Neural correlates of encoding pictures into long-term memory: the influence of advance information

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A dissertation submitted for the degree of
Doctor of Philosophy
of the
University College London.

Institute of Cognitive Neuroscience
University College London

2015

Declaration

I, Danying Wang, confirm that the work presented in this thesis is my own. Where information has been derived from other sources, I confirm that this has been indicated in the thesis.

Abstract

It has been shown that neural activity before an event influences the likelihood that the event will later be remembered. This doctoral thesis aimed to clarify the functional role of anticipatory activity in long-term memory by manipulating the amount of advance information that is available about an upcoming pictorial encoding event. The first three studies employed scalp-recorded electrical brain activity. Experiment 1 investigated how advance information about the physical form of an object (a perceptually impoverished outline or detailed photograph) affects encoding-related processes. In the temporal domain, event-related potentials (ERPs) showed encoding-related differences regardless of type of advance information. In the frequency domain, decreases in theta and alpha power predicted later memory, but only for photographs. Experiment 2 addressed how preparation time (1.5 or 3 s) affects the encoding of photographs. Only when the preparatory interval was long did anticipatory ERP activity predict encoding success. Experiment 3 aimed to induce a brain state conducive to effective encoding by asking participants to prepare for a delayed match-to-sample task known to involve the hippocampus. A memory probe during the anticipation period suggested that encoding was indeed better before an episodic, rather than control, version of the task. Finally, Experiments 4 and 5 used behavioural measures to address the relationship between encoding-related anticipatory processes and overall memory performance. Experiment 4 compared retrieval under full and divided attention conditions. When retrieval resources were limited by a secondary task, memory performance was better following longer preparation times during encoding. This pattern was not seen in Experiment 5, which contrasted easy and difficult secondary task conditions. Together, the doctoral thesis suggests that the more information is available to guide preparation, the more likely it is that anticipatory activity influences encoding. Individuals may be able to actively employ preparatory processes to strengthen memory under certain circumstances.

Acknowledgements

First, I would like to express my sincere gratitude to my supervisor, Dr Leun Otten, who has been always supportive during the past four years. Leun has always been motivating when I wanted to try out things like new experimental paradigms or analyses. She is also the most insightful one to guide me when some of my ideas did not work. I cannot imagine how I can finish my PhD works without her invaluable dedication.

In addition, I would like to thank the past and current lab members of the cognitive electrophysiological group. I want to say thank you especially to Drs Eva Bauch, Giulia Galli and Matthias Gruber, for their kind supports, patience and help when I did not know anything about EEG. I still remember what they taught me in details when I was writing up my works in this thesis. I want to thank Jiangyi Xia for being supportive throughout my time in London. I think of Jiangyi as a best friend, a big sister and someone I really want to talk to when I have difficulties in research or life.

I also would like to thank my friends from the ICN, Chen and Wenjing for the fun discussions on research. I thank the ICN administrative staff for their cares and efforts to make things a lot easier. I thank all my friends in the UK and China for helping me be less stressful.

Most importantly, I want to say thank you to all my family members especially my parents. Because of their supports and love, I started to pursue a PhD in such a faraway country. My dad and mom always believe in me even when I felt difficult. Thank you both for always being there for me. I will always love you both unconditionally.

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Chapter 1: Introduction

The neural pattern after an event is important for whether this event can be successfully encoded into long-term memory. This is revealed by an experimental paradigm called the subsequent memory paradigm. The neural activity elicited by the event is categorised according to whether it can be remembered or forgotten in a subsequent memory test (Wagner, Koutstaal, & Schacter, 1999). The subsequent memory paradigm gives important insights about why some events can be encoded efficiently while other events cannot. Recently, the neural activity before an event has been shown to affect the likelihood that the event is successfully encoded by using the subsequent memory paradigm. This pre-stimulus encoding-related activity has been found in variety of brain imaging methods, for example, scalp-recorded EEG (Galli, Choy, & Otten, 2012; Galli, Gebert, & Otten, 2013; Galli, Griffiths, & Otten, 2014; Galli, Wolpe, & Otten, 2011; Gruber & Otten, 2010; Gruber, Watrous, Ekstrom, Ranganath, & Otten, 2013; Otten, Quayle, Akram, Ditewig, & Rugg, 2006; Otten, Quayle, & Puvaneswaran, 2010), intracranial EEG (Fell et al., 2011), MEG (Guderian, Schott, Richardson-Klavehn, & Düzel, 2009) and fMRI (Adcock, Thangavel, Whitfield-Gabrieli, Knutson, & Gabrieli, 2006; Mackiewicz, Sarinopoulos, Cleven, & Nitschke, 2006; Park & Rugg, 2010). It is suggested that the encoding-related pre-stimulus activity may reflect an active preparatory process in service of encoding a new memory (Otten et al., 2010; Galli et al., 2013). The previous works stress the types of preparatory processes for encoding such as semantic vs. non-semantic preparation, high motivated vs. low motivated preparation or emotional vs. non-emotional preparation. This doctoral thesis focuses on the amount of perceptual preparatory processes for encoding a pictorial event. To see whether anticipatory mechanisms are flexibly engaged in visual long-term memory, the amount of advance information about the upcoming event itself, the time intervals before the event and the way to encode the event was manipulated. Chapter 1 gives an introduction to the relevant literature. Chapter 2 gives a brief introduction to the methodology that was used in the experiments of this thesis. Chapters 3, 4 and 5 are the experimental chapters. Chapter 6 summarizes the results of the experimental chapters and presents a discussion in a broader context with the previous literature and closes with implications and future directions.

1.1 Long-term Memory

1.1.1 General introduction to episodic memory

Our long-term memory can store a variety of information such as the capital city of France is Paris, what President Obama looks like, what we did in the last Christmas holiday, how to ride a bicycle, or how to programme with some computer language. According to the multiple memory systems view, the variety of information in long-term memory is stored in different memory systems (Schacter, 1992; Schacter & Tulving, 1994; Tulving, 1985a; Tulving & Schacter, 1990). Although there is still controversy about the nature and number of memory systems, evidence from amnesia and neuroimaging data strongly supports the distinction between declarative (explicit) and non-declarative (implicit) memory (Squire, 2004). Non-declarative memory refers to learning without consciousness. Results of learning usually can be observed by changes in performance. Non-declarative memory can be divided into procedural or skill learning (for example, playing piano or learning how to ride a bicycle), repetition priming, classical conditioning and non-associative learning. Performance is enhanced although processes of learning are unconscious and hard to be described. In contrast, declarative memory refers to conscious recollection of past events or facts. It can be divided into semantic memory and episodic memory. Semantic memory refers to general knowledge of facts that is not restricted by when and where it is acquired. For example, knowing that the capital city of France is Paris or famous people's faces does not require knowing when and where they were learnt. In contrast, episodic memory involves recollection of past events with their specific time and place (Tulving, 1983). For example, someone can remember where and what he/she ate for yesterday's breakfast. In the laboratory, the recollection of a list of words that was learnt earlier in the experiment is also considered episodic memory as it is the recollection of something learnt in a specific time and place (Tulving, 1972; 1983). The episodic memory system shares many features with the semantic memory system as there must be semantic knowledge included in an event. However, evidence from lesion studies shows that the temporal and spatial characteristics of episodic memory make it more vulnerable than other memory systems. Almost all amnesic patients lack the ability to form new episodic memories while the ability to form new semantic memories or implicit memories is hardly affected (for example, the famous amnesia case HM, see Corkin, 2002; for a review see Squire, 2004).

There are at least three stages affecting episodic memory: encoding, storage and retrieval (Gardiner, 1988; Mayes & Roberts, 2001; Tulving, 1983). Encoding refers to the processes when an event is first perceived and transformed into a lasting memory trace (Tulving, 1983; Wagner et al., 1999). Storage or consolidation processes help to strengthen a representation in long-term memory. Retrieval helps to recover the stored episodic memory when it is needed. These stages do not support episodic memory in isolation. Whether we remember or forget an event is determined by all stages or the interaction between them (Godden & Baddeley, 1975; Morris, Bransford, & Franks, 1977; Nadel & Moscovitch, 1997; Tulving & Thomson, 1973; Tulving, 1974).

Although successful retrieval is the measurable index of memory success, encoding operations can significantly affect the degree of memory performance. In the laboratory, the event can be a to-be-remembered word or a picture in a word or picture lists. After intentionally or incidentally encoding those events, memory for them will be tested. Encoding processes are influenced by internal mental states. This can be seen by manipulating the strategy of studying an event. The participants who were instructed to use visual imagery during encoding displayed better memory performance than the participants who used a conventional intentional encoding strategy such as rehearsal (Bower, 1972). When participants' attention was distracted by irrelevant materials or secondary tasks during encoding, their recall performance decreased (Murdock, 1965; Postman, Adams, & Phillips, 1955). When the intention of encoding is not emphasized, memory performance depends on the depth of encoding (Craik & Lockhart, 1972). When semantic attributes of to-be-remembered events are processed during encoding, memory performance is better than when phonological or perceptual attributes are processed. Memory performance is a function of the depth of processing on a to-be-remembered event. Within semantic processing, the more semantic attributes to a word are processed, the more likely it will be recalled later (Klein & Saltz, 1976). In addition, Hunt and Einstein (1981) showed that when words shared similar semantic attributes processing on item-specific semantic attributes such as judging how pleasant a word is led to better recall. In contrast, if words were not in the same semantic category such as animate vs. inanimate processing on semantic relations of the words led to better recall. This also suggests that processing more semantic attributes during encoding increases memory performance.

1.1.2 Neural models of episodic memory

It can be seen that episodic encoding shares many features with semantic memory. Successful episodic encoding depends on the degree of how meaningful an event can be represented. In computational views of long-term memory formation, both semantic and episodic memory encoding initially depend on the hippocampal areas (McClelland, McNaughton, & O'Reilly, 1995). The connections between cortical areas within neocortex are strengthened through repeated rehearsal over time. Semantic information is stored permanently in the neocortex and independent of hippocampal areas. The interactions between hippocampal areas and cortical areas enable activation of the hippocampal areas to encode new events with previous semantic knowledge (Alvarez & Squire, 1994; Murre, 1996). Neocortex is suggested to play a role in episodic memory consolidation as well (Alvarez & Squire, 1994; Murre, 1996). Connections within neocortex are gradually built as time passes to store representations of individual semantic elements of an event and establish relations between those elements when the connections are strengthened. Compared to the slow processes of storing a memory representation in neocortex, hippocampal areas enable more rapid learning processes, which play a selective role in consolidation of a memory trace. Some other views suggest that contextual aspects of an episode, such as spatial or temporal contexts are stored in the hippocampal areas as long as it needs to be retrieved (Nadel & Moscovitch, 1997; Shastri, 2002). Semantic elements of the episode are stored in neocortex. Rehearsal of contextual information, however, does not transfer storage into neocortex as time passes, which results in that contextual information stored within the hippocampal areas being more stable (Mayes & Roberts, 2001; Nadel & Moscovitch, 1997).

Retrieval usually occurs when a cue triggers a part of stored information. Retrieval is successful when this part of stored information is completed with the missing part of stored information in the whole event. If hippocampal areas are where the unique aspects of an event are stored, then retrieval processes should also take place in hippocampal areas (O’Reilly & Rudy, 2001). If our memory is perfect, then retrieval of an event should be a reproductive process like playing a movie. However, Bartlett (1932) suggested that retrieval is a constructive rather than reproductive process as retrieval happens with errors and semantic knowledge distortion. Features that are shared by other events, which are also stored in neocortex after encoding an episode, may cause retrieval with errors and semantic distortion. Therefore the way to probe memory should also affect retrieval as different ways to probe memory might activate different underlying neural networks. For example, recognition may merely affect the hippocampus but the hippocampus is involved in recollection that makes an event stand out (Mayes & Roberts, 2001). The familiarity of an item should depend on cortical areas as stored memory representations share features with many other inputs. Besides recognition, recall is another important test in assessing episodic memory. Recall includes cued recall and free recall. In a cued recall paradigm, participants encode items in pairs or lists. During the test, an item of the studied pairs or lists is presented as a retrieval cue. Participants recall the rest of the pairs or the lists. In a free recall paradigm, no retrieval cue is presented. Participants have to recall as many items as they can. Free recall is thought to be a process of retrieving episodic memory and mainly depend on the hippocampus (Aggleton & Brown, 1999; Tulving, 1974).

1.1.3 Recollection and familiarity

There are still ongoing arguments about the processes involved in recognition. Single-process models argue that recollection and familiarity are not two distinct processes (Dunn, 2008; McClelland & Chappell, 1998; Squire, Wixted, & Clark, 2007). This view is based on signal detection theory (Green & Swets, 1966). A recognition item is compared with information stored in memory to decide memory strength. Squire et al. (2007) suggest that neural networks, such as the hippocampus, that separate recollection from familiarity actually support strong memories while neural networks supporting familiarity such as the perirhinal cortex might contribute to weak memories. Previous studies show nonlinear activity in the hippocampus by memory strengths. In their views, the measurements used in the previous studies were not in linear scale. They listed evidence from studies compared recall with recognition, which showed that recollection and familiarity could both activate the hippocampus and the perirhinal cortex. Therefore, they suggest that the hippocampal activity is related to strong memories that could include both recollection and familiarity. Similarly, weak memories contain both recollection and familiarity but cannot activate the hippocampus. Dual-process models argue that recollection and familiarity are two qualitatively distinct processes during recognition (Diana, Yonelinas, & Ranganath, 2007; Eichenbaum, Yonelinas, & Ranganath, 2007; Greve, Donaldson, & van Rossum, 2010; Mandler, 1980; Rugg & Yonelinas, 2003; Tulving, 1983). In this view, only familiarity reflects a signal detection process while recollection reflects a threshold process (Yonelinas, 2001a). Recollection depends on different neural substrates from familiarity. Also, processing time for recollection is slower than for familiarity (Yonelinas, 2002). In addition, many experimental manipulations such as encoding types, divided attention, stimulus types, and participants' individual differences have significant effects on recollection more than on familiarity (Jacoby, 1991; Yonelinas, 2001a; 2002). In contrast, delays between study and test or priming seem to have larger effects on familiarity than recollection (Rajaram, 1993; Yonelinas, 2001a). It can be seen that familiarity is more affected by implicit processes while recollection requires more resources to recollect context-related information. Compared to recollection, familiarity is retrieval without recollecting spatial-temporal details. It is like a feeling of knowing you have seen someone before but not knowing when or where you have seen him/her.

Tulving and colleagues (Tulving, 1985b; Tulving & Schacter, 1990; Tulving & Markowitsch, 1998) suggest recollection is a conscious process of remembering while familiarity, or the feeling of 'knowing', resembles semantic memory. It is mentioned that the hippocampal areas play important roles in recollection but not familiarity.

Familiarity depends on entirely different neural networks that include the cortical structures where semantic memory representations are stored. The two underlying distinct neural systems provide evidence for the dual-process models. However, debates focus on whether hippocampal activity also plays a role in familiarity, which suggests it is memory strength related (Squire et al., 2007). Yonelinas, Otten, Shaw, and Rugg (2005) used a recognition test that could distinguish recollection from the degree of familiarity and found there was no overlap in cortical regions between recollection and how confident a familiarity judgment was made. They also found that the hippocampal activity was not a function of the confidence levels of familiarity, which suggests that the role of the hippocampal areas is not simply activation to memory strength.

To dissociate recollection of conscious experience from familiarity, a simple item recognition test that requires distinguishing an old item from new items is not sufficient (Tulving, 1985b). Usually, memory is tested with an additional task, for example, an additional question of ‘when the item was presented’ will be asked to decide whether any contextual details can be recollected to a studied item (Jocoby, 1991; Johnson, Hashtroudi, & Lindsay, 1993). The item is recollected if correct contextual details are recalled. However, whether contextual details can be retrieved might depend on familiarity. For example, a more recent item could more easily trigger its temporal context as it is more familiar (Yonelinas, 2002). This kind of test is considered to rely less on familiarity. Another approach is the Remember/ Know procedure developed by Tulving (1985b). Participants are asked to make one of three responses, remember, know and new when they see an item. Remember means if they can recollect any contextual details about it. Know means if they feel familiar but are not able to recollect any contextual details. New means if they think they have not encountered it. This procedure has been demonstrated to effectively dissociate recollection from familiarity (Gardiner, Ramponi, & Richardson-Klavehn, 2002; Rajaram, 1993; Yonelinas, 2001b).

Nevertheless, as the Remember/ Know procedure is based on subjective responses, it is influenced by how experimental procedure is instructed (Geraci, McCabe, & Guillory, 2009; McCabe & Geraci, 2009). Yonelinas (2002) also suggested that Know responses are not an unbiased index for familiarity. The instruction of making Know responses emphasises absences of recollection. Yonelinas (2002) argued that this might bias the amount of familiarity as instructions should stress that a Know response could be made when an item is simply familiar.

In this doctoral thesis, most studies used a confidence recognition memory test, which is widely used in neuroimaging studies to illustrate encoding and retrieval processes in long-term memory (e.g. Henson, Rugg, Shallice, & Dolan, 2000; Otten, Henson, & Rugg, 2001; Otten et al., 2006). Behavioural evidence of the direct comparisons between Remember/Know paradigm and confidence recognition judgment shows that more ‘Know’ responses tend to be made for familiar items such as non-words more than ‘Remember’ responses while the number of high confidence judgments does not differ from the number of low confidence judgments made to such items (Dunn, 2004). However, when modelling ‘Remember’ and ‘Know’ responses and confidence judgments with signal detection theory, ‘Remember’ responses are related to high confidence judgments and ‘Know’ responses are associated with low confidence judgments (Dunn, 2004). Although there is no direct evidence showing how recollection is represented in a confidence recognition memory test, Yonelinas (2001) suggested recollection should result in more high confidence responses than familiarity (Yonelinas, 2001). While familiarity reflects a different confidence responses range (Yonelinas, 2001). Although the confidence recognition memory test might not be able to provide sufficient information about recollection, it does give a measure of strong memory and weak memory. In a pilot of the studies in the current thesis, the Remember/ Know paradigm could not give an acceptable trial number in each category that is used to compute Event-Related Potentials (ERPs) (Picton et al., 2000). Therefore, a confidence recognition memory test was used in the first two EEG experiments in order to reach an acceptable signal/noise ratio to look at ERP subsequent memory effects. In the third EEG experiment, a revised version of the Remember/ Know procedure was used as the nature of the experiment permits the test to be able to be used. The test asks participants to make one of five instead of three responses: Remember, Confident old, Unconfident old, Unconfident new and Confident new (Yonelinas et al., 2005). This test attempts to resolve the problem that the Remember/ Know procedure might not be able to distinguish high confident familiarity judgments. Further studies that used this procedure show that the five-way procedure is more efficient to dissociate the brain areas that support recollection from the brain areas that support familiarity, which provides clearer evidence that recollection and familiarity are two distinctive processes (Johnson, Suzuki, & Rugg, 2013; Voss & Paller, 2009; Woodruff, Hayama, & Rugg, 2006; Yu & Rugg, 2010).

In conclusion, memory success depends on encoding, consolidation, retrieval and interactions between these stages. Manipulations on encoding and retrieval directly influence memory performance. Although there are still debates on the processes in recognition memory, dual-processes models are favoured. Recognition memory can be consisted of two processes, recollection and familiarity. In order to dissociate such two processes in a recognition memory test, reports of conscious recollection and the feeling of knowing are added on top of the traditional old / new recognition test. More recently, tests using reports of conscious recollection and the strengths of familiarity are demonstrated to effectively dissociate recollection from high confidence familiarity. Restricted by sufficient artefacts-free trial numbers in ERP analyses, two EEG studies of this doctoral thesis used confidence recognition memory test. A third EEG study used the revised version of remember / know paradigm (i.e. five-way responses by Yonelinas et al., 2005).

1.2 Measuring the neural pattern of successful memory formation: The subsequent memory paradigm

Although it was known that episodic memory formation mainly relies on the Medial Temporal Lobe (MTL) from lesion data, there was not a way to study the isolated processes of memory formation in our brain until neuroimaging techniques developed. In an early ERP study, Sanquist, Rohrbaugh, Syndulko, and Lindsley (1980) first found the waveforms elicited by subsequently remembered word pairs were more positive-going than the waveforms elicited by subsequently forgotten word pairs during encoding. Later, Paller, Kutas and Mayes (1987) termed this difference due to memory the ‘Dm’ effect. Subsequent memory approach has been used for decades to investigate the neural correlates of encoding. It provides a way to see why some events are encoded more efficiently than other events.

Studies on neural correlates of encoding using functional Magnetic Resonance Imaging (fMRI) and Positron Emission Tomography (PET) allow understanding of which brain areas underlie encoding. At first, fMRI and PET techniques could only investigate encoding during a block and not trial-by-trial. For example, participants were asked to do semantic encoding in one block and non-semantic encoding in another block (Kapur et al., 1994; Wagner et al., 1998). Activity in the whole semantic encoding block was averaged to compare with activity in the whole non-semantic encoding block. It was shown that the prefrontal cortex was more activated during semantic encoding compared to non-semantic encoding. This kind of blocked design can only show which brain areas are activated during the type of encoding that leads to better memory performance. However, blocked fMRI and PET studies could not tell which brain areas are activated when an event is remembered compared to forgotten within one type of encoding. Event-related fMRI analyses allow understanding why some events can be remembered while others cannot on a trial-by-trial basis.

Brain activity is recorded while participants incidentally or intentionally encode a series of events. In an intentional encoding task, participants are asked to remember the events intentionally. Sometimes they are not told any specific strategy to use. Sometimes they are asked to use a specific strategy such as rote rehearsal or do some encoding tasks such as semantic judgment (Wagner et al., 1999). In an incidental encoding task, participants encode the events incidentally with an encoding task such as semantic or non-semantic judgments, without knowing the main purpose of the task is memory. After a delay, memory about the studied events is tested. Performance on the memory test is used to go back to sort the brain activity recorded during encoding. The difference between brain activity for subsequently remembered events and for the subsequently forgotten events is called subsequent memory effect or encoding-related activity.

The subsequent memory paradigm could be used with both ERP and event-related fMRI studies (e.g. Brewer, Zhao, Desmond, Glover, & Gabrieli, 1998; Wagner et al., 1998; Otten & Rugg, 2001a). It has also been used with other neuroimaging techniques such as magnetencephalography (MEG) (Osipova et al., 2006; Takashima et al., 2006) and intracranial EEG (iEEG) (Fell et al., 2001; Long, Burke, & Kahana, 2013; Sederberg et al., 2006). However, there are some important issues needed to be considered before designing a study with the subsequent memory paradigm. Subsequent memory effects might not be able to index encoding processes in some circumstances. If participants attend to some items but ignore the other items, then there is a correlation between attentional levels and memory performance. The subsequent memory effect found here then reflects attention-related processes to a great extent (Rugg, Otten, Henson, 2002). In such case, an online measure is necessary to guarantee that attention is allocated equally to both remembered and forgotten items. For example, no significant differences in performance during the encoding task such as RT or accuracy between later remembered and forgotten items can ensure subsequent memory effects unlikely to be influenced by non-encoding-related processes such as attention-related processes (Rugg et al., 2002; Wagner et al., 1999). As mentioned above, memory performance does not only rely on encoding or retrieval or storage but interactions between those processes. Therefore, encoding-related activity that is sorted back by memory performance might not solely reflect encoding processes. Otten (2007) showed that even when study materials are consistent, subsequent memory effects are differed in brain regions by how memory is probed. In spite of that, the subsequent memory paradigm is still the most effective way to investigate isolated encoding processes on why some events can be successfully remembered.

1.3 Encoding-related brain activity after an event

1.3.1 Brain regions correlated with encoding success

By using the subsequent memory paradigm we can understand what kind of brain activity and which part of the brain is activated when an event is successfully encoded compared to forgotten. Most fMRI studies show the importance of the PreFrontal Cortex (PFC) and the Medial Temporal Lobe (MTL) to successful encoding of visual events. Those two regions are activated more when items are subsequently remembered compared to forgotten (for a review, see Wagner et al., 1999). The PFC plays a critical role in cognitive control processes such as selective attention or information organisation in working memory tasks (Blumenfeld & Ranganath, 2007; Duncan &

Owen, 2000; Fletcher & Henson, 2001; Simons & Spiers; 2003). In the literature on long-term memory encoding, a sub-region of the PFC called the VentroLateral PreFrontal Cortex (VLPFC) is found to be more activated when an item is subsequently remembered (e.g. Otten et al., 2001; Wagner et al., 1998). The functional role of the VLPFC is goal-directed information selection in working memory processes. Subsequent memory effects were found in the VLPFC during deep level of processing encoding task (e.g. Otten et al., 2001; Wagner et al., 1998). The VLPFC activation during successful encoding might reflect information selection or elaboration during encoding (Blumenfeld & Ranganath, 2007; Simons & Spiers, 2003). The functional role of another sub-region of the PFC, the DorsoLateral PreFrontal Cortex (DLPFC), is information organisation in working memory. It was found to be activated during successful long-term memory encoding especially when item associations are emphasised (e.g. Blumenfeld & Ranganath, 2006; Summerfield et al., 2006). The causal role of the PFC in episodic memory encoding is determined by brain stimulation to the PFC areas during encoding. Memory performance is facilitated or impaired when the PFC areas are subjected to Transcranial Magnetic Stimulation (TMS) during encoding (Epstein, Sekino, Yamaguchi, Kamiya, & Ueno, 2001; Kahn et al., 2005; Köhler, Paus, Buckner, & Milner, 2004; Machizawa, Kalla, Walsh, & Otten, 2010).

The characteristic of episodic memory encoding is a combination of an event and its temporal-spatial features or any other contextual information. Sub-regions of the MTL are critical for receiving a variety of information such as unimodal or multimodal features of an event, as well as interacting with neocortex to process the meaning of the features and finally forming representations of the event for later retrieval (Burgess, Maguire, & O’Keefe, 2002; Davachi, 2006; Diana et al., 2007; Simons & Spiers, 2003; Suzuki & Amaral, 2004). Recently, the role of the Posterior Parietal Cortex (PPC) in episodic memory encoding was also attracted attention. One of its sub-regions, the dorsal PPC, is mostly found to be activated when an item is subsequently remembered (e.g. Otten et al., 2001). The activation of the dorsal PPC is related to top-down or goal-directed attentional control processes in working memory (Berryhill, 2012; Uncapher & Wagner, 2009). Uncapher, Hutchinson, and Wagner (2011) used a spatial cueing paradigm to show that the dorsal PPC was activated when a target picture presented in a valid cued location. The activation of the dorsal PPC also predicted memory success of the target pictures. In contrast, the activity of another sub-region, the ventral PPC, is negatively correlated with subsequent memory performance (e.g. Otten & Rugg, 2001a; Uncapher et al., 2011; Wagner & Davachi, 2001). The activation of the ventral PPC might reflect bottom-up or saliency-related processes. Therefore, it might modulate effective memory encoding by means of its deactivation to suppress task-irrelevant information (Uncapher & Wagner, 2009).

1.3.2 Encoding-related electrical brain activity

The fMRI studies on encoding-related activity after an event reveal the brain areas correlated with effective encoding. EEG, iEEG or MEG studies using the subsequent memory paradigm give understandings about temporal characteristics and type of encoding-related activity. Scalp-recorded ERPs are often more positive-going for subsequently remembered items compared to forgotten items (for reviews, see Paller & Wagner, 2002; Rugg, 1995; Wagner et al., 1999; Werkle-Bergner, Müller, Li, & Lindenberger, 2006). This positive-going effect starts around 300 to 800 ms after stimulus onset. The scalp distributions of the effect depend on encoding type or material type (Friedman & Johnson, 2000; Otten, Sveen, & Quayle, 2007; Otten & Rugg, 2001b; Wagner et al., 1999).

IEEG permits to look at both spatial and temporal features of encoding-related activity. Fernández et al. (1999) used intracranial ERP to find negative-going waveforms after subsequently recalled words compared to unrecalled words in the MTL around 300 to 500 ms after word onset. ERP analyses stress the summation of neural activity locked to an event. Recently, the subsequent memory paradigm has been utilised to look at encoding-related activity in frequency bands of oscillatory brain activity derived from EEG or MEG signals. Oscillatory brain activity is continuous and not specifically locked to the event. Time-frequency analyses sum the continuous activity in a specific time window depending on the frequency of the continuous fluctuating wave patterns (Roach & Mathalon, 2008). Changes of magnitude or phases in different frequency bands usually reflect cognitive processes. For example, encoding-related activity in theta (4 – 8 Hz) and gamma (30 – 100 Hz) in the PFC and the MTL is usually thought to be critical for memory encoding (Fell et al., 2001; Long et al., 2013; Sederberg et al., 2007; Sederberg, Kahana, Howard, Donner, & Madsen, 2003). In addition, scalp-recorded theta, alpha (8 – 12 Hz) and beta (12 – 30 Hz) encoding-related activity is found to play a role in memory formation (Hanslmayr, Staudigl, & Fellner, 2012; Hsieh & Ranganath, 2014; Klimesch, 1999).

This doctoral thesis focuses on the lower frequency bands i.e. theta and alpha. Lisman and Idiart’s computational model (1995) describes how short-term memories are encoded and stored. In the model, each item in short-term memory is represented by a cycle of gamma frequency (35 Hz). Because of the proposed storage capacity of human short-term memory, approximately 7 ± 2 items are stored in 7 ± 2 gamma cycles (35 Hz), nested in a subcycle of theta frequency. Short-term memory of the 7 ± 2 items is maintained via repetition of the theta subcycle. This model is supported by evidence that theta activity increases with working memory load (e.g. Jensen & Tesche, 2002). Further, this model indicates that individual episodic information is stored with a gamma sub cycle and associated with each other by fast N-me-thyl-D-aspartate (NMDA) channels connections to form an episodic memory (Jensen & Lisman, 1996). The episodic memory is retained by a theta cycle. This idea is supported by the finding that theta-gamma-coupling (gamma amplitude changes that coincide with theta range) modulates successful episodic memory encoding (e.g. Staudigl & Hanslmayr, 2013). Each gamma cycle represents item memory while theta activity helps to bind these items together (item-source binding). In memory retrieval, increases in gamma power are found for correctly recognised old items compared to correctly judged new items, but not for source judgments (Gruber, Tsivilis, Giabbiconi, & Müller, 2008). In contrast, increases in theta power are found to be sensitive to source judgments. The authors suggested that gamma power reflects familiarity and theta power recollection. The alpha activity is thought to increase when more attention is paid (Klimesch, 1999). As a result, more alpha activity after a successfully encoded item might be related to more attentional resources given to that item. However, encoding-related synchronised or desynchronised oscillatory brain activity varies and functional roles of theta and alpha activity are still not clear. How encoding-related (de)synchronisation in theta and alpha oscillatory activity varies and what it means is introduced in the next part of this chapter.

1.3.3 Encoding-related activity and encoding manipulations

Encoding-related activity after an event is influenced by encoding manipulations such as material types, encoding types or retrieval manipulations such as retrieval types or interactions between encoding and retrieval. As mentioned above, memory performance is a function of types of encoding (Craik & Lockhart, 1972). Likewise, activity in the prefrontal cortex has been found to correlate with semantic processing during encoding compared to a perceptual or shallow encoding task (Demb et al., 1995; Kapur et al., 1994; Wagner et al., 1998). However, in an event-related fMRI study, similar prefrontal cortex subsequent memory effect was not found only for semantic encoding (Otten et al., 2001). The prefrontal cortex was also more activated for subsequently recognised items under alphabetical encoding task. The same group of researchers used another shallow level of processing task to recruit high-demand phonological processing to items compared with the same semantic task (Otten & Rugg, 2001a). A significant subsequent memory effect was found in the prefrontal cortex only during the semantic encoding task. In contrast, significant subsequent memory effects were found in the posterior parietal cortex for the phonological encoding task, where was also activated for the phonological encoding task regardless of memory performance compared to the semantic encoding task.

In most ERP findings of encoding-related activity after an event, a frontal or frontocentral positive-going subsequent memory effect is found in the deeper processing or semantic encoding task (Friedman & Johnson, 2000; Paller et al., 1987; Rugg, 1995; Sanquist et al., 1980; Wagner et al., 1999). In the shallow processing or non-semantic encoding task, usually no or reduced subsequent memory effect is found (Paller et al., 1987; Sanquist et al., 1980). The findings suggest that shallow and deep processes in episodic encoding are qualitatively similar, but that these processes are invoked to a lesser degree during shallow encoding tasks. However, one ERP study compared encoding-related activity elicited by items in a semantic encoding task to encoding-related activity elicited by items in an alphabetic task and found qualitatively different subsequent memory effects (Otten & Rugg, 2001b). Subsequently recognised words elicited more positive-going waveforms in the semantic encoding task compared to subsequently forgotten words. In contrast, significant negative-going subsequent memory effects were found for the alphabetic encoding task. The different polarities of the two subsequent memory effects might be caused by different neural activity (e.g. excitatory vs. inhibitory) from the same neural generators, equivalent neural activity from different neural generators, or different neural activity from different neural generators. Regardless of the precise neural underpinnings, the observed polarity difference implies that encoding-related neural activity in a shallow task is not a subset of the encoding-related activity found in a deep task. Episodic encoding is supported by multiple neural networks that depend on encoding types. A recent EEG study compared encoding-related oscillatory brain activity in a semantic encoding task to the activity in an alphabetic task (Hanslmayr, Spitzer, & Bäuml, 2009). It was found that alpha power decreased after subsequently recognised words compared to forgotten words in the semantic task in an earlier time window (around 500 ms after word onset). In contrast, theta power increased after subsequently recognised words in the same time window under alphabetic encoding. In a later time window (from 1000 ms after word onset), encoding-related decreases in alpha power were also found in the alphabetic encoding task. The decreases in alpha power might reflect semantic processing in memory encoding as after 1000 ms a semantic process could be involved even in the non-semantic encoding task. This view is supported by a later study conducted by the same group (Fellner, Bäuml, Hanslmayr, 2013). It replicated the encoding-related alpha power decrease effect in a semantic encoding task. Those findings suggest that encoding-related oscillatory activity is also task-specific. Oscillatory brain activity supports successful episodic encoding depending on the types of processing underlying encoding (Hanslmayr & Staudigl, 2014).

Differences in encoding-related activity between semantic or deeper encoding and non-semantic or shallow encoding are often investigated with an incidental encoding task. It is suggested that intentional encoding is more effortful thus participants might utilise more elaborated strategies (Anderson, 1995; Tulving, 1983). However, intentional encoding is more variable in generating more individual differences in stimulus processing or memory strategy compared to incidental encoding, when there is a unified encoding task (Wagner et al., 1999). Most ERP studies using an incidental encoding paradigm found a larger, earlier positive-going subsequent memory effect with a widespread scalp distribution compared to intentional encoding conditions (Fabiani, Karis, & Donchin, 1990; Friedman, 1990; Karis, Fabiani, & Donchin, 1984; Münte, Heinze, Scholz, & Künkel, 1988; Paller, 1990). It seems that the differences in neural correlates between incidental and intentional encoding are in degree rather than type of activity. FMRI findings suggest that the MTL is activated for subsequently memorised items under both incidental and intentional encoding conditions (Martin, 1999; Stark & Okado, 2003). Although one fMRI study failed to find a statistically significant subsequent memory effect in the MTL for the incidental encoding condition, the patterns of material-specific MTL activity were the same as in the intentional encoding condition (Kelley et al., 1998). Neural correlates of incidental encoding thus differ from the neural correlates of intentional encoding in the degree of activity within the same brain area. In turn, this suggests that the engagement of associated cognitive processes is the same across incidental and intentional encoding conditions, but the degree to which they are activatied might differ. Therefore, neural correlates of incidental and intentional encoding should be quantitative rather than qualitative in nature.

Memory performance is also impaired when attention is divided during encoding (Anderson et al., 2000; Craik, Govoni, Naveh-Benjamin, & Anderson, 1996; Craik, Luo, & Sakuta, 2010; Fernandes & Moscovitch, 2000; Iidaka, Anderson, Kapur, Cabeza, & Craik, 2000; Naveh-Benjamin, Craik, Guez, & Dori, 1998; Naveh-Benjamin, Craik, Perretta, & Tonev, 2000). Further, the differences between the ERP activity elicited by the subsequently remembered items and the activity elicited by the subsequently known items are a function of the level of attention (Mangels, Picton, & Craik, 2001). The ERP waveforms of subsequently remembered items were overlapped with the ERP waveforms of subsequently known items under full attention condition in the study done by Mangels et al. (2001). The differences in the ERP waveforms over frontal sites increased as the difficulty for the divided attention tasks increased. The results suggest that insufficient attentional resources influence the engagement of elaborative or semantic processes, which the neural activity of elaborative encoding greatly differentiates from the neural activity of guessing processes. Several PET findings showed that during encoding, activity in PFC and MTL is significantly reduced under divided attention condition compared to full attention condition (Anderson et al., 2000; Fletcher, Shallice, & Dolan, 1998; Iidaka et al., 2000). Additionally, an increase in activation of the PPC was found under divided attention compared to full attention condition during encoding (Iidaka et al., 2000). It can be seen that a secondary task competes for attentional resources with memory encoding, which leads to less brain activity that is critical to memory formation but more activity for attention-related brain areas to allocate resources for the secondary task itself.

