsistencies reported for the RCC effects, although at a more methodological level, a reason for this may also be related to the diverse retro-cue reliability in past studies. The retro-cue reliability is the ratio at which valid and invalid retro-cues are presented, with a lower cost effect when the two cues have the same likelihood to be presented (Gözenman et al., 2014; Gunseli et al., 2015). Moreover, set size – the number of encoded elements– may mask the RCC if it exceeds the WM capacity (Astle et al., 2012). Inconsistent RCC reports may also be due to the participants' strategy used to process the cue.

For instance, participants may neglect it, which suggests a strategic control over the processing of these cues (Souza & Oberauer, 2016). Accordingly, using a delayed matching-to-sample paradigm with retrospective-cues, Berryhill and colleagues asked participants to perform a memory task ignoring the retro-cue information, and therefore assessing participants' awareness as well as their strategic control over the retro-cue effect. The benefit associated with the valid retro-cue persisted, whereas the RCC associated to invalid retro-cues was only evident in response time, and it diminished across blocks. This result was interpreted as an evidence of participants' control over invalid retro-cues (Berryhill et al., 2012).

On the basis of these accounts, we argue that performing invalid retro-cue trials may result in three types of behavioural patterns, which can be used to subdivide participants according to the presence in their performance of: (1) a RCC effect (a negative result when subtracting performance in invalid from neutral retro-cues) (2) an inverted RCC effect (a positive result when subtracting invalid from neutral retro-cues) (3) no significant difference between invalid and neutral retro-cues, "no-cue" subgroup (a value around zero resulting from the subtraction). To assess whether participants falling into these groups are simply ignoring the retro-cue in general (regardless of type), the inverted RCC and the RCC subgroups were also compared in terms of retro-cue benefit. We predicted that if the information carried by the retro-cue is ignored, participants with inverted RCC may also show no retro-cue benefit. Alternatively, if the inverted RCC effect reflects an effective and flexible usage of the retro-cue, there may be higher retro-cue benefit compared to the cost.

One way to better understand the source of variability in processing invalid retro-cues is to explore the neuronal correlates, specifically in terms of resting-state brain activity, which has been linked to crucial cognitive abilities such as selective attention and arousal (Heister et al., 2013; Sala-Llonch et al., 2012a). Recent research demonstrated that resting-state brain activity can be informative about upcoming performance and general cognitive functioning (Klimesch, Doppelmayr, Pachinger, & Ripper, 1997; Klimesch, Vogt, & Doppelmayr, 1999). Specifically, the investigation of spontaneous, task-free brain oscillatory activity (rsEEG) revealed strong correlations with cognitive functions such as attention, language, motor abilities and memory (Heister et al., 2013; MacLean et al., 2012; Oswald et al., 2017; Prat, Yamasaki, Kluender, & Stocco, 2016; Wu, Srinivasan, Kaur, & Cramer, 2014) as well as differences between healthy and clinical populations (Canuet et al., 2011, 2012; Lee et al., 2014; Vecchio et al., 2013). We therefore recorded rsEEG to test whether it can predict participants' ability to manipulate memory representations depending on their task-relevance (Canuet et al., 2011; Garrett et al., 2013; Hata et al., 2016). In the domain of WM, EEG evidence has shown the involvement of the alpha band (8-12Hz) in actively inhibiting task-irrelevant brain regions as well as in actively maintaining task-relevant information (Bonnefond & Jensen, 2012; Hanslmayr, Gross, Klimesch, & Shapiro, 2011; Jensen, Bonnefond, & VanRullen, 2012; Jensen et al., 2002; Poch et al., 2014). rsEEG studies revealed that larger alpha power at rest is associated to better memory performance (Doppelmayr et al., 1998; Klimesch, 1999; Klimesch, Vogt, et al., 1999). In addition, alpha peak amplitude in frontal sites correlates with memory performance in terms of load, intended as a sequence of items to memorize (Clark et al., 2004). Because inhibition and memory are part of a retro-cue paradigm we used, here we focused the rsEEG analyses specifically on the alpha frequency band.

We had two specific hypotheses. First, we hypothesized that participants showing lower cost associated with invalid retro-cues (inverted RCC vs RCC effect) also showed larger magnitude of alpha power at rest. High alpha level at rest is usually associated to an internally oriented attentional state, which may correspond to alpha desynchronization in attentional and sensory posterior regions during task, therefore increasing vulnerability to the detrimental effect of the invalid retro-cue (MacLean et al., 2012). We predicted no specific neural profile associated with the no-cue effect subgroup, since there was no characterization of this group in terms of retro-cue processing. Second, we hypothesized that a flexible manipulation of memory representations is the key cognitive process underlying retro-cue manipulation. We therefore predicted that flexibility in the neural dynamics during resting state may be associated with flexibility in performing the retro-cue.

As a proxy to measure the degree of flexibility of neural dynamics, we capitalized on a measure of long-range temporal correlations, LRTC (Tateishi-Karimata & Sugimoto, 2012). Being a measure of fluctuations across time-scales at specific frequency band data, LRTC has been linked to information processing (Bhattacharya, Edwards, Mamelak, & Schuman, 2005; Chaudhuri, Knoblauch, Gariel, Kennedy, & Wang, 2015; Honey et al., 2012), which is critical for the integration and manipulation of information, and which also constitutes an indicator of correlations across anatomically distributed networks involved in executive functions (Kahana, Seelig, & Madsen, 2001; J. M. Palva et al., 2013). For instance, a recent study on behavioural time series reported a positive correlation between a high degree of LRTC and cognitive flexibility in terms of planning and inhibitory control (Simola, Zhigalov, Morales-Muñoz, & Palva, 2017). A recent study provided further support for the positive association between the dynamic properties of alpha band activity at rest and cognitive performance. This showed higher LRTC associated to better performance in a working memory subcomponent (task-switching) tested via a numeric 2-back task (Mahjoory et al., 2019). Task-switching was measured in terms of a 'switch-cost score' which indicates the difference in participants' ability to withhold answers to incongruent trials and to respond to congruent ones (Hughes, Linck, Bowles, Koeth, & Bunting, 2014). Accordingly, we expected that the ability to resist the interfering effect of invalid retro-cue effect (inverted RCC) may correspond to a higher degree of LRTC in spontaneous EEG activity in the alpha band. This is because reduced cost associated to invalid retro-cue may imply effective executive functions, and specifically the flexible redirection of attention towards memory representations.

We performed two validation analyses. First, in order to demonstrate the discriminant validity of the neural features studied (alpha band power and LRTC), we used multivariate pattern analysis (MVPA) to classify RCC subjects (Haynes & Rees, 2006; Norman, Polyn, Detre, & Haxby, 2006). Second, by using additional cognitive tasks, we tested whether individual RCC variability was attributable to more general cognitive differences amongst participants, and the extent to which any potential associations between electrophysiological measures and our WM paradigm could be broadened to more general memory and attentional components.

5.2 METHODS

5.2.1 PARTICIPANTS

Thirty young participants (21 females, mean ± SD age: 23 ± 3.6 years) provided written informed consent to take part in the study which was approved by the Local Ethics Committee at Goldsmiths, University of London. For all participants, performance data in the retro-cue paradigm as well as 5 minutes of eyes-open rsEEG prior the task execution was collected. Behavioural performance only was also collected in a larger sample (N=32), therefore obtaining a total sample of 62 subjects for behavioural data (overall: 44 females, mean age (24.36) SD ± (3.81)). Data from the second sample was used to investigate the behavioural effect of the retro-cue. To obtain information from a larger and more representative sample, participant classification for EEG analysis was based on normalized data, taking into account the performance of the larger sample (N=62).

All participants taking part in the EEG experiment 1 completed a safety screening questionnaire to ensure their suitability for EEG recording and none of them had a history of neurological or psychiatric disorders, personal or family history of seizures, and was under regular medication. In order to match the requirements of both statistical tests and supervised machine learning analyses, as well as to investigate individual variability, the sample for which EEG data was available was split into three subsamples (RCC effect, inverted RCC effect and no-cue subgroups) of equal size (N=10) based on individual performance in invalid retro-cue trials, relative to the neutral conditions.

5.2.2 EXPERIMENTAL PROCEDURE

Participants were seated in front of a 21" CRT monitor at a viewing distance of 60 cm in a darkened and soundproof room. The task was programmed in MATlab 8.4 (http://www.mathworks.co.uk) using the Cogent toolbox (http://www.vislab.ucl.ac.uk/cogent.php). The resting state fixation cross was programmed and run on ePrime software (Schneider, Eschman, & Zuccolotto, 2002).

Prior to the experimental task, electrophysiological resting state data was collected, during which participants kept their eyes open while staring for 5 minutes at a white dot (visual angle 6 degrees) presented on a black screen. Participants were then given at least one block of practice to familiarize themselves with the paradigm. Data from this block(s) were not included in the analyses. After task completion, additional cognitive tasks (forward and backward Digit and Corsi span, Attentional Network Test) tapping attentional and memory processes were administered. The entire experimental session took around 2 hours and breaks were allowed between blocks and the neuropsychological tests.

5.2.3 EXPERIMENTAL DESIGN

The retro-cue WM task consisted of three blocks of 42 trials each, with 21 valid, 12 neutral and 9 invalid retro-cues in each block (Bays et al., 2009; Borghini et al., 2018) (see Figure 5.1).