Most studies that have reported subsequent memory effects in ERP, fMRI and oscillations used verbal materials. For example, the typical positive-going ERP subsequent memory effects are found in words (Friedman, 1990; Munte et al., 1988; Paller, 1990). The encoding-related activity in the PFC and the MTL is also often found in words (Otten et al., 2001; Otten & Rugg, 2001a; Wagner et al., 1998). In addition, most studies that found encoding-related oscillatory activity used words as materials (Fell et al., 2001; Hanslmayr et al., 2009; Sederberg et al., 2003). Not only words, but also other verbal materials such as names (Fabiani, Karis, & Donchin, 1986) or abstract words (Weiss, Müller, & Rappelsberger, 2000) have been able to show significant subsequent memory effects. There are fewer studies using other kinds of visual stimuli such as object pictures or complex visual scenes. Compared to the frontal or frontocentral positive-going subsequent memory effect found in words, Friedman and Sutton (1987) used line drawings of everyday objects and found a more parietal and earlier subsequent memory effect. An intracranial ERP study showed that the encoding-related activity in the MTL correlated with later memory performance (Elger et al., 1997). The correlation between encoding-related activity in the MTL and memory performance was lateralised according to material type. Activity in the right MTL was positively correlated with later memory performance for pictures, while activity in the left MTL was positively correlated with later memory performance for words. A scalp-recorded ERP study that used unfamiliar faces as stimuli found a frontally-distributed subsequent memory effect (Sommer, Schweinberger, & Matt, 1991). Similarly, the subsequent memory effect found for the unfamiliar faces was also larger over right scalp sites. In an fMRI study that compared encoding-related activity for words and pictures, it was found that encoding-related Blood-Oxygen-Level Dependent (BOLD) signals are larger in the left hemisphere for words and in both hemispheres for pictures (Kirchhoff, Wagner, Maril, & Stern, 2000). Another fMRI study compared encoding-related activity for words, pictures of everyday objects and pictures of unfamiliar faces (Kelley et al., 1998). Similar results were found in that activation of dorsal frontal regions was left-lateralised by words, bilateral by objects and right-lateralised by faces. Most studies investigated encoding-related oscillatory brain activity used words as stimuli and found frontal increases in theta power and parietal decreases in alpha power (Hanslmayr et al., 2009; Klimesch, Doppelmayr, Schimke, & Ripper, 1997; Sederberg et al., 2003; Summerfield & Mangels, 2005). There are few studies using pictorial stimuli. An MEG study used scenes of landscapes and buildings as stimuli and found an encoding-related theta power increase over right parietotemporal areas (Osipova et al., 2006). Also, a scalp-recorded EEG study directly compared encoding-related theta and upper alpha (10 -12 Hz) activity of words and faces (Molle, Marshall, Fehm, & Born, 2002). Theta synchronisation and upper alpha desynchronisation were found to predict successful word encoding over left frontotemporal scalp sites and predict successful face encoding over right parietal scalp sites.

It seems that subsequent memory effect is found to be activated in different brain networks depending on material types. However, in an ERP study, Petten and Senkfor (1996) used meaningless novel visual patterns and found no significant subsequent memory effect produced by them. They suggested that the reasons why no subsequent memory effect was found were that no pre-experimental knowledge was associated with those patterns. Therefore, neural activity contributes to successful encoding might be cancelled out due to failure in later retrieval of any associative pre-knowledge about the patterns. Otten et al. (2007) compared encoding-related brain activity for words and non-words, with non-words being meaningless but pronounceable and orthographically legal letter strings. This reduces the confounds in Petten and Senkfor’s study (1996) that different encoding tasks (semantic vs. non-semantic) were used. The encoding task in the study of Otten et al. (2007) was a syllable judgment that can be done for both words and non-words. A frontally distributed positive-going subsequent memory effect was found for words while successfully encoded non-words elicited a negative-going effect over widespread scalp regions. The findings suggest that compared to familiar information, there is a different brain network supporting learning of novel information, which can be evident in encoding processes.

Emotional or saliency attributes of stimuli can also influence encoding-related activity. The amygdala is suggested to be a key brain region for the encoding of emotionally arousing stimuli (Canli, Zhao, Brewer, Gabrieli, & Cahill, 2000; Dolcos, LaBar & Cabeza, 2004). Its activation can predict later memory performance for emotional stimuli. Saliency or novelty of stimuli can also be manipulated by reward. Reward could modulate MTL to enhance memory formation (Wittmann et al., 2005;

Wittmann, Schiltz, Boehler, & Düzel, 2008). Reward-related activity in MTL could also be modulated by positive emotional stimuli and then interact with activity in the amygdala to improve memory performance (Wittmann et al., 2008). This suggests that neural processes underlying reward and positive emotional valence have an addictive effect on episodic encoding regardless of material types (Wittmann et al., 2008).

In conclusion, there are multiple neural networks supporting successful encoding. They are modulated by how information is encoded and what kind of information is encoded.

1.3.4 Encoding-related activity and retrieval manipulations

Encoding-related activity is neural activity categorised according to subsequent memory performance. Therefore, how memory is probed should also influence encoding-related activity. The frontal or frontocentral positive-going subsequent memory effects in ERP findings seem to be shown in recall test and recognition test (Friedman, 1990; Karis et al., 1984; Munte et al., 1988; Paller et al., 1988; Paller, 1990). There is a graded difference in the subsequent memory effects between recall and recognition. Namely, the size of the subsequent memory effect is larger in the comparison between subsequently recalled and forgotten items than the comparison between subsequently recognised and forgotten items (Munte et al., 1998). Magnitude of subsequent memory effect is more evident when an item is ‘really remembered’ rather than ‘guessed’. Robust subsequent memory effects are often shown when subsequent ‘remember’ responses are made rather than ‘know’ responses in the Remember/Know paradigm (Duarte, Ranganath, Winward, Hayward, & Knight, 2004; Friedman & Trott, 2000). In another study using the Remember/Know paradigm, subsequent memory effects were also compared between encoding conditions under different degree of attention diversion (Mangels et al., 2001). In easy and difficult divided attention conditions, there was no difference between items subsequently judged as ‘know’ and ‘new’, which suggests that when attentional resources are not sufficient, ‘know’ responses are close to ‘guessed’ and generate weak memory representation similar to forgotten items. A similar result was found in a study using five-way judgments (Yonelinas et al., 2005). Only subsequently recollected and confidently judged as old items elicited positive-going waveforms relative to items subsequently judged as new (Voss & Paller, 2009). Likewise, robust subsequent memory effects found in fMRI studies usually concern high confident old judgments (Brewer et al., 1998; Otten et al., 2001; Wagner et al., 1998). More recently, qualitative differences are found between familiarity-related encoding activity and recollection-related encoding activity in fMRI studies (Davachi, Mitchell, & Wagner, 2003; Henson, Rugg, Shallice, Josephs, & Dolan, 1999; Otten, 2007). The activation of the hippocampus and the posterior parahippocampal cortex predicts subsequent recollection with source, while the activation of perirhinal cortex predicts subsequent item recognition without source recollection (Davachi et al., 2003). In the other fMRI studies, the PFC was additionally activated to predict later remember but not know judgments (Henson et al., 1999; Otten, 2007).

As discussed above, Otten (2007) found that how memory is probed can modulate encoding-related activity. Successful encoding of visual words activated left fusiform gyrus, right frontal and occipital cortices if the words were tested with spoken words. In contrast, if the words were tested with pictures, activation in the left superior temporal gyrus, left superior frontal gyrus and right lateral parietal cortex predicted successful encoding. An ERP study also showed that subsequent memory effect is affected by study-test congruency (Bauch & Otten, 2012). A frontal positive-going subsequent memory effect was found when a picture was tested with the same picture format while the effect was more over posterior scalp sites if the picture was tested with a word format. Interestingly, Staudigl and Hanslmayr (2013) found that the study-test congruency could also modulate encoding-related theta power. They manipulated context during encoding and retrieval. During encoding, a word was presented on top of a video clip. If the word was tested with the same video clip as presented with during study, increased theta power predicted later successful retrieval. In contrast, if the word was tested with a different video clip from when it was presented with before, decreased theta power was related to later recognised items. They suggested that previous studies with different directions of encoding-related theta effect could be interpreted by this context-congruency modulation.

In summary, the PFC, the MTL and the PPC are three critical brain regions for encoding. However, encoding manipulations such as encoding tasks or material types could influence the neural networks engaged in successful encoding. EEG and MEG studies also show that different types of encoding-related activity are involved depending on encoding tasks. In addition, encoding-related activity is influenced by retrieval manipulations such as retrieval types. The overlaps between encoding and retrieval and how a memory is probed vary neural correlates of successful encoding. There may be multiple neural networks supporting successful encoding, which reflect underlying cognitive processes during encoding.

1.4 How brain activity before an event influences processing on the event

In our daily life, anticipation or expectation might help people avoid harm or increase performance. In cognitive neuroscience, anticipation or preparation has been found to affect brain activity in a few seconds before an upcoming event (Brunia, van Boxtel, & Böcker, 2012). The earliest research on neural correlates of expectation can be tracked back to 1964. Walter, Cooper, Aldridge, McCallum and Winter (1964) presented a series of irregular or regular pairs of stimuli. In the irregular presentation, stimuli were presented at an interval of 3-10 seconds while regular pairs of stimuli were presented at a regular interval of 1 or 1.5 second(s). The first stimulus (S1) was a click and the second stimulus (S2) was a flash. Participants needed to press a button when they saw the flash. A slow negative deflection was observed over frontocentral scalp sites and reached its maximum around 20 μV just before S2 of the regular pairs. Walter et al.'s findings indicate that the second stimulus in the regular pairs is the key point. The Contingent Negative Variation (CNV) disappeared when S2 was not presented and restored when the second stimulus was re-presented. Therefore, the CNV has been thought to reflect preparation for responses to S2. However, Walter et al. also indicated that the CNV could be observed as long as participants kept being attentive and pressed buttons immediately. This was criticised because the CNV may not only reflect preparation for the responses but also attention to S1 (Järvilehto & Fruhstorfer, 1970). There were at least two components of the observed CNV. One was an earlier frontally distributed waveform that was related to S1 and the other was a late centrally distributed waveform just before S2. The latter one was called a 'readiness potential'. The later potential reflected a preparation for responses to S2. Correlations between RTs of responses to S2 and magnitude of the later waveforms seem to support this idea. The more negative waveforms before S2 were, the faster RTs to S2 were (Brunia & Vingerhoets, 1980; Hillyard, 1969). More recently, CNV is thought to be an index of anticipation timing, i.e. temporal expectation (Nobre, Correa, & Coull, 2007). In the studies investigating temporal expectation, the temporal information of the fore period was manipulated by changing S1. If S1 indicates the fore period is more predictable and short before S2 onset, not only the RTs to S2 are faster but also amplitudes of CNV are larger before S2 (Miniussi, Wilding, Coull, & Nobre, 1999; Zanto et al., 2011). Macar and Vidal (2003) asked participants to compare durations between S1 and S2 with the target duration 2 s. Participants had to press a button to indicate whether the duration was same (yes) or different (no) compared with 2 s when S2 was presented. Magnitude of CNV reached their maximum at the estimated target time point even when the duration was longer than 2 s. This suggests that the peak of CNV amplitudes might not only reflect preparation for actions but also internal evaluation of temporal information. The late CNV amplitudes are also affected by an interaction between motivation and attentional resources. A recent study by Schevernels, Krebs, Santens, Woldorff and Boehler (2014) found that when S1 indicated that the task of S2 was more difficult and monetary reward was given, CNV amplitudes were larger than when S1 indicated the task of S2 was easier. No differences in CNV amplitudes between difficult and easy tasks in no reward trials were found, as there might be no motivation to spend more effort on preparing for a more difficult task. RTs to S2 were faster when the differences of CNV amplitudes between difficult and easy tasks were larger but only in reward trials. These findings suggest that CNV amplitudes reflect both motor preparation and attention to an upcoming event. As an index of preparatory processes, CNV can be influenced by reward in terms of allocating preparatory effort.

It has been suggested that the later component of the CNV reflects a ‘readiness potential’ that is related to motor preparation (Järvilehto & Fruhstorfer, 1970). Differently from CNV which is a component between two stimuli, the ‘readiness potential’ is a component that reflects preparation before a movement whether a stimulus is or is not presented. It is also known as the Bereitschaftspotential (BP), which is termed by Kornhuber and Deecke (1965). BP is also a slow negative shift over central scalp sites, starts from 2 s and shows an increase in negativity very shortly before a movement is made (for a review, see Shibasaki & Hallett, 2006). BP is observed by asking participants to do voluntary movements for example pressing buttons at self-paced rates. The source of BP is suggested to be motor cortex and lateralised depending on response hands (Cunnington, Windischberger, Deecke, & Moser, 2003; Shibasaki &

Hallett, 2006). There is another component related to anticipation or preparation but more reflecting attention rather than action preparation. It is termed as Stimulus-Preceding Negativity (SPN) and was observed in a time estimation task (Damen & Brunia, 1988). Damen and Brunia (1988) asked participants to press buttons once per 20 s. A stimulus was presented 2 s after button presses as a feedback of the time that participants made responses. This distinguished the component of motor preparation from anticipation to a stimulus. The BP was found largest contralateral to the movement side before button pressing while another negative shift (SPN) was found largest over the right hemisphere before the feedback stimulus regardless of the movement side. They suggested SPN reflects a different process from BP due to its scalp distribution. SPN may be the component of attentional preparation for upcoming stimulus. Overall, preparation on actions or upcoming events can be observed by slow negative EEG waveforms preceding actions or stimulus. SPN reflects purely non-movement-related attentional anticipation. BP is a preparatory component on movement. CNV might be an ensemble of BP and SPN that include both anticipation to action and stimulus.

The early studies of CNV mainly used a warning stimulus as S1 to indicate the other stimulus is going to be presented. More recently, an S1 is not merely a warning stimulus but contains information about fore periods or locations of S2. The anticipatory process is from ‘expecting an event’ to ‘knowing what to expect’. Reaction times are significantly faster if a valid cue indicates orientations or temporal positions of a stimulus (Nobre et al., 2007; Posner, 1980). Information of a valid cue might play a role of top-down control in anticipation of an event. It was found that a visual cue that indicates whether colour or motion of an upcoming stimulus needs to be attended could activate brain areas that are responsible for colour and motion processing in the pre-stimulus period (Shibata et al., 2008). It was also suggested that when different category of objects are instructed to be attended, corresponding brain areas are activated even before stimulus onset (Driver & Frith, 2000). In a working memory task, Bollinger, Rubens, Zanto and Gazzaley (2010) used informative cues to indicate categories of upcoming pictures (faces or scenes) compared with non-informative cues. They found that working memory performance was significantly better after informative cues than non-informative cues. In addition, the Fusiform Face Area (FFA) was activated and showed more functional connectivity with only the prefrontal cortex when the category of an upcoming picture was known to be a face. A recent study investigated how anticipation optimises brain activity in working memory updating (Yu, FitzGerald, & Friston, 2013). The dopaminergic midbrain and striatum was activated when high probability of working memory updating was cued. In another working memory study, cue-related activity could predict subsequent working memory performance (Murray, Nobre, & Stokes, 2011). These findings suggest that if pre-stimulus cues contain valid information about properties of upcoming events, both pre-stimulus brain activity and behaviour on upcoming events could be optimised. The valid information about upcoming events might enable imagining processes to optimise brain activity (Driver & Frith, 2000). If any information about the properties of a target is given beforehand, for example, the category of an upcoming picture will be a face, and then imagining a template of a face could activate the FFA.

Unfortunately, in our daily life, sometimes there is no cue to guide our behaviour or brain. Things are happening by series. In this case, it was suggested by Barton, Kuzin, Polli and Manoach (2006) that knowledge about upcoming events in a series could be obtained by maintaining and updating information of rules of the series, which involves executive processes especially working memory. In addition, attention can tune the precision of perceptual expectation. Using Multivariate Pattern Analysis (MVPA), Jiang, Summerfield and Egner (2013) found that attention helped to differentiate neural patterns of expected stimuli from unexpected stimuli. Additionally, using MVPA, Haynes et al. (2007) showed that activity in the Medial PreFrontal Cortex (MPFC) could predict participants' intentions as to which task they were going to do. Most importantly, in that study, participants were asked to choose one of two tasks freely and hold their decision in their minds for variable delays before stimulus onset. MPFC, rather than lateral PFC, patterns predicted later task selection. The MPFC is related to goal-directed information selection processes and this predicted participants' later intentions most accurately. This might be due to participants choosing a task freely, which is different from that a task goal is decided by the experimenter. This finding suggests that preparatory brain activity for a specific task may be under participants' strategic control.

Some brain states can also help later perception or responses if no information is available before the stimulus. For example, a stimulus presented after decreased phase coupling in alpha frequency band is more likely to be perceived (Hanslmayr et al., 2007; Mathewson, Gratton, Fabiani, Beck, & Ro, 2009). Likewise, power increases in pre-stimulus alpha activity over occipital regions can impair later visual discrimination (van Dijk, Schoffelen, Oostenveld, & Jensen, 2008). In a go/ no-go paradigm, larger occipital alpha power before stimulus onset led to more errors in the task (Mazaheri, Nieuwenhuis, van Dijk, & Jensen, 2009). The findings indicate that increases in pre-stimulus alpha activity reduce accuracy in perception. In contrast, performance is better when less pre-stimulus alpha activity is available. Pre-stimulus alpha activity might gate visual stream to play an inhibitory role in perceiving an upcoming visual event (Jokisch & Jensen, 2007; Mazaheri et al., 2009).

1.5 Encoding-related brain activity before an event

The preparatory processes or brain activity before an event do not only influence our perception, attention or motor responses but also influence higher-level cognitive processes such as working memory (Bollinger et al., 2010), task-switching (Poljac & Yeung, 2014) or problem-solving (Kounios et al., 2006). In the memory domain, Tulving (1983) proposed that an appropriate cognitive set supports to treat an event as a retrieval cue to retrieve stored episodic information. The development of neuroimaging techniques allow to study the neural correlates of this cognitive set. Neural activity preceding an event influences the efficiency with which information is retrieved from long-term memory storage (Rugg & Wilding, 2000; Wilding & Ranganath, 2012). A recent study found that pre-stimulus theta power increase leads to correct source memory retrieval (Addante, Watrous, Yonelinas, Ekstrom, & Ranganath, 2011). From the first study on brain activity before an event that predicts memory encoding (Otten et al., 2006), there has been a good number of studies on investigating how neural correlates before an event influence memory formation.

Using the subsequent memory paradigm, it has been demonstrated that the brain activity elicited by an event is important to memory encoding of that event. Otten et al. (2006) found that neural activity elicited by a cue before an event could also predict subsequent memory performance. In their study, ERP waveforms elicited by the pre-stimulus cue were categorised by subsequent memory performance. The waveforms before subsequently recognised words were significantly more negative than the waveforms before subsequently forgotten words over frontal scalp sites. This frontal negative-going pre-stimulus subsequent memory effect was only found after a cue that indicated a semantic encoding task needed to be done on the upcoming word. In a later fMRI study, a monetary incentive cue was presented before a target event to indicate reward value if the event was memorised (Adcock et al., 2006). Intervals between a reward cue and a target were jittered between 2.5 and 6.5 s to avoid BOLD signals overlap across trials. It was found that only after high reward cues, activation in hippocampal areas before target event onset predicted later memory performance. An

MEG study showed a pre-stimulus encoding-related theta power increase effect regardless of whether the encoding task was semantic or non-semantic (Guderian et al, 2009).

What is the functional role of encoding-related pre-stimulus activity? In the study by Otten et al. (2006), such encoding-related pre-stimulus activity was evident only when pre-stimulus cues indicated a semantic encoding task about upcoming words. Therefore, they suggested the frontal negative-going pre-stimulus subsequent memory effect reflected a semantic preparatory process. Participants may have used the information of the cue to engage a more elaborated semantic preparation for later successful formation of memory representations. Further, this frontal negative-going pre-stimulus subsequent memory effect is not modality-specific (Otten et al., 2010). Otten et al. (2010) used cues to indicate the modality of upcoming words. In a supplementary result figure from Otten et al. (2006) study, a visual cue signalling a presentation of an auditory word elicited larger P2 amplitude than a visual cue signalling a presentation of a visual word. Switching modalities between visual cues and auditory words requires more attention, which may impair preparation for encoding upcoming auditory words. Therefore, Otten et al. (2010) kept the modalities of cues and stimulus consistent. As a result, frontal negative-going pre-stimulus subsequent memory effects were found in both auditory and visual conditions. Such effects may reflect a wide role of semantic preparation in forming a verbal memory representation. This frontal negative-going pre-stimulus subsequent memory effect is also found when using free recall test (Galli et al., 2012; 2013). In both studies, the effects were evident only when there was opportunity to employ more elaborate strategies to memorise words, which suggests a role of the frontal negative-going pre-stimulus subsequent memory effect in semantic preparation.

Similar to encoding-related activity after an event, encoding-related activity before an event might be qualitatively different if different anticipatory processes are engaged. In an ERP study, Gruber and Otten (2010) used monetary reward cues to indicate reward value when a word was memorised. A more sustained positive-going widespread scalp distributed pre-stimulus subsequent memory effect was found only when the cue indicated a high reward value. This suggests that high monetary motivated preparation for verbal memory formation might be a different mechanism from semantic preparation. High monetary motivation also activated dopaminergic midbrain and MTL before stimulus onset and the activations predicted better subsequent memory performance (Adcock et al., 2006). In addition, high monetary motivation increased pre-stimulus theta power to modulate memory encoding (Gruber et al., 2013). Only when pre-stimulus cue indicated high reward value, frontal theta power increased before remembered words. Positive-going pre-stimulus subsequent memory effects were also found when anticipating an emotionally negative scene (Galli et al., 2011; 2014). Pre-stimulus cues indicated the valence of upcoming pictures. ERP waveforms elicited by a cue indicating that the upcoming picture would be an emotionally negative scene were significantly more positive-going before remembered pictures than forgotten pictures. It was suggested the preparatory processes engaged in encoding of a negative picture might be similar to the preparatory processes of memorising a high rewarded word as reward and emotion might share similar motivational mechanisms (Galli et al., 2011). Galli et al. (2011) also suggested that the frontal negative-going pre-stimulus subsequent memory effect probably reflects different preparatory processes that are more cognitively oriented. In an ERP study, Padovani, Koenig, Brandeis and Perrig (2011) directly compared semantic preparation and emotional preparation. A pre-stimulus cue indicated whether participants needed to make semantic or emotional decisions about upcoming words. A frontal negative-going pre-stimulus subsequent memory effect was found before semantic decisions while a more central positive-going pre-stimulus subsequent memory effect was found before emotional decisions. The results suggest there might be multiple preparatory neural mechanisms supporting memory formation.

The above findings indicate that encoding-related pre-stimulus activity might not reflect random fluctuations. Instead, such activity may reflect a beneficial state for later encoding, similar to the role of pre-stimulus activity in the perception domain (Busch, Dubois, & VanRullen, 2009; Hanslmayr et al., 2007; Mathewson et al., 2009). In contrast to that domain, however, encoding-related pre-stimulus activity might be under strategic control (Galli et al., 2013; Gruber & Otten). Strategic control is often recruited in executive functions such as prospective memory, task switching or the monitoring of conflicts when cognitive resources are limited (Bartholow et al., 2005; Botvinick, Braver, Barch, Carter, & Cohen; Braver, Reynolds, & Donaldson, 2003; MacDonald, Cohen, Stenger, & Carter, 2000; McDaniel & Einstein, 2001). Strategic control should be self-initiated by an individual and effortful (MacDonald et al., 2000; McDaniel & Einstein, 2001). In the domain of long-term memory, Kuhl and Wagner (2009) suggested that strategic control processes help resolve conflicts between memory representations and irrelevant representations. The control processes play a role in selecting what needs to be encoded, stored and retrieved (Benjamin, 2007). For example, strategic processes can be reflected in time allocation when the difficulty of to-be-encoded items is manipulated (Son & Metcalfe, 2000). More study time is allocated to more difficult items. In addition, the strategic selectivity in encoding can be reflected by different values of to-be-encoded items (Castel, Benjamin, Craik, & Watkins, 2002). Participants tend to remember more words with higher point values to get higher sum scores. These findings suggest that participants strategically allocate limited cognitive resources to encode items to adjust performance.

In a similar vein, encoding-related pre-stimulus activity does not seem to reflect automatic processes. Such pre-stimulus activity is only found under certain circumstances, such as semantic preparation or preparation for encoding negative scenes. This suggests that encoding-related pre-stimulus activity might reflect effortful processes. Encoding-related pre-stimulus activity is also sensitive to the availability of cognitive resources. The activity is engaged in helping memory encoding only when sufficient cognitive resources are available (Galli et al., 2013). When participants have to switch modality between pre-stimulus cues and to-be-encoded items, no significant pre-stimulus subsequent memory effect was found in encoding auditory items (Otten et al., 2006). When the modality was consistent between pre-stimulus cues and to-be-encoded items, pre-stimulus activity helped to encode auditory words (Otten et al., 2010). Finally, preparatory processes are self-initiated by an individual. Pre-stimulus activity is engaged when preparing for encoding a word in a high, but not low, monetary reward condition (Gruber & Otten, 2010). Therefore, not only processes after a stimulus are controlled strategically, but also the processes before a stimulus to aid successful encoding.

Some fMRI studies found that the critical brain regions for pre-stimulus subsequent memory effects depend on the information that pre-stimulus cues hold. Uncapher et al. (2011) found that activation of the dorsal parietal cortex preceding stimulus predicts successful encoding by using valid spatial pre-stimulus cues. Pre-stimulus activity in the amygdala is also positively correlated with later recognition performance when a cue informs of an aversive upcoming picture (Mackiewicz et al., 2006). Most fMRI studies showed the MTL was more activated prior to remembered event (Adcock et al., 2006; Mackiewicz et al., 2006; Park & Rugg, 2010). An MEG study (Guderian et al., 2009) and an iEEG study that recorded directly from the hippocampus (Fell et al., 2011) both have observed increases in theta power before word onset associated with successful memory encoding. Both of the two studies suggest that the MTL theta activity reflected contextual activation before event onset. Larger theta power in the MTL could pre-activate information of episodic context for binding with the later item (Fell et al., 2011; Guderian et al., 2009).

Yoo et al. (2012) shows that the Parahippocampal Place Area (PPA) was less activated before remembered scenes than forgotten scenes. Then, they presented a scene after the PPA BOLD signals were larger or less than a pre-defined reference signal. Memory performance for the scenes presented after less PPA activity was significantly better than for the scenes presented after larger PPA activity. This study suggests that memory performance can benefit if an appropriate neural context is in place. However, there have been very few studies describing how memory benefits from appropriate preparation. Hanslmayr, Leipold and Bäuml (2010) used a think / no-think paradigm and found that when pre-stimulus cues informed the think / no-think task in advance, the proportion of forgotten items following ‘no-think’ cue were significantly larger than forgotten items presented with ‘no- think’ cue spontaneously. Nevertheless, they did not find a better performance for remembering when there was pre-stimulus cue due to ceiling effect of the task. There are three studies showing better memory performance benefitted from informative category cues, valid spatial cues or a longer pre-stimulus interval (Bollinger et al., 2010; Summerfield & Mangels, 2006; Uncapher et al., 2011). They all suggest this is due to more attention to upcoming events modulated by top-down control. Galli et al. (2013) found pre-stimulus subsequent memory effects only when sufficient cognitive resources were available before encoding a word. However, overall memory performance did not show any advantage when sufficient cognitive resources were available during preparation. These results suggest that overall memory performance is not necessarily improved when pre-stimulus activity is engaged before encoding. If encoding-related activity before an event is a determinant of successful retrieval, then memory performance should also depend on interactions between encoding-related activity before and after an event, consolidation and retrieval.

In summary, so far at least two kinds of pre-stimulus ERP activity have been found to predict successful encoding. Frontal negative-going pre-stimulus subsequent memory effect is thought to reflect semantic preparation. Positive-going widespread pre-stimulus subsequent memory effect may suggest motivational mechanisms. The critical brain region for encoding-related pre-stimulus activity is suggested to be the hippocampus. Only a few studies show differences in overall memory performance between informative cues and non-informative cues or between with pre-stimulus cues and without pre-stimulus cues, which suggests that presence of encoding-related pre-stimulus activity does not have to enhance later memory performance as other memory stages may compensate later overall memory performance (Galli et al., 2013).

1.6 Neural correlates of retrieval

Using a variety of event-related neuroimaging methods, the neural correlates of successful episodic retrieval are mainly investigated with the ‘old / new’ paradigm (Hanslmayr et al., 2012; Rugg, 1995; Vilberg & Rugg, 2008; Wilding & Ranganath, 2010). The difference between neural activity elicited by correctly recognised studied items and correctly judged unstudied items is called the ‘old/new effect’ or retrieval-related activity. Sanquist et al. (1980) were the first group of researchers who reported an ERP old / new effect. They found that correctly recognised old items elicited significant larger positive waveforms than correctly rejected items over a parietal electrode site in a late post-stimulus time window around 450 – 750 ms. Wilding and Rugg (1996) showed that this late parietal old / new effect was associated with retrieval of source. The effect was evident only when the gender of voices of old words during encoding was correctly judged. The effect between 500 and 800 ms after words onset was over left parietal sites. This effect is therefore termed the left-parietal ERP old / new effect (Rugg, 1995). It has been widely supported that the left-parietal ERP old / new effect might be an index of recollection. As an index of recollection, the amplitudes of the left-parietal old / new effect have been positively correlated with number of correct source judgments (Wilding, 2000). In addition, the effect has been found to be associated with Remember judgments but not Know judgements, or was significantly larger for Remember than Know judgments in the Remember / Know paradigm (Duarte et al., 2004; Düzel, Yonelinas, Mangun, Heinze, & Tulving, 1997). These findings suggest that the left-parietal ERP old / new effect might be related to the amount of information that can be retrieved from episodic memory.

In the study by Wilding and Rugg (1996), they found another positive-going old / new ERP effect in a later time window and over more frontal and right-lateralised scalp sites compared to the left-parietal old / new effect, which was also associated with correct source judgment. The time window of this right frontal old / new effect was from 800 ms until 1400 ms after stimulus onset. As this time window was quite close to the end of the recording epoch they used in the study, they suggested that the effects might reflect post-retrieval processes that influenced organisations of information in previous events. However, not all the studies showed a consistent result for the right frontal old/ new effect. For example, Senkfor and Petten (1998) did not find that the right frontal old/ new effect was restricted to correct source retrieval. Further, confidently recognised items without recollection have been found to elicit a right frontal old / new effect (Woodruff et al., 2006). Hayama, Johnson and Rugg (2008) showed that right-frontal old / new effects were robust for both episodic source retrieval task and semantic task on top of an old / new judgment. Therefore, compared to the left-parietal old / new effect, the late right-frontal old / new effect has not been widely agreed to be related to episodic recollection.

According to dual-process models, there should be a separate neural network supporting familiarity-based recognition memory. Rugg et al. (1998) observed an earlier old / new effect before left-parietal old / new effect over frontal scalp sites. This effect started from 300 ms after stimulus onset until 500 ms. In the study, the authors also compared studied words that attracted correct judgments with new words that attracted correct judgments as a function of levels of processing. They found that from 300 ms to 500 ms, the old / new effects did not differ in levels of processing during study phase while after 500 ms, the correctly recognised words of deep processing elicited significantly more positive-going waveforms than the waveforms elicited by both correctly judged new items and correctly recognised items of shallow processing. Therefore, they suggested that the early mid-frontal old / new effect could reflect familiarity of item recognition. Later, there are more studies supporting the idea that this mid-frontal old / new effect is different from left-parietal old / new effect in its functions and could thus be an index of familiarity (Azimian-Faridani & Wilding, 2004; Curran, 2000; Curran & Cleary, 2003; Woodruff et al., 2006).

Functional MRI studies have also suggested that recollection and familiarity depend on different brain networks. The main idea is that increased hippocampal activity reflects recollection but not familiarity, while familiarity is positively correlated with activation of the perirhinal cortex (Diana et al., 2007). In addition, the PFC is a critical region that is thought to contribute to recollection (Simons, Owen, Fletcher, & Burgess, 2005; Skinner, Grady, & Fernandes, 2010; Yonelinas, 2002). However, a recent study that used five-way judgments to dissociate recollection and high-confident familiarity suggested that previous findings on the role of the PFC in recollection might be attributed to high confidence in familiarity (Yonelinas et al., 2005). In the study, they also proposed a network of recollection that the PPC contributes to recollection of episodic association. There is a view about the role of the PPC suggesting that it is activated by both recognised old items and false alarms compared to correct rejections and missed items (Wagner, Shannon, Kahn, & Buckner, 2005). Thus, the PPC might contribute to recollection by activating subjective experience of familiarity, which could lead to false memories.

Similarly to ERP correlates of familiarity and recollection, theta power elicited by ‘Know’ responses was larger than ‘Remember’ responses in the early time window of retrieval, while theta power was larger for ‘Remember’ responses in a later time window than ‘Know’ responses (Klimesch et al., 2001). By using a source memory paradigm, Gruber et al. (2008) found that successful source retrieval was associated with larger theta activity while larger gamma activity was related to successful item memory but not source memory. Theta activity is thought to be crucial for recollection (Düzel, Penny, & Burgess, 2010). Recently, it was found that larger theta power could predict successful source retrieval before a retrieval cue, which suggests that a better brain state for source retrieval may be reflected in a larger magnitude of theta oscillations (Addante et al., 2011).

1.7 Research aims

In this doctoral thesis, I mainly investigate the functional role of encoding-related pre-stimulus activity. At least two kinds of encoding-related pre-stimulus ERP activity have been found (e.g. Galli et al., 2011; 2014; Gruber & Otten, 2010; Otten et al., 2006; 2010). These two kinds of pre-stimulus ERP activity are qualitatively different depending on the preparatory processes. Semantic preparation is reflected by a frontal negative-going pre-stimulus subsequent memory effect. A widespread positive-going pre-stimulus subsequent memory effect is thought to indicate motivational processes.

Although there is evidence of qualitatively different pre-stimulus effects, it is currently unknown whether the same pre-stimulus effect can be invoked to different degrees. In other words, it is unknown whether encoding-related activity before event onset can be graded in nature.

In the previous studies, effects have been found in one condition but not another, depending on the type of task or stimulus indicated by a pre-stimulus cue. For example, in Otten et al. (2006), a task cue indicated whether the encoding task of an upcoming word was semantic or non-semantic in nature. A pre-stimulus frontal negative subsequent memory effect was only observed when the cue indicated a semantic encoding task. The absence of a pre-stimulus subsequent memory effect in the non-semantic condition might be explained by the lack of engaging semantic preparatory processes. A question of interest is whether, when semantic preparatory processes are needed in different conditions but to varying degrees, pre-stimulus activity will similarly vary in magnitude. If so, this would strengthen an interpretation of pre-stimulus activity as reflecting an active preparatory nature of pre-stimulus activity. In support of this idea, Gruber and Otten (2010) demonstrated that pre-stimulus activity can be strategically engaged in supporting encoding. In the study, pre-stimulus activity was only engaged to form a new memory representation when a high monetary reward was given. The high monetary reward condition was also associated with better memory performance. On the assumption that high monetary rewards encourage participants to use more efficient encoding-related processes, the findings suggest that engaging pre-stimulus activity that benefits encoding is, at least to some extent, under an individual’s control. If this interpretation is correct, individuals may be able to engage pre-stimulus processes to different degrees depending on the circumstances. In turn, this would be expected to lead to subsequent memory effects of different amplitudes (Otten & Rugg, 2005). Therefore, in this doctoral thesis, the research question is how amount of advance information influences encoding-related pre-stimulus activity to assess whether the preparatory processes that benefit encoding can be engaged to different degrees.

Pictures of daily objects were used as stimuli. First, pictures are found to have different subsequent memory effects from verbal materials (for a review, see Wagner et al., 1999). Pre-stimulus subsequent memory effects for pictures might also differentiate from those seen for verbal materials, which might suggest a perceptual preparatory process as pictures contain more perceptual details than verbal materials. To my knowledge, there have only been two EEG studies that investigated pre-stimulus encoding-related activity for pictures and their focuses are how emotional control contributed to encoding-related activity before emotional scenes (Galli et al., 2011; 2014). Second, compared to verbal materials, pictures hold more perceptual information than words. Therefore, the amount of perceptual information could be manipulated to see whether the neural correlations of preparation are accordingly varied. To dissociate encoding-related activity before and after an event efficiently, EEG was the neuroimaging technique for investigating the neural correlates of successful memory formation in the thesis, which is briefly introduced in Chapter 2.

This thesis addresses three main questions: first, is pre-stimulus encoding-related activity influenced by amount of advance information? Chapter 3 reports three ERP experiments to address this question. The first experiment used detailed grey-scale photos and perceptually impoverished line drawings as stimuli. Pre-stimulus cues indicated the amount of perceptual information to prepare for encoding. The letter ‘P’ signalled the presentation of a detailed grey-scale photo, an ‘O’ a perceptually impoverished outline, and an ‘X’ that either could occur. All advance information concerned the perceptual nature of a stimulus. If perceptual preparatory processes are under strategic control, participants may be able to use the advance information to strategically adjust encoding-related preparatory activity to be larger when more perceptual information is available to guide preparation (i.e. prior to a photo rather than impoverished outline). Bollinger et al. (2010) suggested that when a face was expected to be encoded, face-related regions (FFA) were functionally connected with a frontoparietal network of region. Therefore, it would be expected that anticipation to a perceptually rich picture would activate more perceptual preparatory processes than anticipation to a perceptually impoverished picture. When a pre-stimulus cue is non-informative about the amount of to-be-encoded perceptual information, the preparatory process might be insensitive to the amount of perceptual information. One possible expectation could be that participants might not be able to recruit preparatory activity for encoding in that condition.

As discussed above, when cognitive resources are limited, strategic control processes may be recruited to help allocate resources for optimising actions. To optimise encoding processes, more resources must be allocated for more preparation. Less preparation needs less cognitive resources. Therefore, the degree in preparatory processes cannot only be manipulated by the amount of information to prepare, but also by the opportunity to prepare. To manipulate the opportunity available for preparation, different amounts of preparation time were used for preparing for encoding grey-scale photos in the second experiment. Advance information indicated the amount of preparation time. The letter ‘L’ indicated that participants had a relatively long preparation time (3 s). An ‘S’ indicated a preparatory interval of 1.5 s. The letter ‘N’ was a non-informative cue, which could be followed by either a 1.5 or 3 s interval. As to-be-encoded stimuli were always grey-scale photos, the same preparatory processes should be engaged in preparing for encoding the pictures in all three cases. The advance information was expected to guide preparatory activity to strategically engage in memory encoding. ‘L’ was expected to elicit larger encoding-related preparatory activity than ‘S’. Galli et al. (2013) suggested that sufficient cognitive resource is important for developing encoding-related pre-stimulus activity, which means preparation for memory encoding might depend on the opportunity to engage such pre-stimulus activity. Therefore, it would be expected that a long pre-stimulus interval gave more opportunity to employ preparation for encoding an upcoming event. Differently from the non-informative cues used in Experiment 1, here, the non-informative cue condition would be informative once the short preparatory interval elapsed. Therefore, participants might also be able to prepare even if the cue is non-informative in the present case. Uncapher et al. (2011) found that pre-stimulus dorsal parietal cortex was activated only when a pre-stimulus cue validly signalled the location of an upcoming picture. More importantly, such activity was positively correlated with later encoding success on the objects that were presented after valid location cues. Different neural networks in ventral parietal cortex were involved in bottom-up attention in the invalid cue condition. This suggests that the pre-stimulus subsequent memory effects after a cue signalling the cue length might be qualitatively different from the pre-stimulus subsequent memory effects after a non-informative cue.

The final ERP experiment attempted to induce different preparatory brain states by manipulating advance information of pre-stimulus cues. The pre-stimulus cues indicated the Delayed Match-to-Sample (DMS) task participants needed to prepare. The conjunction DMS task is suggested to involve the hippocampus, which participants need to remember a combination of an object and its location in a short delay (Olson, Page, Moore, Chatterjee, & Verfaellie, 2006). In contrast, the feature DMS task that requires participants to remember only a location of an object does not involve the hippocampus. In half of the trials, a critical stimulus, a colour image of an object was presented 3 s into a 5 s preparatory interval. As mentioned above, pre-stimulus hippocampal activity can predict successful episodic memory encoding (e.g. Park &

Rugg, 2010). If preparation for the conjunction DMS task can activate the hippocampus, it would be expected that a colour image of an object that was presented after the preparation was more likely to be remembered in a later recognition memory test than a colour image of an object that was presented after preparation for the feature DMS task.

The second question is how amount of advance information influences encoding-related theta and alpha oscillatory states prior to stimulus onset. The three EEG experiments were analysed in the time-frequency domain to address this question in Chapter 4. The third question is the relationship between encoding-related anticipatory processes and overall memory performance. Galli et al. (2013) demonstrated that encoding-related pre-stimulus activity is influenced by cognitive resources before an event. However, the overall memory performance was not affected by whether cognitive resources before an event were sufficient to engage pre-stimulus activity for encoding. Galli et al. (2013) suggested other memory stages such as consolidation or retrieval might compensate weaker memory representations during encoding. In Chapter 5, two behavioural experiments (Experiment 4 and 5) manipulated cognitive resources during retrieval to prevent the engagement of the compensatory mechanisms during retrieval. During encoding, the design was the same as the second ERP experiment. If longer preparation time enables more opportunity to engage pre-stimulus activity for encoding processes, then the memory representations after longer preparation time should be stronger than the memory representations after shorter preparation time. It would be expected if there was no sufficient cognitive resources to engage such compensatory mechanisms during retrieval, weaker memory representations were more likely to be unsuccessfully retrieved than stronger memory representations.

1.8 Summary of introduction

Episodic memory success depends on encoding, consolidation, retrieval and interactions between these processes. In the laboratory, episodic memory is usually investigated via a study phase and test phase. Brain activity can be recorded during study and / or test phase. The brain activity can be categorised by later test performance. The subsequent memory paradigm refers to brain activity recording during the study phase, categorised by subsequent memory performance. The subsequent memory paradigm is widely used to investigate episodic memory encoding. Memory retrieval is investigated via the old / new paradigm. Brain activity during the test phase is categorised by separating correct old and new judgments. The MTL is a crucial brain area for both encoding and retrieval. A positive-going ERP subsequent memory effect is usually found for verbal materials. There are two main ERP old / new effects. One is over mid-frontal scalp sites and seen in a time window around 300 – 500 ms after stimulus onset. This effect is thought to reflect familiarity. The other effect is over left parietal scalp sites in the 500 – 800 ms time window, and thought to reflect recollection. Recently, oscillatory brain activity has attracted attention in its cognitive meaning. Theta, gamma, alpha and beta are the main frequency bands that have been suggested to be important for memory formation and retrieval.

By using the subsequent memory paradigm, it has become clear that not only activity after, but also activity before, an event can support memory formation. At least two types of pre-stimulus encoding-related ERP activity have been found so far. A frontal negative-going pre-stimulus subsequent memory effect is thought to reflect semantic preparation. A positive-going widespread pre-stimulus subsequent memory effect may instead suggest motivational mechanisms. It has been demonstrated that such encoding-related preparatory activity might not reflect random fluctuations, but active strategic control processes. The critical brain region for the encoding-related preparatory processes is suggested to be the hippocampus. However, some studies suggest that hippocampal activity might not be specific to encoding operations, which argues against an active role of encoding-related pre-stimulus activity. Moreover, few studies show that the presence of encoding-related pre-stimulus activity enhances later overall memory performance. The exact functional roles of the encoding-related pre-stimulus activity are still largely unknown. In this doctoral thesis, to investigate whether encoding-related pre-stimulus activity is graded by the degree in preparatory processes, the amount of advance information was manipulated in the first two EEG experiments. The third EEG experiment aimed to investigate if there is a certain brain state conducive to episodic memory encoding. The other two behavioural experiments aimed to find a relationship between encoding-related preparatory processes and overall memory performance.

Chapter 2: General methods

2.1 Studying the relationship between the brain and cognitive processes with electroencephalography

In this doctoral thesis, electroencephalography (EEG) will be the main method to investigate the relationships between cognitive functions and brain activity. Electrical potentials are generated by activations of large populations of neurons. When placing a couple of electrodes on the scalp, the electrical potentials can be measured by the differences between one electrode and a reference electrode. The voltage differences over time are referred to as EEG signals (Coles & Rugg, 1995; Gazzaniga, Ivry, & Mangun, 2009). In 1875, Caton (1875) first reported electrical brain activity from the skulls of mammals, which paved the way for the future research on rhythmic activity in EEG. In 1929, Berger first reported rhythmic EEG activity from the human scalp (Bastiaansen, Mazaheri, & Jensen, 2012). From then on, EEG has become a popular functional neuroimaging technique to investigate how neural activity supports cognitive processes. The difference in voltages between an electrode site and a reference site measured from the scalp is a summation of activity of a large group of neurons that are activated synchronously and share similar spatial directions (Coles & Rugg, 1995). In order to generate currents that can be detected on the scalp, the neurons have to be aligned in a parallel direction. If the directions of the neurons are random, the current flow can be cancelled out from each other. A dipolar field with a group of parallel neurons is known as ‘open fields’ (Coles & Rugg, 1995). However, if the sources of electrical fields are too far away from the scalp such as the thalamus, even ‘open fields’ might not be able to be detected on the scalp (Coles & Rugg, 1995). It is suggested that post-synaptic potentials of cortical pyramidal neurons instead of axonal action potentials are the main generators of scalp EEG signals because pyramidal neurons have a larger population and more sustained synchronisations in the same geometrical orientations than axons (Coles & Rugg, 1995; Luck, 2005).

The amplitudes of scalp EEG signals are usually in the order of microvolts. To convert such tiny analog signals into digital form, EEG recording systems always have amplifiers. An Anolog-to-Digital (AtoD) converter transforms analog waveforms into digits that can be stored and manipulated in the computer. The digital resolution of an AtoD converter is a power of 2 (Picton et al., 2000). For example, the resolution of the AtoD converter used in this doctoral thesis was 12 bits, which means the analog EEG voltages are represented by 2^{12} or 4096 values. The gain of an EEG recording system can be calculated by the factor of the amplification and the resolution of the AtoD converter (Picton et al., 2000). For example, if the amplification factor is 20,000, the range of the AtoD converter that signals are blocked is ±5 V, the resolution of the system can be calculated as 10/20,000/4096, which is 0.122 μV/bit. The digital data points can be reconstructed into waveforms that reflect real voltages of EEG signals.

As digital data points that are converted by an AtoD converter are discrete, how many data points can be converted from a continuous EEG waveform depends on how many samples there are in one second, that is, the sampling rate. According to the Nyquist theorem, the sampling rate must be at least twice the highest frequency in the data (Luck, 2005). For example, if the highest frequency of interest is 35 Hz (within Gamma frequency band) then the sampling rate must be more than 70 Hz.

However, there might be some high frequency noise such as 50 Hz line noise while sampling. In that case, a low-pass filter will help to cut off the noise higher than a selected frequency without aliasing problem caused by slowing down the sampling rate (Luck, 2005). At the same time, some low frequency artefacts such as skin potentials caused by sweat might result in saturation of the digital signals. To avoid such problems, a high-pass filter can be used to cut off the drifts slower than a selected frequency.

However, filters might lead to distortion in amplitudes and latency of the data (Luck, 2005). In the studies in this doctoral thesis, online band pass analog filters were between 0.01 Hz and 35 Hz, which removes high-frequency noise such as 50 Hz but might still leave some muscle artefacts and some slow drifts. However, these band pass filters allow looking at slow modulations and most ERP activity such as subsequent memory effects and oscillatory activity in theta (4 - 8 Hz) and alpha (8 - 12 Hz) frequency bands.

In cognitive neuroscience research, EEG activity is recorded while human subjects do tasks that include presenting a series of stimuli. Usually, EEG activity will be extracted into epochs. Each epoch might be time-locked to the stimulus and segregated by the manipulations of the tasks or the stimulus. Such event-related EEG signals can be analysed by two approaches: ERP and time-frequency analyses. Compared to fMRI, EEG has poorer spatial resolution and it is hard to interpret where the intracranial sources are. What is observed on the scalp is the summation of neural activity from different parts of the brain. However, EEG has a temporal resolution in milliseconds, which allows dissociating brain activity before a stimulus from that after the stimulus (Otten et al., 2006; Rugg et al., 2002; Wagner et al., 1999). In this doctoral thesis, pre-stimulus and post-stimulus encoding-related activity will be investigated by EEG and analysed with both ERP and time-frequency approaches. ERPs have been widely used to investigate cognitive processes since the 1960s. Recently, attention to oscillations has increased (for a review, see Bastiaansen et al., 2012). Both approaches will be generally introduced in this chapter.

2.2 Event-related potentials

In the ERP approach, many segregated epochs are averaged depending on experimental manipulations to exclude the background noise of EEG signals that are random fluctuations and not related to the cognitive tasks (Rugg & Coles, 1995). To increase the signal-to-noise ratio, there usually need to be sufficient EEG trials in each experimental condition. The signal-to-noise ratio increases as a function of the square root of the trial number (Luck, 2005). The averaged waveforms are the ERP, which are thought to represent changes attributable to the experimental manipulations over time. Taking the subsequent memory effect as an example, ERP waveforms belonging to subsequently remembered stimuli might have different deflections than waveforms that belong to subsequently forgotten stimuli over different time courses.

In order to interpret the relationships between cognitive processes and ERP waveforms, one can use prior knowledge such as ERP components. An ERP waveform is represented by positive and negative deflections of different amplitudes across time series. ERP components are used to decompose such continuous waveforms into discrete parts in terms of polarity, amplitude and latency to try to associate them with underlying cognitive or neural processes (Kappenman & Luck, 2012). Although there have been many arguments on defining the term ERP component (for reviews, see Kappenman & Luck, 2012; Luck, 2005; Coles & Rugg, 1995), in practice an ERP component can be defined in terms of its specific polarity, duration, scalp distribution and sensitivity to experimental manipulations (Donchin & Heffley, 1978). For example, as discussed above, the CNV is a component that indicates anticipation to an upcoming event. It was first defined in a study by Walter et al. (1964) as a negative deflection over frontocentral scalp sites before S2 when S1 is a warning stimulus. Apart from the CNV, three components that are thought to be related to attention are also of interest. When comparing the cue-related activity elicited by informative or non-informative cues irrespective of memory performance, the three components N1, P2, and P300 can provide evidence about whether the processing of informative cues attracts more attention than the processing of non-informative cues, which can indicate participants’ overall preparation for an upcoming stimulus guided by more amount of advance information. The N1 is a component that has a negative peak elicited by a stimulus and is thought to have many subcomponents (for a review, see Näätänen & Picton, 1987). In this doctoral thesis, the N1 component is defined as a negative deflection and considered to reflect visual selective attention (Mangun, 1995). In a time window after the N1 component, a positive deflection over posterior scalp sites also reflects attention to the visual stimulus. This is termed the P2 component (Kotchoubey, Wascher, & Verleger, 1997). The P300 component is defined by an 'oddball' paradigm, which the P300 is a large positive deflection elicited by a salient stimulus compared with another identical stimulus within an experimental series (Coles & Rugg, 1995). The P300 component is suggested to reflect higher-level cognitive processes such as context updating (Donchin, 1981) or the level of effort devoted to a task (Isreal, Chesney, Wickens, & Donchin, 1980).

Although it seems difficult to define an ERP component, ERP components provide a way to bridge across experiments (Otten & Rugg, 2005). If no prior knowledge about ERP components is available, the interpretations between cognitive processes and ERP waveforms can be made by considering amplitudes, polarities, scalp distributions and time courses (Otten & Rugg, 2005). Differences in amplitudes of ERP waveforms often reflect the same cognitive processes but engaged in quantitatively different ways. For example, larger P300 amplitudes may reflect greater updating processes. However, if the amplitude differences are in reversed polarities, it might indicate some qualitative differences as the reversed scalp polarities might be generated from different neural sources (e.g. Otten & Rugg, 2001b). In addition, differences in scalp distribution point to qualitative differences in cognitive processes. Along with the information from the time course, the differences between two ERP waveforms can be related to a certain cognitive process (Otten & Rugg, 2005). For example, retrieval processes can be reflected by differences between the ERP waveforms elicited by correctly remembered old items and correctly rejected new items, which are called old / new effects (Rugg, 1995). The start of old / new effects, as any ERP differences, indicates an upper bound on differences occurring in underlying processes of discriminating a remembered item from new items. As discussed in the previous chapter, two old/ new effects differ in time and scalp distribution. The first old / new effect is between 300 and 500 ms after event onset and largest over frontal scalp sites. The second old / new effect is between 500 and 800 ms and largest over left parietal scalp sites. The two effects reflect the involvement of different neural patterns underlying recognition memory over time due to their different time courses and scalp distributions. The two effects indicate that there may be qualitatively different cognitive processes that happen at different times in recognition memory (Otten & Rugg, 2005).

There are usually two ways to quantify ERP amplitudes. Peak amplitude measures consist of finding the maximum amplitude of a waveform in a defined time window. The other one is averaging the amplitudes in a defined time window of the waveform (Luck, 2005). The ERP analyses in this doctoral thesis used the mean amplitude method to quantify the ERPs. Peak amplitude measures assume that ERP components are reflected by maximum voltage values. Therefore, when measuring an ERP component, the peak amplitude measures usually need to involve a relatively wide measuring time window because the latency of a peak varies across subjects, electrode sites or conditions (Luck, 2005). The mean amplitude method does not measure the peak amplitude, but the average amplitude in a specified interval. This type of measurement is less affected by noise in the signal, although at the expense of being able to assess latency differences across conditions. Use of a relatively narrow time window can remedy this problem to some extent. Care should be taken that the selection of a time window is justified by existing knowledge, and not arbitrary and without justification since this has been shown to lead to biased statistics (Kilner, 2013). As different temporal intervals were used in Experiment 1 from Experiments 2 and 3, the chosen time windows will be introduced in each *Results* section in Chapter 3.

The statistical analyses of subsequent memory effects or other comparisons were done via analyses of variance (ANOVA). When an ANOVA was done for any factor with more than two levels, the Greenhouse-Geisser correction was incorporated to avoid violations of sphericity (Keselman & Rogan, 1980). The Greenhouse-Geisser correction can decrease the degrees of freedom when there are more than two levels in one factor. Then the p value is increased to protect the analyses from type I errors caused by nonsphericity. The results of this thesis will report the corrected degrees of freedom and p values when ANOVAs were done with factors more than two levels. In addition, the data were scaled by the max/min method to remove overall amplitude differences between conditions (McCarthy & Wood, 1985). McCarthy and Wood (1985) suggested that a significant interaction between scalp sites and experimental conditions does not necessarily indicate that the effects in the two experimental conditions are qualitatively different due to different scalp distributions. Such significant interactions might be caused by overall larger amplitudes in one condition than amplitudes in the other condition because EEG data are multiplicative and ANOVAs are additive. Therefore, McCarthy and Wood (1985) suggested scaling the data by the data point value – minimum value / the maximum value – the minimum value. If the interaction between experimental condition and electrode site for the scaled data is significant, at least the significant interaction is not confounded by an overall amplitude difference. In that case, it can be concluded the effects in the two experimental conditions have different scalp distributions. The results of this doctoral thesis reported ANOVAs for the original data and scaled data.

2.3 Time-frequency analyses

Given that the first report of human scalp rhythmic EEG activity was published in 1875 by Caton, it seems to be a long time that oscillatory brain activity has re-attracted interest in its relation with cognitive functions (Bastiaansen et al., 2012). To investigate oscillatory brain activity in relation to cognitive processes, time-locked EEG epochs are still segregated by experimental manipulations similar to ERP analyses. However, the epochs cannot be averaged as this will cancel out non-phase-locked activity that ERP treats as ‘background noise’ (Roach & Mathalon, 2008).

EEG can be modelled as sine waves in the time and frequency domain. Each sine wave has its own frequency, i.e. how fast a sine wave cycle changes. At each time point of the sine wave, a phase angle can be measured by where the time point is within one cycle. Magnitude can be measured by the height of the wave at a time point. The phases of certain oscillatory activity to a stimulus could vary across experimental trials (Bastiaansen et al., 2012). For example, at the time point of event onset, there may be two signals with the same magnitude in two trials. One signal starts with a positive phase angle, the other starts with a negative angle. ERP analyses would average them, which leads to a zero potential at this time point as ERP only considers phase-locked activity (Herrmann, Grigutsch, & Busch, 2005). Therefore, there needs to be a new approach to analysing non-phase-locked event-related EEG signals.

EEG oscillations can be decomposed into magnitude and phase information in different frequencies. This is called spectral decomposition or time-frequency decomposition (Roach & Matholon, 2008). The power of magnitude signals the strength of activity in a frequency band. The phase is the direction of a waveform at a frequency and measured by unit of angle. The power / phase decomposition of EEG signals ensures that event-related oscillations will not be cancelled out due to variable phases to stimulus onset. Time-frequency representations of each epoch are averaged across trials within the same experimental condition. The time-frequency analyses generate information of magnitude and / or phases of oscillatory activity in each frequency band and time point.

There are many ways of transforming EEG data into time-frequency information (Herrmann et al., 2005; Roach & Matholon, 2008). The principle to choose an approach to do time-frequency transformation is the balance between temporal and frequency resolution. Basically, a longer time window gives high frequency resolution but poorer temporal resolution. In this doctoral thesis, Morlet wavelet decomposition as implemented in EEGLAB was used to transform time-frequency information. Wavelets might have a problem in frequency bleeding (i.e. power of a frequency bleeds to neighbouring frequencies) but wavelets are sensitive to detect signals, which means wavelets have less trade-off between time and signal amplitude (van Vugt, Sederberg, & Kahana, 2007). The frequency bleeding issue should not be a major concern in this doctoral thesis. When fixed cycles were used, van Vugt et al. (2007) demonstrated that compared to another spectral analysis method (multitapers), wavelets led to more frequency bleeding only when the frequency of interest was 40 Hz or higher. The frequency specificity did not differ in spectral analysis methods (wavelets, multitapers or P_{episode}) for lower frequencies of interest. In this doctoral thesis, the frequencies of interest are in the low frequency bands (4 – 12 Hz). A fixed number of waveforms (4 cycles) was used for the wavelets analysis (cf. Gruber et al., 2013). More cycles (7 cycles) that provide higher frequency resolution have been used to compare the frequency specificity with 4 cycles in Experiment 1, and the results did not show any difference. In conclusion, the frequency bleeding issue should not affect the results in this doctoral thesis. As the lowest frequency of interest in this doctoral thesis is 4 Hz, fewer cycles (4 cycles) were used to have a relatively higher temporal resolution (Roach & Matholon, 2008).

The frequencies are separated into different frequency bands: Delta (0-4 Hz), Theta (4 – 8 Hz), Alpha (8 – 12 Hz), Beta (13 – 30 Hz) and Gamma (30 – 80 Hz) (Herrmann et al., 2005). The different frequency bands provide information at which rate a large population of neurons works together. Although the above is a common separation of frequency bands, the separation can vary depending on the experimental manipulations. For example, when investigating encoding-related pre-stimulus theta power, Fell et al. (2011) used 4 – 7 Hz for the rhinal cortex and 3 – 7 Hz for the hippocampus. Nenert et al. (2012) investigated the role of alpha power in maintaining working memory. They used 8 – 14 Hz, separated into low (8 – 10 Hz) and high (12 Hz) depending on whether there existed a correlation between alpha power and performance. Klimesch (1999) defined the traditional alpha frequency band is 7.5 – 12.5 Hz. However, he suggested that alpha frequency can be defined by observed largest power of a frequency within that frequency range. To be consistent across experiments, theta and alpha frequency bands were always 4 – 8 Hz for theta and 9 – 12 Hz for alpha in this doctoral thesis. The bands were chosen based on the traditional frequency bands separation (Herrmann et al., 2005; Niedermeyer, 2005), but with a separation between theta and alpha bands. When wavelets cycles are fixed, spectral bandwidths of the Gaussian function will increase as the centre frequency increases (Roach & Matholon, 2008). Therefore, having some separation between frequency bands can reduce the chance that adjacent frequencies might be picked up more than twice (Herrmann et al., 2005; Mazaheri & Picton, 2005), which helps avoid Type I error in further statistical analyses.

As discussed above, theta and alpha activity both play important roles in memory formation (for reviews, see Düzel et al., 2010 and Hanslmayr et al., 2012). Increases and decreases in theta and alpha power seem to influence memory encoding depending on the cognitive processes during encoding (Hanslmayr & Staudigl, 2013).

Theta and alpha activity before an event can also predict later encoding success (e.g. Fell et al., 2011; Gruber et al., 2013; Guderian et al., 2009). In this doctoral thesis, the analyses focus on the power information of non-phase-locked oscillations at theta and alpha frequency bands. The event-related oscillations are mainly compared by the subsequent memory approach to see what kind of oscillatory activity (synchronisation or desynchronisation) contributes to memory formation.

ERPs mainly reflect the phase-locked activity to a stimulus over time, while oscillations are non-phase-locked to the stimulus and exist independent of the stimulus. Therefore, understanding about the relationships between ERPs and oscillations can provide more insights about processing of the stimulus in a specific neural context (ongoing oscillations) and neural patterns elicited by the stimulus (ERP). The relationships between ERP and oscillations have been controversial over years. The phase-resetting model argues that ERPs are the result of phase-resetting of ongoing oscillations by a stimulus, which suggests that ERPs and oscillations reflect similar neural processes (for reviews, see Bastiaansen et al., 2012; Sauseng et al., 2007). In an opposing view, (that is, the additive model), the stimulus-evoked ERPs are an additive component to the background oscillations, which suggests that ERPs and oscillations reflect two independent neural processes (Bastiaansen et al., 2012; Sauseng et al., 2007).

The evidence does not favour either the phase-resetting model or the additive model. For example, Makeig et al. (2002) suggested that visual evoked ERPs such as the N1 component are caused by increases in Inter-Trial-Coherence (ITC) in alpha phase after stimulus onset. Such findings indicate that stimulus-evoked ERPs are evident when phases of oscillations are reset by stimulus onset. Another finding that supports the phase-resetting model is that the post-stimulus power does not change at the time point of stimulus onset compared to pre-stimulus power, which argues against the additive model that adding a stimulus-evoked ERP to the background oscillations leads to larger post-stimulus power compared to pre-stimulus power (Hanslmayr et al., 2007). However, Mazaheri and Picton (2005) argued that increases in ITC can also be found when simply adding an ERP to the background oscillations. Additionally, Hanslmayr et al. (2007) suggested that background oscillatory power decreases during the time of stimulus onset, which might bias the amount of changes in the overall post-stimulus power. The findings cannot completely support the idea that no overall post-stimulus power change reflects the phase-resetting view.

On the other hand, some evidence supporting the additive model seems to not be stable either. For example, Shah et al. (2004) used intracortical recording for monkeys and showed that ERPs can be generated after stimulus onset independent of pre-stimulus oscillatory power. The finding is against the phase-resetting view as it suggests that phase-resetting occurs when ongoing oscillations exist during a pre-stimulus period. However, the intracortical activity might not be comparable with scalp EEG where most phase-resetting phenomena are found (Sauseng et al., 2007). Further, Mäkinen, Tiitinen and May (2005) suggested that if ERPs are generated by phase-resetting of ongoing oscillations, a decrease in amplitude variance should be found at the time point of stimulus onset. Mäkinen et al. (2005) found increases, rather than decreases in amplitude variance at the time of stimulus onset across trials. Nevertheless, Klimesch, Hanslmayr, Sauseng and Gruber (2006) commented on the method that Mäkinen et al. (2005) used and suggested that amplitude variance is not a good index to support the additive model or be against the phase-resetting model. Klimesch et al. (2006) suggested that not only amplitude variance but also phase concentration should be considered to argue against the phase-resetting view. To consider the role of phase in either model, Mazaheri and Jensen (2006) used a phase preservation index (PPI) as a measure to investigate the relationship between the phases of ongoing oscillations and the phases after stimulus onset. They found that the relationship between the phases of ongoing oscillations and after stimulus-evoked responses does not change, which supports that no phase-resetting to the background oscillations is shown when stimulus-evoked potentials happen. However, because the PPI is not preserved after stimulus onset as compared to the pre-stimulus period, it cannot be concluded that phase-resetting happens. The measure might be biased by an additive stimulus-evoked response. The additive evoked response can cause phase perturbations from the pre-stimulus oscillations (Bastiaansen et al., 2012; Sauseng et al., 2007).

As no consistent evidence supports one model over the other, some researchers suggest that ERPs and oscillations might share the same neural generators, which is termed the ‘shared generators view’ (e.g. Mazaheri & Picton, 2005). In that view, ongoing oscillations and stimulus-evoked responses can be generated by the same group of neurons. Therefore, stimulus onset may yield evoked responses when the neurons are inactive. In such case, an additive component is generated independent of ongoing oscillations. At the same time, stimulus onset might also be able to activate the neurons to produce an induced event-related synchronisation that is time-locked to the stimulus. In addition, stimulus onset might be able to change neurons that generate existing ongoing oscillations to phase-lock to the stimulus. During the changes, event-related synchronisations might be found from a lower or higher frequency band than the ongoing oscillations while event-related desynchronisations might be found from the frequency of the ongoing oscillations. This view explains findings that cannot be explained by either the phase-resetting or additive view, for example, an ERP generated with or without background oscillations or ongoing oscillatory power decreases when an ERP occurs.

Although there is not a universal view explaining the relationships between ERPs and oscillations, either model suggests that it would be valuable to look at the EEG data in both domains in one data set. The additive model suggests ERPs and oscillations reflect two different neural processes, which suggests that such processes might support cognitive processes in different ways. For example, in terms of pre-stimulus encoding-related activity, Otten et al. (2006) showed pre-stimulus encoding-related ERP activity only in semantic preparation condition while Guderian et al. (2009) showed that pre-stimulus theta activity predicts later memory success regardless of preparatory task. These findings suggest that there might be two underlying mechanisms to support preparation for memory encoding. However, the experimental manipulations were different across the two studies. Therefore, it is difficult to conclude whether the findings are caused by different experimental settings or different underlying mechanisms represented by ERPs and oscillations.

On the other hand, the phase-resetting view suggests ERPs are part of ongoing oscillations, which indicates that two measures might share common mechanisms underlying cognitive processes. As discussed in Chapter 1, studies that focused on ERPs and oscillations found that encoding-related activity in a semantic condition is qualitatively different from encoding-related activity in a non-semantic condition (alphabetical order judgments) (Hanslmayr et al., 2009; Otten & Rugg, 2001b). The frontocentral positive-going subsequent memory effect in the ERP study reflects semantic processing, which might be associated with alpha desynchronisation found in the semantic encoding in the oscillations study. Again, it is difficult to directly compare the findings due to the different experimental settings.

Therefore, considering the data in both ERP and oscillations domains is interesting under either the phase-resetting view or the additive view. In this doctoral thesis, three EEG experiments were analysed in both ERP and time-frequency domains to address the question how the amount of advance information influences pre-stimulus encoding-related activity. To complement the ERP analyses, Event-Related Spectral Perturbation (ERSP) that allows looking at non-phase-locked EEG activity locked to time (an event) was used to analyse the data in the time-frequency domain (Makeig, Debener, Onton, & Delorme, 2004). For each experimental condition, power was averaged across trials at each time point, each frequency and each electrode. Thus, each participant had a data structure with the number of time points by the number of frequency by the number of electrodes in each experimental condition. To conduct statistical analyses on each frequency band of interest (theta and alpha), the data points were collapsed into 4 - 8 Hz (theta) and 9 - 12 Hz (alpha). The data points were also collapsed into time windows of 500 ms as 500 ms enables at least two oscillatory cycles of the lowest frequency of interest (4 Hz), which is suggested to be a sufficient representation of the existence of oscillations (Bastiaansen et al., 2012). Permutation tests were used to test the statistical differences in oscillatory power between conditions to protect the analyses from a type I error caused by multiple comparisons (Addante et al., 2011; Gruber et al., 2013; Hanslmayr et al., 2009). Permutation tests were done on all the scalp electrodes, all the time windows and both frequency bands in the experimental comparisons. The details of the permutation tests used in the statistical analyses will be introduced in the *Methods* sections in Chapter 4.

2.4 Behavioural analyses of recognition memory

To effectively measure recognition memory, a discrimination index (Pr) of the two-high threshold model was used (Snodgrass & Corwin, 1988). The two thresholds refer to the threshold of recognising old items (Po) and the threshold of discriminating new items (Pn). Pr is the common threshold that Po is assumed to equal Pn. The model suggests that within the recognised old items, some of them are really recognised and some of them are luckily guessed. Pr reflects the probability of real recognised items while the proportion of False Alarms (FA) reflects the probability of guessing that an item is old.

Therefore, the proportion of hits (hit rate) equals Pr plus FA rate. Pr is the proportion of hits minus the proportion of false alarms.

There is another index in the two-high threshold model, the response bias index (Br). Br is defined as how likely participants guess ‘yes’ to items that they are not sure about (Snodgrass & Corwin, 1988). When participants give an ‘old’ response to a new item, this is termed a false alarm. Participants tend to make ‘yes’ responses in uncertain circumstances (Br) and cannot distinguish new items from old items (1 - Pr). Therefore, the false alarm rate equals Br multiplied by (1 – Pr). There are also many other models measuring recognition memory such as signal detection models, which is based on single processing models of recognition memory (e.g. Murdock & Dufty, 1972). In this doctoral thesis, the reasons why the two-high threshold model was used are because first, it is the simplest measurement. The focus of this thesis is the neural activity for efficient memory not the behavioural models of recognition memory, so the relatively simple behavioural measure was used. In addition, the two-high-threshold model is demonstrated to be more sensitive to be affected by discrimination and bias and the two measures are well distinguished from each other (Snodgrass & Corwin, 1988).

The significance level of all the statistical tests for the behavioural analyses, ERP analyses and permutation tests for oscillatory analyses was 0.05 in this doctoral thesis. The 0.05 alpha level means there is a 5 percent probability that rejecting the null hypothesis H_0 is an error (Type I error). Adopting this criterion is common in cognitive neuroscience studies (e.g. Gruber & Otten, 2010; Gruber et al., 2013; Otten et al., 2010).

Chapter 3: Does amount of advance information influence pre-stimulus encoding-related activity?

3.1 Experiment 1: The influence of graded perceptual preparation on pre-stimulus encoding-related activity

3.1.1 Introduction

So far, studies on encoding-related pre-stimulus activity have focused on different types of preparation for memory encoding, such as semantic preparation (e.g. Galli et al., 2012; 2013; Otten et al., 2006; 2010), preparation for encoding success with high monetary reward (Gruber & Otten, 2010) or preparation for negative emotional events (Galli et al., 2011; 2014). Two kinds of encoding-related pre-stimulus activity were found in these studies. Frontal negative-going pre-stimulus subsequent memory ERP effects were shown when semantic preparation was engaged. When preparing for encoding a word with high monetary reward or a negative emotional scene, widespread positive-going subsequent memory ERP effects were found. As discussed in Chapter 1, the two different kinds of pre-stimulus subsequent memory effects reflect two different preparatory processes. The frontal negative effect might reflect semantic preparation while the widespread positive-going effect might suggest motivational processes (Galli et al., 2011).

Preparatory processes might be under strategic control according to pre-stimulus cue information. If preparatory processes for memory encoding are under strategic control, when more advance information about an upcoming event is available, the better preparation should be engaged before memory encoding. If less advance information is available, less degree of preparation will be engaged before memory encoding. However, it is still not clear whether pre-stimulus activity for encoding is in an all-or-none fashion, for example, the activity might be engaged regardless of amount of information to be prepared under certain type of appropriate preparation. Therefore, the research question is whether a pre-stimulus subsequent memory effect is graded as a function of the amount of advance information.

In other cognitive domains, for example attention, many studies show that when pre-stimulus information validly cues a location or time of the presentation of a stimulus, both behaviour and brain activity is enhanced (Downing, 1988; Gruber, Müller, Keil, & Elbert, 1999; Rohenkohl & Nobre, 2011; Zanto et al., 2011). In the memory domain, the accuracy of a recognition memory test and a working memory task is better when pre-stimulus cues contain information about the stimulus category than when pre-stimulus information does not indicate a specific category of stimuli (Bollinger et al., 2010). Behavioural performance is better when advance information is more specific about an upcoming event. Pre-stimulus activity can also be engaged in supporting encoding success. Uncapher et al. (2011) showed that cue-related activity from dorsal parietal cortex was positively correlated with encoding success when a cue indicated the location of an upcoming object. When a cue indicated an opposite location of the upcoming object, cue-related activity from parietal cortex was negatively correlated with encoding success. The findings suggest that the more advance information is available to guide preparation, the more likely pre-stimulus activity can be engaged in supporting encoding success.

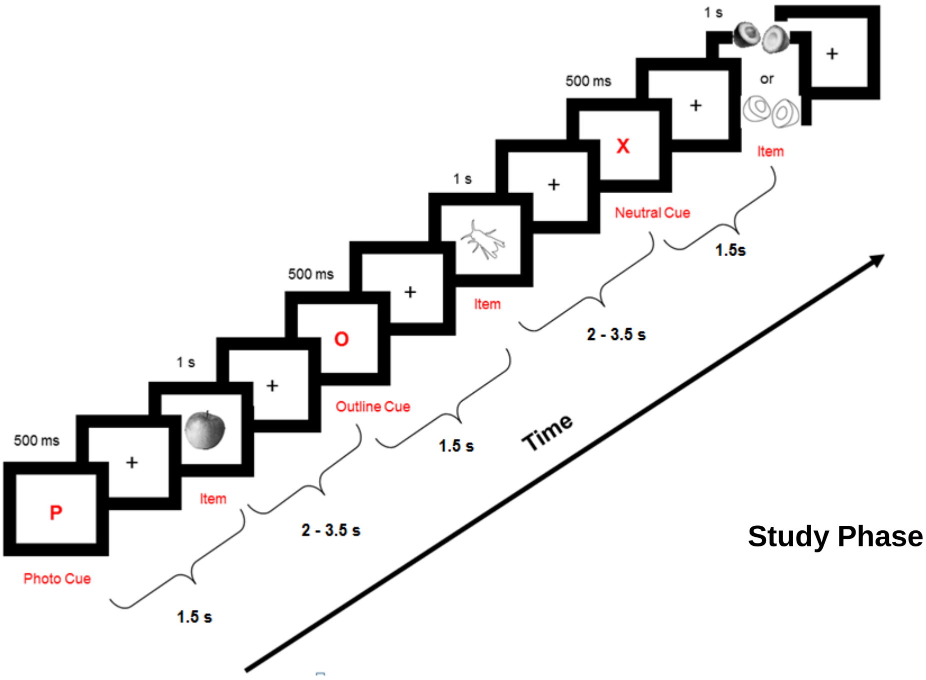
To address the question of whether encoding-related pre-stimulus activity is graded as a function of amount of information to be prepared, pictures of everyday objects were used as experimental stimuli. The richness of perceptual details of the pictures was manipulated. Greyscale photographs with more perceptual details and line drawings with less perceptual details were used. An informative pre-stimulus cue signalled the type of an upcoming picture. Participants prepared for different amount of perceptual information. In addition, a non-informative cue did not signal the type of the upcoming picture. In that case, the amount of perceptual information to be prepared was unknown. If pre-stimulus subsequent memory effect is graded rather than operating in an all-or-none fashion, then preparation for different amount of perceptual information should elicit graded pre-stimulus subsequent memory effects. The non-informative cue might not elicit any pre-stimulus subsequent memory effect. The cue signalled a presentation of a line drawing would elicit less degree of pre-stimulus subsequent memory effect. The cue signalled a presentation of a greyscale photo elicit largest pre-stimulus subsequent memory effect.