In each trial, a stimulus array followed the presentation of a black fixation cross (0.8° diameter) centrally presented on a grey background. The stimulus array consisted of four arrows presented for 1s in a random orientation and in four out five possible colours (yellow, blue, red, green and white); two of the arrows were presented on the right and two on the left of the fixation cross. 1000 ms after stimulus presentation, the fixation cross (retro-cue) could either remain on the monitor with no change of colour (neutral cue), or change for 100 ms into a colour that either correctly (valid retro-cue), or incorrectly (invalid retro-cue) matched the colour of the probe. After 3000s, participants had maximum 3500msec to match the orientation of the probe to the item in the initial display, using a computer mouse.

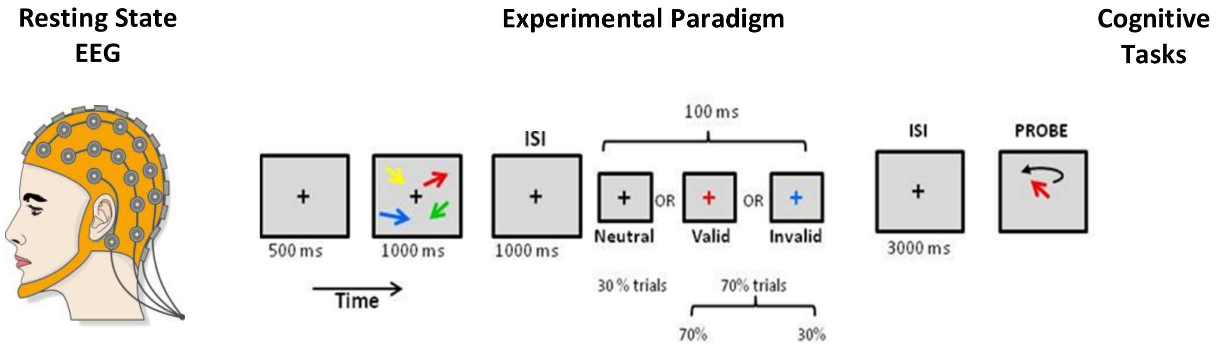

Figure 5.1 Experimental procedure and paradigm. After 1s from a stimulus array' presentation, a retro-cue (providing color feature) was or not presented (neutral condition). When shown, the retro-cue could match the item probed afterwards (valid cue), or **was** not (invalid cue). After 3000s, participants matched the probed orientation to the original one. Before task execution, eyes-open electrophysiological (EEG) activity was recorded, at rest. After task execution, cognitive tasks were administered.

5.2.4 WM PERFORMANCE INDICES

WM performance was measured in terms of accuracy (recall precision), source of errors and response time. RTs correspond to the difference between the probe onset and the response. Since response times reflect also the time spent rotating the mouse (before the actual answer), they should be interpreted with caution. The measures reflecting the source of errors were obtained using an established probabilistic model (see Bays and Husain, 2008, Bays et al, 2011).

5.2.4.1 Accuracy

Recall precision: is calculated as 1/circular standard deviation of error in response, namely the discrepancy between the veridical and the participant's orientation of each arrow stimulus. Higher values refer to higher recall precision (better performance). These values were averaged separately for the different retro-cue conditions.

5.2.4.2 Source of errors

Probability to respond to the target stimulus, pT: it refers to the Gaussian variability in reporting the orientation of the target item. Higher values refer to higher probability to respond to the target stimulus (better performance). pT values were averaged separately for the different retro-cue conditions.

Probability to respond to the no-target stimulus, pNT: it measures the probability of responding to a non-probed item and is an index of misbinding. This refers to responses whereby items that were not probed (no-target items) corrupted the probe's memory such that participants report the orientation of an item of a different colour to the target one. Higher values refer to higher probability to respond to the no-target stimulus (worse performance). pNT values were averaged separately for the different retro-cue conditions.

Random guess, pU: it corresponds to the probability of responding with a random orientation. Higher values refer to higher random responses (worse performance). pU values were averaged separately for the different retro-cue conditions.

Kappa, κ: defined as "concentration parameter", it provides a measure of the variability of recall of the target feature, whereby higher κ corresponds to lower variability. Higher values refer to higher variability (worse performance). Kappa values were averaged separately for the different retro-cue conditions.

Among these measures of VWM performance, we mostly referred to the probability of responding to the target item (pT) because of its strong link with the cognitive processes (selective attention, prioritization etc.) crucial for the retro-cue effect (for a review see (Souza & Oberauer, 2016).

5.2.5 ADDITIONAL COGNITIVE TASKS

We administered additional cognitive tasks to test whether any differences in RCC and inverted RCC subgroups were related to general attentional and memory abilities rather than to the manipulation of memory representations based on retro-cue information. These tests also provide a form of independent assessment of the cognitive abilities tapped by our paradigm. Specifically, we used the Digit Span in its forward condition –a measure of verbal short-term memory (Kessels, Van Den Berg, Ruis, & Brands, 2008) and its backward condition as a measure of verbal working memory and inhibition (Conklin, Curtis, Katsanis, & Iacono, 2000). The test corresponds to series of digits read by the experimenter at a rate of one digit per second, and repeated in the same (forward) or reverse order (backward) by the participants, with no time constraints. One point is awarded for each sequence correctly recalled, for a maximum of 16 points for the forward order, and 14 for the backward. The task is discontinued after a sequence is incorrectly recalled twice.

The Corsi Span assesses visuo-spatial short-term (forward version) and working memory as well as inhibitory control (backward version) (Kessels, Van Zandvoort, Postma, Kappelle, & De Haan, 2000). The task consists of a board with nine cubes randomly located, labelled by numbers from one to nine only visible to the experimenter, who taps a series of blocks sequences. After each sequence, participants tap the block sequence in the same (forward) or in the reverse order (backward) with no time constraints. One point is awarded for each sequence correctly recalled, for a maximum of 9 points for the forward order, and 8 for the backward. The task is discontinued after a sequence is incorrectly recalled twice.

To investigate attention and its main sub components (alerting, orienting and conflict) the *Attentional Network Test (ANT)* was used (Fan, McCandliss, Fossella, Flombaum, & Posner, 2005; Fan, McCandliss, Sommer, Raz, & Posner, 2002). Here participants determine the direction of the target stimulus –an arrow centrally presented– which could be the same (congruent) or different (incongruent) to two arrows presented on each side of the target. Performance scores (RTs) provide information about *alerting*, the ability to achieve and sustain an alert state (mean RT of the central cue condition minus the mean RT of the no-cue condition); *orienting*, directing attention to target items (mean RT of the spatial cue minus the central cue condition); *conflict* between responses (mean RT of congruent minus incongruent conditions regardless of cue type).

5.2.6 STATISTICAL ANALYSIS

5.2.6.1 Behavioural data

Non-parametric (Wilcoxon signed-rank) test was used for planned paired comparison between the retro-cue conditions, as the assumption of normality (Kolmogorov-Smirnov test) was violated. Response times for retro-cue conditions were compared using Kruskal-Wallis

Test, since these data were also not normally distributed; retro-cue condition (valid, invalid and neutral retro-cue) was included as factor. Correlation analyses were conducted by using Spearman coefficient.

5.2.6.2 Electrophysiological data

Significant differences in the alpha frequency band both in the spectral power and LRTC (both discussed in Chapter 2) were estimated using two-sided (alpha level=.025) cluster-based permutation (1000 randomization), applied in paired comparison between the subgroups based on behavioural performance (Oostenveld, Fries, Maris, & Schoffelen, 2011).

For MVPA, we assessed whether cross-participants classification accuracy was significantly above chance by estimating the chance level using permutation tests. Note that the theoretical chance level of 50% for a two-class (group) classification is often violated in the case of small sample size (Combrisson & Jerbi, 2015). However, permutation tests can overcome this issue by estimating the appropriate chance level from the data (Herrojo Ruiz et al., 2014).

5.3 RESULTS

5.3.1 BEHAVIOURAL RESULTS

Across all performance indexes obtained from the probabilistic model, 20 data points for the large sample (N=62) (.02%)[3], and 9 for sub-sample (N=30) (.02%)[1] were excluded from the analyses as over 2.5 standard deviations (SD) from the group mean.

Participants in the large sample showed higher probability to respond to the target orientation (pT) in trials with valid compared to invalid retro-cues (*Z*=2.435, *p*=.015), but not in neutral relative to invalid (*Z*=1.879, *p*=.060), see Table 5.1. No other effects reached significance. The sub-sample for which EEG data was recorded had a similar tendency, although no significant retro-cue effect was found in any of the measures used (precision, pT, pNT, pU, Kappa) (Table 5.1).

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[3] Note that 5 data points for each participant were extracted. Each data point corresponded to the 5 performance indices explained in pages 100-101.

Table 5.1 Performance in the retro-cue WM paradigm. Mean and standard error (in bracket) for the whole sample (N=62) and for participants for which EEG was available (N=30) for response times (RTs), accuracy (Precision) and source of error (pT, pNT, pU, Kappa) from the probabilistic model (Bays et al., 2009)

	62 subjects						**30 subjects**					
Retro- cue condition	*RTs*	*Precision*	*pT*	*pNT*	*pU*	*Kappa*	*RTs*	*Precision*	*pT*	*pNT*	*pU*	*Kappa*
Valid	1918.21 (28.16)	1.25 (.04)	.79 (.02)	.12 (.01)	.08 (.01)	.3.06 (.24)	1974.74 (35.13)	1.20 (.04)	.78 (.03)	.11 (.02)	.07 (.02)	2.79 (.20)
Invalid	1997.45 (31.59)	1.25 (.06)	.72 (.03)	.21 (.05)	.11 (.02)	5.39 (1.88)	2069.34 (40.17)	1.14 (.04)	.71 (.04)	.17 (.03)	.12 (.04)	3.98 (.64)
Neutral	1993.89 (32.47)	1.19 (.04)	.77 (.02)	.16 (.02)	.04 (.01)	3.25 (.30)	2036.69 (38.13)	1.16 (.05)	.76 (.04)	.14 (.02)	.05 (.02)	2.80 (.27)

For the larger sample, response times were not significantly modulated by retro-cue type (*p* >.05), although they were on average faster for the valid condition, followed by neutral and the invalid, Table 5.1. Similar results were found in the smaller sample with no significant effect of retro-cue type *(p* >.05), Table 5.1.