3.1.2 Methods

Participants. The experimental procedures were approved by the University College London Research Ethics Committee. 24 healthy adults were paid at a rate of £7.50/h to participate. The mean age was 22 years (range of 18-27 years) and 11 of them were female. All of the volunteers were naive about the purpose of the experiment. Each volunteer completed a written informed consent form before participating and reported they had normal or corrected-to-normal vision, were right-handed, native English speaking and did not have a neurological or psychiatric history.

Stimulus Material. Stimuli were randomly selected from a pool of 261 pairs of greyscale pictures of everyday objects (e.g. food, toys, and furniture) and animals. 261 objects could fit in a shoebox in their real size and the other 261 objects could not fit in a shoebox (i.e. their real size is larger than a shoebox). 261 pictures were presented as photographs (photo) while the other 261 pictures were presented as line drawings (outline). Outlines were created by Adobe Photoshop (Adobe Systems, Inc.) by keeping the outline of each greyscale photo and filtering each photo’s inside perceptual details. Each picture was presented equally often as a photo or an outline across subjects. Each subject saw only one version of an object. The object was not presented as both a photo and an outline within a subject. Six sets of 56 pictures (336 critical items) were pseudo-randomly selected to create a study list and the remaining 3 sets of 56 pictures (168 unstudied items) were joined to create a test list (504 critical items in total). 9 additional pairs were used as filler items (6 pairs for the study phase and an additional 3 pairs for test phase). The number of objects that could fit in a shoebox was always equivalent to the number of objects that could not fit in a shoebox. Also, the number of photos was equal to the number of outlines in study, test and practice phases. The photos and outlines were randomly intermixed. The numbers of pictures in each pre-stimulus cue condition were equal. 112 photos followed pre-stimulus cues that signalled presentation of photos. 112 outlines followed pre-stimulus cues that signalled presentation of outlines. 56 photos and 56 outlines followed non-informative pre-stimulus cues.

All pictures were presented in central vision on a white background using the Cogent 2000 Toolbox (Wellcome Laboratory of Neurobiology: http://www.vislab.ucl.ac.uk/cogent.php) and MATLAB (The MathWorks, Inc.). During the study phase, each picture was preceded by a cue that indicated the type of picture or did not indicate the type of picture. When the cue was a ‘P’, the upcoming picture would be a photo. If the cue was an ‘O’, the upcoming picture would be an outline. If the cue was a non-informative cue (or neutral cue - ‘X’), the upcoming picture would either be a photo or an outline. All three kinds of cues were written in red. They were always shown 1.5 s before picture onset and presented for 500 ms, followed by a fixation cross for 1 s until picture onset. The picture was presented for 1 s followed by a fixation cross. The interval between picture onset and the onset of the next cue was a variable period from 2 to 3.5 s. During the test phase, the procedure was almost the same as the study phase except that the cues in the test phase were replaced by exclamation marks in red. The interval between exclamation mark onset and item onset was 1 s. An exclamation mark was just a neutral warning cue to warn the onset of the next stimulus.



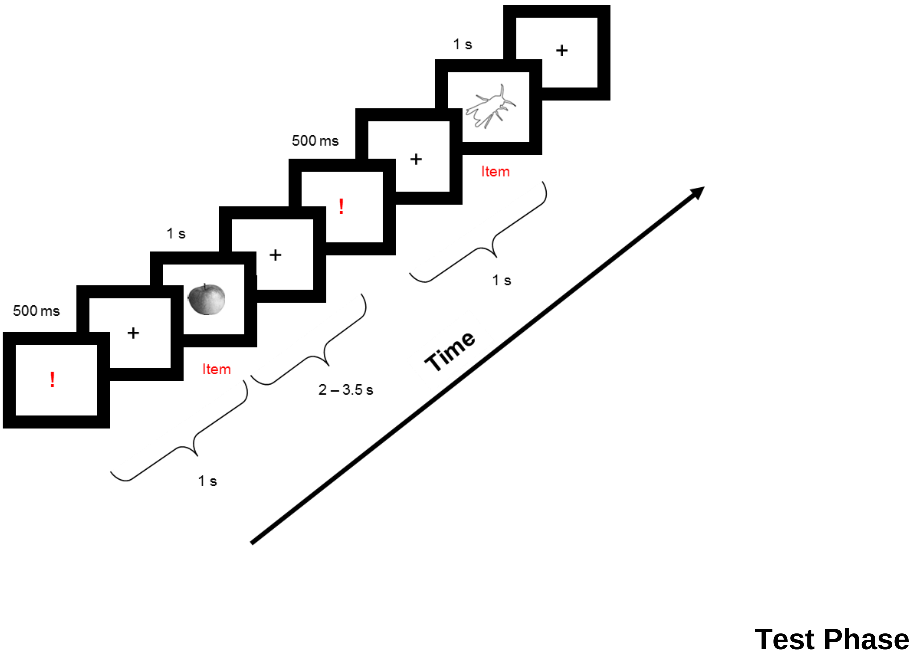


Figure 1. Experimental procedure of study and test phases in Experiment 1

In the study phase, an informative cue indicated the type of the upcoming picture. A non-informative cue was followed by either a grey scale photo or an outline. The incidental encoding task during the study phase was a size judgment task. At test, the procedure was the same except pre-stimulus cues were replaced by exclamation marks.

Procedure. Pilot experiments used the Remember / Know paradigm (Tulving, 1985b) in the test phase, and the test phase was run immediately after the study phase. Only two out of five pilot participants had sufficient forgotten trials. To increase the number of forgotten trials, the design was changed and the test phase was run one day after the study phase. One out of three pilot participants did now not have sufficient numbers of remembered trials. To reach an acceptance level of trial numbers for both remembered and forgotten trials, confidence rather than Remember / Know judgements were used for the test phase in following pilot work, with study and test phases run on separate days. Four pilot participants were run with that design, all resulting in acceptable trial numbers. This design was therefore chosen for the EEG experiment.

The final design is shown in Figure 1. On the first day, participants only did the study phase. They were told to make decisions about a series of pictures. Before each picture, cues indicated what kind of pictures they would see next. Participants were encouraged to use the cue to help them make decisions. They were then asked to press one of two buttons to indicate whether or not the object fitted in (in their real size) a shoebox. Assignments of response hands were counterbalanced across participants. Before the formal experiment, there was a practice phase for them to become familiar with the whole procedure and key pressing. They were given oral feedbacks about whether their answers during the practice were correct in order to make sure that they understood the task.

The participants were asked to return to the lab at the same time on the second day. They were asked to do a surprise recognition test on the previous day’s pictures. Participants were instructed to give old / new recognition judgments with confidence judgments to each item by pressing one of four buttons with two hands. If they were sure that they had seen the picture in the study phase, they should give an old sure response; if they thought the picture was in the study phase but they were not sure, they should give an old unsure response. If they were sure they had never seen the picture in the study phase, they should give a new sure response; if they thought the picture had not been in the study phase the previous day but were not sure, they should give a new unsure response. Old / new assignments of response hands were counterbalanced across participants. Participants saw exactly the same objects in the same picture format as they had seen in the study phase along with pictures they had never seen in the study phase. Studied pictures were in mirror-reversed direction as in the study phase to make the items less familiar (Groh-Bordin, Zimmer, & Mecklinger, 2005). Pilot experiments also showed that participants tended to make fewer 'old' judgments when the orientation of the test probes was mirror-reversed. In both study and test phases, participants were told that both accuracy and response speed were important.

EEG acquisition. The EEG was only recorded on the first day. The EEG was recorded from 32 scalp sites using silver/silver-chloride electrodes fitted in an elastic cap. The electrodes were positioned according to an equidistant electrode montage (www.easycap.de/easycap/e/electrodes/13_M10.htm). Vertical and horizontal eye movements (EOG) were recorded bipolar from electrodes above and below the right eye and the outer canthi of each eye. All online data were recorded with reference to channel Fz according to the international 10-20 system. All impedances were kept below 5kΩ and all data were amplified, band pass filtered between 0.01 and 35 Hz (3 dB roll off), and digitized (12-bit resolution) at a rate of 500 Hz.

EEG analyses. The EEG data were digitally filtered offline between 0.05 and 20 Hz (96 dB roll off), downsampled to 1 point/8 ms (125Hz) and algebraically re-referenced to averaged left and right mastoids (reinstating the online reference site). The continuous EEG elicited by cues and pictures was segmented separately into epochs of 2048 ms duration including a 100 ms baseline before cue and picture onsets. These epochs were used to create ERP waveforms for each subject and electrode site by averaging them separately for items in the study phase according to the later ‘old sure’, ‘old unsure’, ‘new sure’, ‘new unsure’ judgments that participants gave in the test phase. Epochs with horizontal eye movements, muscle artefacts, analog-to-digital saturation, drifts exceeding ±50 µV and trials with no response in the test phase were excluded from the averaging process. The blink artefacts were minimized by estimating and correcting their contribution to the ERP waveforms with a standard regression technique (Rugg, Mark, Gilchrist, & Roberts, 1997). There were at least 12 artefact free trials in each condition for each subject’s averaged ERPs (for trial ranges in each condition see Table 1). This criterion for inclusion mimics previous works investigating encoding-related ERP activity (e.g. Gruber & Otten, 2010; Kim, Vallesi, Picton, & Tulving, 2009). Only one subject contributed the minimum trial number in some of the critical experimental conditions. The ERPs for the remaining 23 subjects were based on more than 15 artefact free trials. Supplemental ERP analyses were done on those 23 subjects who had more than 15 artefact free trials. The pattern of results did not differ from that seen across all the 24 subjects. The trials in the neutral cue condition were not separated into photos and outlines as trial numbers were not sufficient to look at ERPs in each individual condition after neutral cue onset.

The main analyses focused on the comparisons of ERP waveforms between later recognized trials and later forgotten trials for activities elicited by cues. To keep the analyses consistent with previous research on pre-stimulus encoding related activity (Otten et al., 2006, 2010), studied trials were classified as ‘recognized’ only when they were given a confident recognition judgment (‘old sure’ judgment). To maximize the signal-to-noise ratio, studied trials were classified as ‘forgotten’ if they were given a non-confident new judgment or confident new judgment. For all comparisons, mean ERP waveforms were created for 24 subjects in each condition. The mean trial numbers in each condition are shown in Table 1. Repeated measures analysis of variance

(ANOVAs) were used to test the differences between each comparison incorporating the Greenhouse-Geisser correction for violations of nonsphericity (Keselman & Rogan, 1980). ANOVAs were based on all 32 scalp electrodes.

Table 1. Mean trial numbers in each condition for pre-stimulus cue period in Experiment 1 (Range in brackets)

	Photo Cue Condition	Outline Cue Condition	Neutral Cue Condition
Recognized trials	42 (16 to 69)	44 (23 to 73)	43 (17 to 71)
Forgotten trials	33 (15 to 51)	29 (12 to 50)	31 (12 to 55)

Table 2. Mean trial numbers in each condition for post-stimulus cue period in Experiment 1 (Range in brackets)

	Photo Cue Condition	Outline Cue Condition
Recognized trials	41 (16 to 70)	43 (21 to 71)
Forgotten trials	32 (17 to 49)	28 (13 to 53)

3.1.3 Results

Task Performance

Study. Performance for the study phase is summarized in Table 3. Although the trial numbers of photos and outlines in the neutral cue condition were half of the trial numbers in the photo (outline) cue condition, the performance of size judgments could be biased if the level of perceptual richness was not a factor in the analyses. Therefore, the analyses used ANOVA with two repeated measures factors of amount of advance information (informative, non-informative) and level of perceptual richness (photos, outlines). Reaction times were significantly different in level of perceptual richness, $F(1, 23) = 18.939$, $p < 0.001$. The reaction time for the size judgment of photos was significantly faster than the reaction time for outlines regardless of cue conditions. Reaction time for the informative cue condition was faster than reaction time for the non-informative cue condition. However, this advantage was not statistically significant, $F(1, 23) = 3.558$, $p = 0.072$. There was no difference in accuracy of size judgments (as judged by the experimenter) as a function of either amount of advance information, F(1,

23) = 2.013, *p* = 0.169, or level of perceptual richness, *F*(1, 23) = 4.062, *p* = 0.056. This might be due to the shoebox task performance being at ceiling (see Table 3). However, the judgments in the shoebox task were quite subjective, that is, objects could be classified as fitting or not fitting inside a shoebox depending on how an object was envisaged. Accuracy of the task performance was therefore not considered further.

Reaction times were categorised according to later recognition memory test to be consistent with subsequent memory ERP analyses. ANOVAs were done in three factors, amount of advance information (informative, non-informative cues), level of perceptual richness (photo, outline) and recognition memory performance (confident old, forgotten (unconfident and confident new)). These analyses showed that reaction times for size judgments of objects followed informative cues were significantly faster than followed non-informative cues, *F*(1, 23) = 6.588, *p* = 0.017. This might be caused by the fact that items subsequently given unconfident old judgments or not given any judgments were excluded due to ERP analyses criteria. Photos were made significantly faster size judgments than outlines, *F*(1, 23) = 12.078, *p* = 0.002, which was consistent with the earlier analyses. Later recognised items were given faster size judgments than later forgotten items, but this did not reach level of significance, *F*(1, 23) = 3.962, *p* = 0.059. The interaction between amount of advance information and subsequent memory did not reach significance although there was a trend (*F*(1, 23) = 3.182, *p* = 0.088). To understand this trend, pairwise comparisons were conducted between remembered and forgotten items in the informative and non-informative cue conditions. These suggested that the interaction might reflect larger differences between reaction times for subsequently remembered and forgotten items in the non-informative cue conditions (informative cue conditions, *F*(1, 23) = 1.191, *p* = 0.191, non-informative cue conditions, *F*(1, 23) = 4.259, *p* = 0.051).

Table 3. Study task performance in Experiment 1

		photo cue	outline cue	neutral cue (photo & outline)	neutral cue (photo)	neutral cue (outline)
Accuracy	M	0.83	0.81	0.83	0.84	0.83
	SD	0.04	0.05	0.04	0.04	0.05
Response times (ms)	M	944	994	983	969	997
	SD	249	270	255	243	272

Values are across-subject means. n=24.

Test. Recognition memory performance is summarized in Tables 4 and 5. The discrimination index Pr was used to assess individuals' ability to discriminate between old and new items. The response bias index Br was used to assess individuals' propensity to give old judgments. Pr was not significantly different depending on either amount of advance information or level of perceptual richness, regardless of type of confidence judgments (photo cue: 0.44; outline cue: 0.48; neutral cue photo: 0.45; neutral cue outline: 0.47; all ps > 0.1). No significant differences were found either when only confident old judgments were considered (photo cue: 0.33; outline cue: 0.37; neutral cue photo: 0.35; neutral cue outline: 0.37; all ps > 0.15). This was done as later ERP analyses focus on the comparison between confident old judgments and all new judgments. Similar results were found when Br values were compared. Br regardless of recognition type did not differ depending on either amount of advance information or level of perceptual richness (photo cue: 0.39; outline cue: 0.45; neutral cue photo: 0.40; neutral cue outline: 0.45; all ps > 0.05). However, outlines tended to attract old judgments than photos when participants were uncertain ($F(1, 23) = 4.125$, $p = 0.054$). When comparing Br values for confident old judgments, no significant differences were found (photo cue: 0.13; outline cue: 0.11; neutral cue photo: 0.14; neutral cue outline: 0.11; all ps > 0.07). Nevertheless, there was a tendency for more confident old judgments for photos than outlines when participants were uncertain ($F(1, 23) = 3.440$, $p = 0.077$). For confident old hits, the discriminations between old and new items were significantly greater than zero, $p \leq 0.001$. Reaction times for confident old judgments were significantly faster than reaction times for the unconfident old judgments, $F(1, 23) = 49.618$, $p < 0.001$.

Table 4. Mean proportion of recognition memory responses in Experiment 1

Condition		Recognition Type			
		Confident old	Unconfident old	Unconfident new	Confident New
Informative cue	photo	0.41 (0.15)	0.25 (0.12)	0.23 (0.08)	0.10 (0.05)
	outline	0.43 (0.15)	0.28 (0.15)	0.21 (0.09)	0.07 (0.05)
Non-informative cue	photo	0.43 (0.17)	0.24 (0.14)	0.23 (0.09)	0.10 (0.06)
	outline	0.43 (0.17)	0.27 (0.15)	0.23 (0.10)	0.07 (0.05)
	photo & outline	0.43 (0.16)	0.26 (0.14)	0.23 (0.09)	0.08 (0.43)
New	photo	0.08 (0.07)	0.14 (0.06)	0.44 (0.13)	0.33 (0.15)
	outline	0.07 (0.07)	0.17 (0.08)	0.46 (0.11)	0.31 (0.14)

Values are across-subject means (SD). n=24.

Table 5. Mean RTs (ms) of recognition memory responses in Experiment 1

Condition		Recognition Type			
		Confident old	Unconfident old	Unconfident new	Confident New
Informative cue	photo	1054 (215)	1313 (299)	1324 (302)	1231 (273)
	outline	1063 (236)	1270 (278)	1299 (293)	1278 (372)
Non-informative cue	photo	1053 (215)	1325 (327)	1311 (310)	1324 (459)
	outline	1052 (230)	1330 (341)	1313 (341)	1210 (368)
	photo & outline	1052 (219)	1327(325)	1312 (315)	1337(420)
New	photo	1185 (279)	1365 (391)	1287 (294)	1214 (278)
	outline	1168 (435)	1311 (366)	1285 (278)	1236 (332)

Values are across-subject means (SD). n=24. The reaction times shown above are based on 24 participants except new outline confident old judgments: these are based on 22 participants as two participants did not have any trials for that condition.

Summary of behavioural findings

The reaction times for the encoding task (size judgments) were significantly faster for photos than outlines regardless of the amount of advance information that was provided. The more perceptual details a picture had, the easier a decision was made about an object’s size. Although more advance information nominally led to faster decisions in the size judgment task, this difference was not statistically significant.

The Pr and Br values for the recognition memory test did not show any significant effects related to the amount of advance information or level of perceptual richness. However, there were trends that for photos, a more liberal response criterion was used than for outlines when a confident old judgment was made. When both confident old and unconfident old judgments were combined, a more liberal response criterion was used for outlines than photos.

Encoding-related activity preceding pictures

Neural activity related to successful encoding was identified with the subsequent memory paradigm. Studied items were categorized into subsequent recognized and forgotten items according to subsequent memory performance in the test phase. ERP waveforms elicited by cues could therefore be contrasted depending on whether the following items were recognized or forgotten. As can be seen from Figure 2, ERPs elicited by photo cues differed in later recognised and forgotten categories. The pre-stimulus ERPs before later recognised items were more positive-going than later forgotten items. In contrast, ERPs elicited by the other two kinds of cues almost overlapped between later recognised and forgotten categories.

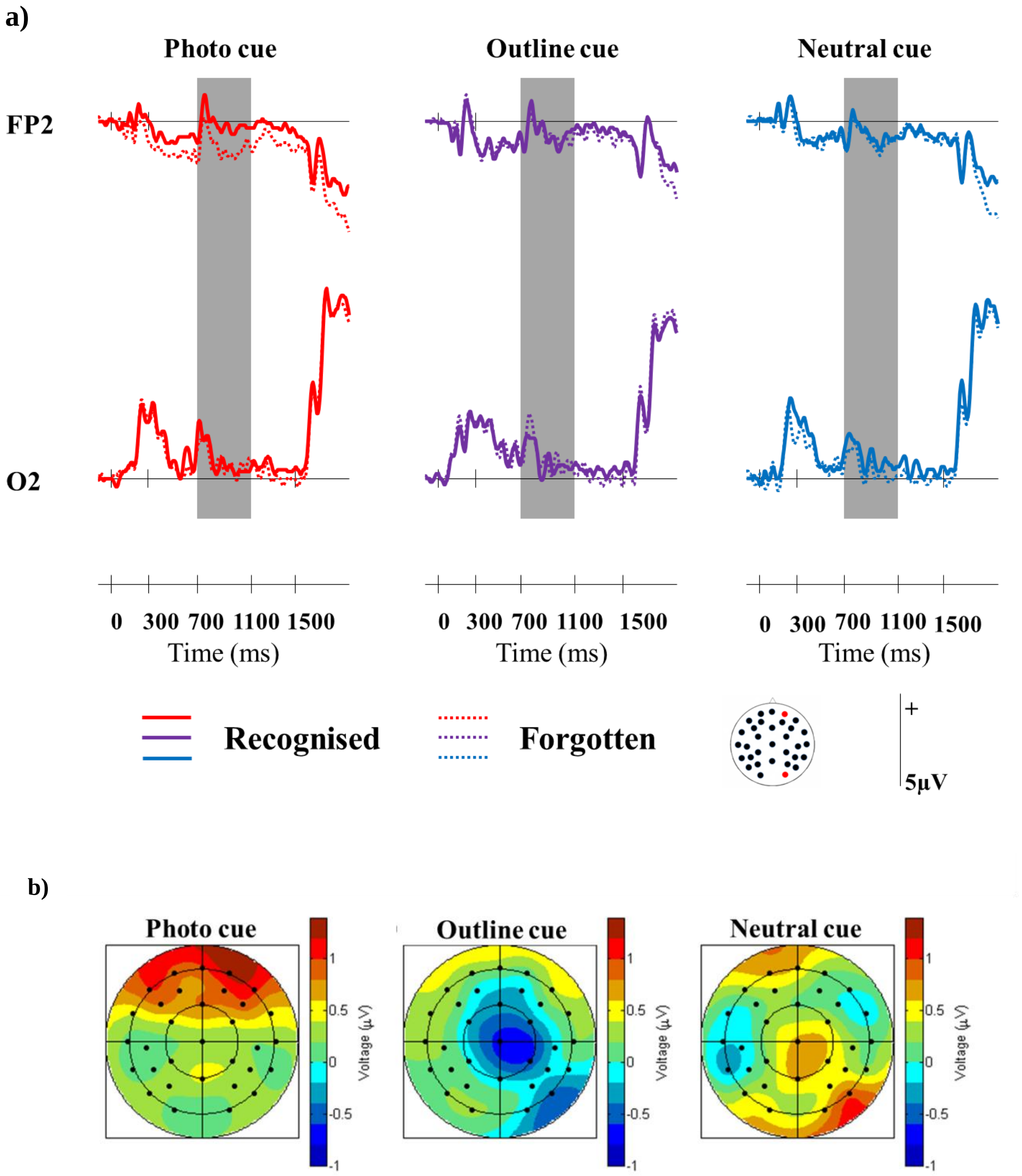


Figure 2. Pre-stimulus subsequent memory effect in Experiment 1

a) Group-averaged ERP waveforms elicited by photo cues (left), outline cues (middle) and neutral cues (right) at a frontal and an occipital electrode sites (sites FP2 and O2 from montage 10, www.easycap.de/easycap/e/electrodes/13_M10.htm), where the frontal electrode site showed the positive-going subsequent memory effect most visibly. The occipital electrode site is the symmetric site to the frontal electrode. Positive values are plotted upwards. 0 is the time point of cue onset. b) Voltage spline maps showing the distributions of the subsequent memory effects across the scalp in the 700 ms to 1100 ms time window after cue onset. The maps are scaled to the difference between maximum and minimum across conditions to highlight the topographical differences and magnitude of the modulations in each condition.

ANOVAs were based on all the 32 sites. To quantify the observed pre-stimulus subsequent memory effect in the photo cue condition, mean amplitudes were calculated in the intervals of 300 to 700 ms, 700 to 1100 ms and 1100 to 1500 ms after cue onset, to be consistent with a previous study (Galli et al., 2011). Although Galli et al. (2011)

focused on pre-stimulus subsequent memory effect regulated by emotion and the stimulus material was emotional scene pictures, they showed a similar positive-going pre-stimulus subsequent memory effect for pictures, which might be most comparable to Experiment 1. Statistical analyses showed a significant pre-stimulus subsequent memory effect only in the time interval 700 to 1100 ms (main effect of subsequent memory: $F(1, 23) = 5.665$, $p = 0.026$, all other ps > 0.08). No interaction between pre-stimulus subsequent memory effect and cue condition was revealed. The spline map of the pre-stimulus subsequent memory effect in the photo condition showed a focal frontal distribution. Therefore the ANOVAs incorporating the factor of electrode site with all 32 levels might not be able to capture the pre-stimulus subsequent memory effect in the photo condition. An ANOVA was done for 24 electrode sites that could be partitioned into four equal quadrants (left anterior, right anterior, left posterior, right posterior, cf. Galli et al., 2011). The resulting ANOVA incorporated factors of subsequent memory (recognised, forgotten), cue condition (photo, outline, neutral), position (anterior/ posterior), hemisphere (left/ right) and electrode site (six sites). This ANOVA did not reveal any significant interactions involving subsequent memory and cue condition. This suggests that the absence of an interaction between subsequent memory and cue condition in the 32-site analysis was not caused by the number of electrode sites submitted to the ANOVAs.

The results suggested that the pre-stimulus subsequent memory effect observed from the grand average waveforms in the photo cue condition must be so subtle that statistics was not able to reveal the interaction. One possible reason could be variability across participants. Questionnaires that were answered after the experiment showed that 15 participants said ‘no’ to the question ‘Have you done anything in the interval between cues and pictures?’ the other 9 participants said they prepared somewhat before they saw pictures according to each kind of cues. The grand average ERP waveforms of the two groups showed differences (see Figure 3). As can be seen from the grand average waveforms, the difference between the activity preceding later recognised photos and forgotten photos started around 300 ms after cue onset for the ‘prepared’ group (N=9) and sustained until around 1100 ms. ANOVAs based on 24 subjects showed a marginal significant pre-stimulus subsequent memory effect in the time window of 300 to 700 ms, $F(1, 23) = 3.190$, $p = 0.088$. The effect for the ‘non-prepared’ group (N=15) started later around 700 ms after cue onset. From the spline maps (see Figures 3b and 3c) the amplitudes of pre-stimulus subsequent memory effects also differed in two groups. The amplitudes of the pre-stimulus subsequent memory effects in the prepared group were larger than in the non-prepared group in both time windows. However, these effects were unable to be showed statistically due to insufficient numbers of subjects in each group.

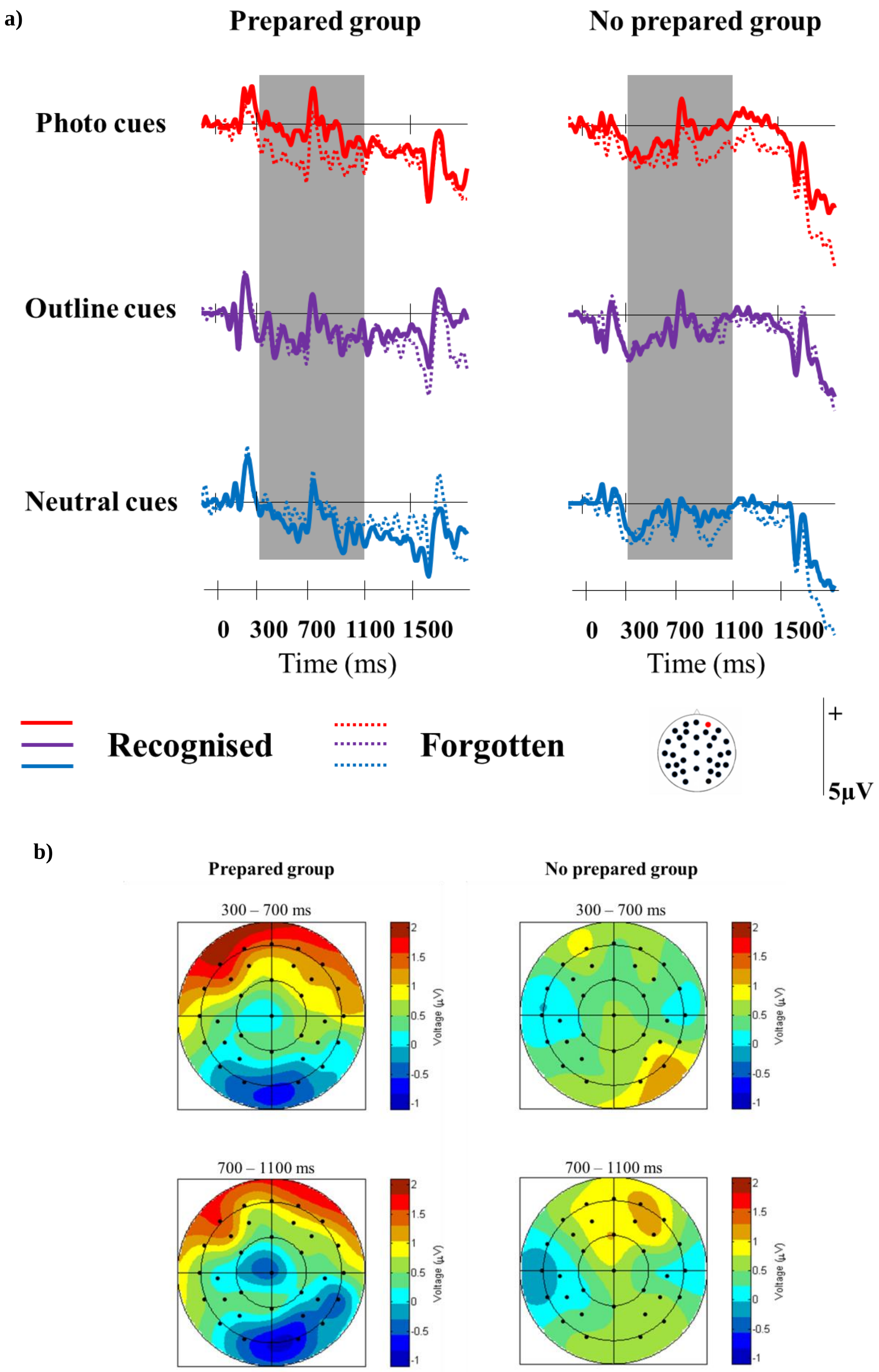


Figure 3. Pre-stimulus subsequent memory effect across groups in Experiment 1

a) Group-averaged ERP waveforms elicited by photo cues (top), outline cues (middle) and neutral cues (bottom) at a representative frontal electrode site (site Fp2 from montage 10) where the effects were most visible for the photo cue condition. 0 is the time point of cue onset. Left: the prepared group includes 9 participants who claimed to have done preparation when they saw different types of cues. Right: the no prepared group includes 15 participants who said they did the same for different types of cues or ignored cues. b) Voltage spline maps showing the distributions of the subsequent memory effects across the scalp in the 300 ms to 700 ms and 700 ms to 1100 ms time windows in the photo cue condition for the prepared group (left) and no prepared group (right). The maps are scaled to the difference between maximum and minimum across conditions to highlight the topographical differences and magnitude of the modulations in each condition.

Encoding-related activity after pictures

Another possible reason why the pre-stimulus subsequent memory effect did not statistically differ in cue conditions might be that preparatory processes for different amount of perceptual information were the same. Therefore, encoding-related neural activity elicited by pictures was also assessed with the subsequent memory approach to see whether memory processes per se were modulated by amount of perceptual information. The post-stimulus subsequent memory effects for the photos and outlines following neutral cues were not able to be analysed individually due to insufficient trial numbers. Therefore the post-stimulus subsequent memory ERP analyses focused on the photo cue and the outline cue conditions. More positive-going waveforms were elicited by later recognized pictures than forgotten pictures for both photos and outlines over frontocentral scalp sites (Figure 4). The effect started from around 200 ms onwards. The effects were pronounced in both picture conditions.

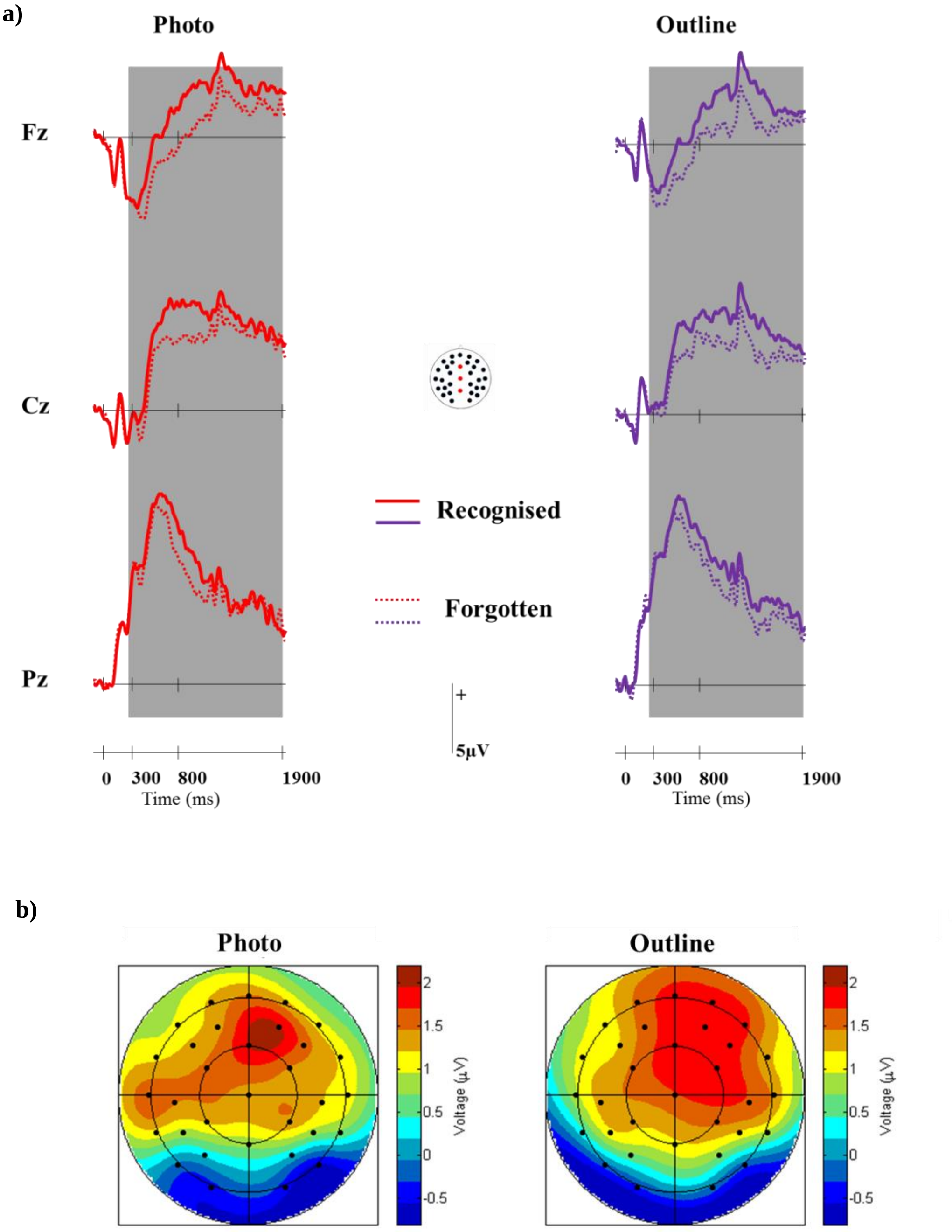


Figure 4. Post-stimulus subsequent memory effect across groups in Experiment 1

a) Group-averaged ERP waveforms elicited by photos (left) and outlines (right) at three midline electrode sites (sites Fz, Cz and Pz from montage 10), showing frontocentral subsequent memory effects. 0 is the time point of picture onset. Positive values are plotted upwards. b) Voltage spline maps showing the distributions of the subsequent memory effects across the scalp in the 300 to 1900 ms time window after picture onset. The subsequent memory effects showed positive, frontocentral maximum distributions. The maps are scaled to the difference between maximum and minimum across conditions to highlight the topographical differences and magnitude of the modulations in each condition.

ANOVAs were also based on all the 32 electrodes on the scalp. As discussed in Chapter 1, typical post-stimulus subsequent memory effect is found to be positive-going in a time window of 300 – 800 ms and over frontal and centro-parietal scalp sites depending on encoding operations (Friedman & Johnson, 2000; Paller & Wagner, 2002; Werkle-Bergner et al., 2006). However, the studies used pictorial stimuli showed an earlier subsequent memory effect from 100 or 200 ms after stimulus onset (e.g. Bauch & Otten, 2012; Friedman & Sutton, 1987). Therefore, mean amplitudes were calculated in the intervals of 100 to 300 ms, 300 to 800 ms, 800 to 1100 ms and 1100 to 1900 ms. The interval of 100 to 300 ms aimed to depict the early effect found in the pictorial stimuli. The intervals of 300 to 800 ms and 800 to 1100 ms were two intervals that typical positive-going subsequent memory effect was found in verbal material (Friedman & Johnson, 2000; Werk-Bergner et al., 2006). The last interval of 1100 to 1900 ms aimed to capture the sustained later subsequent memory effect (e.g. Galli et al., 2011; 2014). Main effects of subsequent memory were found in three time intervals starting from 300 ms (300 ms to 800 ms, $F(1, 23) = 10.124$, $p = 0.004$, 800 ms to 1100 ms, $F(1, 23) = 21.422$, $p < 0.001$, 1100 ms to 1900 ms, $F(1, 23) = 11.009$, $p = 0.003$). For all the three intervals, there were interactions between subsequent memory and scalp site after the Greenhouse-Geisser correction (300 ms to 800 ms, $F(3.3, 75.1) = 7.153$, $p < 0.001$, 800 ms to 1100 ms, $F(4, 92) = 9.074$, $p < 0.001$, 1100 ms to 1900 ms, $F(4.4, 101.9) = 5.359$, $p < 0.001$). The interactions confirmed the fronto-central scalp distribution of the subsequent memory effects observed in both picture conditions (Figure 4b), which resembles the previous findings of ERP subsequent memory effects in deep processing tasks(Otten & Rugg, 2001b; Paller et al., 1987; Sanquist et al., 1980). An ANOVA that incorporated factors of subsequent memory (recognised, forgotten), scalp site (32 sites) and time interval (300 ms to 800 ms, 800 ms to 1100 ms, 1100 ms to 1900 ms) showed that there was no interaction between subsequent memory effect, scalp site and time interval, $F(9.3, 319.6) = 1.425$, $p = 0.175$. This suggests that the subsequent memory effects found in the three intervals might reflect one sustained post-stimulus subsequent memory effect that did not differ across time.

No interaction between subsequent memory effect and level of perceptual richness of pictures was found. However, interactions between level of perceptual richness of pictures and scalp site were found in the intervals of 100 to 300 ms (main effect of level of perceptual richness of pictures, $F(1, 23) = 17.361$, $p < 0.001$, the interaction between level of perceptual richness of pictures and scalp site, $F(3.4, 79.1) = 23.866$, $p < 0.001$) and 300 to 800 ms (the interaction between level of perceptual richness of pictures and scalp site, $F(2.8, 64.4) = 4.810$, $p = 0.005$). In the time window of 100 to 300 ms, ERP activity elicited by photos was more negative-going than ERP activity elicited by outlines over frontocentral scalp sites but more positive-going over occipital scalp sites (Figure 5). In the time window of 300 to 800 ms, the activity elicited by photos was more negative-going over frontal scalp sites but more positive-going over occipital scalp sites than the activity elicited by outlines (Figure 5). In addition, a three-way interaction was found between level of perceptual richness of pictures, scalp sites and time interval (100 to 300 ms, 300 to 800 ms) after scaling the data with the max / min method (McCarthy & Wood, 1985), $F(3.3, 151.5) = 3.157$, $p = 0.023$, which suggests the two effects showed different scalp distributions (Figure 5). Although levels of perceptual richness of a picture did not affect the encoding-related activity of that picture, the overall processes of perceiving two kinds of pictures with different level of perceptual richness were different. This was confirmed when analysing the overall picture-related activity regardless of memory performance. When collapsing recognised pictures and forgotten pictures, there were sufficient trials for non-informative cues. Therefore, ANOVAs with factors of amount of advance information (informative, non-informative) and level of perceptual richness (photo, outline) were done. The same interaction between level of perceptual richness, scalp site and time interval (100 to 300 ms, 300 to 800 ms) was found for the scaled data, $F(2.7, 123.1) = 5.197$, $p = 0.003$.

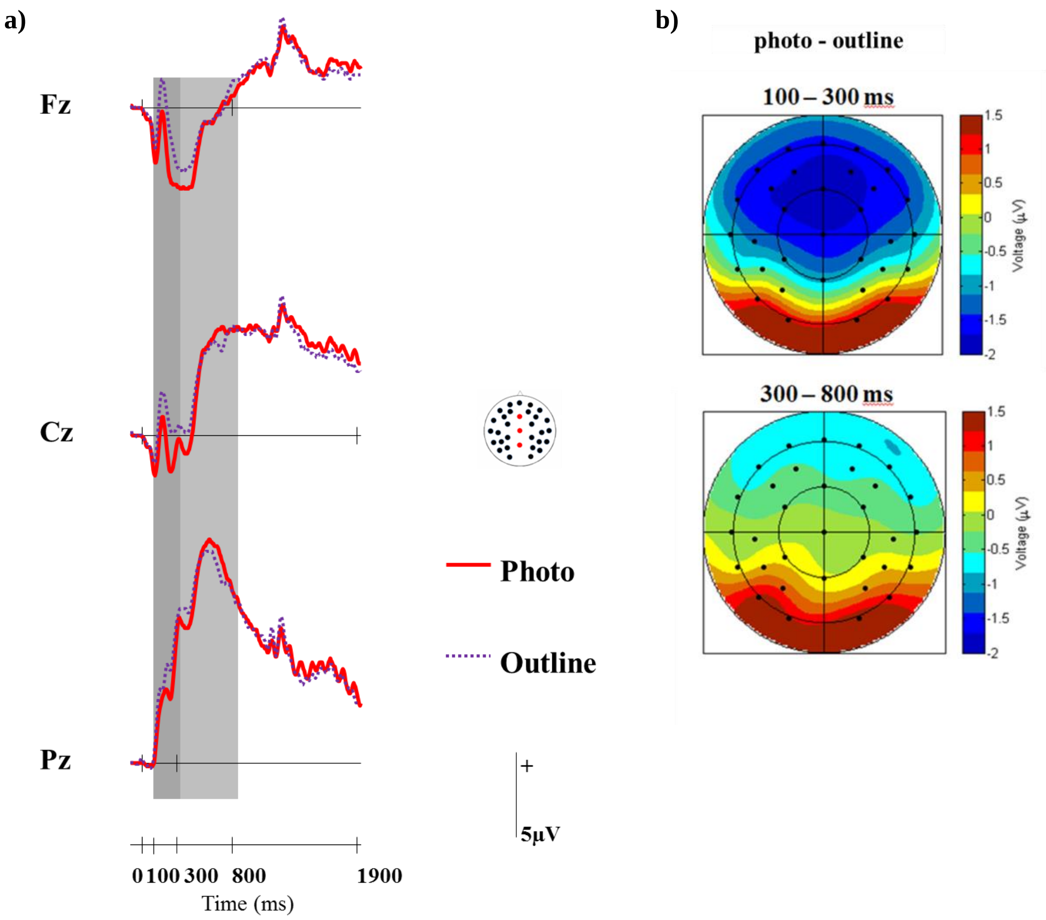


Figure 5. Post-stimulus picture-related activity regardless of memory performance in Experiment 1

a) Group-averaged ERP waveforms elicited by photos and outlines at three midline electrode sites (sites Fz, Cz and Pz from montage 10), where show the trends of the scalp distributions of the differences between picture-related activity elicited by two kinds of pictures. 0 is the time point of picture onset. Positive values are plotted upwards. b) Voltage spline maps showing the distributions of the differences between two kinds of pictures across the scalp in the time windows of 100 to 300 ms and 300 to 800 ms after picture onset. The maps are scaled to the difference between maximum and minimum across conditions to highlight the topographical differences and magnitude of the modulations in each condition.

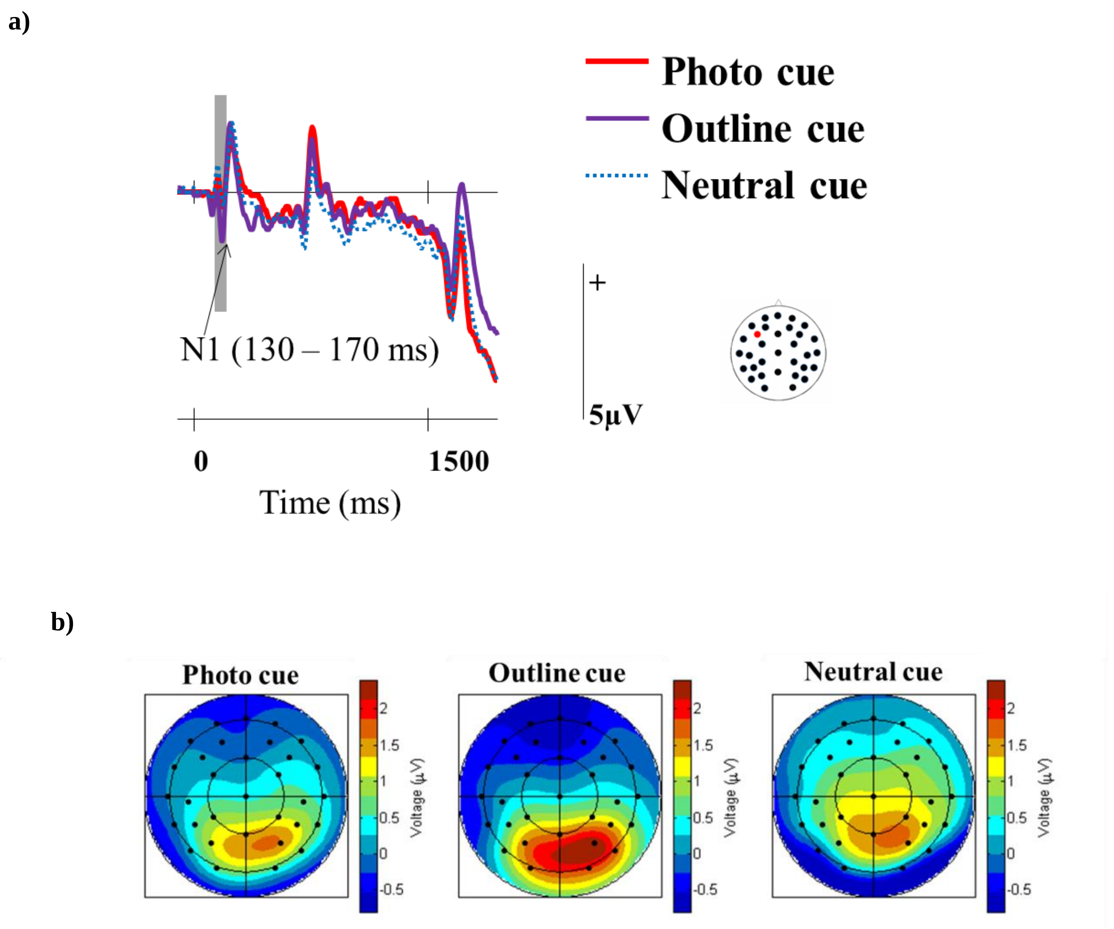


Figure 6. Pre-stimulus overall activity regardless of memory performance in Experiment 1

a) Group-averaged ERP waveforms elicited by three types of cues at a representative temporal electrode site (site 33 from montage 10) where the most visible difference was showed. Positive values are plotted upwards. b) Voltage spline maps showing the distributions of the activity elicited by photo cues (left), outline cues (middle) and neutral cues (right) across the scalp in the 130 to 170 ms time window after cue onset that represents N1 component. The maps are scaled to the difference between maximum and minimum across conditions to highlight the topographical differences and magnitude of the modulations in each condition.

Cue-related activity preceding pictures irrespective of subsequent memory

The picture-related activity showed that participants processed photos and outlines in different ways. Therefore, although no interaction between cue condition and pre-stimulus subsequent memory effect was found, the neural activity elicited by cues indicating different kinds of pictures might differ. The ERPs elicited by photo, outline and neutral cues regardless of subsequent memory performance were analysed. Outline cues elicited a more negative-going ERP waveform than photo cues and neutral cues over frontal scalp electrode sites in an early time window (Figure 6). This negative deflection might reflect modulation of the N1 component that is influenced by attention (Mangun, 1995). N1 was measured in an interval of 130 to 170 ms (e.g. Otten et al., 2010). The analyses revealed a significant interaction between cue condition and scalp site, $F(6.2, 142.9) = 10.1$, $p < 0.001$. The significant interaction was still observed after scaling the data ($p < 0.001$). This result confirmed the observation that outline cues elicited the most negative-going N1 amplitudes than the other two cue conditions over frontal scalp sites (Figure 6).

3.1.4 Discussion

Experiment 1 used an incidental encoding paradigm in which amount of advance information about a visual event was varied to address the question whether encoding-related pre-stimulus activity is dependent on degree of perceptual preparation. ERP results suggest pre-stimulus and post-stimulus subsequent memory effects irrespective of amount of advance information and level of perceptual richness of pictorial stimuli. This indicates that both the preparatory processes for encoding and processes during encoding were not influenced by level of perceptual richness of a to-be-encoded picture. However, ERP results suggest that overall processes on perceptually rich photos and perceptually impoverished outlines were different. This is consistent with the behavioural results. The reaction times to size judgments of outlines were significantly slower than the reaction times to size judgments of photos. In addition, outline cues elicited largest amplitudes in one attention-related component N1. Such results imply that participants might engage more overall preparatory processes for an upcoming outline as the outline was more difficult to make a size judgment.

The pre-stimulus subsequent memory found in Experiment 1 was from 700 to 1100 ms after cue onset irrespective of cue conditions. The effect was more positive-going and not restricted to any specific scalp distribution. It should be noted that there are three other studies showing a similar positive-going pre-stimulus subsequent memory effect. Gruber and Otten used a reward intentional encoding paradigm and words as stimuli (Gruber & Otten, 2010). The other two studies used emotional pictures as stimuli and an incidental encoding task (Galli et al., 2011). It also showed a positive going pre-stimulus subsequent memory effect before negative emotional pictures. Those studies suggest that positive-going widespread pre-stimulus subsequent memory effect might reflect motivational processes, which are different from semantic preparatory processes (Galli et al., 2011). The positive-going pre-stimulus encoding-related activity indicating motivational processes might be able to interpret the individual differences in the preparatory activity for encoding found in Experiment 1. Grand average waveforms show that the ‘prepared group’ (N=9) had a larger and earlier pre-stimulus subsequent memory effect than the ‘non-prepared’ group (N=15) in the photo cue condition. Although the numbers of subjects in the two groups are not sufficient to do statistical analyses, this hints at the possibility the individuals who prepared more had an earlier and larger pre-stimulus subsequent memory effect. In contrast, if participants treated pre-stimulus cues the same, the pre-stimulus subsequent memory effect emerged just right before stimulus onset. The ‘prepared group’ might have stronger motivation to engage preparatory mechanisms for encoding.

Another possible reason why no interaction between pre-stimulus subsequent memory effect and cue condition might be the encoding processes per se were not influenced by amount of perceptual information of a to-be-encoded picture. Therefore, preparatory processes for encoding the picture would also not be influenced by amount of perceptual information. There was no interaction between post-stimulus subsequent memory effect and level of perceptual richness. The post-stimulus subsequent memory effects of photos and outlines were both frontocentrally focused in an extended time window of 300 to 1900 ms, which resembles the classical subsequent memory effect for verbal material in semantic encoding task (e.g. Otten & Rugg, 2001b). This means when participants encoded a photo or an outline, they might just extract their semantic meaning of the object portrayed in the image. An interesting trend was found for Br in the outline condition. Collapsed across confident and unconfident old judgments, the response criterion for outlines tended to be more liberal than for photos. As outlines have fewer perceptual details, fewer distinctive features were included, which might lead to a memory representation of an outline being more similar to an internal representation that already exists (Snodgrass & Corwin, 1988). The encoding of an outline might engage more semantic rather than episodic processing. Similar semantic representations may be activated during retrieval, leading to higher familiarity levels for both old and new items. However, the trend did not reach statistical significance. Moreover, if the higher Br means more semantic processing for the outlines, the typical fronto-central subsequent memory effect should be larger for outlines than photos. The subsequent memory effect did not differ in level of perceptual richness of a picture, which might suggest that the differentiation in processing a photo and an outline was still unable to affect encoding-related ERP activity. Therefore, the preparatory processes could also be similar to semantic preparation, but not differ in the amount of perceptual information. In addition, the positive-going pre-stimulus encoding-related activity might be cancelled out by the neural activity of such semantic preparation that is reflected by a negative-going pre-stimulus subsequent memory effect (e.g. Otten et al., 2006; 2010).

Regardless of subsequent memory performance, there were some hints that participants used advance information to differentially prepare for pictures with different degrees of perceptual details. First, reaction times for pictures after informative cues were faster relative to after non-informative cues when only considering confident recognition judgments. These results are consistent with previous studies that used valid cues to enhance future behaviour (e.g. Bollinger et al., 2010; Uncapher et al., 2011).

However, the comparison between reaction times for pictures after informative cues and pictures after non-informative cues did not differ significantly when all memory categories were included (*p* = 0.072). On the whole, the decision about the size of an object might not be influenced by its physical form or the amount of perceptual information beforehand. Such advance information might not be informative enough, which leads to an unreliable cueing effect. In addition, the difference between reaction times for recognised and forgotten pictures after non-informative cues was larger than informative cues. Subsequently recognised pictures were given faster size judgments than subsequently forgotten pictures when pre-stimulus cues were non-informative. This suggests that when advance information is less informative, encoding a picture may rely on attention in a greater extent than when more advance information about an upcoming stimulus is available. However, this interaction between subsequent memory and amount of advance information did not reach statistical significance either, *p* = 0.088, which suggests that in either informative cue conditions or non-informative conditions, reaction times for the size judgment task did not differ as a function of later memory performance. Therefore, attention should not be a candidate in interpreting the differences between different cue conditions in encoding processes.

Second, both pre-stimulus and post-stimulus ERPs showed significant differences in level of perceptual richness regardless of subsequent memory. Outline cues elicited larger N1 amplitudes than photo cues and neutral cues. The N1 component reflects a selective attention process (Mangun & Hillyard, 1995). The anterior N1 is usually observed in an earlier time window than the posterior N1. Both anterior and posterior N1 components are found to be larger in amplitude for items after valid relatively to invalid cues in the Posner spatial cueing task (Hillyard, Vogel, & Luck, 1998). Hillyard et al. (1998) suggested that the earlier anterior N1 reflects motor preparation for later responses while the posterior N1 might reflect identity discrimination processes in visual search. The N1 was mainly frontally distributed in Experiment 1. Impoverished perceptual richness of the outlines might make these objects most difficult to process. The reaction times of the encoding task can also be used to infer that outlines were more difficult to be recognised.

Larger frontal N1 amplitudes elicited by outline cues might reflect that outline cues were attended to more than the other two kinds of cues in order to engage more motor preparation. The cue-related activity mainly reflects processing of the cue information and ensuing preparation for upcoming items. It is reasonable that no posterior N1 was found as the need to discriminate cue information should be equal. In addition, outlines elicited a more positive-going waveform from 100 to 300 ms after picture onset than photos, which is the time range of P2 component (Luck & Hillyard, 1994). P2 also reflects target-related processes (Luck & Hillyard, 1994). Both pre-stimulus and post-stimulus ERPs suggest that outlines were selected to be paid more attention from a pre-stimulus interval when a cue indicated a presentation of an outline. Therefore, participants used advance information to engage preparatory activity to optimise the performance. It is noted that in a later post-stimulus time window (300 to 800 ms), photos elicited larger amplitudes than outlines over posterior scalp sites. This time window was the same as where one of the post-stimulus subsequent memory effects was found and also reflects P300 component (Sanquist et al., 1980). Compared to P2, P300 reflects activity elicited by a more complex target (Luck, 2005). Differed from the frontocentral subsequent memory effect, the posterior scalp distribution might reflect context updating for photos (Polich, 2012). Compared to outlines, photos had more perceptual information to be processed and updated, which led to larger amplitudes in P300. The other interesting trend for Br was found in photos. Differently from the trend for outlines, the response criterion for photos was more liberal when confident old judgments were made. Although the encoding processes might be less distinctive for photos as they were just daily objects, more perceptual details might make the response to a test probe more confident as more perceptual details might be easier to fit into internal memory representations. Unfortunately, the trend did not reach statistical level, which means that the amount of perceptual details of a picture might not affect confident recognition judgments to a test probe. As a matter of fact, encoding-related ERP activity was not influenced by level of perceptual richness. The perceptual processing differences could not be reflected by encoding processes. Different scalp distributions and no interaction suggest that perceptual processing and encoding seemed to be two independent processes.

In summary, amount of perceptual information does not influence either post-stimulus or pre-stimulus encoding-related activity. However, both pre-stimulus and post-stimulus ERPs irrespective of subsequent memory performance were modulated by amount of perceptual information. The behavioural results also indicate more advance information could enhance performance. Pre-stimulus encoding-related activity is not graded by amount of perceptual information to be prepared. More experiments need to be done to understand how amount of the other kinds of advance information influences encoding-related pre-stimulus activity.

3.2 Experiment 2: The influence of amount of time available before an event on pre-stimulus encoding-related activity

3.2.1 Introduction

Experiment 1 showed a positive-going pre-stimulus subsequent memory effect irrespective of amount of perceptual information. Such positive-going encoding-related pre-stimulus activity might reflect motivational processes (Galli et al., 2011). Experiment 1 indicated that such activity was not influenced by amount of perceptual information to be prepared. It is not clear whether encoding-related pre-stimulus activity is influenced by amount of other kinds of advance information. Experiment 2 addressed a question about whether advance information signalling amount of time available to prepare before an event influences pre-stimulus encoding-related activity.

Experiment 1 manipulated the amount of perceptual information about a to-be-encoded picture to investigate if encoding-related pre-stimulus activity is graded by amount of perceptual information to be prepared. The absence of interaction between the pre-stimulus subsequent memory effect and amount of perceptual information might reflect general preparatory brain signals that are not restricted to strategies (Haynes et al., 2007). Galli et al. (2013) suggested that pre-stimulus activity for memory encoding depends on the opportunity to engage such activity. Preparatory activity for encoding can be investigated by manipulating not only the amount of information about a to-be-encoded stimulus but also the opportunity to engage the activity. Therefore, the amount of preparation time, instead of the stimulus itself, was manipulated in Experiment 2.

As discussed in Chapter 1, the anticipation time is of great interest in the other cognitive domains such as perception or attention. Both behavioural and EEG data shows that when a cue indicates when an upcoming stimulus is coming up, performance and neural activity is enhanced compared to an invalid or a non-informative cue (e.g. Miniussi et al., 1999; Zanto et al., 2011). However, such enhancement is only shown when the cue signals a short interval before the stimulus onset compared to an unexpected short cue-item interval. Miniussi et al. (1999) suggested that participants were able to re-direct their attention to unexpected long cue-item interval once they realised the stimulus was not presented in a short interval. Brain activity can be flexibly engaged in anticipating a target by using the cue information. The tasks that were used in those studies are usually easy perceptual tasks such as detection or discrimination tasks. Therefore, the temporal informative cue just helps raise the attention level to a target at the time point the cue predicts. Such preparatory brain activity might help fine-tune perception for the target (Rohenkohl, Cravo, Wyart, & Nobre, 2012). However, it is not clear whether, in the memory domain preparatory activity for encoding can also be enhanced by a predictable short interval. First, the cue-item interval in Experiment 1 was 1.5 s. No significant interaction was found to support that 1.5 s was sufficient to prepare for encoding a greyscale photo. Second, Galli et al. (2013) used divided attention tasks to manipulate the level of cognitive resources in a pre-stimulus interval. A difficult divided attention was also slower to be made a judgment so that less preparation time was left before item onset. This study indirectly suggests that engagement of preparatory activity for encoding might need sufficient time.

To address whether amount of time available to prepare influences encoding-related pre-stimulus activity; two durations for preparation were used. One was 1.5 s or short and the other was 3 s or long. An informative cue indicated the length of a cue-item interval. Participants might have more opportunity to engage preparatory activity in a long interval for memory encoding. A non-informative cue did not indicate the length of the cue-item interval. Therefore, participants did not know how much opportunity they would have to engage preparatory activity for encoding. Greyscale photos were used as experimental stimuli as encoding-related preparatory activity for photos was the most visible among three cue conditions in Experiment 1, although statistically it did not reveal any significant effect. As encoding-related preparatory activity did not merely reflect attention (Otten et al., 2006), a temporal informative cue signalling more opportunity to engage preparatory activity for encoding rather than a temporal informative cue signalling a short interval was expected to elicit significant encoding-related activity. As brain activity can be quite flexible for using cue information to prepare (Miniussi et al., 1999), participants might wait until no presentation of a target and re-engage preparatory activity in an unpredictable long interval.

3.2.2 Methods

Participants. The experimental procedures were approved by the University College London Research Ethics Committee. 24 healthy adults were paid at a rate of £7.50/h to take part. The mean age was 22 years (range of 18-29 years) and 15 of them were female. They met all the criteria described in Experiment 1.

Stimulus Material. Stimuli were randomly selected from the same pool of pictures as used in Experiment 1. The only difference was that all the pictures were greyscale photographs. Pictures were assigned the same way as in Experiment 1. Four sets of 84 pictures (336 critical items) were pseudo-randomly selected to create a study list and the remaining two sets of 84 pictures (168 unstudied items) were joined to create a test list (504 critical items in total). There were 24 additional filler items (16 items for the study phase and an additional 8 unstudied items for the test phase). The numbers of pictures in each pre-stimulus cue condition were ¼ of the number of whole pictures. 84 pictures followed predictable short intervals. 84 pictures followed predictable long intervals. 84 pictures followed unpredictable short intervals and 84 pictures followed unpredictable long intervals.

All pictures were presented in central vision on a white background using the Cogent 2000 Toolbox (Wellcome Laboratory of Neurobiology:

http://www.vislab.ucl.ac.uk/cogent.php) and MATLAB (The MathWorks, Inc.). During the study phase, each picture was preceded by a cue that indicated how long a participant would have to wait until a picture came up. If the cue was an ‘S’ (short) a picture would come up after 1.5 s. If the cue was an ‘L’ (long) a picture would come up after 3 s. If the cue was an ‘N’ (non-informative or neutral) the cue-picture interval would either be 1.5 s or 3 s. All three kinds of cues were written in red and presented for 500 ms, followed by a fixation cross until picture onset. Pictures were presented for 500 ms followed by a fixation cross. Trials with long cue-picture intervals had a variable duration that varied randomly between 5 and 6.5 s. Trials with short cue-picture intervals had a variable duration from 3.5 to 5 s. During the test phase, the procedure was similar to that in the study phase except that the temporal cues were replaced by exclamation marks. An exclamation mark just signalled the upcoming picture as a neutral warning. The duration between exclamation mark and a picture was 1.5 seconds. Each trial had a variable duration between 3.5 to 5 s.

15 participants had a study list and a test list with the same sequence of cue conditions due to a programming mistake when assigning conditions to pictures. In the study and test lists, condition codes were randomly assigned therefore participants were not able to predict the condition of each trial. The programming mistake made this one random sequence of condition codes assigned to those 15 participants instead of changing the sequence for each participant. However this should not cause any order effect as the probability to see each condition was totally random across the sequence. In addition, orders of the pictures were changed for each participant so that the effects found in the current experiment were not caused by processing on a particular picture either.

Procedure. The experimental procedure was generally the same as in Experiment 1. Pilot experiments were done to adjust the delay between study and test phases to get participants' performance to acceptable levels. When study and test phases were run on the same day with short delays (immediately and after 30 min), the numbers of forgotten trials were too few for most participants (8 out of 12 participants). Therefore, the two sessions were run on separate and consecutive days in Experiment 1. In Experiment 2, response speed to the encoding task (size judgment task) was emphasized. Participants were encouraged to use cues to prepare their responses during the cue-item interval and asked to respond as fast as possible.

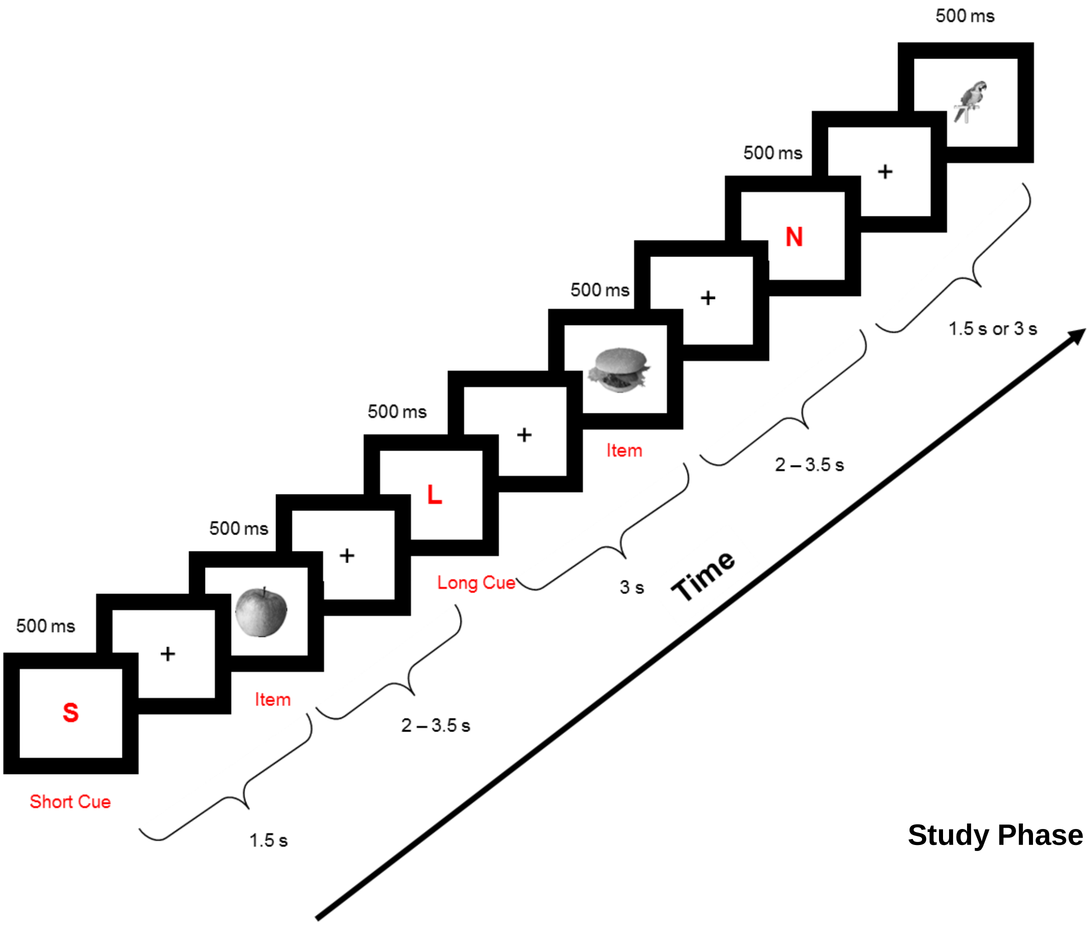


Figure 7. Experimental procedure of study phase in Experiment 2

The study phase was similar to that in Experiment 1. An informative cue indicated the time before the upcoming picture. A non-informative cue was followed by either a short or a long cue-picture interval. The incidental encoding task during the study phase was a size judgment task.

EEG acquisition. The EEG was only recorded on the first day. The EEG was recorded from 37 scalp sites using silver/silver-chloride electrodes fitted in an elastic cap. Compared to the montage used in Experiment 1, four central sites were added to capture CNV activity, which is suggested to be largest over frontocentral scalp sites in previous literature (e.g. Walter et al., 1964). An additional occipital site was also added to cover more occipital scalp areas. Other details about the EEG acquisition were the same as in Experiment1.

EEG analyses. Offline, the data were digitally filtered between 0.05 and 20 Hz (96 dB roll off) and algebraically re-reference to linked mastoids (reinstating the online reference site). The continuous EEG elicited by cues was downsampled to 1 point/13 ms (around 77Hz) and segmented separately into epochs of 3312 ms duration including a 100 ms baseline before cue onset. The EEG elicited by pictures was downsampled to 1 point/8ms (125Hz) and segmented into epochs of 2048 ms duration including a 100 ms baseline before picture onset. The way to categorise the epochs for computing subsequent memory effect was similar to Experiment 1. But here, the epochs of 'old sure' and 'old unsure' judgments were collapsed into one 'old' category. Since there were not sufficient artefact free trials for all subjects if 'old sure' judgments were considered in isolation. The artefact corrections were done with the same criteria as described in Experiment 1. There were at least 15 artefact free trials in each condition for each subject's ERPs.

The main analyses focused on the comparisons of ERP waveforms between later recognized and later forgotten trials separately, for activity elicited by cues and pictures. The comparisons between cues regardless of memory performance were also of interest to see how pre-stimulus cues were used by subjects. As discussed in Chapter 1, the CNV component is an index of preparation for motor responses and attention on an upcoming stimulus. Therefore, the CNV was also of interest. The CNV was computed in a time window of 300 ms before picture onset in both cue intervals as this time interval showed largest negativity even in the short cue interval. Mean amplitudes in this time window were averaged from five central electrodes (sites Cz, 3, 4, 6, 7 from montage 10) as the CNV is usually reported to be largest over frontocentral scalp sites (Brunia, 1988). Additional analyses based on classifying 'old sure' as 'recognized' were also done for 15 subjects who had more than 15 'old sure' artefact free trials to see if there was any qualitative differences between these two confidence judgments. Studied trials were classified as 'forgotten' if they were given a non-confident new judgment or confident new judgment as described in Experiment 1. For all comparisons except 'old sure' vs. 'forgotten', mean ERP waveforms were created for 24 subjects in each condition. Mean ERP waveforms were created for 15 subjects in each condition for 'old sure' vs. 'forgotten' comparison. Mean trial numbers in each condition are shown in Table 6. Repeated measures analysis of variance (ANOVAs) was used incorporating the Greenhouse-Geisser correction for violations of sphericity (Keselman & Rogan, 1980). The ANOVAs were based on all 37 electrodes.

Table 6. Mean trial numbers in each condition for pre-stimulus ERPs in Experiment 2 (Range in brackets)

	Predictable short	Predictable long	Unpredictable short	Unpredictable long
Recognized trials	44 (25-64)	44 (29-64)	43 (27-57)	44 (24-62)
Forgotten trials	27 (16-44)	26 (16-53)	27 (18-43)	26 (18-48)

Table 7. Mean trial numbers in each condition for post-stimulus ERPs in Experiment 2 (Range in brackets)

	Predictable short	Predictable long	Unpredictable short	Unpredictable long
Recognized trials	47 (25-67)	47 (25-63)	47 (32-59)	45 (25-61)
Forgotten trials	29 (16-44)	26 (15-43)	29 (19-47)	27 (17-43)

3.2.3 Results

Task Performance

Study. Performance for the study phase is summarized in Table 8. The analyses used ANOVA with repeated measure factors of amount of advance information (informative, non-informative) and amount of time (short 1.5s, long 3s). Reaction times in the informative cue condition were significantly faster than reaction times in the non-informative cue condition, $F(1, 23) = 12.488$, $p = 0.002$. There was no interaction between amount of advance information and amount of time (all other *p*s > 0.8). Accuracy of the size judgment task revealed an interaction between amount of advance information and amount of time, $F(1, 23) = 8.821$, $p = 0.007$. Follow-up pair-wise comparisons showed that the accuracy of size judgment after a predictable short interval was significantly better than the accuracy of predictable long condition, $t(23) = 2.76$, $p = 0.011$. Reaction times of the size judgment task were also categorised by subsequent memory performance (see Table 9). ‘Confident old’ and ‘unconfident old’ were collapsed into a ‘recognised’ category and ‘confident new’ and ‘unconfident new’ were collapsed into a ‘forgotten’ category to be consistent with ERP results. A main effect of amount of advance information was found, $F(1, 23) = 11.438$, $p = 0.003$, which is consistent with the previous ANOVAs. A main effect of subsequent memory was also found. The reaction times for the subsequently recognised items were significantly faster than those for the subsequently forgotten items, $F(1, 23) = 6.077$, $p = 0.022$.

Table 8. Study task performance in Experiment 2

		Predictable short	Predictable long	Unpredictable short	Unpredictable long
Accuracy	M	0.82	0.80	0.81	0.82
(proportion)	SD	0.05	0.06	0.05	0.05
Response	M	807	805	823	824
times (ms)	SD	148	145	149	154

Values are across-subject means. n=24.

Table 9. RTs in study task categorised by subsequent memory performance in Experiment 2

	Predictable short		Predictable long		Unpredictable short		Unpredictable long	
	old	new	old	new	old	new	old	new
Response M	828	830	823	838	835	853	835	850
times (ms) SD	157	160	151	165	145	166	155	169

Values are across-subject means. n=24.