5.3.1.1 Individual differences in invalid retro-cue usage analysis

Lack of significant retro-cue effects at the group-level may be due to inter-individual variability (Lim et al., 2018). Indeed, an inspection of the data especially in the invalid retro-cue condition, indicated that some participants had higher RCC values than others and slower response times (above 2SDs from the group average).

Low or no RCC effect in some participants may be because they either ignored the information carried by the retro-cue (either valid or invalid) or because they used it effectively, which may reflect higher cognitive flexibility. This means that participants with high cognitive flexibility may benefit from the valid retro-cue and exhibit no cost from the invalid retro-cue. If so, we expect reduced cost (RCC) and benefit (RCE) values to positively correlate. To test this possibility, two analyses were performed. In the first, valid and invalid trials were used as variables in a correlation analysis. These values were interpreted as equivalent to the cost and benefit variables since for each subject, they were calculated by subtracting performance in invalid and valid trials by the same neutral ones. Bivariate Spearman correlation highlighted a positive relation between valid and invalid trials ($r_{s(28)}$=.49, p= .007), because higher pT values in the valid retro-cue condition correlated with higher (positive) pT values in the invalid condition, see Figure 5.2.

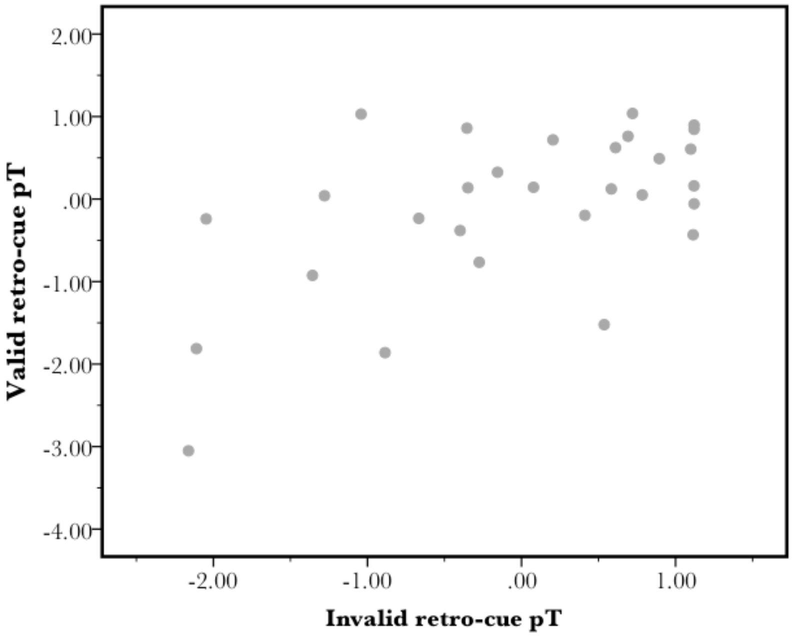

Figure 5.2. Correlation between participants' probability of responding to the target orientation in invalid and valid retro-cues (pT); scores obtained from the smaller sample (N=30).

The second analysis aimed at obtaining a measure of this relationship minimizing the possibility that it merely resulted from using the same common term (neutral condition) for both variables (cost and benefit). For this, rather than using modelled data, a discrepancy value deriving from the raw data was calculated, corresponding to the difference in degrees of angle between the veridical position of the target item and the position selected by the participant. This value is conceptually similar to the precision parameter (mentioned on page 103). This method allowed us to obtain two independent sets of neutral trials by dividing trial by trial data into two equal blocks. Cost and benefit were then calculated by subtracting from valid and invalid cues trials the value of neutral trials from two independent sets, in a balanced order across participants (i.e. in half of the participants cost and benefit were subtracted from block one and in the other half from block two).

Spearman correlation performed between these cost and benefit discrepancy values was positive ($r_{s(30)}$=.541, p=.002), such that the lower the discrepancy for valid trials (minus neutral), i.e the higher the benefit, the lower the discrepancy for invalid trials (minus neutral), namely the lower the cost.

This positive correlation continued to be significant ($r_{s(30)}$=.417, p=.022) even when the order of the subtracted neutral blocks was swapped (i.e. when the cost and benefit initially subtracted from block one, were now subtracted from block two; and the opposite for block two).

These results indicate that individual variability in the RCC effect is unlikely to result from simply suppressing all retro-cue information, regardless of its condition, as participants with higher level of retro-cue benefit also showed resistance to the invalid retro-cue cost.
This suggests that cognitive flexibility in the inverted RCC participants allowed them to both effectively use or disregard information presented during the maintenance period, depending on the retro-cue conditions.

To further explore individual variability in retro-cue processing, and in order to match the requirements of electrophysiological analysis methods (demanding balanced group), the

EEG sample was divided in to three subgroups of 10 participants each, corresponding to the three behavioural patterns, specifically RCC, inverted RCC and no cue-effect. In order to make it representative of a larger population, the EEG sample (N=30) was normalized, by summing each value to the mean and dividing by the standard deviation of the larger sample (N=62).

5.3.1.2 Additional cognitive tasks

No significant difference (*p*>.05) was found between the RCC and inverted RCC subgroups when compared on short-term memory (Corsi and Digit Span) and attentional tasks (ANT) using a one-way ANOVA with group as a between-subjects factor.

5.3.2 ELECTROPHYSIOLOGICAL RESULTS

5.3.2.1 Power spectral density analysis

The differences in the magnitude of excitability fluctuations (power spectral density) between the three subgroups (RCC, inverted RCC and no cue-effect) were used to examine the spontaneous neural activity which may account for the different behavioural responses to the invalid retro-cue.

Cluster based permutation tests applied on the three subsamples to resting-state spectral power in the alpha band showed a trend (*p*=.08) towards a larger magnitude in the inverted RCC relative to the RCC subgroup over parieto-occipital electrodes (Figure 5.3 a, b). No

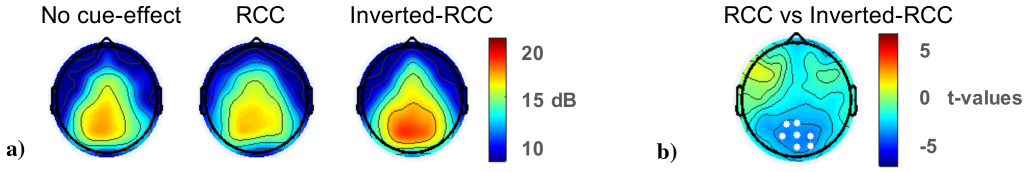

Figure 5.3: a) Topographical representation of the averaged power spectral density for each sub-group: no cue-effect, retro-cue cost (RCC), inverted RCC, for the alpha frequency band; b) The power difference after paired comparisons between the retro-cue cost (RCC) and the inverted RCC subgroups

significant differences were found when the RCC or inverted RCC were compared to the no retro-cue effect group.

Next, power spectral density was extracted from the marginally significant parieto-occipital cluster and correlated to the additional visuo-spatial cognitive tasks from the whole sample (N=30). This showed a positive correlation ($r_{s(28)}$=.46, p=.03) between the alpha power and working memory performance (Corsi Block Backwards).

5.3.2.2 Long-range temporal correlation analysis

To test whether participants showing an inverted RCC effect and higher cognitive flexibility also had stronger brain dynamics at rest, we assessed the degree of long-range temporal correlations (LRTC) using detrended fluctuation analysis (DFA) in the alpha band.

DFA exponents in the alpha frequency band were extracted and averaged across channels for each participant from the entire sample (N=30) and correlated with pT cost scores (invalid minus neutral retro-cue). Spearman correlation (pT cost values * DFA exponents) highlighted a significant positive association such that stronger LRTC (higher DFA coefficients) corresponded to lower cost values ($r_{s(28)}$=.40, p= .02), see Figure 5.4a.

To investigate whether this relationship was reflected in significant differences in DFA between subgroups, we compared averaged DFA values for each participant, between the RCC and inverted RCC subgroups. No significant difference emerged (p>.05), although the inverted RCC showed overall higher DFA coefficients compared to the inverted RCC (M:.61, SE:.03), (M:.67, SE:.01), see Figure 5.4 b.

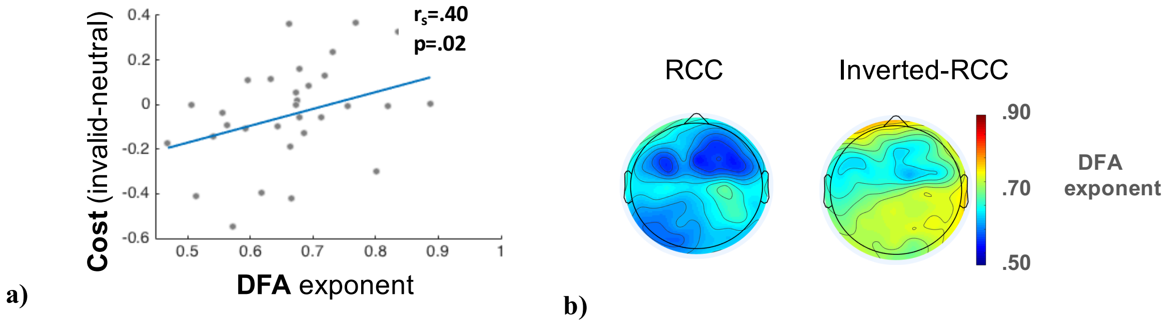

Figure 5.4: Positive correlation between the alpha-band detrended fluctuation (DFA) exponents averaged across the 64 channels, and the cost values in the probability of responding to the target item (pT); b) Topographical representation of the DFA exponents for the retro-cue cost (RCC) and inverted RCC subgroups respectively.