Test. Recognition memory performance is summarized in Table 10. The analyses did not show any significant effect in terms of amount of advance information, amount of time or their interactions in either Pr or Br across all four conditions regardless of recognition confidence. Pr in the predictable short condition was 0.33, in the predictable long 0.34, in the unpredictable short condition 0.34 and in the unpredictable long 0.34 (all ps > 0.4). For Br, the corresponding values were 0.43, 0.44, 0.43, 0.43 (all ps > 0.3). For confident old hits, the discriminations between old and new items were significantly greater than zero, $p \leqslant 0.001$. In addition, for unconfident old hits, the discriminations between old and new items were significantly greater than zero, all ps $\leqslant 0.005$, which suggests that the unconfident old judgments reflected reliable memory in Experiment 2. Thus, collapsing unconfident old trials and confident old trials into one recognised response category for the ERP analyses should not decrease power for the analyses. Reaction times for old sure judgments or for old judgments (collapsing old sure and old unsure to be consistent with ERP analyses) did not differ in either amount of advance information or amount of time, all ps > 0.5. Reaction times for the confident old judgments were significantly faster than reaction times for the unconfident old judgments, $p < 0.001$, which is consistent with the result in Experiment 1.

Table 10. Recognition memory performance in Experiment 2

Condition	Recognition Type			
	Confident old	Unconfident old	Unconfident new	Confident New
Proportion of responses				
Old				
Predictable short	0.35 (0.17)	0.27 (0.15)	0.23 (0.11)	0.15 (0.12)
Predictable long	0.37 (0.15)	0.27 (0.15)	0.23 (0.10)	0.14 (0.12)
Unpredictable short	0.37 (0.15)	0.25 (0.13)	0.23 (0.10)	0.15 (0.09)
Unpredictable long	0.36 (0.14)	0.27 (0.15)	0.23 (0.11)	0.14 (0.12)
New	0.10 (0.08)	0.20 (0.08)	0.40 (0.17)	0.32 (0.20)
Mean reaction time (ms)				
Old				
Predictable short	1031 (121)	1281 (273)	1301(343)	1144 (241)
Predictable long	1041 (131)	1282 (285)	1299 (294)	1192(268)
Unpredictable short	1038 (118)	1307(296)	1280 (319)	1140(262)
Unpredictable long	1039 (127)	1288 (276)	1295(326)	1164 (217)
New	1121(209)	1312 (315)	1273 (282)	1157 (220)

Values are across-subject means (SD). n=24. The reaction times shown above are based on 24 participants except predictable short confident new judgments, predictable long unconfident old judgments and confident new judgments, unpredictable short confident new judgments, unpredictable long unconfident old judgments, new pictures unconfident old judgments, which are based on 23 participants as one participant did not have any trials for the above conditions, unpredictable long confident new judgments, which are based on 22 participants as two participants did not give any button press for that condition.

Summary of behavioural findings

More advance information led to significantly faster decisions in the size judgment encoding task, irrespective of amount of preparation time. In the recognition test, no significant effects were found for either Pr or Br.

Encoding-related activity preceding pictures

Neural activity related to successful encoding was identified by the subsequent memory paradigm. Additional analyses were done for comparison between ‘old sure’ and collapsing ‘new sure’ and ‘new unsure’ judgments for 15 subjects. However, the findings were similar to what was found in the contrast between ‘old’ (collapsing ‘old sure’ and ‘old unsure’) and ‘new’ (collapsing ‘new sure’ and ‘new unsure’). Figure 8 shows grand average waveforms at a frontal electrode and a parietal electrode elicited by cues preceding items that were later recognized and forgotten in each condition. From the grand average waveforms, only the predictable long and unpredictable long cue conditions show a pre-stimulus subsequent memory effect. The activity elicited by predictable and unpredictable long cues was more positive-going before later recognized pictures than later forgotten pictures. From the grand average waveforms, this effect started from 300 ms onwards (see Figure 8) in the predictable long cue condition. According to the spline maps (Figure 8b, 8c), the effect was most pronounced over frontal scalp sites in the predictable long cue condition, while the effect was more specific to parietal scalp sites in the unpredictable long cue condition.

ANOVAs are based on all 37 scalp sites. Mean amplitudes were calculated in the intervals of 300 – 700 ms, 700 – 1100 ms, 1100 – 1500 ms, to be consistent with Experiment 1. As after 1500ms, only predictable and unpredictable long cue conditions were still in cue-item interval, analyses of intervals after 1500ms were based only on those two conditions. Mean amplitudes were calculated in 300 ms time windows from 1500 ms onwards i.e. 1500 – 1800 ms, 1800 – 2100 ms, 2100 – 2400 ms, 2400 – 2700 ms, 2700 – 3000 ms. No significant effect was found for the three intervals before 1500 ms (all *p*s > 0.05). An interaction between amount of time and pre-stimulus subsequent memory effect was found to approach significant in the 300 – 700 ms time window, $F(1, 23) = 4.275$, $p = 0.05$. Subsidiary analyses on each cue length showed a significant effect of pre-stimulus subsequent memory only in the long cue conditions irrespective of amount of advance information, $p = 0.025$. A marginal significant pre-stimulus subsequent memory effect was found in the interval of 700 – 1100 ms, $F(1, 23) = 4.303$, $p = 0.05$. A waveform preceding remembered items was more positive-going than a waveform preceding forgotten items. No further interaction was found, which replicated the findings in Experiment 1.

From 1500 ms onwards, a main effect of pre-stimulus subsequent memory was found in each 300 ms time window (see Table 11). In the interval of 1500 – 1800 ms, a significant interaction between amount of advance information and scalp site was found after the Greenhouse-Geisser correction, $F(3.9, 90) = 3.168$, $p = 0.018$. A three-way interaction between pre-stimulus subsequent memory effect, amount of advance information and scalp site was found in the interval of 1800 – 2100 ms, $F(4.8, 110.9) = 2.446$, $p = 0.04$. The interaction in the interval of 1800 – 2100 ms approached significant, $p = 0.058$, after scaling the data. Further analyses were done to 28 scalp sites that allow dividing the scalp to into anterior-posterior and left-right regions (Galli et al., 2011; see Figure 9) to understand the scalp distributions of the interactions. ANOVAs showed that a significant interaction was found between amount of advance information and scalp anterior-posterior position in the 1500 – 1800 ms interval, $p = 0.018$. The interaction was still significant after scaling the data ($p = 0.037$), which demonstrates that a waveform elicited by predictable long cues were more positive-going than a waveform elicited by unpredictable long cues over posterior sites, irrespective of subsequent memory performance (see Figure 10). A significant three-way interaction was found between pre-stimulus subsequent memory, amount of advance information and scalp anterior-posterior position in the 1800 – 2100 ms interval after scaling the data, $p = 0.032$. Subsidiary analyses on each scalp position and each cue condition were done to understand the interaction. A significant pre-stimulus subsequent memory effect was found in the anterior scalp position in the predictable long cue condition, $p = 0.03$, while a significant pre-stimulus subsequent memory effect was found in the posterior scalp position in the unpredictable long cue condition, $p = 0.049$, which confirms the scalp distributions of two different pre-stimulus subsequent memory effects in the predictable and unpredictable cue conditions (Figure 8).

After 2100 ms, there were no further interactions found (all *p*s > 0.15). ANOVAs were done with factors of subsequent memory (recognised, forgotten), scalp site (37 sites) and time interval (2100 – 2400 ms, 2400 – 2700 ms, 2700 – 3000 ms). A main effect of pre-stimulus subsequent memory was found through the three time intervals, $p < 0.001$. No interaction or main effect of time interval was found, which means a sustained positive-going pre-stimulus subsequent memory effect started from 900 ms before picture onset (both *p*s > 0.35).

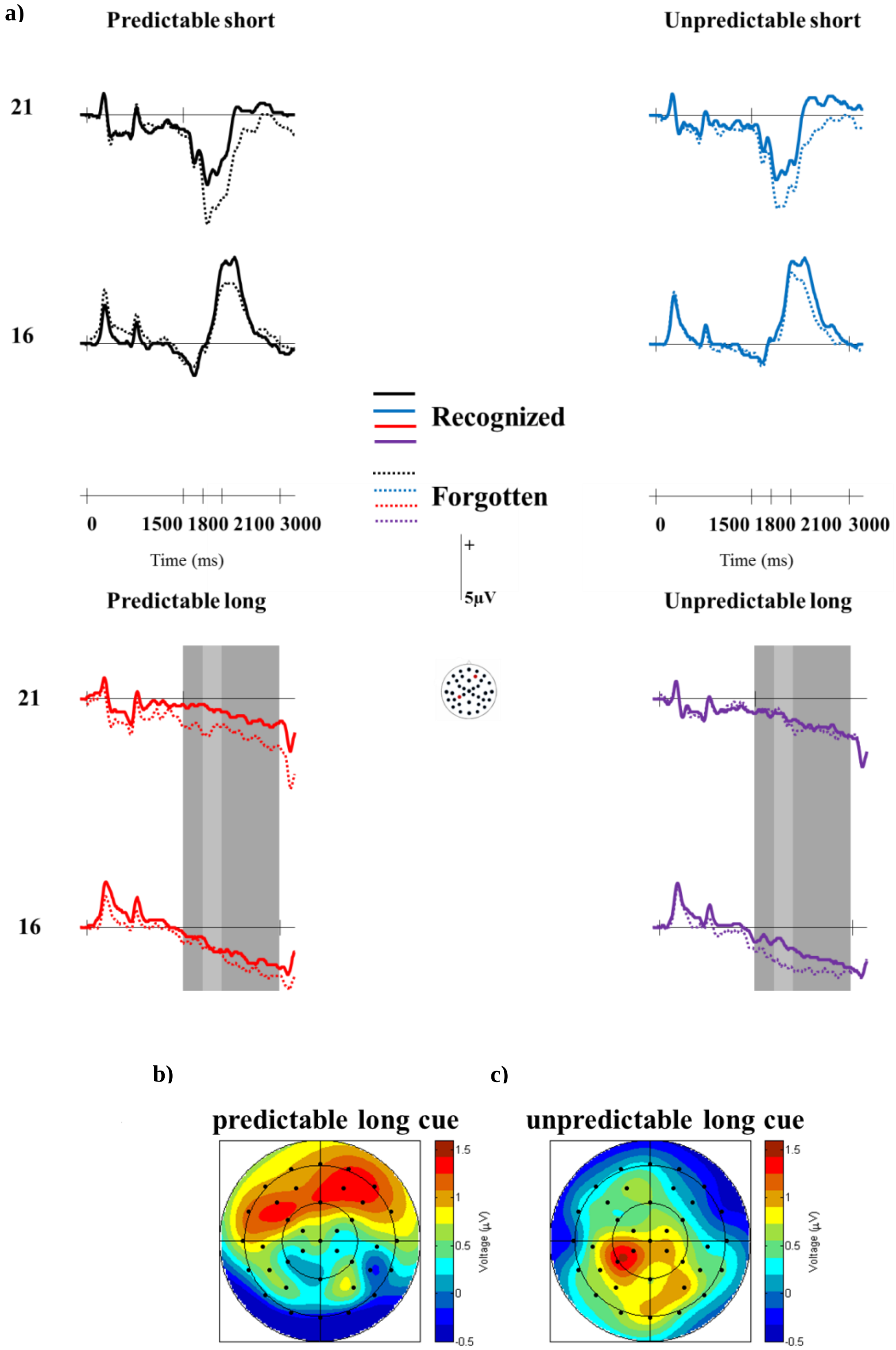


Figure 8. Pre-stimulus subsequent memory effect in Experiment 2

a) Group-averaged ERP waveforms elicited by pre-stimulus cues at two representatives frontal electrode sites (site 21 front and site 16 back from montage 10, www.easycap.de/easycap/e/electrodes/13_M10.htm), where showed the largest positive-going pre-stimulus subsequent memory effects in the two long preparation time conditions. Positive values are plotted upwards. Waveforms were low pass filtered at 12.9 Hz for graphical purposes. b) Voltage spline map showing the distribution of the subsequent memory effect across the scalp in the 1800 ms to 2100 ms after predictable long cue onset. The pre-stimulus subsequent memory effect showed a positive, frontally maximum distribution. c) As in b, but the effect shown here is from the unpredictable long cue condition. The pre-stimulus subsequent memory effect was positive-going over parietal scalp sites. The maps are scaled to the difference between maximum and minimum across conditions to highlight the topographical differences and magnitude of the modulations in each condition.

Table 11. F statistics and p values of pre-stimulus subsequent memory effects in all the intervals after 1500 ms in Experiment 2

Time Interval	F	p
1500 – 1800 ms	F(1, 23) = 4.804	p = 0.039
1800 – 2100 ms	F(1, 23) = 7.959	p = 0.010
2100 – 2400 ms	F(1, 23) = 8.144	p = 0.009
2400 – 2700 ms	F(1, 23) = 6.785	p = 0.016
2700 – 3000 ms	F(1, 23) = 6.371	p = 0.019

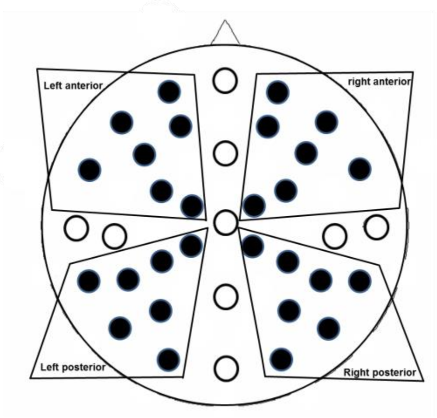


Figure 9. The 28 scalp electrodes used for the ANOVAs

Scalp sites were separated into four quadrants: left anterior, right anterior and left posterior, right posterior. The sites used in the analyses are in black.

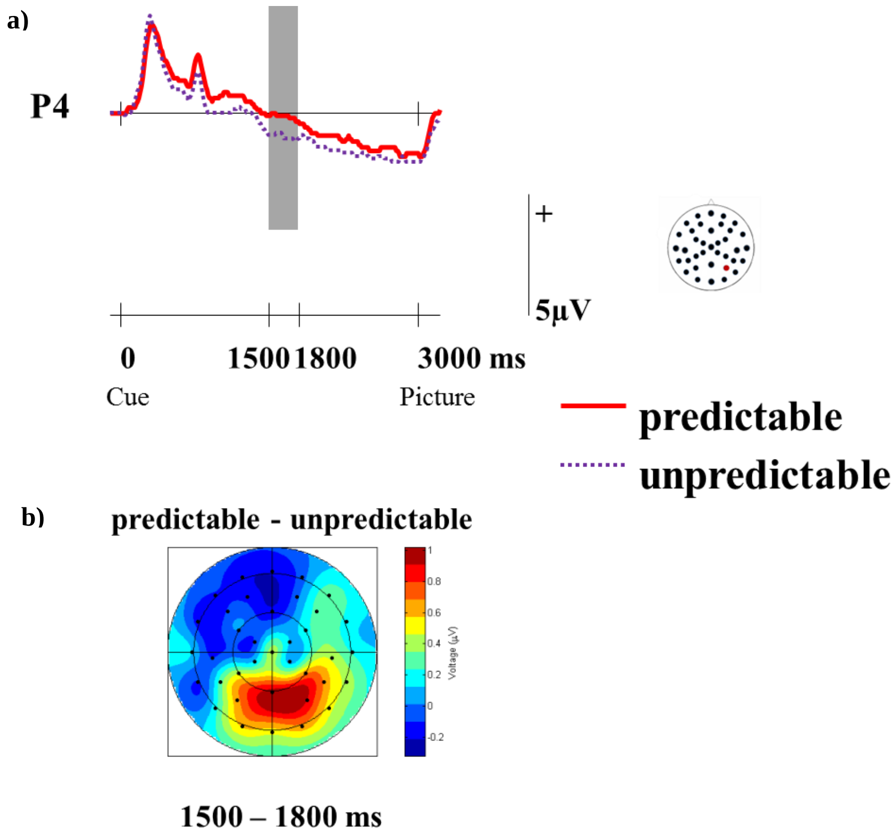


Figure 10. Pre-stimulus overall activity in long cue intervals regardless of memory performance

a) Group-averaged ERP waveforms elicited by predictable long and unpredictable long cues at a representative parietal electrode site (site P4 from montage 10) where showed the largest cue-related differences between the predictable long and the unpredictable long cue conditions. Positive values are plotted upwards. Waveforms were low pass filtered at 12.9 Hz for graphical purposes. b) Voltage spline map showing the distribution of the difference between two cue conditions across the scalp in the 1500 ms to 1800 ms after cue onset. The predictable long cue elicited a more positive-going activity over parietal scalp sites.

Encoding-related activity after pictures

Encoding-related neural activity elicited by pictures was also assessed with the subsequent memory approach to see if amount of preparation time and amount of advance information would affect post-stimulus activity. The effects were similar to the findings in the Experiment1 that a more positive-going waveform was elicited by later recognized pictures than forgotten pictures over frontocentral scalp sites. The effects were pronounced in all four cue conditions (Figure 11).

ANOVAs were based on all 37 scalp electrodes. To be consistent with Experiment 1, intervals of 100 to 300 ms, 300 ms to 800 ms, 800 ms to 1100 ms, 1100 ms to 1900 ms were chosen. The main subsequent memory effects were found in the two intervals starting from 300 ms (300 – 800 ms, $F(1, 23) = 26.420$, $p < 0.001$, 800 –

1100 ms, $F(1, 23) = 16.982$, $p < 0.001$). For all the four intervals, interactions between subsequent memory and scalp sites were found after the Greenhouse-Geisser correction (all ps < 0.001, see Table 12). These interactions confirmed the observation of a fronto-central scalp distribution of the subsequent memory effect in all four cue conditions (Figure 11b), which was consistent with the findings in Experiment 1 and previous studies (Galli et al., 2011; Otten & Rugg, 2001b). Differently from Experiment 1, an ANOVA that incorporated factors of subsequent memory (recognised, forgotten), scalp site (37 sites) and time interval (100 to 300 ms, 300 to 800 ms, 800 to 1100 ms, 1100 to 1900 ms) revealed a significant interaction between subsequent memory, scalp site and time interval after scaling the data, $p < 0.001$. This suggests that the subsequent memory effects found in the four intervals were four separate effects.

Three-way interactions between subsequent memory effect, scalp site and amount of advance information were found in the earliest (100 – 300 ms) and latest time windows (1100 – 1900 ms). In the earliest time window (100 – 300 ms), significant subsequent memory effects were showed only when the cues were informative, irrespective of amount of preparation time, $F(3.8, 86.3) = 2.847$, $p = 0.032$. In the time window of 1100 – 1900 ms, the frontocentral subsequent memory effects in the predictable cue conditions were significantly larger than the effects in the unpredictable cue conditions, regardless of amount of preparation time, $F(6.3, 145.4) = 2.694$, $p = 0.015$. The interaction was still significant after scaling the data for the later time window 1100 – 1900 ms, $p = 0.034$, which demonstrates a reliable scalp distribution difference between the subsequent memory effects in the predictable cue conditions and the effects in the unpredictable cue conditions (see Figure 11).

Table 12. F statistics and p values of interactions between post-stimulus subsequent memory effect and scalp site in all the intervals in Experiment 2

Time Interval	F	p
100 – 300 ms	$F(3.7, 84.6) = 7.095$	$p < 0.001$
300 – 800 ms	$F(4.2, 97.2) = 22.026$	$p < 0.001$
800 – 1100 ms	$F(4.5, 102.6) = 10.237$	$p < 0.001$
1100 – 1900 ms	$F(5.7, 132.0) = 9.760$	$p < 0.001$

Degrees of freedom and p values are after the Greenhouse-Geisser correction.

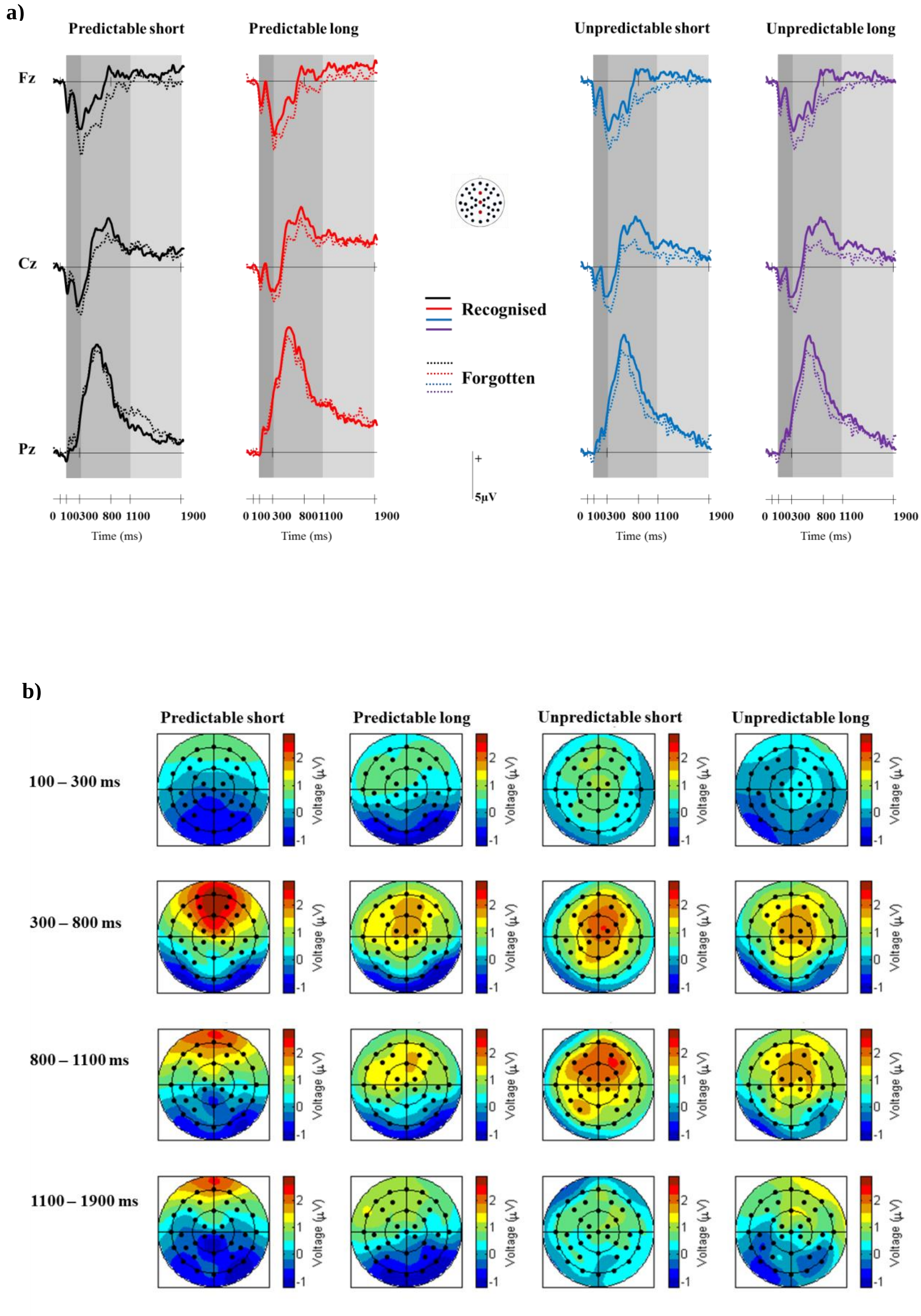


Figure 11. Post-stimulus subsequent memory effect in Experiment 2

a) Group-averaged ERP waveforms elicited by pictures at three midline electrode sites (sites Fz, Cz and Pz from montage 10) where show the trends of the frontocentral subsequent memory effects in the four conditions. Positive values are plotted upwards. b) Voltage spline maps showing the distributions of the subsequent memory effects across the scalp in the 100 ms to 300 ms, 300 ms to 800 ms, 800 ms to 1100 ms and 1100 ms to 1900 ms time windows after picture onset. The subsequent memory effects showed positive, frontocentral maximum distributions. The maps are scaled to the difference between maximum and minimum across conditions to highlight the topographical differences and magnitude of the modulations in each condition.

Relationship between reaction time of encoding task and CNV

As discussed above, the CNV amplitudes reflect attention and preparation for stimulus responses. The CNV amplitudes are significantly more negative before stimulus onset for predictable short time interval than an unpredictable short time interval, which suggests that participants used the cue information to direct their attention (Miniussi et al., 1999; Zanto et al., 2011). The ANOVAs were first based on all the scalp sites to compare the mean amplitudes of all four cue conditions in 300 ms before stimulus onset. No significant difference was found in amount of advance information (all ps > 0.4). The mean amplitudes in the long cue conditions were significantly more negative than the mean amplitudes in the short cue conditions regardless of amount of advance information, $F(1, 23) = 44.752$, $p < 0.001$. The longer a cue interval was the more negative mean amplitudes were. Then, the CNV amplitudes were calculated by mean amplitudes of five central scalp sites in 300 ms before item onset as mentioned in the Methods section. The CNV amplitudes were significantly less than zero in all four cue conditions (see Table 13). No significant difference was found in the mean amplitudes of selected central scalp sites (Figure 11) in terms of amount of advance information (all ps > 0.2). Longer cue intervals had more negative CNV amplitudes than shorter cues intervals, $F(1, 23) = 40.148$, $p < 0.001$. In addition, larger CNV is found before stimuli that preceded faster responses, which suggests that CNV negativity reflects preparation for motor responses (Brunia & Vingerhoets, 1980; Hillyard, 1969). Therefore, reaction times of the size judgment task and CNV amplitudes were analysed by Bivariate Correlations for each cue condition across subjects. Positive correlations were found in the unpredictable short cue condition and predictable long conditions (Figure 12). The faster responses a subject made in those two conditions, the larger CNV they had (unpredictable short, Pearson's $r = 0.444$, $p = 0.030$, predictable long, Pearson's $r = 0.458$, $p = 0.024$).

Table 13. CNV amplitudes (μv) and one-sample t-test t values and p values

	Predictable short	Predictable long	Unpredictable short	Unpredictable long
M	-0.89	-3.13	-0.98	-2.73
SD	2.05	2.72	1.66	2.34
t	-2.13	-2.89	-5.63	-5.72
p	0.044	0.008	<0.001	<0.001

Values are across-subject means. n=24.

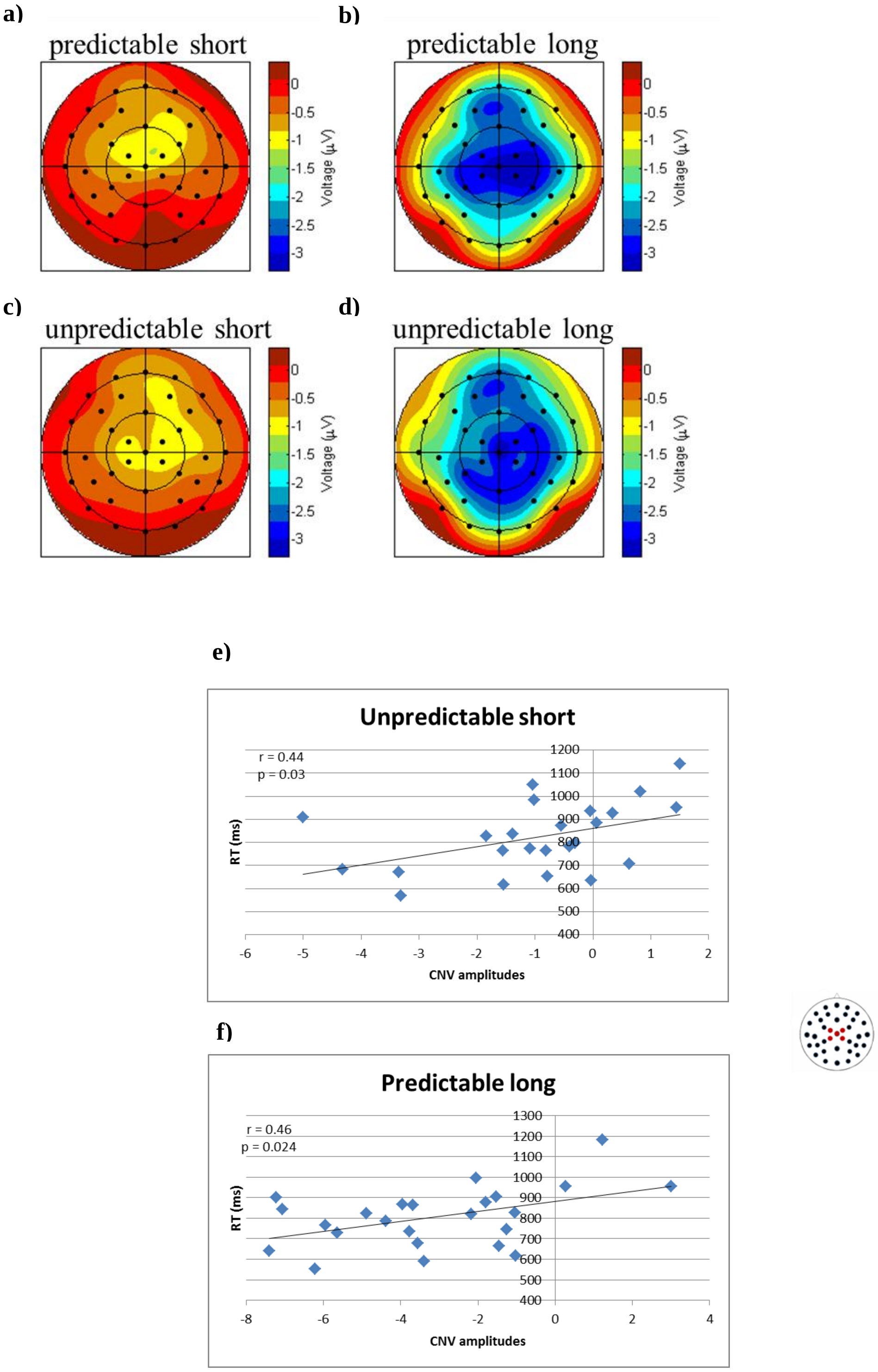


Figure 12. Relationship between reaction time of encoding task and CNV amplitudes

a) Voltage spline map showing the distribution of the amplitudes in the predictable short cue condition across the scalp 300 ms before picture onset. b) As in a, but shown here is from the predictable long cue condition. c) As in a, but shown here is from the unpredictable short cue condition. d) As in a, but shown here is from the unpredictable long cue condition. The maps are scaled to the difference between maximum and minimum across conditions to highlight the topographical differences and magnitude of the modulations in each condition. e) The correlation between CNV amplitudes and task RT in the unpredictable cue condition. Each blue point represents the one participant. X-axis represents CNV amplitudes (mean amplitudes of five central electrodes shown on the left in the 1200 – 1500 ms time window). Y-axis represents reaction times of the size judgment task. f) As in e, but shown here is from the predictable long condition.

3.2.4 Discussion

In Experiment 2, an informative pre-stimulus cue indicated the amount of time before an event. A cue-picture interval could be as long as 3 s or as short as 1.5 s. Non-informative cues did not give temporal information about the intervals. ERPs before picture onset predicted later memory of the picture, but only when the cue interval was long. The encoding-related pre-stimulus activity started from 1500 ms. In an early time window, the pre-stimulus subsequent memory effect was found over anterior scalp sites for the predictable long cue condition while the effect in the unpredictable long conditions was over posterior scalp sites. After 2100 ms, no interaction between cue predictability and subsequent memory or scalp distribution was found. The activity persisted until picture onset.

In Experiment 2, sustained negative deflections were found before stimulus onset in all of the cue conditions. Response speed was emphasised in Experiment 2, which might enable the paradigm to be more similar to the classic S1-S2 paradigm (Järvilehto & Fruhstorfer, 1970; Walter et al., 1964). The more negative CNV amplitudes correlated with faster reaction times in the predictable long cue and unpredictable short cue conditions across subjects. These suggest that CNV as a neural measure does serve a role in preparatory process for upcoming events. Different from previous studies (Miniussi et al., 1999; Zanto et al., 2011), the CNV amplitudes shown here were only affected by amount of time but not amount of advance information. Behaviourally, reaction times were faster after both predictable intervals than after unpredictable intervals, regardless of amount of time. These findings suggest that participants in Experiment 2 might not deploy their attentional resources to only a stimulus after a predictable short interval. In addition, reaction times of size judgment for subsequently recognised pictures were significantly faster than them for subsequently forgotten pictures. A waveform preceding subsequently recognised pictures was more positive-going than a waveform preceding subsequently forgotten pictures, which is opposite to that CNV negativity predicts faster reaction times for stimuli responses. Therefore, preparatory processes for encoding found in Experiment 2 could not be simply explained by negative shifts or CNV.

The findings in Experiment 2 replicated the findings in Experiment 1. First, the positive-going pre-stimulus subsequent memory effect is similar to the pattern in Experiment 1. In terms of its direction, the effect in Experiment 2 is also similar to findings in Galli et al. (2011) and Gruber and Otten (2010). Compared to these findings, the pre-stimulus subsequent memory effect in Experiment 2 started quite late and was more sustained. The latency of the effect in Experiment 2 might be more comparable with findings from Otten et al. (2006). In Experiment 1 of their study, a 2.7 s cue-word interval was used. The pre-stimulus subsequent memory effect developed gradually and persisted until word onset. Such sustained and gradually built encoding-related pre-stimulus activity right before item onset might suggest a preparatory brain state for successful encoding (Yoo et al., 2012). Second, the pre-stimulus subsequent memory effect before 1.5 s was subtle, which suggests that 1.5 s might not be sufficient for engaging pre-stimulus activity in preparing for encoding a pictorial stimulus in Experiment 1. Previous studies demonstrated a solid pre-stimulus subsequent memory effect in a cue interval of 1.5 s (Galli et al., 2011; Otten et al., 2006; 2010) in encoding of words and emotional memory. But it was unknown whether the time is sufficient to prepare for forming a memory for objects of greyscale photographs used in Experiments 1 and 2, which might involve perceptual processes to a greater extent (Galli & Otten, 2011). In Experiment 2, it suggests 3 s is sufficient amount of time for preparing memory encoding on pictures. The positive-going pre-stimulus subsequent memory effect was suggested to reflect motivational processes (Galli et al., 2011; 2014; Gruber & Otten, 2010). The findings in Experiment 2 suggest that encoding-related pre-stimulus activity is not only under voluntary control but also depends on the opportunity to engage such activity before a to-be-encoded item.

Moreover, the encoding-related pre-stimulus activity is affected by amount of advance information. Previous literatures on advance information on other cognitive domains such as attention, perception or working memory have demonstrated that higher pre-stimulus cue validity or predictability enables a better performance and changes of neural responses (Bollinger et al., 2010; Miussi et al., 1999; Sauseng et al., 2005; Yu et al., 2013; Zanto et al., 2011). In Experiment 2, advance information about the amount of preparation time guided preparation to faster reaction times in the size judgment task and also changes in encoding-related pre-stimulus activity. Predictable long cues elicited a frontal positive-going pre-stimulus subsequent memory effect. While a parietal positive-going pre-stimulus subsequent memory effect was found in the unpredictable long cue condition. Of note, the time window of the effect initiation in the unpredictable long cue condition is 300 ms after short cue intervals ended. This means at this time point, participants should be able to realise there was still 1.5 s to go until item onset. The effect had a more parietal scalp distribution. This might indicate a different preparatory process from the one found in the predictable long cue condition. This parietal pre-stimulus subsequent memory effect occurred shortly after the time point that subjects realized it could be a long interval. The effect is more likely to reflect an attention-related or information (time) updating process (Kutas & Federmeier, 2011) that would benefit later memory encoding. The two different pre-stimulus subsequent memory effects in the predictable long cue and unpredictable long cue conditions reflect that different strategic preparatory processes are utilized according to advance information. This can also be indicated by the differences between activity elicited by predictable long cues and unpredictable long cues at the time point that short intervals just ended. Around 1.5 s, activity in the predictable long cue condition was significantly more positive-going than activity in the unpredictable long cue condition over parietal scalp sites. Around 1.5 s, unpredictable cues might be treated as predictable short cues due to its uncertainty about cue length. Miniussi et al. (1999) found that in a time window of 540 – 560 ms (very close to target onset), short interval had more negative activity than long interval in parietal scalp sites. Although the intervals used in Experiment 2 are much longer than that interval and no significant difference showed around short intervals ended between predictable short and long cue conditions, the grand average waveform does show that activity in predictable short cue condition was more negative than predictable long cue condition around short intervals ended. Therefore, subjects might use a strategy which could be like treating non-informative cues as predictable short cues and after around 1.5 s if there was still time, then treating it as long intervals.

Interestingly, even encoding-related post-stimulus activity was influenced by amount of advance information. Three-way interactions between subsequent memory effect, amount of advance information and scalp site were found in an early and a late time windows. In the late time window, the anterior subsequent memory effects were significantly larger in the predictable cue conditions than in the unpredictable cue conditions. The interaction was still significant after scaling the data. Although it did not keep significant after scaling the data, the post-stimulus subsequent memory effects started earlier (100 ms after picture onset) in the predictable cue conditions than unpredictable cue conditions regardless of amount of preparation time. The advance information about a cue interval influenced the degree of post-stimulus encoding-related activity. The results indicate that predictable cues might help get ready to encode a memory more efficiently. There were main effects of amount of preparation time regardless of memory performance or cue predictability found from 100 ms onwards in all intervals. The long cue interval conditions had a more positive-going activity than the short cue interval conditions. This might be attributed to baseline shift due to larger and longer lasting negativity in the long cue interval conditions before picture onset (Miniussi et al., 1999; Woldorff, 1993). However, it did not seem to affect the results, as there was no interaction between amount of preparation time and subsequent memory.