5.3.2.3 Multivariate pattern classification analysis (MVPA)

MVPA investigated whether single-subject RCC and inverted RCC during rest membership could be classified from the multivariate patterns of spectral alpha-band power distributed across all the 64 channels. Significant, above-chance decoding accuracy was found using MVPA with the averaged alpha power spectral density values (2-fold cross-validation, accuracy: 70%, p=0.03).

To complement the correlation results between stronger LRTC and lower pT values for RCC, MVPA also applied to the patterns of the DFA scaling exponents across the 64 channels in order to explore further whether the patterns of LRTCs in the alpha band are discriminative of the performance in the task. MVPA successfully classified participants from the two subgroups (2-fold cross-validation, 75%, p = .01).

5.4 DISCUSSION

In this study, we investigated whether variability in retrospective attention in the context of working memory may reflect variability in cognitive flexibility towards memory representations. We tested whether this flexibility may be linked and predicted by spontaneous oscillatory activity recorded at rest, conducting power spectral density and long-range temporal correlation (LRTC) analyses, specifically on the alpha frequency band.

5.4.1 THE EFFECT OF INDIVIDUAL VARIABILITY ON THE RCC EFFECT

We found a significantly lower probability of responding to the target item (pT) in invalid relative to valid retro-cues in the large sample, consistent with past findings (Borghini et al., 2018; Gunseli et al., 2015; Pertzov, Dong, Peich, & Husain, 2012; Rerko et al., 2014). This effect also emerged in the subsample for which EEG data was recorded, although it was not significant, possibly due to high individual variability. To characterise the impact of such variability on performance, participants were divided in three distinct groups based on their RCC values: those showing either a retro-cue cost (RCC), reduced cost (inverted RCC) or no cue effect. These findings are in line with the idea of reconciling the existing views on RCC since different effects may co-exist in the same sample, with some participants showing RCC as result of the *protection/removal* accounts, others not showing any cost, supporting the *prioritization* hypothesis, or only slower responses, resulting from the cognitive conflict induced by the invalid retro-cue (Pertzov et al., 2013). In other words, while the no-cue effect subgroups may reflect the ability to fully filter out the information carried by the cue regardless of its condition (Berryhill et al., 2012), the remaining participants could show divergent response to the invalid cue: either showing or not the related behavioural cost (RCC subgroup and inverted RCC respectively).

In the inverted RCC subgroup, a positive cost value may suggest a “benefit” rather than a cost associated to invalid trials. A possible explanation can be that the retro-cue influenced and enhanced the maintenance of information of more than one item held in memory (Camos et al., 2018). Based on this explanation, when more than a single item is held in memory, the prioritization of the cued one might extend the attentional resources and “refresh” the memory representations of the adjacent items, in line with the idea that item prioritization actually promotes item-context associations (Oberauer, 2013). Thus, prioritizing a memory representation, either by a valid or an invalid retro cue, may allocate resources to uncued representations, ultimately enhancing working memory performance.

Altogether, these findings move on from the previous literature, by introducing and testing a new concept of flexibility applied on the retro-cue paradigm.

5.4.2 The link between Power Spectral Density and Long-Range Temporal Correlations with RCC effect

Power spectral analysis showed marginally larger parieto-occipital alpha power magnitude in the inverted RCC subgroup relative to the RCC subgroup. Moreover, we found a correlation between performance cost (RCC) and the degree of LRTC. Both power and LRTC decoding analyses (using MVPA) supported the subgroups classification (RCC and inverted RCC) by successfully discriminating RCC and inverted RCC alpha profiles. The correlation between performance in additional cognitive tasks and cost values further supported the distinction between subgroups as related to their responses to invalid retro-cues, rather than in more general factors such as short-term memory, WM capacity and attentional processes. Power spectral density indicated that larger alpha power at rest predicts the flexible manipulation of memory representations, as reflected in distinct patterns of memory performance (Klimesch et al., 1999; Oswald et al., 2017) and possibly attentional states (MacLean et al., 2012).

Previous research has shown that the type and direction of power change depend on whether it is based on spontaneous or event-related brain activity (Doppelmayr et al., 1998; Klimesch, Vogt, et al., 1999). Consequently, task demands which are usually associated to alpha power suppression, may predict alpha power increment at rest. Considering our findings, we suggest that the behavioural differences in our subgroups may reflect the dependency of event-related activity on the spontaneous one (Doppelmayr et al., 1998). According to the 'Inhibition-timing Hypothesis' (Klimesch, Sauseng, & Hanslmayr, 2007) alpha oscillations are actively involved in top-down functional inhibition, by regulating the engagement or disengagement of sensory regions depending on task demands (Haegens et al., 2012; Jensen et al., 2002), but they are also linked to the timing over action potentials, ultimately facilitating access to information (Klimesch, 2012). The power increment at rest in the inverted RCC subgroup may therefore correspond to a power suppression of task-relevant regions during task execution, which may have increased arousal and vigilance and released inhibition towards un-cued items (Haegens et al., 2012; Jensen et al., 2002). Power increment at rest could may also indicate improved timing for accessing WM contents that become relevant after invalid probe presentation. Therefore, participants in a high state of readiness (characterized by larger power at rest) may approach the task with more resources (Olivers & Nieuwenhuis, 2005, 2006), and using the information coming from the cue more effectively, in line with the 'Inhibition-timing Hypothesis' (Doppelmayr et al., 1998). The parieto-occipital cluster identified by the power analysis also correlated with a measure of spatial working memory (Corsi backward). This suggests that the larger power magnitude corresponding to no-cost in WM performance may reflect a generally more efficient WM capacity, predicting inter-individual variability (Haegens, Cousijn, Wallis, Harrison, & Nobre, 2014; Oswald et al., 2017).

The LRTC analysis supported the hypothesis that attenuated effect of invalid cued items corresponded to larger scaling exponents within the range of long-range temporal correlations, and thus to a higher level of neural flexibility (Nikulin & Brismar, 2004; Simola et al., 2017; Tateishi-Karimata & Sugimoto, 2012). The positive correlation between LRTC and inverted RCC scores finds theoretical ground in the fact that efficient executive functions (in this context resisting to misinformation carried by the invalid retro-cue) typically involves stronger temporal coordination of neuronal activity across time scales and cortical areas (Simola et al., 2017). Similarly to the link between behaviour and cortical excitability (Haegens et al., 2012; Herrmann, Strüber, Helfrich, & Engel, 2016), stronger LRTCs in neuronal oscillations may relate to a balance between cortical states switches, resulting in higher cognitive performance (Poil, Hardstone, Mansvelder, & Linkenkaer-Hansen, 2012; Samek et al., 2016). In the current study, evidence of a link between the LRTC in the alpha frequency band and cognitive performance aligns with previous findings which have associated stronger LRTC with higher performance in executive functions, such as the ability to suppress task-irrelevant upcoming information (Mahjoory et al., 2019; Simola et al., 2017). Our results extend this association to the ability to selectively manipulate information held in memory based on task-relevance.

5.5 CONCLUSION

This study used a probabilistic WM retro-cueing paradigm and the analyses of amplitude and fluctuations of rsEEG alpha oscillations to investigate the cognitive processes underlying variability in cost-related effects. Individual differences in the ability to flexibly manipulate memory representations corresponded to and were decoded from distinct patterns of spontaneous alpha brain activity, recorded prior to task execution.

CHAPTER 6: ENDOGENOUS NEURAL ACTIVITY CORRELATIONS WITH FLEXIBLE MANIPULATION OF VISUAL WORKING MEMORY REPRESENTATIONS IN AGEING

In the previous chapter, we emphasized the role of spontaneous brain activity to elucidate the cognitive processes underlying the variability in the "RCC effect" associated with invalid retro-cues. Based on the spectral density power and long-range temporal correlation, our previous results indicated that in young adults, brain activity at rest could predict the effective usage of task-relevant attention processes during the manipulation of memory representations. Here, we extended this investigation to an older adult sample, as interference from task-irrelevant information is known to increase with ageing. This chapter first investigates whether RCC in ageing is vulnerable to individual variability and secondly it aims at investigating the possible role of brain activity recorded at rest to distinguish and predict the ability to effectively manipulate memory representations.

6.1 INTRODUCTION

There is a general consensus that retro-cue effects (retro-cue cost, RCC, and retro-cue benefit, RCE) lie in the ability to prioritize items and therefore to resist the interference from task-irrelevant ones, especially when invalidly probed (Newsome et al., 2015; Rerko et al., 2014). A factor that inevitably increases vulnerability to interference is age (Hasher & Zacks, 1988; Lustig, Hasher, & Zacks, 2008). Indeed, many studies have shown that older adults are less accurate or slower when required to inhibit irrelevant information (Berry, Zanto, Rutman, Clapp, & Gazzaley, 2009; Wais & Gazzaley, 2014). In our study on young adults (Chapter 5), we have shown that retro-cue cost (RCC) values negatively correlated with retro-cue effect (RCE) values, such that the higher the benefit deriving from valid retro-cues, the lower the cost associated to the invalid retro-cues. This suggests an effective and flexible usage of the retro-cue information, depending on its validity (Myers et al., 2017). Whether this would be also the case for older adults has been overlooked. We predict that older adults may show: (1) no-cue effect, that is no difference in performing valid and invalid trials when compared to the neutral condition; this is expected considering age-related decreased ability in prioritizing information based on task-relevance (Gazzaley, Cooney, Rissman, & D'Esposito, 2005); (2) a cost, modulated by invalid retro-cues (RCC effect), possibly together with the beneficial effect of the valid retro-cue (RCE); this scenario would suggest residual ability to prioritize information (involved in RCE) and to redirect attention towards task-relevant information, which could be indicative of working memory flexibility.

Research into retro-cue processing in older population presents contradictory results. Some studies showed a beneficial effect of valid trials when compared to the neutral condition (RCE) either in accuracy, time responses or electrophysiological signatures (Loaiza & Souza, 2018; Mok, Myers, Wallis, & Nobre, 2016, Newsome et al., 2015). However, this was not the case in other studies (Borghini et al., 2018; Duarte et al., 2013). Discrepancies could be due to crucial methodological differences; for instance, the inclusion of only one retro-cue condition (valid but not invalid) besides the neutral (Duarte et al., 2013; Mok et al., 2016; Newsome et al., 2015), which is likely to influence the trust participants may develop towards cued information (Souza & Oberauer, 2016). A recent study on older adults which included valid, invalid and neutral retro-cue conditions, did not show a RCE effect. However, it highlighted an enhanced behavioural cost (RCC) for older adults' performance when compared to younger adults (Borghini et al., 2018). The authors interpreted these results as evidence of the susceptibility to the detrimental aspects of invalid retro-cue effect in ageing, in support of an age-related decline in the ability to resist to the interference from task-irrelevant stimuli. Moreover, when parietal alpha-tACS (transcranial alternating current stimulation) was delivered, older adults participants improved their performance more strongly in the invalid retro-cue condition, suggesting not only flexibility in the inhibitory ability underlying invalid retro-cue processing but also its causal link to brain oscillations (Borghini et al., 2018).

In the study reported in this chapter, in order to complement these findings as well as to test whether cognitive processes underlying the retro-cue manipulation (i.e. inhibitory and/or selective attention) could be predicted prior to task performance, spontaneous brain oscillatory activity was analysed in combination to the RCC effect. This investigation is inspired by previous evidence suggesting a relationship between ageing cognition across different domains, and spontaneous brain dynamics across different frequency oscillations. For instance, despite the association between alpha frequency band (8-12 Hz) and age (Chiang, Rennie, Robinson, van Albada, & Kerr, 2011; Clark et al., 2004; Grandy et al., 2013; Klimesch, Doppelmayr, Schimke, et al., 1997) inconsistencies in the literature has been found: some studies have shown positive relationship between alpha power or individual alpha peak (iPAF) and general cognitive performance in ageing (Clark et al., 2004), whereas others have shown an inverse pattern (Trammell, MacRae, Davis, Bergstedt, & Anderson, 2017) or no relationship at all (Finnigan & Robertson, 2011). Similar inconsistent results have been found for delta (1-3 Hz) and theta (4-7 Hz) oscillation (Trammell et al., 2017). Significant and marginal positive correlations were found between delta oscillation and measures of executive functions, perceptual speed and short-term memory in some studies (Trammell et al., 2017; Vlahou, Thurm, Kolassa, & Schlee, 2014, respectively) but not in others (Finnigan & Robertson, 2011). Likewise, regarding theta oscillations, discrepant findings have also been reported. Some studies showed a positive correlation between theta power and cognitive impairment (Jelic et al., 2000; Prichep et al., 2006), whereas others showed the opposite pattern, characterized by positive correlation between frontal theta and higher cognitive functions such as working memory (Cummins, Broughton, & Finnigan, 2008; Finnigan & Robertson, 2011; Vlahou et al., 2014).

An additional oscillatory measure, theta-to-alpha ratio (TAR) has proven to be a more consistent indicator of cognitive abilities in ageing (Bian et al., 2014; Moretti, 2015; Trammell et al., 2017). Specifically, TAR distinguishes between healthy older adults who typically show increased TAR, and ageing adults suffering from a wide range of pathologies (amnesic Mild Cognitive Impairment, Alzheimer's and Parkinson's disease) (Bian et al., 2014; Moretti, 2015). Recently, increased TAR was also found in association with normal age-related changes compared to younger sample (Trammell et al., 2017).

In this study, we ought to extend prior behavioural findings regarding the RCC effect (Borghini et al., 2018) by first determining whether this response is negatively associated to the RCE effect (see chapter 5 for similar rationale). Such association would be evidence of residual flexibility in manipulating memory representations in ageing. Additionally, we investigated whether spontaneous brain activity reflected information associated to participants' RCC performance.

To address these questions, we first analysed performance in 36 older adults tested with the same paradigm used by Borghini and colleagues (2018) (as well as in chapter 5) based on three retro-cues conditions (valid, invalid and neutral). To elucidate the relationship between the RCC and spontaneous brain activity, electrophysiological activity was recorded at rest (rsEEG) in a smaller sample of ageing adults (N=21), prior to task execution.

Two electrophysiological measures were used: power spectral density and long-range temporal correlations. These measure were applied on three frequency band oscillations: alpha (8-12 Hz) theta (4-7 Hz), theta-alpha ratio(TAR) and delta (1-3 Hz), considering their established role in age-related cognition (Buchan et al., 1997; Finnigan & Robertson, 2011; Gordon et al., 2018; Jelic et al., 2000; Klimesch, Vogt, et al., 1999).

We expected a positive correlation between the inverted RCC effect, power spectral density and TAR power magnitude at rest. These predictions are based on our finding that power spectral density is linked to flexible manipulation of memory representation (Chapter 5), and that TAR power magnitude cognitive performance is linked to alpha, theta and delta in younger adults.

As long-range temporal correlation represents a measure of complex variability characterizing high cognitive functions (as VWM abilities, see Chapter 5) in a positive relationship, we reasoned that alpha, theta and delta band DFA values might be positively associated to resistance to retro-cue cost (inverted RCC). Alternatively, as the ageing brain is characterized by a general loss of complexity in physiological processes, including brain oscillations (Goldberger et al., 2002; Lipsitz & Goldberger, 1992), we hypothesized that potential associations between RCC effect and LRTC might be too weak to emerge.

6.2 METHODS

6.2.1 PARTICIPANTS

Twenty-one right-handed participants (F=12, M=9; mean age= 70.14±3.6) with normal or corrected vision provided written consent to participate in our study that was approved by the local Ethics Committee. All participants were assessed for colour blindness and none of them showed impairment in colour perception. Moreover, none of the participants had past history of neurological or psychiatric disorders, personal or family history of seizures or was under regular medication. All participants received the Mini Mental State Examination (MMSE, Folstein et al, 1975) and achieved a score of 28 or greater, suggesting that their cognitive faculties were within the normal range. In addition, all participants completed safety screening questionnaires to ensure the candidates' suitability for EEG recording and non-invasive brain stimulation.

Behavioural performance with no EEG was also collected in an additional sample (N=15) (7 females, mean age (70.9) SD ± 3.8), who took part into a brain stimulation study.

6.2.2 EXPERIMENTAL PROCEDURE AND TASK

Participants included in the analyses took part in two independent studies (one including 21 participants and the other 15), in which the condition of no-stimulation (sham) corresponded to their control condition/baseline, collected in randomized order at least one week apart from the other brain stimulation conditions. For the purpose of this study, we used only data deriving from this no-stimulation testing session which took approximately 1 hour each (and additional 30 minutes for the participants undertaking the EEG recording).

Although the experimental procedure and the task was identical to that reported in Chapter 5, a direct comparison between younger and older adults with age group as a between-subject factor was not carried out in this research project. This was because of the possible practice effect deriving from a no-stimulation session randomly assigned before or after the stimulation session. Specifically, the analysis of younger participants' performance (Chapter 5) was based on baseline data, corresponding to participants' first exposure to the task. Such a contrast may have informed on the neural spontaneous predictors of working memory performance across the life span, a comparison already investigated at behavioural level (Borghini et al, 2018) (see 6.1 for further information).

6.2.3 STATISTICAL ANALYSIS FOR BEHAVIOURAL DATA

As the assumption of normality was violated (Kolmogorov-Smirnov test), a non-parametric test (Wilcoxon signed-rank) was used for planned paired comparison between the retro-cue conditions. Correlation analyses were conducted using Spearman coefficient.

6.2.3 EEG RECORDING AND STATISTICAL ANALYSIS

The EEG recordings were identical to those used in Chapter 5. Differently to the previous chapter, EEG analyses (power spectral density and LRTC) were also extended to theta frequency band. As no group analysis was carried out (preventing Cluster based permutation tests), a priori midline regions were identified for power extraction (Fronto (Fz), Central (Cz), Parietal (Pz)) (Finnigan & Robertson, 2011; Trammell et al., 2017).

6.3 RESULTS

6.3.1. BEHAVIOURAL RESULTS

6.3.1.1 Working memory retro-cueing task

Participants in the larger sample (N=36) showed a significant lower probability to respond to target orientation (pT) in the invalid retro-cue condition compared to the valid ($Z = -2.705$, $p = .007$) and neutral ones ($Z = -2.949$, $p = .003$). Moreover, the probability to respond to the no-target orientation (pNT) or misbinding error was significantly higher for the invalid retro-cue condition compared to neutral ($Z = -2.561$, $p = .010$).