The larger and earlier post-stimulus subsequent memory effects occurred regardless of preparation time although no pre-stimulus subsequent memory effect was found in predictable short intervals. The pre-stimulus subsequent memory effects were shown after 1.5 s in the unpredictable long cue condition, which suggests that another 1.5 s might be sufficient to prepare for forming a new memory. Why pre-stimulus subsequent memory effect was absent in the predictable short cue condition? It might be caused by the instructions of the encoding task. In the incidental encoding task, response speed was emphasised. This might make the size judgment task to be like a secondary task to memory encoding. Actually, the reaction times of the size judgment task were found to be a function of subsequent memory performance. Subsequent recognized items were responded faster than subsequent forgotten items in the size judgment task. This might reflect a resource competition between memory encoding and encoding task. If more time was spent on a picture, more likely the picture could be forgotten, which suggests that the size judgment task might be like a secondary task to memory encoding. If this is true, the preparation for memory encoding and responses might also be resource competing. Therefore encoding-related pre-stimulus activity could only be able to be developed when there are sufficient processing resources for both memory encoding and task responses (Galli et al., 2013). As unpredictable cues might be treated as predictable short cues in short intervals then after short intervals ended there was sufficient resource for the unpredictable long cue condition to build the preparatory state specific to memory encoding.

In conclusion, the encoding-related pre-stimulus found in Experiment 2 was influenced by amount of time to prepare and amount of advance information about preparation time. The preparatory processes for encoding cannot be simply explained by CNV. This indicates that pre-stimulus cues can guide a strategic assignment of preparatory processes. Preparatory processes are not automatically engaged to help memory encoding. Such preparatory activity for encoding also depends on the opportunity to engage the activity. The pre-stimulus activity influences successful memory formation on a trial-by-trial basis, but only when preparation time is sufficient. Therefore, pre-stimulus activity may reflect an active preparatory process that plays a direct role in the ability to create a new memory. Although the engagement of encoding-related preparatory activity did not enhance overall memory performance in Experiment 2, it should be noted that encoding-related activity after the to-be-encoded events was also engaged, and even larger, when preparation time was short. Galli et al. (2013) suggested that the lack of effects on overall memory performance might be due to the engagement of compensatory processes during consolidation and / or retrieval. Therefore, the larger encoding-related post-stimulus activity observed after picture onset reflect encoding processes compensate for weaker preparatory processes. This idea will be tested in Chapter 5.

3.3 Experiment 3: Probing memory before a delayed match-to-sample task influences memory performance and memory-related brain activity associated with the encoding and retrieval of the probes

3.3.1 Introduction

The results from Experiment 2 suggest that it needs to take 3 seconds to develop pre-stimulus activity for encoding a picture. Such slow and sustained activity may reflect a brain state that supports the encoding of information into long-term memory (Fernández, Brewer, Zhao, Glover, & Gabrieli, 1999; Otten, Henson, & Rugg, 2002; Yoo et al., 2012). The scalp distribution difference between the informative cue condition and the non-informative cue condition suggests the development of the encoding-related pre-stimulus activity in the two conditions might be supported by different cognitive processes. A brain state that supports memory encoding might depend on simultaneous cognitive processes underlying preparation (Craik, 2002). Experiment 3 tried to induce different brain states by asking participants to prepare for two kinds of delayed match-to-sample (DMS) tasks. The tasks were demonstrated to involve different neural networks. In one task, participants needed to remember a conjunction of an object and its location in a short delay. In the other task, participants only needed to remember a feature of the conjunction, in Experiment 3, namely, the location of the object in a short delay. Olson et al. (2006) suggested that the task of remembering a conjunction in a short delay involved the hippocampal areas, which are important brain areas for forming an episodic memory. In contrast, the task of remembering an individual feature in a short delay did not necessarily involve the hippocampus (Olson et al., 2006). Experiment 3 addressed whether preparing for a conjunction DMS task can induce a brain state that supports episodic memory encoding.

A previous study using real-time fMRI manipulated brain states for learning (Yoo et al., 2012). The authors monitored brain activity in the PHC that is related to encoding a scene picture. They first measured BOLD activity in the PPA that is a functional region within the PHC while asking participants to remember a series of scenes with the purpose of defining good or bad brain states. The pre-stimulus BOLD activity was significantly lower before remembered scenes than before forgotten scenes. Therefore, BOLD signals in the PPA could be used to control a brain state for efficient encoding or encoding failure prior to a to-be-remembered picture. Secondly, series of scene pictures were presented when they detected that the activity in the PPA was less than a reference activity that was the activity when participants viewed scenes, objects and faces (a good brain state) or more than the reference activity (a bad brain state). They found that later memory performance for pictures presented after a good brain state was significantly better than pictures presented after a bad brain state.

In Experiment 3, such brain states were controlled by asking participants to prepare for different DMS tasks. In the study by Olson et al. (2006), MTL lesion participants and healthy participants were asked to do the DMS tasks. There was no significant difference in their performance of feature DMS tasks. In contrast, MTL lesion participants' performance on the conjunction DMS task was significantly worse than the controls' performance. The effect was significant for a DMS task that participants needed to remember a conjunction or a feature in 1 s. Therefore, Olson et al. (2006) suggested that remembering a conjunction of features in a delay as short as 1 s also involved the hippocampus. This idea is demonstrated by other lesion and fMRI studies (e.g. Finke et al., 2008; Piekema, Kessels, Mars, Petersson, & Fernández, 2006). As discussed in Chapter 1, the hippocampus is also the crucial brain region for encoding-related pre-stimulus activity (Fell et al., 2011; Guderian et al., 2009; Park & Rugg, 2010). If preparation for a conjunction DMS task can activate the hippocampus, then an item that is presented after such brain state should be more likely to be remembered.

To address whether a brain state conducive to effective encoding can be induced by asking participants to prepare for a DMS task known to involve the hippocampus, a cue was presented 5 s before the DMS task. A conjunction cue signalled a conjunction DMS task. A feature cue signalled a feature task that participants needed to remember only the location of an object in a short delay. Participants prepared for the involvement of the hippocampus or no involvement of the hippocampus. In order to enable sufficient time to engage encoding-related pre-stimulus activity, a probe was inserted 3 s after cue onset in half trials. Memory for the probe was tested later. If preparation for a conjunction DMS task can induce a brain state for successful memory encoding, then encoding-related activity and memory performance should be enhanced for the probe inserted 3 s after a conjunction cue.

3.3.2 Methods

Participants. The experimental procedures were approved by the University College London Research Ethics Committee. 24 healthy adults were paid at a rate of £7.50/h to take part. The mean age was 22 years (range of 19-35 years, 13 females). They met all criteria described in the previous experiments.

Stimulus Material. Stimuli for the DMS tasks were 352 greyscale photographs of everyday objects randomly selected from the same pool as used in the previous experiments. These 352 pictures were used to create 256 critical trials of the DMS tasks. Each trial consisted of the consecutive presentation of three grayscale pictures of objects, each presented in one of 9 locations of a 3X3 black grid on a white background (see Figure 12). A comparison stimulus followed 3 s later on the 3X3 black grid. The type of the comparison stimulus depended on the task type. If it was a feature task in which subjects were asked to remember the locations of the objects, the comparison stimulus was a black dot presented in one of the locations where the three objects were presented. If it was a conjunction task in which subjects were asked to remember the objects with their specific locations, the comparison stimulus was one of the objects presented before and presented in a location that would be its specific location or another location. Within each trial, an object was presented without replication. As there were not enough objects presented without replication between trials (3 x 256 objects were needed to avoid replication between trials), some objects might be replicated between trials. Trial numbers of feature and conjunction tasks were equal (128 trials in each task condition). Within each task, trial numbers of ‘match’ answers and ‘mismatch’ answers to the task were equal as well. ‘Match’ and ‘mismatch’ trials were randomised in each task. Trials of the feature task were intermixed with trials of the conjunction task. 39 additional filler items were used to create a practice list that consisted of 24 trials.

Stimuli for the long-term memory (LTM) probes were 192 colour photographs of everyday objects on white backgrounds, randomly selected from the Hemera Photo Objects collection (Volumes 1 and 2, Hemera Technologies, Inc.). The stimuli for the LTM probes were different objects than the 352 objects of the DMS tasks. The objects for the LTM probes were twice the size of the objects for the DMS tasks (see Figure 12). Four sets of 32 pictures (128 critical items) were pseudo-randomly selected to create a list for study phase and the remaining 2 sets of 32 pictures (64 unstudied items) were added to create a list for test phase (192 critical items in total). 64 critical items were inserted into preparation phase for 64 feature task trials and 64 critical items were inserted into preparation phase for 64 conjunction task trials. The trials of ‘match’ and ‘mismatch’ answers were also equal for the trials with LTM probes. They were all intermixed. There were 18 additional filler items for the LTM probe stimuli (12 items for the study phase and 6 additional unstudied items for the test phase) for the practice lists.

All stimuli were presented in central vision on a white background using the Cogent 2000 Toolbox (Wellcome Laboratory of Neurobiology:

http://www.vislab.ucl.ac.uk/cogent.php) and MATLAB (The MathWorks, Inc.). During the DMS tasks, each stimulus was presented for 500 ms with a 13 ms Inter-Stimulus-Interval (ISI) that was a blank black grid on a white background in each consecutive presentation of three objects. The blank black grid lasted 3 s after the last object of the three pictures series disappeared until the presentation of the comparison stimulus. The comparison stimulus was also presented for 500 ms. Before each DMS trial, a letter cue indicating a feature (‘L’) or conjunction task (‘C’) was presented for 1 s. The interval between the cue and the DMS trial was 5 s. A blank black grid was presented for 500 ms just before each DMS trial. Intervals between a DMS trial and the cue for the next trial were jittered between 2.5 – 4 s. In the 5 s cue interval, a LTM probe was presented 3 s into the interval in half the trials in order to avoid participants’ intentional processes on the probe, which could bias the purpose of the experiment. The LTM probe was presented for 1 s. A fixation cross was always presented in the centre of the screen except when stimuli were presented in the centre of the screen. After the completion of the DMS tasks, a surprise recognition task was given for the LTM probes. During the test phase, the procedure was similar as in the previous experiments except that each picture was presented for 1 s. An exclamation mark was presented for 500 ms as a neutral warning to signal the beginning of each trial. There was 1.5 s from an exclamation mark onset to a picture onset. Each trial had a variable period from 2.5 to 4 s randomly.

Several pilot behavioural experiments were carried out to optimise the length of the whole experiment and participants’ performance. In the initial experiment, there were 40 critical LTM probes per DMS task condition. During the DMS tasks, each stimulus was presented for 1 s instead of 500 ms. The delay between the last stimulus of a DMS test sequence and the comparison stimulus was 6 s. The comparison stimulus was presented for 1 s. Six participants took part in the initial pilot. Most of them (4 out of 6) made too few old judgments in the later test phase. Therefore, in the second pilot experiment, more critical trials were added. The delay between the last stimulus of a DMS sequence and the comparison stimulus was reduced to 4 s to shorten the whole experiment. Both the old judgments and new judgments given to the LTM probes reached satisfactory levels for 5 out of 6 participants. To decrease the experiment time, the interval between a cue and a DMS trial was 4 s in the third pilot experiment. Each DMS stimulus was presented for 500 ms. The delay between the last stimulus of the DMS sequence and the comparison stimulus was 3 s. The comparison stimulus was presented for 500 ms. Four participants took part in this pilot. Half of them did not have sufficient trials for judging old LTM probes. The last pilot experiment used the same parameters as described in the above paragraph. The trial numbers reached acceptable levels for most participants (5 out of 6) and the whole experiment did not take as long as the second pilot experiment. Thus, this version was used as the final paradigm for the EEG experiment.

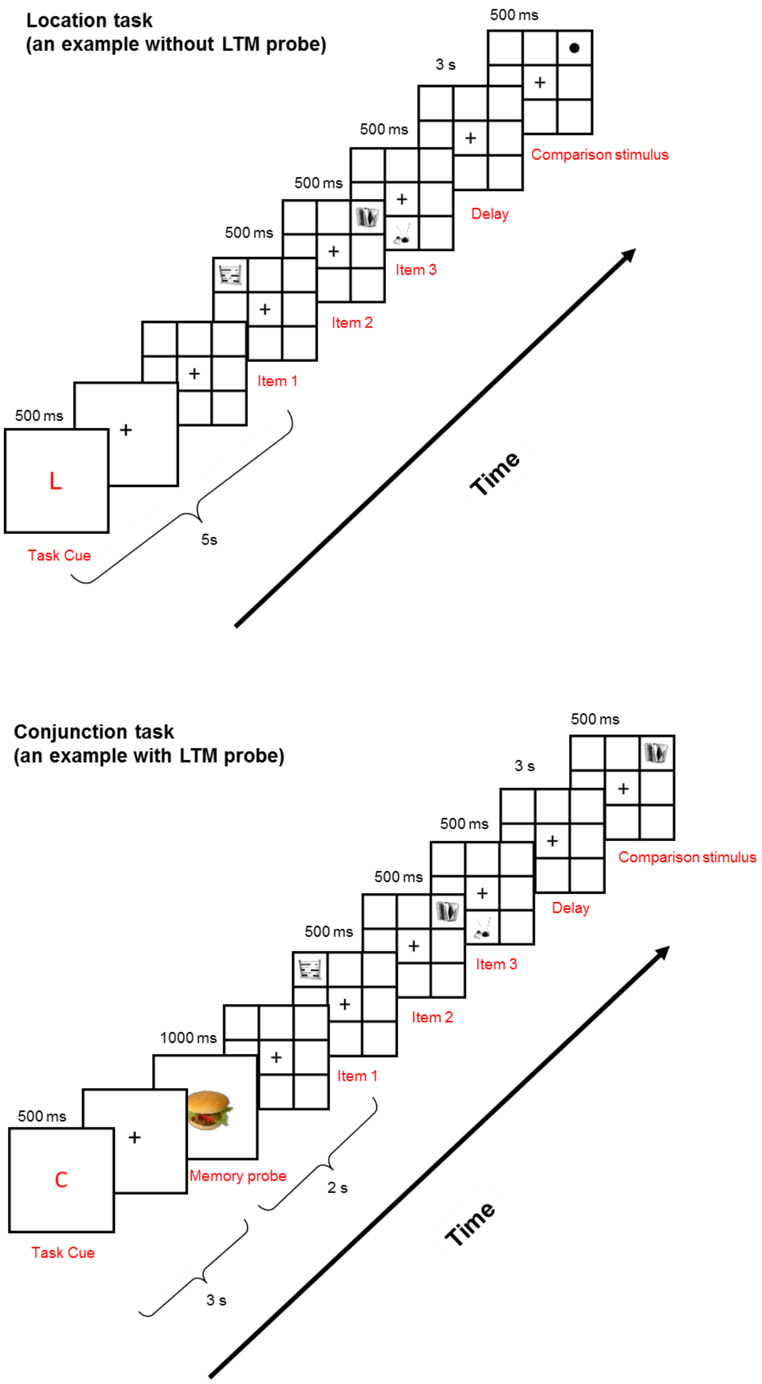


Figure 13. Experimental procedure of DMS tasks in Experiment 3

A letter cue indicated the type of the DMS task. At the top is a feature DMS task without LTM probe. ‘L’ indicated that only the locations of the three objects needed to be remembered. The first item was presented 5 s after ‘L’ onset. The comparison stimulus was always a black dot appearing in an old or new location. At the bottom is a conjunction DMS task with LTM probe. ‘C’ indicated that both the objects and their specific locations needed to be remembered. 5 s after ‘C’ onset, an LTM probe was presented for 1 s on half of the trials. The first item was also presented 5 s after cue onset. The comparison stimulus was always one of the three objects. It might be in its specific location or in another location.

Procedure. In the DMS tasks, participants were asked to prepare for different DMS tasks when they saw the letter cues. If it was an ‘L’ cue that meant participants only had to remember the location of the three objects. The comparison stimulus was always a black dot presented in a location where one of the three objects had appeared earlier or in a new location on the 3X3 black grid. Participants were asked to give a ‘match’ response if the black dot appeared in one of the locations where the three objects had appeared before and give a ‘mismatch’ response if the black dot appeared in a new location by pressing one of two buttons. If it was a ‘C’, they had to remember the identities of the three objects combined with their particular locations. The comparison stimulus was always one of the three objects but it might appear in its particular location or in another location. Again, participants needed to press one of the two buttons to indicate whether it was a ‘match’ (i.e. the object appeared in its particular location) or a ‘mismatch’ (i.e. the object did not appear in its own location but another location). Assignments of response hands were counterbalanced across participants.

A colour image of an object was presented as the LTM probe 3 s after cue onset in half the trials. Participants were asked to always focus their eyes on the centre of the screen to make sure that they did not miss any colour image. They were told their main task was the DMS tasks and both accuracy and response speed were important so that they should prepare for the following DMS tasks during the 5 s cue intervals. They were told sometimes a colour image would be presented before a DMS task but they did not have to do anything about the image. A practice phase was given before the formal task. Participants would get feedback after the practice to make sure that they understood the task. Participants were also asked whether the letter cues were useful for them to make sure that they utilised the cues to prepare for the DMS tasks.

After the completion of the DMS tasks, participants were asked to do a surprise recognition test about the LTM probes. They were instructed to give an old/new response incorporating five-way judgments to each item by pressing one of five buttons with their right hand (Yonelinas et al., 2005). If participants were certain they had seen the colour image during the anticipation phase of the DMS tasks, and were able to recall any detail connecting to that item (recollection), they were asked to make an ‘R’ response. In that case, they should press the leftmost or rightmost button depending on the assignment of the response. If they were certain that they had seen the colour object in the anticipation phase of the DMS tasks but were not able to recollect any detail about the item, they were asked to give an old sure response by pressing the second left or right button. If they thought the picture was in the anticipation phase of the last task but they were not sure, they were asked to give an old unsure response by pressing the middle button. If they were sure they had never seen the picture in the cue interval of the DMS tasks, they were asked to give a new sure response by pressing the rightmost or leftmost button. If they thought the picture had not been in the cue intervals of the DMS tasks but they were not sure, they were asked to give a new unsure response by pressing the second right or left button. Assignments of response fingers were counterbalanced across participants. Participants were instructed that both accuracy and response speed were important and asked to spread out their responses across five judgments (Yonelinas et al., 2005). A practice phase of the recognition test was given before the formal test. Participants were asked why they gave such responses to each item after the practice to make sure that they understood the meaning of each response.

EEG acquisition. The EEG was only recorded during the DMS tasks and the recognition test. Other details about the EEG acquisition can be found from the EEG acquisition session of Experiment 2.

EEG analyses. Offline, the data were digitally filtered between 0.05 and 20 Hz (96 dB roll off) and algebraically re-referenced to linked mastoids (reinstating the online reference site). As the in-house ERP analysis software is only able to process data with

256 data points, data were downsampled to different sample rates to have longer or shorter epochs. First, the continuous EEG elicited by DMS task cues was downsampled to 1 point/20 ms (50 Hz) and segmented separately into epochs of 5120 ms duration including a 100 ms baseline before cue onset to see the preparatory activity along the whole pre-stimulus period for the DMS tasks. Second, the continuous EEG elicited by DMS task cues was downsampled to 1 point/14 ms (around 72 Hz) and segmented into epochs of 3584 ms duration including a 100 ms baseline before cue onset to see encoding-related pre-stimulus activity associated with the LTM probes. The EEG activity elicited by LTM probe pictures was downsampled to 1 point/10 ms (100 Hz) and segmented into epochs of 2560 ms duration including a 100 ms baseline before LTM probe picture onset to see encoding-related post stimulus activity associated with the LTM probes. The EEG activity elicited by the LTM probe pictures in the recognition test was downsampled to 1 point/8 ms (125 Hz) and segmented into epochs of 2048 ms duration including a 100 ms baseline before picture onset to see the retrieval-related activity associated with the LTM probe pictures. The epochs of the 5 s DMS cue intervals were averaged according to the DMS task conditions when LTM probes were, or were not inserted to create ERP waveforms for each participant and electrode as there was probe-related activity when LTM probes were inserted, but the statistical analyses were done to compare preparatory activity between two DMS task conditions irrespective of whether LTM probes were or were not inserted. The epochs before and after the LTM probe pictures were averaged by the later ‘R’, ‘old sure’, ‘old unsure’, ‘new unsure’ and ‘new sure’ judgments that participants gave during the recognition test. The epochs of the test phase were also averaged by the ‘R’, ‘old sure’, ‘old unsure’, ‘new unsure’ and ‘new sure’ judgments. The artefact corrections were done with the same criteria described in the previous experiments. There were at least

13 artefact free trials in each condition for each subject's averaged ERPs (See Tables 14 to 17).

The analyses focused on trials with correct answers to the DMS tasks in order to ensure that participants were involved in preparation for the following DMS tasks most efficiently. The comparisons of the ERP waveforms between later remembered and forgotten trials for activities before and after LTM probes in the DMS tasks were of interest. The criteria for categorising subsequently remembered trials were when participants gave confident judgments ('R' and 'old sure' responses) in the recognition test. The criteria for subsequently forgotten trials were when participants gave unconfident old or new, or confident new judgments in the recognition test to maximize the signal-to-noise ratio. The analyses of retrieval-related activity focused on the comparison between old items that were confidently judged as old ('R' and 'old sure' responses) and new items that were judged as new or unconfidently judged as old ('new sure', 'new unsure' and 'old unsure' responses) to be consistent with the criteria during encoding. Otten and Rugg (2001b) demonstrated that ERP subsequent memory effects seen for confident hits relative to unconfident hits collapsed with misses do not differ from effects seen for confident hits relative to only misses. In the first study investigating pre-stimulus encoding-related electrical brain activity, the same criterion was used to categorise remembered trials (recollected and confidently recognised items) and forgotten trials (unconfidently recognised items and misses). Although fewer than 12 participants had more than 13 artefact free trials for the former contrast in each ERP analysis, the grand average waveforms showed no difference from the grand average waveforms showed no difference from the waveforms resulting from the latter contrast. Behaviourally, the discriminations between old and new items that attracted unconfident old judgments did not differ from zero (*p* values in both conjunction and feature conditions > 0.3 for all 24 subjects and those 18 subjects who were included in the memory-related ERP analyses). Therefore, the unconfident old response category may be reasonable to be considered as equivalent to forgotten items (cf. Voss & Paller, 2009). Retrieval-related activity also differed between old items that attracted confident old judgments and old items that attracted unconfident old judgments. In contrast, the activity did not differ between old items that attracted unconfident old judgments and new items that attracted new judgments (Woodruff et al., 2006). Thus, the decision to collapse unconfident hits and misses is unlikely to affect the aims for the ERP analyses in Experiment 3. The comparisons between activities elicited by two kinds of DMS cues were also of interest to see the overall preparation for the feature and the conjunction tasks. Repeated measures analysis of variance (ANOVAs) was used to test each comparison, incorporating the Greenhouse-Geisser correction for violations of sphericity (Keselman & Rogan, 1980). The ANOVAs were conducted on all 37 scalp sites.

Table 14. Mean trial numbers in each condition in the DMS task cue-related ERPs (Range in brackets)

	Feature task	Conjunction task
With LTM probe	43 (23-61)	42 (18-57)
Without LTM probe	45 (25-57)	43 (23-59)

Table 15. Mean trial numbers in each condition in pre-LTM probe ERPs (Range in brackets)

	Feature task	Conjunction task
Recognized trials	23 (14-39)	24 (16-41)
Forgotten trials	28 (15-43)	24 (14-35)

Table 16. Mean trial numbers in each condition in post-LTM probe ERPs (Range in brackets)

	Feature task	Conjunction task
Recognized trials	24 (15-40)	25 (18-42)
Forgotten trials	28 (15-44)	26 (14-36)

Table 17. Mean trial numbers in each condition in retrieval ERPs in Experiment 3 (Range in brackets)

Feature task Hits	Conjunction task Hits	Correct rejections
21 (13-36)	22 (14-40)	41 (24-54)

3.3.3 Results

Task Performance for 24 participants

Task performance for all 24 participants is shown in this section. As only 18 participants have sufficient artefact free trial number to create ERPs to look at subsequent memory effect and retrieval old/new effect, so the task performance for these 18 participants will be shown in the following section.

DMS task performance. Performance for the DMS tasks is summarized in Table 18. An ANOVA with factors of type of DMS task (feature, conjunction) and response (match, mismatch) showed main effects of DMS task type and response in task accuracy. The accuracy in the feature task was significantly better than the accuracy in the conjunction task, $F(1, 23) = 15.635$, $p = 0.001$. Participants were significantly more accurate when a 'match' answer should be made than when a 'mismatch' answer should be made, $F(1, 23) = 5.434$, $p = 0.029$. Similarly, an ANOVA on reaction times also showed main effects of DMS task type and response type. Reaction times of the feature task were significantly faster than the conjunction task, $F(1, 23) = 95.383$, $p < 0.001$. It was significantly faster to make responses to 'mismatch' trials than 'match' trials, $F(1, 23) = 7.669$, $p = 0.011$. An interaction between DMS task type and responses type was found $F(1, 23) = 6.701$, $p = 0.016$. Pairwise comparisons showed that only in the pair of the conjunction task, reaction time in ‘mismatch’ trials was significantly faster than reaction time in ‘match’ trials, $t(23) = 3.569$, $p = 0.002$. The DMS task performance replicated the previous findings reported in Olson et al. (2006).

To see whether LTM probes affected later DMS task judgments, analyses were conducted to compare accuracy and reaction times between DMS trials after LTM probes and DMS trials without LTM probes. There was no significant difference. Accuracy and reaction times of the DMS tasks were also categorised by subsequent memory performance of the LTM probes to see whether memory of the LTM probes was affected by following DMS tasks. No significance differences were found in terms of subsequent memory performance of the LTM probes (all ps > 0.1).

Table 18. DMS tasks performance

		Feature match	Feature mismatch	Conjunction match	Conjunction mismatch
Accuracy	M	0.99	0.98	0.96	0.92
(proportion)	SD	0.02	0.02	0.03	0.10
Response	M	815	791	1043	981
times (ms)	SD	195	170	211	180

Values are across-subject means. n=24.

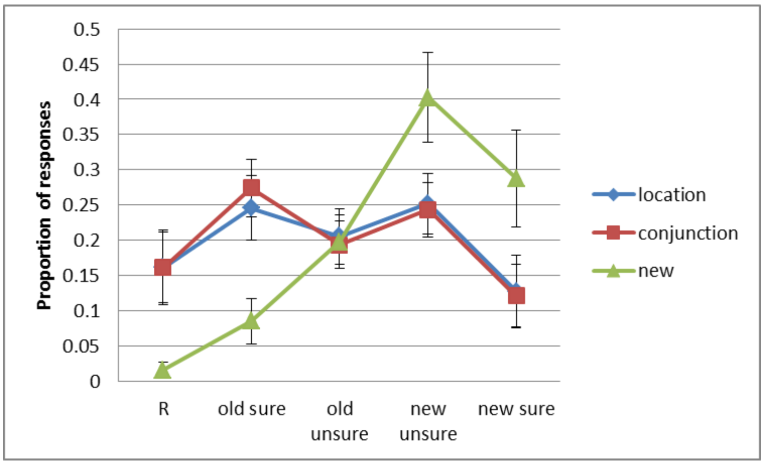
Recognition Test. Recognition memory performance for the LTM probes is summarized in Table 19. The analyses did not show any significant effect in terms of DMS task type in either Pr or Br regardless of recognition memory type (Pr in the feature condition 0.31 and in the conjunction condition 0.31, $p = 0.36$; Br in the feature condition 0.44 and in the conjunction condition 0.44, $p > 0.6$). The comparison between Pr associated with remembered items (hits collapsed across ‘R’ and ‘old sure’ responses minus false alarms given ‘R’ and ‘old sure’ judgments) in the feature and conjunction conditions did not reach significance (feature, 0.31 and conjunction, 0.33, $t(23) = 1.782$, $p = 0.088$, see Figure 14). The same comparison in Br also did not reveal a significant difference (0.15 versus 0.16 in the feature and conjunction conditions, respectively, $p > 0.2$). For both confident hits (‘R’ and ‘old sure’), the discriminations between old and new items were significantly greater than zero, both p values ≤ 0.001. An ANOVA with factors of DMS task type (feature, conjunction) and memory type (‘R’, ‘old sure’ or ‘old unsure’ for old items) revealed main effects of DMS task type, $F(1, 23) = 5.569$, $p = 0.027$, and memory type, $F(1.864, 42.869) = 32.947$, $p < 0.001$ after Greenhouse-Geisser correction, in reaction time. Hits for LTM probes before the conjunction task were significantly faster made than hits for LTM probes before the feature task (feature, 1638 ms, conjunction, 1591 ms, see Figure 14). Pair-wise comparisons indicated that the reaction times of ‘R’ judgment were significantly faster than the other two memory types (‘R’ vs. ‘old sure’, $p = 0.001$, ‘R’ vs. ‘old unsure’, $p < 0.001$). Reaction times for ‘old sure’ judgment were significantly faster than reaction times for ‘old unsure’ judgment, $p < 0.001$. Another ANOVA was done to see the effects of factors of DMS task type and memory type of only ‘R’ and ‘old sure’ judgments as these two judgments were used to create subsequently remembered ERPs. An effect of DMS task type showed a trend but did not reach significance, $F(1, 23) = 3.641$, $p = 0.069$. Reaction times of ‘R’ and ‘old sure’ judgments for the LTM probes before the conjunction task were faster than before the feature task (feature, 1532 ms and conjunction, 1489 ms).

Table 19. Recognition memory performance in Experiment 3

Condition	Recognition Type				
	Recollection	Confident old	Unconfident old	Unconfident new	Confident New
Proportion of responses					
Old					
Feature	0.16 (0.12)	0.25 (0.11)	0.21 (0.09)	0.25 (0.10)	0.13 (0.12)
Conjunction	0.16 (0.12)	0.27 (0.10)	0.19 (0.08)	0.24 (0.09)	0.12 (0.11)
New	0.02 (0.03)	0.09 (0.08)	0.20 (0.09)	0.40 (0.15)	0.29 (0.16)
Mean reaction time (ms)					
Old					
Feature	1425 (355)	1639 (346)	1850 (384)	1705 (434)	1544 (319)
Conjunction	1396 (337)	1583 (306)	1795 (395)	1706 (391)	1619 (333)
New	1832 (505)	1585 (435)	1825 (378)	1692 (365)	1504 (265)

Values for recognition accuracy are across-subject means (SD). n=24. The reaction times shown above are based on 24 participants except the feature condition confident new judgments, which are based on 21 participants, the conjunction condition confident new judgments, which are based on 22 participants and the new recollection judgments, which are based on 11 participants as some participants did not have any trials for the above judgments of the above conditions.

a)



b)

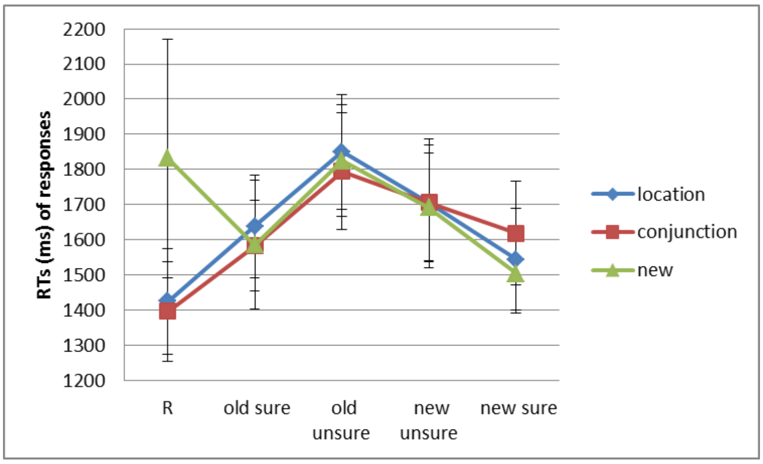


Figure 14. Recognition memory performance in Experiment 3

a) Proportion of responses for the recognition memory test (y-axis) as a function of type of recognition memory (x-axis) in the three picture conditions (location, conjunction or new). b) As for a) but the y-axis is RTs of responses for the recognition memory test.

Relationship between DMS task performance and recognition accuracy for the LTM probes. Although recognition accuracy for the probes before a conjunction task was higher than recognition accuracy for the probes before a feature task, it was not statistically significant. One possible reason was subjects' variability in whether they prepare for DMS tasks properly. Therefore, bivariate correlations were conducted between DMS task performance and recognition accuracy for the LTM probes across participants to see the relationship between preparation for DMS tasks and the recognition memory performance for the LTM probes. The correlations were done between conjunction task performance and recognition accuracy for the LTM probes before conjunction tasks, and between feature task performance and recognition accuracy for the LTM probes before feature task. A significant positive correlation was found between reaction time for the DMS conjunction task and recognition accuracy of confident responses (Hits (‘R’ + ‘old sure’) – False alarms (‘R’ + ‘old sure’)) for the LTM probes before the conjunction DMS task, Pearson’s $r = 0.428$, $p = 0.037$. The faster a participant responded in the conjunction DMS task, the better was their ability to later discriminate conjunction probes (Figure 15).

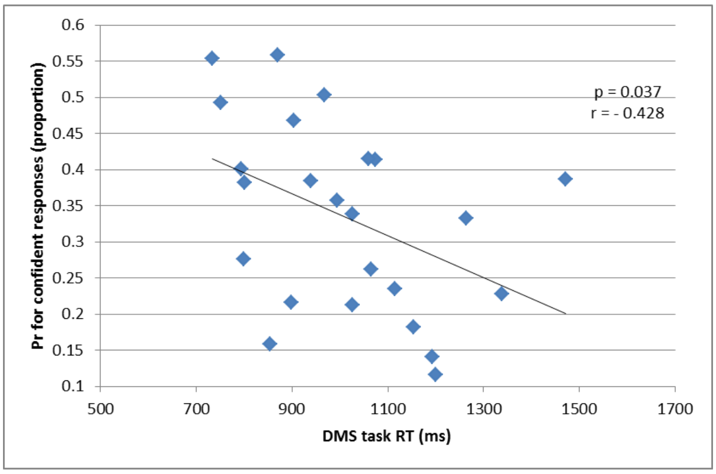


Figure 15. Relationship between reaction time for the DMS conjunction task and recognition accuracy of confident responses for the LTM probes before the conjunction DMS task.
Each blue point represents one participant’s reaction time in the conjunction DMS task (x-axis) and corresponding recognition accuracy of confident responses (Pr) for the LTM probes before the conjunction DMS task for that participant (y-axis).

Task Performance for 18 participants

DMS task performance. Performance for the DMS tasks of 18 participants is summarized in Table 20. Statistical analyses results were similar as the results for 24 participants.

Table 20. DMS tasks performance based on 18 participants

		Feature match	Feature mismatch	Conjunction match	Conjunction mismatch
Accuracy	M	0.99	0.98	0.95	0.91
(proportion)	SD	0.02	0.02	0.03	0.11
Response	M	810	781	1037	970
times (ms)	SD	198	174	216	188

Values are across-subject means. n=18.

Recognition Test. Recognition memory performance based on 18 participants for the LTM probes is summarized in Table 21. Statistical analyses results were similar as the results for 24 participants except that reaction times did not differ between DMS task conditions.

Table 21. Recognition memory performance based on 18 participants in Experiment 3

Condition	Recognition Type				
	Recollection	Confident old	Unconfident old	Unconfident new	Confident New
Proportion of responses					
Old					
Feature	0.19 (0.12)	0.26 (0.10)	0.20 (0.10)	0.25 (0.10)	0.10 (0.09)
Conjunction	0.19 (0.12)	0.30 (0.09)	0.18 (0.08)	0.24 (0.09)	0.09 (0.07)
New	0.02 (0.03)	0.10 (0.08)	0.18 (0.08)	0.44 (0.15)	0.25 (0.14)
Mean reaction time (ms)					
Old					
Feature	1361 (309)	1645 (380)	1814 (350)	1672 (360)	1593 (313)
Conjunction	1377 (366)	1571 (299)	1792 (354)	1679 (344)	1606 (321)
New	1838 (516)	1618 (455)	1782 (324)	1644 (334)	1532 (252)

Values are across-subject means (SD). n=18. The reaction times shown above are based on 18 participants except the feature condition confident new judgments, which are based on 15 participants, the conjunction condition confident new judgments, which are based on 16 participants and the new recollection judgments, which are based on 9 participants as some participants did not have any trials for the above judgments of the above conditions.

Summary of behavioural findings

Both accuracy and reaction times were enhanced in the feature relative to conjunction DMS tasks, which is consistent with the previous findings of Olson et al. (2006).

In the recognition test for the LTM probes, Pr based on confident judgments (recollected and confident hits) showed a trend for better memory following the conjunction than feature DMS task condition. However, the difference was not statistically significant. Moreover, reaction times for confident judgments were faster for the probes from the conjunction condition, although again this difference did not reach significance. The reason why the two effects did not reach significance appears to be variability in performance across participants. A significant Pearson’s correlation showed that participants who responded faster in the conjunction DMS task were better at discriminating the LTM probes from the conjunction condition from new items in the recognition test.

Overall preparatory activity preceding DMS task onset

ERPs elicited by different DMS task cues were compared to see if overall preparatory activity was affected by anticipating the different DMS tasks. The analyses were based on all 24 participants as all of them had sufficient trials for computing the ERPs of the overall preparatory activity. Cues signalling a conjunction DMS task elicited a more positive-going waveform after 200 ms. The overall preparatory activity shortly before conjunction DMS task onset was more positive-going over frontal scalp sites but more negative-going over posterior scalp sites than before feature DMS task onset.