Similarly, in the smaller sample for which EEG was available, significant retro-cue effects were found in the probability to respond to the target orientation (pT) and the probability to respond to the no-target stimulus (pNT). Specifically, target responses (pT) were lower (worse performance) in invalid trials compared to neutral ($Z = -2.295$, $p = .022$) and valid ones ($Z = -2.013$, $p = .044$). Similarly, no-target responses (pNT) were higher (worse performance) in invalid compared to valid ($Z = -2.633$, $p = .008$) and neutral trials ($Z = -2.094$, $p = .036$). Retro-cue effect did not reach significance in other behavioural parameters (all $p>.05$). A retro-cue effect was also present in response time ($F_{(2,36)} = 3.275$, $p=.049$, $\eta_p^2=.15$), although none of the comparisons between retro-cue conditions survived post-hoc tests ($p > .05$).

Table 6.1. Performance in the retro-cue WM paradigm. Mean and standard error (in bracket) for the larger (N=36) and smaller (N=21) sample in terms of accuracy (Precision) and source of error (pT, pNT, pU, Kappa) from the probabilistic model *(Bays et al., 2009)*.

		36 Participants					21 Participants					
		Precision	*pT*	*pNT*	*pU*	*Kappa*	*RT*	*Precision*	*pT*	*pNT*	*pU*	*Kappa*
Retro-cue condition	Valid	1.11 (.05)	.71 (.05)	.23 (.03)	.16 (.08)	2.86 (.54)	1979.28 (272.79)	1.12 (.05)	.80 (.04)	.19 (.03)	.08 (.01)	6.52 (.27)
	Invalid	1.09 (.06)	.61 (.06)	.32 (.04)	.17 (.07)	2.82 (.40)	2065.34 (286.62)	1.07 (.04)	.65 (.05)	.35 (.04)	.11 (.02)	3.24 (.45)
	Neutral	1.17 (.04)	.81 (.02)	.14 (.02)	.16 (.09)	3.04 (.49)	2039.44 (276.20)	1.11 (.04)	.78 (.05)	.27 (.05)	.04 (.01)	2.30 (.23)

6.3.1.1 Individual differences in invalid retro-cue performance

Next, we investigated whether variability in the RCC effect (invalid minus neutral) may reflect variability in cognitive flexibility. This link was observed in the younger adults' sample (see Chapter 5), and here we tested whether this effect held true also for the older adults too. Specifically, we examined whether higher values of inverted RCC effect which indicate resistance to the behavioural cost associated to invalid trials, may correspond to higher value in RCE, reflecting the benefit associated to valid trials.

For consistency with the previous chapter, we used valid and invalid retro-cue values extracted from the pT parameter, as well as cost and benefit extracted from discrepancy values with independent sets of neutral trials. Both approaches were used to assess cognitive flexibility also in this age group (see Chapter 5). A bivariate correlation between valid and invalid trials showed a significant positive association in both the larger ($r_{s(34)}$= .50, *p*= .003) and the smaller sample ($r_{s(19)}$= .46, *p*= .04).

A similar pattern of results was found when cost and benefit from discrepancy values were used as variables. Spearman correlation showed a positive association between cost and benefit discrepancy values ($r_{s(21)}$=.575, *p*=.006), which held when the order of the subtracted neutral blocks was swapped ($r_{s(21)}$=.545, *p*=.011).

Taken together, these analyses extend the association between valid and invalid conditions and possibly the inverted RCC and RCE effects to the older adults' sample (Figure 6.1).

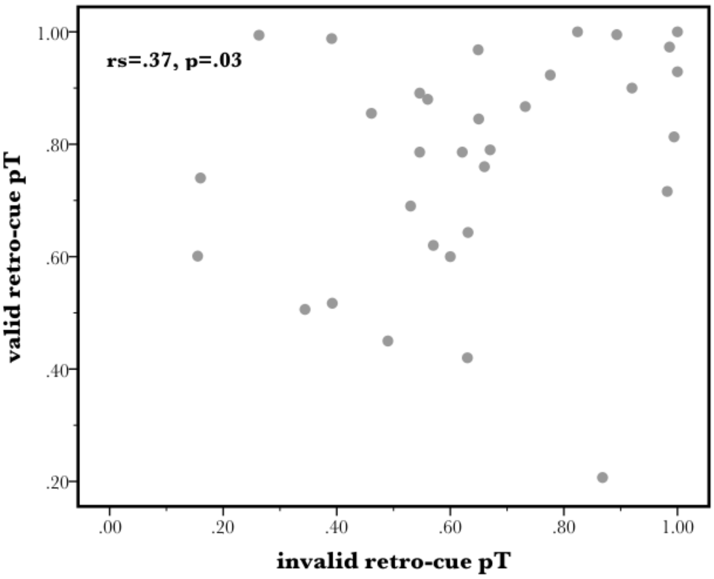

Figure 6.1. The positive correlation between valid and invalid values in the probability to respond to the target item (pT).

6.3.2. EEG RESULTS

6.3.2.1 Power Spectral Density Analysis

Correlation between power in the three selected frequency bands and the values for the RCC effect (invalid–neutral retro-cue type) in target responses (pT) highlighted a positive association between delta power from the Pz site and RCC values (r_s= .48, *p*= .02) and negative correlations with TAR in all the selected sites (Fz: r_s= .46, *p*= .03; Cz: r_s= .49, *p*= .02; Pz: r_s= .50, *p*= .01).

With the exception of parietal TAR (Figure 6.2), all correlations did not reach significance after Bonferroni correction, therefore these results are presented descriptively with uncorrected p-values.

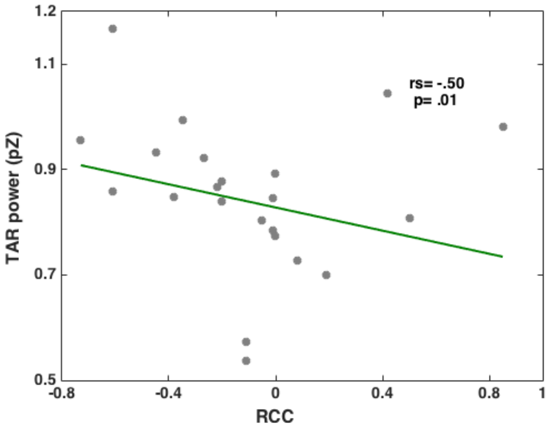

Figure 6.2 The negative association between parietal power in Theta to Alpha ration (TAR) and the RCC effect in the probability to respond to the target orientation (pT).

Bivariate correlations between alpha and theta bands power spectral density and RCC effect did not show any significant association (expect for a marginal positive relationship between theta band from frontal cluster and RCC effect (r_s= .37, *p*= .09)).

6.3.2.1 Long-Range Temporal Correlations

There were no significant (*p*>.05) bivariate correlations between LRTC extracted from the alpha, theta and delta bands and the RCC effect.

6.4 DISCUSSION

The present study aimed to investigate the cognitive processes underlying retro-cue manipulation in ageing. Specifically, we focused on flexible working memory abilities and we tested whether such flexibility could be associated to spontaneous oscillatory activity at rest.

At the behavioural level, consistent with previous findings (Borghini et al., 2018), older adults' ability to recall the orientation of both the target and no-target item (respectively pT and pNT) was influenced by retro-cue type. More specifically, older adults' performance worsened in trials with invalid retro-cues (namely, RCC), and did not benefit from the valid retro-cue condition relative to neutral (known as RCE). The weaker performance in invalid trials may result from reduced attentional resources towards memory representations, which underlies working memory, which has been shown to decline with age (Hasher & Zacks, 1988; Wais & Gazzaley, 2014; Ziegler et al., 2018). Crucially, despite the cost driven by invalid cues and the lack of benefit from valid retro-cue, there was a positive correlation between the inverted RCC and RCE, which rules out the possibility that reduced RCC results from merely filtering out the information carried by the cue. These results support previous findings suggesting residual memory functioning in older adults' memory, given the difference in performance between the three types of retro-cue conditions (Borghini et al., 2018). Second, by showing an association between the variability in the valid and invalid retro-cue values, this study suggests a common underlying cognitive ground in these effects, entailing the ability to prioritize information and to re-direct attention to new relevant information, which could be interpreted as a form of working memory flexibility (Myers et al., 2017). The same type of relationship was also found in younger adults (Chapter 5), suggesting that this ability is maintained across age.

At the neural level, the parietal theta to alpha ratio (TAR), which has been used a marker of ageing cognition, showed a relation with the RCC effect because increased TAR was associated with decrease in RCC (namely, inverted RCC effect). This means that the smaller the cost associated to invalid retro-cue, the larger the theta/alpha ratio. This is consistent with previous research that found an increase in low frequencies ratios correlating with cognitive decline in healthy and pathological ageing, and supports the view that increased theta power might be associated to hippocampal atrophy, vulnerable to ageing (Abuhassan, Coyle, Belatreche, & Maguire, 2014; Bian et al., 2014; Moretti, 2015; Trammell et al., 2017). Additionally, the topography of our effect is in accordance with previous findings linking lower oscillations ratios and memory functioning in ageing (Moretti, Paternicò, Binetti, Zanetti, & Frisoni, 2013). Generally, negative correlations were also found for the other selected topographies (Fz and Cz) and RCC values, although they did not reach statistical significance after corrections for multiple comparisons. This may be due to the sample being underpowered and the use of two-tailed (non-directional) testing. Conversely, it is unlikely that the lack of an association between long-range correlation and RCC values could be solely explained by our sample size, which was larger than the minimum number recommended in the literature (n=10) (Nikulin & Brismar, 2005; Tateishi-Karimata & Sugimoto, 2012).

Previous studies have shown how age and diseases accompany the breakdown of brain dynamics complexity which is the fundamental physiological function underlying long-range temporal correlations (Andrews-Hanna et al., 2007; Goldberger et al., 2002; Lipsitz & Goldberger, 1992). This could be possibly explaining our lack of associations. Moreover, we restricted our investigation to the association between this measure of neural dynamics and RCC values, not including other potential associations that have been observed when other factors as gender, power and age are considered (Nikulin & Brismar, 2005).

Future studies could investigate the specific interaction with healthy aging and the complex measure of fluctuations across time-scales and frequency bands, represented by LRTC, characterizing at around which "age stage" the perturbation of the association between higher cognitive functions and LRTC begins.

In summary, our findings, add some clarity to the new literature regarding the behavioural cost associated to the ability to prioritize and re-direct attention towards memory representations, known to decline with age. These abilities share common components possibly rooted in working memory flexibility, and associated spontaneous brain activity.

CHAPTER 7: CONCLUSIONS

This chapter draws an overview of the findings on the cognitive and neural factors in VSTM and VWM. Each study's contribution is discussed and directions for further research are suggested.

7.1 INTRODUCTION

In line with the continuous allocation resource models (Bays & Husain, 2008b; Wilken & Ma, 2004), two paradigms assessing memory and the quality of memory processes were used in this thesis. Participants made a two-alternative forced choice on the location and orientation in which a probe item had been displayed (Chapter 3 and 4), or matched a stimulus to a probed item (Chapter 5 and 6), while the magnitude of this change varied parametrically and probabilistically, respectively.

The specific focus of this work was to assess the cognitive and neural factors that modulate the maintenance and the manipulation of memory representations. Previous research has indicated the crucial role of cognitive factors such as perceptual, memory load and inhibitory processes (Beck & Kastner, 2009; Shapiro & Miller, 2011), but their combined contribution specifically controlling for perceptually accuracy has been overlooked. Furthermore, past studies provided inconsistent findings as to whether flexibility may be the key factor to modulate the manipulation of memory representations across the life-span.

Based on these premises, the present thesis aimed at:

1. Assessing the combined and individual contribution of perceptual, memory and inhibitory factors' load on recognition performance, while directly controlling for perceptual discrimination accuracy (Chapter 3);

2. Investigating the influence of perceptual discrimination accuracy on the maintenance period, by analysing its electrophysiological activity and potential link with spontaneous activity, prior to task performance (Chapter 4);
3. Testing whether individual variability in cognitive flexibility in the context of memory representations could be decoded by spontaneous oscillatory activity recorded prior to task performance (Chapter 5);
4. Extending the previous aim to an ageing sample considering the vulnerability of processes underlying flexibility with the increase of age (Chapter 6);

The following sections will expand on these aims, providing relative findings, discussions and future directions.

7.2 COGNITIVE FACTORS MODULATING VISUAL SHORT-TERM MEMORY'S TASK

Chapter 3 aimed at investigating the individual and joint contribution of perceptual, memory and inhibitory load in a VSTM task. This was done by manipulating in a new paradigm the difference in orientations' degree (load) between the stimuli to be encoded, the probe-to-target and the probe-to-no target stimuli, respectively. Specifically, in this task participants first made an explicit discrimination of the orientation of the initial stimuli and after a short delay, compared target and probe stimuli on binding information (orientation and location relative to a fixation dot).

In line with visual attentions theories (Shapiro & Miller, 2011), VSTM accuracy decreased with the increase of load, specifically between initial stimuli to be encoded and a probe compared to a target stimulus (namely, perceptual and memory load). This is also in accordance with previous findings that observed VSTM capacity decrement with high object perceptual complexity (Alvarez & Cavanagh, 2004).

Crucially, by introducing an explicit perceptual judgment, results showed that recognition performance was higher in trials preceded by accurate discrimination, and that the no-target load effect emerged. This result was also replicated in the study reported in Chapter 4. Indeed, only in trials preceded by correct perceptual discrimination, differences between no-target stimulus load were statistically significant. This result represents a novel finding in the VSTM domain, as it identifies a *sine qua non* condition for the no-target stimulus to be critical in a retrospective manner. If not deeply encoded and discriminated when presented, the memory representation of no-target stimuli may not emerge and this could be misinterpreted as successful suppression of its interfering effect.

Controlling for perceptual accuracy was relevant in the case of no prior information about the identity of target and no-target stimuli as in this specific paradigm, and provided support to our methodological decision to explicit assess that. It is noteworthy that this choice implied introducing a second task based on binding processing and no-target stimulus representation, hence low accuracy for the memory recognition judgment was expected (Craik, 2014).

One of the aims of this first study was also to induce a deeper and level of stimulus encoding to facilitate recognition and provide further information about its contributing factors, specifically, perception, memory and inhibition (Kang, Hong, Blake, & Woodman, 2011; McConnell & Quinn, 2000). Results of mixed models showed that the factor most impacting on recognition accuracy is the orientation difference between the probe and the target stimulus, in the specific condition of high load. An additional and significantly detrimental effect on accuracy was found when high memory load was associated with high perceptual load and low inhibition load (Rosenholtz, 2001). These results were maintained when the analyses focused only on trials accurately discriminated in the perceptual task. This specific finding is in the direction of continuous rather than discrete memory models as it shows that despite the fact visual stimuli were encoded and stored, the fidelity of their representations decreased as memory load increased (Bays, Wu, & Husain, 2011). Our paradigm allows us to explore the quality of encoding and to extend continuous memory processing to load – in terms of stimulus complexity rather than number of items.

The choice of this experimental paradigm does deserve two main considerations. First, as discussed in Paragraph 4.3.2 and 4.3.3, the low level of memory performance, which was close to chance, means the results should be interpreted with caution. Second, in this particular paradigm, load may have been manipulated beyond stimulus complexity. Indeed, when perceptual load was low (two identical stimuli are presented), participants may have stored one rather than two memory representations as a result of perceptual grouping. This may have extended the effect of load intended to number of memory items. This applies to the results of both Chapter 3 and 4.

Taken together, the behavioural results reported in Chapter 3 and 4 highlighted the importance of obtaining a measure of the quality of the perceptual and memory processes in VSTM. In line with resource allocation models, in which VSTM success is facilitated by the quality of the memory representation, this study also showed recognition performance being particularly dependent on an initial accurate perceptual discrimination of the stimuli and its stability against load and task-irrelevant information.

7.3 NEURAL SIGNATURES AND CORRELATES OF VSTM MAINTENANCE

As indicated in Chapter 3, VSTM performance is influenced by the load of specific cognitive factors, some of which emerged only by controlling for the initial perceptual encoding of the stimuli.

However, these results may have been influenced by the processes occurring during the maintenance of the memory representations, another crucial stage of VSTM (Trapp & Lepsien, 2012). Stimuli representation although deriving from an accurate encoding could still be challenged by overwriting or by concurrent processing demand such as syntactic processing (Just & Carpenter, 1992; Oberauer & Kliegl, 2006). Therefore, a second study in Chapter 4 used the same VSTM paradigm to investigate the load effect on memory representations, specifically in trials where both perceptual and memory judgments were correct. This was based on analysing the electrophysiological (EEG) correlates of holding memory representations during and prior to task performance.

When accurate in both judgments, memory representations were characterized by theta oscillations increasing with the decrease of load. This effect was constant throughout the entire maintenance interval, following a parietal-frontal topography in line with previous studies suggesting similar brain network for holding information in memory (Liebe et al., 2012; Sarnthein et al., 1998; Siegel et al., 2009).

However, the direction of the effect indicating higher theta magnitude for low load is not in line with some previous findings (Gevins et al., 1997; Jensen & Tesche, 2002; Klimesch, Doppelmayr, Pachinger, et al., 1997). This may be due to the way in which the stimuli were manipulated since studies reporting theta power increment proportional with load presented stimuli sequentially and controlled load by changing set size, rather than feature similarity as in this study. Accordingly, recent studies using simultaneous rather than sequential presentation found a decrease rather than increase in theta power associated with load (Bastiaansen et al., 2002; Pan et al., 2018).

Additional support of our evidence of higher theta magnitude for low load could be found in the analysis of endogenous brain activity during rest. A negative correlation was found between frontal-theta power extracted prior to task execution and performance. This is in line with established theories linking power decrement at rest with successful memory performance (Klimesch, Doppelmayr, Pachinger, et al., 1997; Klimesch, Vogt, et al., 1999), specifically in regions included in the Default Mode Network, relevant in higher order cognitive task such as memory (Scheeringa et al., 2008). Crucially, this association between performance and frontal theta power was only significant for trials correct in both judgments but not in any other performance outcomes (i.e. only correct for perceptual or incorrect for both judgments). The specificity of this relationship further strengthened our view of the link of memory representations and frontal theta.

Moreover, the inverse association of task-related and spontaneous brain activity may be linked to pre-stimulus theta power during encoding which can predict subsequent successful recollection of items (Otten, Quayle, & Puvaneswaran, 2010). Indeed, we found an increase of theta power for the load condition associated with higher accuracy.

In accordance, it should be noted that a direct comparison between correct memory trials preceded by inaccurate versus accurate perceptual discrimination could not be performed in task-related EEG activity, therefore we could not identify what distinguishes these two scenarios at the neural level. Future studies using this paradigm with a balanced number of correct and incorrect trials, may investigate the time course of load effect during maintenance for trials that incorrectly recognised despite an initial correct perception discrimination, or the opposite. A physiological candidate mechanism could be theta-gamma coupling (Jafarpoura, Horner, Fuentemilla, Penny, & Duzel, 2013) since these oscillations are responsible for the coordination of the information replay/rehearsal, because memories 'fire' during each theta cycle and they are stored within a gamma cycle (Jensen & Colgin, 2007; Lisman, 2010). For instance, a recent study has shown that the link between theta and gamma can predict memory accuracy (Axmacher et al., 2010). Applied on our paradigm, theta-gamma coupling may inform whether results change depending on perceptual discrimination of the stimuli to be remembered.

7.4 VWM FLEXIBILITY ACROSS AGE

Re-directing attention during the maintenance interval could be done by providing a retrospective cue (retro-cue), which leads to the prioritization of a stored item. This usually has a beneficial effect on memory performance, known as retro-cue effect, RCE (Griffin & Nobre, 2003; Gunseli et al., 2015; Souza & Oberauer, 2016). This operation requires a degree of flexibility within our WM ability, and an even greater amount is requested when a mis-informative rather than an informative and reliable (valid) retro-cue is provided. Such condition is defined as "invalid" and consists of the presentation of a cue that directs attention to an item that will not be probed in the retrieval phase. Therefore, in invalid retro-cues participants are required to suppress the prioritized item and retrieve another one from the initial stimuli array. This operation results in a retro-cue cost (RCC); however previous studies have reported inconsistent findings of cost (Gressmann & Janczyk, 2016).

Chapters 5 and 6 of this thesis used a retro-cue WM paradigm to investigate top-down attentional processes occurring during stimulus maintenance, to shed light on potential factors underlying previous findings of individual variability. Specifically, we proposed that individual variability in cognitive flexibility towards memory representations may reconcile previous inconsistencies on the RCC effect.

Chapter 5 assessed these processes in younger adults and Chapter 6 in older adults, using the same retro-cue paradigm (Borghini et al., 2018). Direct comparisons between the two age groups were beyond the scope of this thesis and prevented by procedural differences (Paragraph 6.2.2 for more information); therefore, results are reported and discussed separately for each age group.

In the younger adults' sample, since there was no RCC effect at the group level, we hypothesized that different behavioural patterns may have been taken place. Specifically, we tested whether participants were negatively affected by the invalid retro-cues (RCC), ignored them (no-RCC) or effectively suppressed the misleading information carried by the invalid retro-cue ("inverted RCC").

The inverted RCC group showed an "advantage" from a mis-informative retro-cue (invalid) relative to the condition in which no cue is provided during maintenance (neutral) because they benefitted from prioritization processes extended to adjacent items (Camos et al., 2018). We suggest that this may correspond to high cognitive flexibility, especially if supported by the presence of RCE in the valid retro-cue condition.

By correlating the probability of recalling the target item in valid and invalid retro-cue conditions in younger adults', a positive association was found because the larger the benefit related to valid retro-cue (RCE), the larger is the resistance to the cost related to invalid retro-cue (inverted RCC). On one hand, these results supported previous findings suggesting the key for a successful performance within WM relies on the flexible manipulation of memory representations (Woodman, Vogel, & Luck, 2012). On the other, provided a way to quantify it by accounting for individual variability (see also the next section).

With this in mind, Chapter 6 further extended these findings including an ageing sample, as this population is known for having impoverished cognitive flexibility as well as reduced ability to suppress task-irrelevant information (Berry et al., 2016; Clapp, Rubens, & Gazzaley, 2010; Zanto & Gazzaley, 2009). Results in this sample showed both a retro-cue cost (RCC) and a benefit (RCE) at the group level, indicating residual ability to prioritize information within memory representations in ageing (Borghini et al., 2018; Mok et al., 2016). Crucially, a positive correlation between valid and invalid retro-cue conditions values was also found, indicating that the larger the retro-cue benefit (RCE), the smaller is the cost (RCC), ultimately representing further evidence of resilient flexibility maintained throughout age. At a more general level, one could argue that retro-cue effects (cost and benefit) may result from an 'alerting' effect intrinsic in the retro-cue presentation during the interval delay, regardless of its task-relevance (Coull, Nobre, & Frith, 2001; Thiel & Fink, 2007). The retro-cue effect has been shown to be persistent across the life-span (Wiegand & Sander, 2019). A recent study has tested this hypothesis, including, aside from the canonical retro-cue conditions (valid, invalid and neutral), another retro-cue condition carrying colour information that was never part of the stimulus display (i.e. in pink colour) (Borghini et al., 2018). Under this condition of 'task-irrelevant cueing', younger and older adults' performance was not as affected as for the other task-relevant retro-cues, therefore excluding the suggestion that the mere presentation of a cue during maintenance interval may have a distracting, alerting effect, independently of its task-relevance.

To summarize, the results reported in Chapters 5 and 6 provided a novel way to investigate flexibility in working memory with a valid method regardless of age differences, which can ultimately reconcile inconsistencies in the RCC effect literature. Further studies will aim at tracking flexibility in working memory across the whole life span, including a middle age sample in order to define potential differences and their neural underpinnings.

7.5 VWM NEURAL CORRELATES ACROSS AGE

In order to investigate the processes underlying variability in the RCC effect in both age groups, we carried out an analysis of endogenous oscillations recorded prior to task performance.

Endogenous, spontaneous resting-state EEG activity, and specifically alpha frequency band, was chosen for this purpose as it is known for modulating crucial cognitive abilities embedded in a VWM task, such as encoding and task-irrelevant information suppression (Klimesch, 2012; Klimesch et al., 2007), attentional investment and arousal (MacLean et al., 2012; Sala-Llonch et al., 2012b).

Therefore, Chapters 5 and 6 are based on the reasoning that behavioural inconsistencies driven by individual variability may correspond to neuronal patterns underlying brain activity at rest. In the younger adults' sample, based on participants' RCC effect, three equal subgroups were identified: those exhibiting a retro-cue cost (RCC), a reduced (inverted RCC) or no cue effect. Alpha power spectral analysis between these subgroups showed larger power magnitude in the inverted RCC subgroup relative to the RCC one. These results and their posterior topography were in accordance with previous findings suggesting that alpha synchronization at rest (power increment) is reflected to a more easily desynchronization (power reduction) during task performance. Since power magnitude depends on task demands, the increase reflects the suppression of task-irrelevant brain regions, which may correspond to those underlying un-cued items (Bonnefond & Jensen, 2012; Doppelmayr et al., 1998; Haegens, Osipova, Oostenveld, & Jensen, 2010). Moreover, based on the "Inhibition-timing processing", the synchronization of alpha could also indicate a higher capacity to time and access the necessary information. Therefore the inverted RCC subgroup may have inhibited the invalid retro-cue, and possibly improved the timing for accessing WM contents (Klimesch, 2012). Furthermore, the RCC and inverted RCC subgroups differed in an additional electrophysiological measure in the alpha-band, which is positively related to cognitive flexibility, namely long-range temporal correlation (Simola et al., 2017; Tateishi-Karimata & Sugimoto, 2012). This result supports a difference between participants prior to task performance, and is based on the finding that successful performance in higher order cognition is linked to stronger temporal correlations of neuronal activity across time scales and cortical areas (Bhattacharya et al., 2005; Bhattacharya & Petsche, 2001; Simola et al., 2017). Further support to these findings was obtained by applying multivariate pattern analysis to successfully decode the subgroups membership of participants, based on both alpha power spectral density values and long-range temporal correlations.

The same approach was also applied to the older adults' sample (Chapter 6), however because cost and benefit effects were significant at the group level, no subgroups comparisons were performed. Bivariate correlation analyses between electrophysiological measures at rest and RCC effect highlighted a positive relationship between the theta to alpha ration (TAR) over parietal sites and inverted RCC. No other EEG indices in power or long-range temporal correlation was found in association with the RCC effect in older adults.

The positive correlation found between TAR index and RCC is consistent with previous research showing an increase in low frequency ratios correlating with cognitive decline in healthy and pathological ageing. This also supports the view that increased theta power might be associated to hippocampal atrophy, which is vulnerable to ageing (Abuhassan et al., 2014; Bian et al., 2014; Moretti, 2015; Trammell et al., 2017). Additionally, while the topography of our effect is in accordance with previous findings linking lower oscillation's ratios and memory functioning in ageing (Moretti et al., 2013), the effect lying in the interactions between frequency bands represents a further evidence of the combined oscillatory effort involved in working memory (Miller, Lundqvist, & Bastos, 2018; Roux & Uhlhaas, 2014).

Further studies, together with the ones ongoing in our laboratory, should extend this investigation including the entire life span, may affect and change the interaction between endogenous activity and flexible cognition, in order to detect sensitive measures of crucial abilities underlying many everyday life activities.

7.6 SUMMARY

Our ability to maintain and manipulate memory representations underlies many everyday life activities. Despite this, its underlying factors and whether they could explain individual variability in performance have been overlooked. This thesis attempts to address this via: decomposing the steps intrinsic in a visual short-term memory task and proposing a behavioural profile for flexible working memory abilities. The latter aspect was assessed using an ageing perspective, considering its vulnerability to memory impairment, as well as the investigation of neural correlates modulating and predicting the flexible manipulation of memory information.

Collectively, this thesis highlights the relevance of the explicit assessment of perceptual processes preceding recognition and proposes a cognitive and neural profile that could reconcile contrasting findings on our ability to flexibly manipulate memory representations.

The extent to which these mechanisms can account for individual variability in cognitive flexibility across the entire the life span remains a fruitful venue where methods, hereby suggested, could be implemented.

APPENDIX

Means and Standard deviations of accuracy for each perceptual load and proportion for type of response (same/different)

Type of Response	Perceptual load condition	Accuracy
Same .82 (.13)	Low	.82 (.13)
Different .73(.15)	Medium	.76 (.20)
	High	.67 (.20)

Means and Standard deviations of accuracy for each memory load and type of response (same/different)

Type of Response	Memory load condition	Accuracy
Same .87 (.04)	Low	.87 (.04)
Different .42(.13)	Medium	.47 (.16)
	High	.38 (.16)

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