To capture the positive-going deflections, mean amplitude values were computed in time windows of 200 – 300 ms (P2 component), 300 – 600 ms (P3 component), 600 – 1100 ms and 1100 – 1500 ms after cue onset (Gruber & Otten, 2010). In the time window of 300 – 600 ms, ANOVA with factors of task cue type (conjunction, feature) and electrode site (37 sites) revealed an interaction between task cue type and electrode site, $F(2.9, 67.2) = 3.339$, $p = 0.025$, which confirms a posterior scalp distribution of the larger P3 deflection elicited by conjunction cues (Figure 16). This significant interaction, however, did not reach the significance level after scaling the data ($p > 0.1$). No significant effects were found in the other time windows (all *p*s > 0.3). After 1500 ms, mean amplitude values were computed in each 300 ms time window to be consistent with Experiment 2. No significant differences were found in all the time windows (all *p*s > 0.4). After 3000 ms, ERPs were created according to whether there was a LTM probe or not as LTM probes elicit large potentials, therefore it was necessary to separate activity from when there was no LTM probe. Mean amplitude values of each 400 ms time window were calculated i.e. 3000 – 3400 ms, 3400 – 3800 ms, 3800 – 4200 ms, 4200 – 4600 ms and 4600 – 5000 ms. Interactions between task cue type and electrode site were found in the time windows of 3800 – 4200 ms, $F(4.3, 97.8) = 3.086$, $p = 0.017$, and 4200 – 4600 ms, $F(5.2, 119.8) = 3.059$, $p = 0.011$, no matter whether there was an LTM probe or not. Both interactions were still significant after scaling the data (3800 – 4200 ms, $p = 0.020$, 4200 – 4600 ms, $p = 0.027$). The effects in the two intervals did not differ from each other when ANOVAs were done with factors of task cue type (conjunction, feature), electrode site (37 sites) and time window (3800 – 4200 ms, 4200 – 4600 ms) for the scaled data (all *p*s > 0.5), which suggests that a sustained positive-going activity was elicited by conjunction cues over frontal scalp sites and by feature cues over posterior scalp sites shortly before DMS task onset (Figure 16).

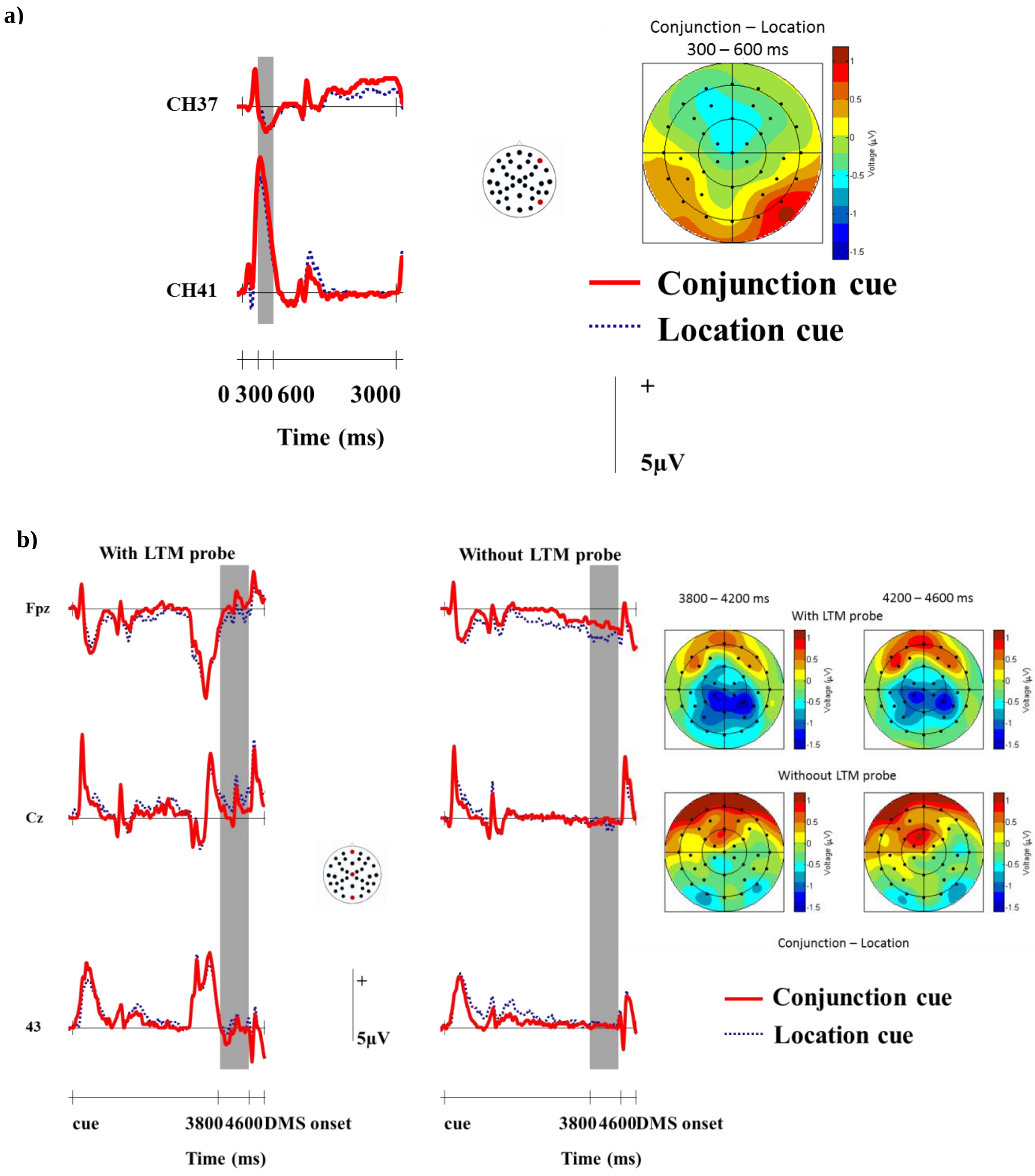


Figure 16. Overall preparatory activity preceding DMS task onset

a) Left: group-averaged ERP waveforms elicited by DMS task cues at a frontal and a posterior electrode sites (sites 37 and 41 from montage 10), where site 41showed the largest amplitudes difference of the P300 component between the conjunction and the feature conditions. Site 37 is a symmetric frontal site to site 41. 0 is the time point of cue onset. Positive values are plotted upwards. Waveforms were low pass filtered at 15.5 Hz for graphical purposes. Right: voltage spline map showing the distribution of the difference between two DMS task cue conditions across the scalp in the 300 ms to 600 ms after cue onset. b) Left: as in a, but separated by with/without LTM probe and at three midline electrode sites (sites Fpz, Cz and 43 from montage 10) where representatively show the differences between the conjunction and the feature conditions across scalp. Right: as in a, but separated by with/ without LTM probe and in two different time windows (3800 – 4200 ms and 4200 – 4600 ms). All the spline maps are scaled to the difference between maximum and minimum across conditions to highlight the topographical differences and magnitude of the modulations in each condition.

Encoding-related activity preceding LTM probes

Neural activity related to successful encoding of LTM probes was identified with the subsequent memory paradigm. Analyses were based on 18 participants who had sufficient artefact free trials to compute subsequent memory effects. The contrast was focused on collapsing confident recognised judgments (‘R’ and ‘old sure’) vs. the other judgments (‘old unsure’, ‘new unsure’ and ‘new sure’). As can been seen from Figure 17, ERPs of recognised LTM probes elicited by feature DMS task cues were more positive-going than ERPs of the forgotten LTM probes. In contrast, recognised LTM probes before the conjunction DMS task showed more negative-going waveforms than forgotten LTM probes preceding the LTM probes. Based on visual inspection of the grand average waveforms, the subsequent memory effects preceding LTM probes started from 300 ms onwards.

To quantify the effects, mean amplitudes were calculated in the intervals of 300 – 700 ms, 700 – 1100 ms, 1100 – 1500 ms, 1500 – 1800 ms, 1800 – 2100 ms, 2100 – 2400 ms, 2400 – 2700 ms and 2700 – 3000 ms after DMS task cue onset to be consistent with the ERP analyses for the pre-stimulus encoding-related activity in Experiment 2. In the early time window of 300 – 700 ms, a significant interaction between DMS task cue condition and pre-stimulus subsequent memory effect was found, $F(1, 17) = 12.694$, $p = 0.002$. Pairwise comparisons revealed main effects of pre-stimulus subsequent memory in both DMS cue conditions. The activity elicited by feature task cues was more positive-going before recognised LTM probes than forgotten LTM probes, $F(1, 17) = 15.05$, $p = 0.001$. In contrast, the activity elicited by conjunction task cues was more negative-going before recognised LTM probes than forgotten LTM probes, $F(1, 17) = 4.785$, $p = 0.043$. In the time window of 700 – 1100 ms, a significant interaction between DMS task cue condition and pre-stimulus subsequent memory effect was missed, $F(1, 17) = 4.32$, $p = 0.053$. Significant interactions were found in the following three time windows (1100 – 1500 ms, $F(1, 17) = 6.297$, $p = 0.023$, 1500 – 1800 ms, $F(1, 17) = 4.604$, $p = 0.047$ and 1800 – 2100 ms, $F(1, 17) = 7.730$, $p = 0.013$). Subsidiary analyses on each DMS task condition showed significant pre-stimulus subsequent memory effects in the feature condition but not in the conjunction condition in all three time windows (all ps < 0.05). An ANOVA that incorporated with factors of subsequent memory (recognised, forgotten), DMS task condition (conjunction, feature) and time interval (1100 – 1500 ms, 1500 – 1800 ms, 1800 – 2100 ms) revealed that the effect in each time interval did not differ from each other (all ps > 0.3). This suggests a sustained interaction between the pre-stimulus subsequent memory effect and DMS task condition from 1100 ms to 2100 ms after cue onset. No other significant effects were found after 2100 ms (all ps > 0.1).

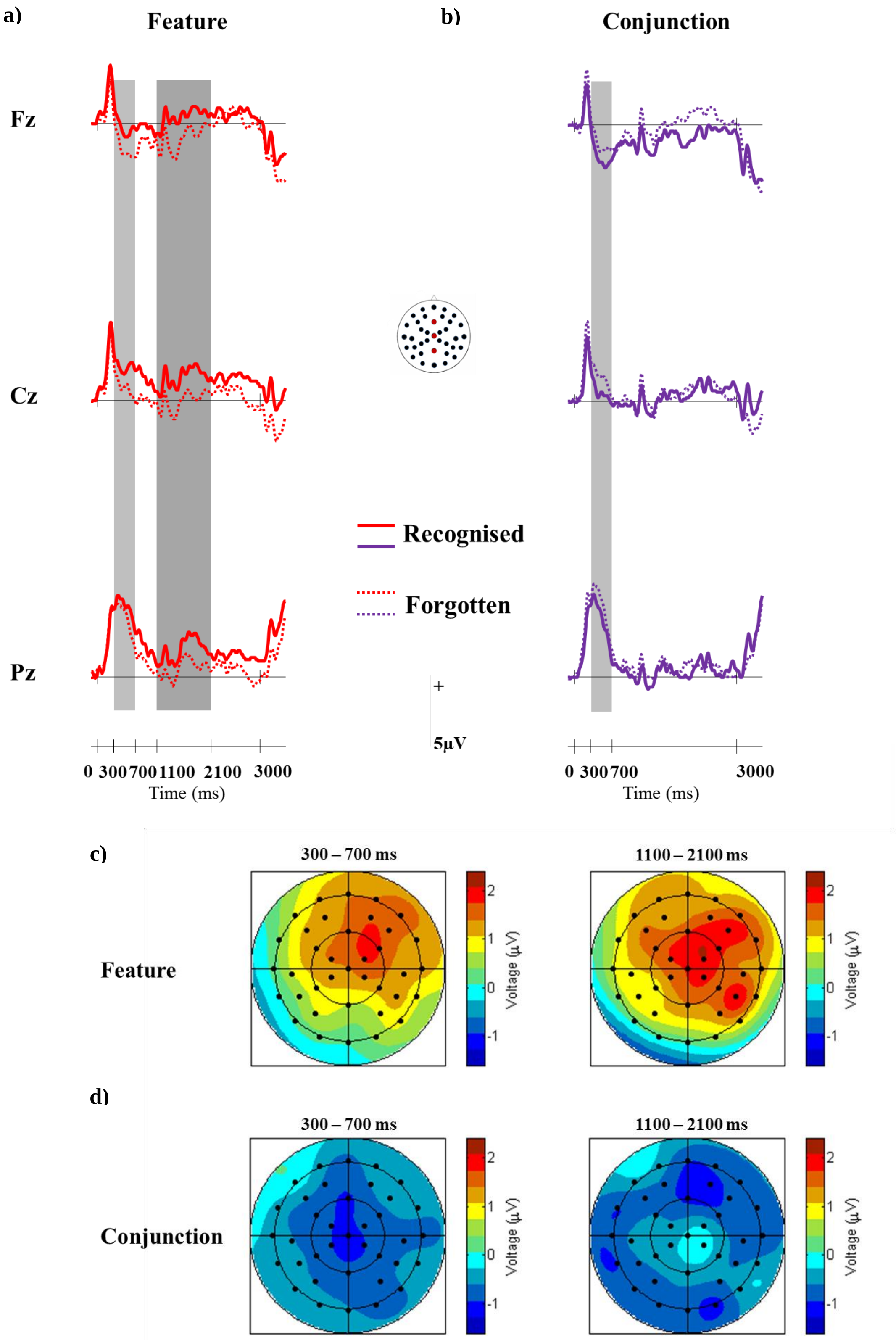


Figure 17. Pre-LTM probe subsequent memory effect

a) Group-averaged ERP waveforms elicited by feature DMS task cues at three midline electrode sites (sites Fz, Cz and Pz from montage 10). Positive values are plotted upwards. Waveforms were low pass filtered at 11 Hz for graphical purposes. The waveforms still look quite noisy because only 18 participants had sufficient trial numbers to compute ERPs. b) As in a, but elicited by conjunction DMS task cues at the three midline electrode sites. c) Voltage spline maps showing the distributions of the subsequent memory effect across the scalp in time windows of 300 – 700 ms, 1100 – 2100 ms after feature DMS task cue onset. d) As in c, but the effect shown here is from the conjunction condition. The maps are scaled to the difference between maximum and minimum across conditions to highlight the topographical differences and magnitude of the modulations in each condition.

Encoding-related activity elicited by LTM probes

Encoding-related neural activity elicited by LTM probes was also assessed with the subsequent memory approach to see whether anticipation of a conjunction DMS task would enhance encoding-related brain activity. The analyses were again based on 18 participants from the analyses on encoding-related activity preceding LTM probes. From the grand average waveforms (Figure 18), probes from both feature and conjunction DMS conditions elicited a positive-going subsequent memory effect over anterior scalp sites. Probes from the feature DMS condition had a larger and earlier subsequent memory effect than probes from the conjunction DMS condition.

Mean amplitudes were calculated in the time windows of 100 – 300 ms, 300 – 800 ms, 800 – 1100 ms and 1100 – 1900 ms after LTM probe onset to be consistent with Experiments 1 and 2. Differently from the results of the previous two experiments, a significant main effect of subsequent memory was found from the later time window of 800 – 1100 ms, $F(1, 17) = 6.006$, $p = 0.025$. An interaction between subsequent memory effect and scalp site was found after the Greenhouse-Geisser correction, $F(2.8, 48.2) = 4.150$, $p = 0.012$. The significant interaction between subsequent memory effect and scalp site confirms the frontocentral scalp distribution (see Figure 18), which is consistent with the findings in Experiments 1 and 2. A significant interaction was also found between subsequent memory and DMS task condition, $F(1, 17) = 14.157$, $p = 0.002$. Subsidiary analyses on each DMS task condition revealed a significant subsequent memory effect only in the feature condition, $p = 0.001$. In the time window of 1100 – 1900 ms, a significant interaction between subsequent memory and scalp site was found after the Green-Geisser correction, $F(2.9, 50.1) = 4.830$, $p = 0.005$. No interaction between subsequent memory effect and DMS task condition was found in this time window. The frontocentral subsequent memory effects found in the two time windows did not differ from each other (all ps > 0.2) when conducting an ANOVA with factors of subsequent memory (recognised, forgotten), scalp site (37 sites) and time window (800 to 1100 ms, 1100 to 1900 ms). The frontocentral subsequent memory effect found in Experiment 3 was later than the effects found in Experiments 1 and 2 but was sustained until 1900 ms after LTM probe onset, which is consistent with the finding in Experiments 1 and 2.

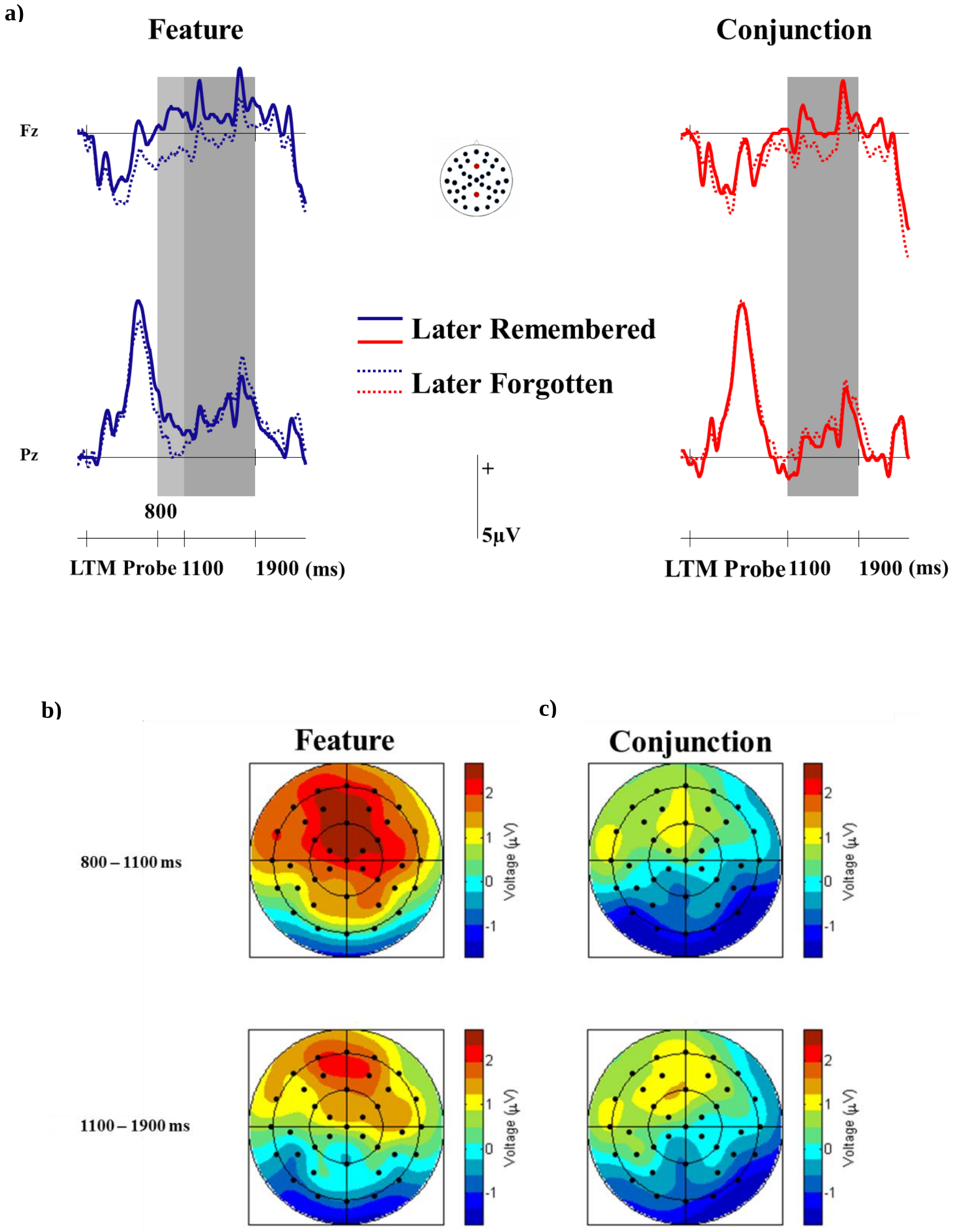


Figure 18. Post-LTM probe subsequent memory effect

a) Group-averaged ERP waveforms elicited by LTM probe at two midline electrode sites (sites Fz and Pz from montage 10) where show the trends of the positive-going frontocentral subsequent memory effects for the probes in the two DMS task conditions. Positive values are plotted upwards. Waveforms were low pass filtered at 15.5 Hz for graphical purposes. Note that a blank 3 X 3 grid was presented 1500 ms after LTM probe onset, where shows the evoked responses. b) Voltage spline maps showing the distributions of the subsequent memory effect across the scalp in the 800 ms to 1100 ms and 1100 ms to 1900 ms time windows after LTM probe onset from the feature condition. The subsequent memory effect showed a positive, frontocentral maximum distribution. c) As in b, but from the conjunction condition. The maps are scaled to the difference between maximum and minimum across conditions to highlight the topographical differences and magnitude of the modulations in each condition.

Retrieval-related activity elicited by LTM probes

Retrieval-related neural activity elicited by LTM probes during the recognition test was identified by the old-new paradigm (Rugg, 1995). To be consistent with the analyses on encoding-related activity, the correct judgments for the old items were collapsing confident judgments that included recollection and old sure judgments. The correct judgments for the new items were collapsing old unsure, new unsure and new sure judgments. The activity elicited by old items that attracted the recollection and confident old judgments was more positive-going than the activity elicited by new items that attracted the unconfident old, confident new and unconfident new judgments in both feature and conjunction conditions. The grand average waveforms showed that retrieval-related activity from the conjunction condition was larger than from the feature condition especially over the frontal scalp sites (Figure 19).

Mean amplitudes were calculated in the time windows of 300 – 500 ms, 500 – 800 ms, 800 – 1400 ms, 1400 – 1700 ms, 1700 – 1900 ms. As mentioned in Chapter 1, the time window 300 – 500 ms is a latency that is thought to be related to familiarity (Rugg et al., 1998). The following two time windows are the two latencies that are thought to be related to recollection (Wilding et al., 1995; Wilding & Rugg, 1996). The last two time windows were selected to see later sustained differences between retrieval-related activities elicited by LTM probes from two DMS task conditions. Interactions of old-new effect by scalp sites were found in all time windows. Therefore, to assess the scalp distributions of the old-new effects, further ANOVAs were conducted on 28 scalp sites that allow dividing the scalp into anterior-posterior and left-right regions like the analyses on pre-stimulus encoding-related activity in Experiment 2 (Figure 9). Such partitioning has been demonstrated to capture the old-new effects in at least the 300 – 500 ms and 500 – 800 ms time windows (Galli & Otten, 2010).

Main effects of old-new were found in the first three time windows (300 – 500 ms, $F(1, 17) = 6.589$, $p = 0.02$, 500 – 800 ms, $F(1, 17) = 29.165$, $p < 0.001$, 800 – 1400 ms, $F(1, 17) = 6.634$, $p = 0.02$). In the time window of 300 – 500 ms, a significant interaction was found between the old-new effect and anterior-posterior scalp position. Subsidiary analyses on each scalp position showed that a significant old-new effect was only found over the anterior scalp sites, $F(1, 17) = 9.216$, $p = 0.007$, not the posterior scalp sites, $F(1, 17) = 1.046$, $p = 0.322$. This is consistent with previous literature (Ranganath & Paller, 2000; Rugg et al., 1998; for a review, see Wilding & Ranganath, 2012) that in this latency an old-new effect should be found over frontal scalp sites, which is usually known as mid-frontal or the FN400 old-new effect (Rugg & Curran, 2007). The old-new effect found in the time window of 300 – 500 ms had a significant three-way interaction with DMS task condition and anterior-posterior scalp position, $F(1, 17) = 4.599$, $p = 0.047$. Subsidiary analyses revealed that a main old-new effect was only found in the LTM probes from the DMS conjunction condition over the frontal scalp sites, $F(1, 17) = 16.618$, $p = 0.001$, but not in the LTM probes from the DMS feature condition, $F(1, 17) = 2.165$, $p = 0.160$. However, the interaction did not remain significant after scaling the data. A supplemental analysis was done on six mid-frontal electrode sites (Fp1, 34, Fpz, Fz, Fp2, 21) to depict the activity from the mid frontal areas some of which were not included in the earlier partitioning. An ANOVA that incorporated factors of old-new statues (old, new), DMS task condition (conjunction, feature), hemisphere (left, midline, right) and site (two sites) revealed a main effect of old-new status ($F(1, 17) = 10.793$, $p = 0.004$). This further highlights the mid-frontal old-new effect also found in the partition analysis.

In the following time window of 500 - 800 ms, a significant interaction of old-new effect by anterior-posterior scalp position and left-right scalp hemisphere was found, $F(1, 17) = 10.497$, $p = 0.005$. Subsidiary analyses showed that significant old-new effects were found in all four quadrants but the largest effect was found over the left posterior scalp sites (left anterior, *F*(1, 17) = 15.805, *p* = 0.001, right anterior, *F*(1, 17) = 13.734, *p* = 0.002, left posterior, *F*(1, 17) = 34.130, *p* <0.001, right posterior, *F*(1, 17) = 10.390, *p* = 0.005). This is consistent with previous literatures that a left-parietal old-new effect is found typically from 500 to 800 ms (Rugg, 1995; for a review, see Wilding & Ranganath, 2012). Again, an interaction of old-new effect by DMS task condition and anterior-posterior scalp position was found, *F*(1, 17) = 5.446, *p* = 0.032. Significant old-new effects were found in both DMS task conditions over posterior scalp sites (conjunction, *F*(1, 17) = 18.676, *p* <0.001, feature, *F*(1, 17) = 11.176, *p* = 0.004). However, a significant old-new effect was found over anterior scalp sites only in the conjunction condition, *F*(1, 17) = 39.378, *p* < 0.001, but not in the feature condition, *F*(1, 17) = 2.428, *p* = 0.138. The interaction approached significance after scaling the data, *p* = 0.053.

In the following time window 800 – 1400 ms, an interaction between old-new effect and anterior-posterior scalp position and left-right hemisphere was found, *F*(1, 17) = 13.979, *p* = 0.002. Subsidiary analyses on each quadrant showed that significant old-new effects were found in left and right anterior scalp sites and left posterior scalp sites. Left anterior scalp sites showed the largest old-new effect among the four quadrants (left anterior, *F*(1, 17) = 8.584, *p* = 0.009, right anterior, *F*(1, 17) = 6.934, *p* = 0.017, left posterior, *F*(1, 17) = 8.127, *p* = 0.011). Previous literature also found a frontal old-new effect after the latency of the left-parietal old-new effect, which is thought to be related with recollection of contextual information (Wilding & Rugg, 1996). But the effect they found was more right lateralised rather than left distributed.

An interaction between old-new effect and DMS task condition and anterior-posterior scalp position was found in the time window of 1400 – 1700 ms, *F*(1, 17) = 5.655, *p* = 0.03. A significant old-new effect was found over anterior scalp sites only for the LTM probes from the conjunction DMS condition, *F*(1, 17) = 6.052, *p* = 0.025. The interaction still remained significant after scaling the data, *p* = 0.038. In the last time window 1700 -1900 ms, a significant interaction between old-new effect and DMS task condition was found, *F*(1, 17) = 6.027, *p* = 0.025. Subsidiary analyses on each DMS task condition showed that neither the feature nor the conjunction condition had a significant old-new effect (feature, *F*(1, 17) = 0.343, *p* = 0.564, conjunction, *F*(1, 17) = 3.648, *p* = 0.073). In both time windows of 1400 – 1700 ms and 1700 – 1900 ms, three-way interactions between old-new effect, anterior-posterior scalp position and left-right scalp hemisphere were found (1400 – 1700 ms, *F*(1, 17) = 5.179, *p* = 0.036, 1700 – 1900 ms, *F*(1, 17) = 5.285, *p* = 0.035). An ANOVA that incorporated factors of old-new status (old, new), scalp position (anterior, posterior), scalp hemisphere (left, right) and time window (1400 – 1700 ms, 1700 – 1900 ms) demonstrated the two interactions did not differ from each other, which suggests that the late old-new effect was a sustained effect with a right frontal scalp distribution (Figure 19).

To see if the differences of old-new effects between DMS task conditions contributed to the slightly better recognition test performance for the probes from the conjunction DMS condition, bivariate correlations were conducted between mean amplitude values differences of retrieval activity in the different DMS task conditions and recognition memory test performance (recognition judgments proportions, Pr and reaction times) across participants. As three-way interactions between old-new effect, DMS task condition and anterior-posterior scalp position approached significance in the time window of 500 – 800 ms and remained significant in the time window of 1400 – 1700 ms after scaling the data, the differences between the old-new effects in the two DMS conditions in these two time windows were used to conduct the correlations. The activity elicited by old items from the DMS conjunction condition that attracted correct confident judgments minus the activity elicited by old items from the DMS feature condition that attracted correct confident judgments over anterior scalp sites that were used in the ANOVAs and showed significant old-new effects in the conjunction condition in the two time windows (averaged across sites Fp1, Fp2, 49, 37, F7, F8, 34, 21, LF, RF, 18, 10, 7, 3 from montage 10, see Figure 9) was significantly correlated with the recollection judgments made for items from the conjunction DMS condition (500 – 800 ms, Pearson's $r = 0.486$, $p = 0.041$, 1400 – 1700 ms, Pearson's $r = 0.472$, $p = 0.048$). The more the difference of the retrieval-related activity between conjunction and feature conditions was, the more recollection judgments were likely to be made for the probes from the conjunction condition (Figure 20).

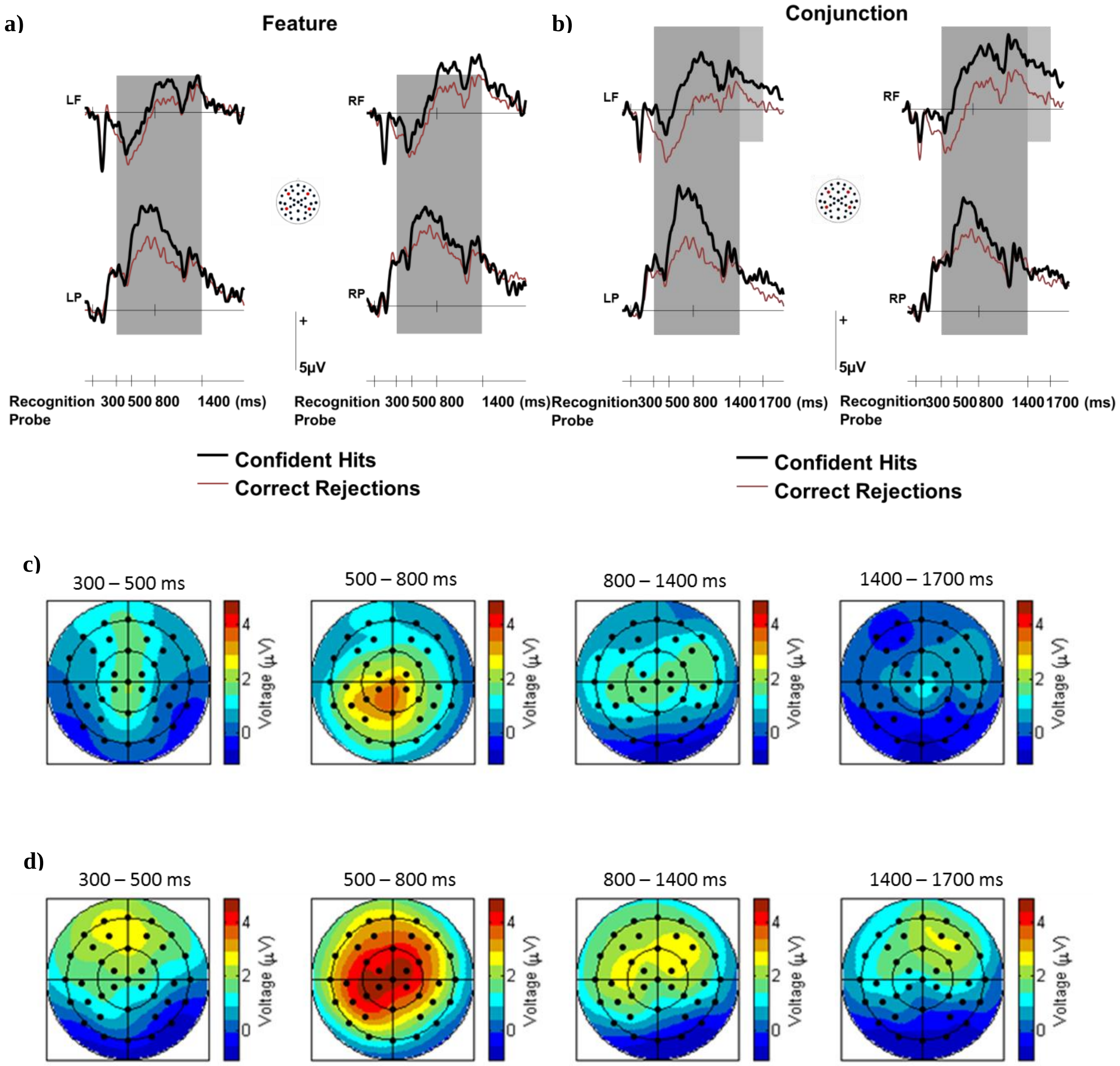


Figure 19. Old-new effect for the LTM probes from different DMS task condition

a) Group-averaged ERP waveforms elicited by probes from the feature DMS condition compared with waveforms elicited by new items at 4 representative electrode sites (site LF, RF, LP and RP from montage 10). Positive values are plotted upwards. b) As in a, but the probes were from the conjunction DMS condition. c) Voltage spline map showing the distribution of the old-new effect for the probes from the feature DMS condition across the scalp in the 300 ms to 500 ms, 500 ms to 800 ms, 800 ms to 1400 ms and 1400 to 1700 ms after recognition item onset. d) As in c, but the probes were from the conjunction DMS condition. The maps are scaled to the difference between maximum and minimum across conditions to highlight the topographical differences and magnitude of the modulations in each condition.

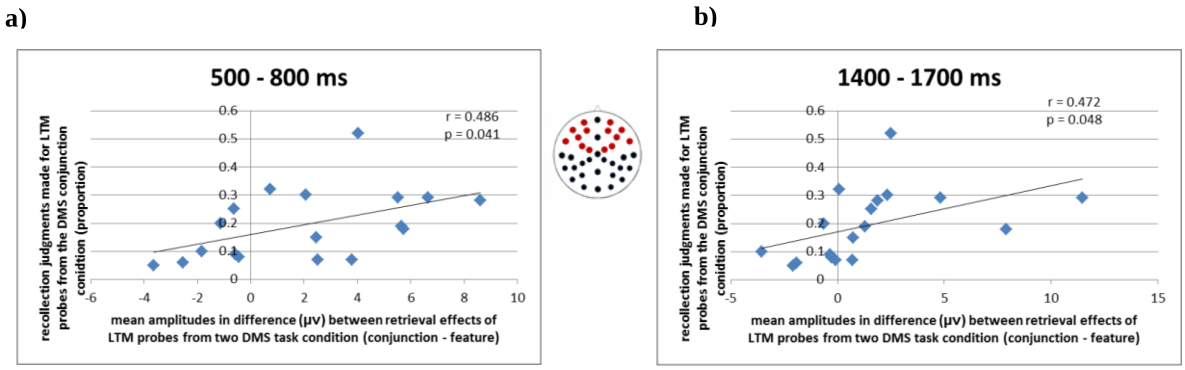


Figure 20. Relationship between difference of frontal retrieval effects for probes from the conjunction DMS condition and the feature DMS condition and recollection hits made for probes from the conjunction DMS condition across participants

a) The correlation between mean amplitudes of ERP difference over anterior electrode sites in retrieval effects of probes from the DMS conjunction and feature conditions in the time window of 500 to 800 ms and recollection judgments made in the conjunction DMS task. Each blue point represents one participant. X-axis represents ERP amplitudes. Y-axis represents proportion of the recollection judgments made for the probes from the DMS conjunction condition during the recognition test. b) As in a, but in the time window of 1400 to 1700 ms.

3.3.4 Discussion

In Experiment 3, a cue signalling the type of a DMS task was presented 5 s before DMS task onset. A long-term memory probe was inserted 3 s after cue onset to see if preparation for a DMS task known to involve the hippocampus (the conjunction task) could induce a brain state conducive to effective encoding. Recognition memory accuracy and reaction times were slightly better for the LTM probes that were inserted before conjunction tasks than the LTM probes that were inserted before feature tasks. The overall preparatory activity elicited by conjunction cues was more positive-going than the overall preparatory activity elicited by feature cues. In addition, the LTM probes from the conjunction condition also elicited larger retrieval-related activity over anterior scalp sites over an extended time period. The above findings generally supported the idea that a brain state conducive to effective memory formation can be induced by asking participant to prepare for a conjunction DMS task. However, encoding-related activity for the LTM probes was larger in the feature than the conjunction condition, which is against the idea that preparation for a conjunction DMS task enhances memory encoding.

Cues signalling the presentation of a conjunction task elicited larger P3 amplitude than cues signalling the presentation of a feature task. The larger P3 amplitude might reflect that more effort was made to preparatory processes for a conjunction task (Luck, 2005). Gruber and Otten (2010) showed that cues signalling potential high monetary rewards for remembering an upcoming word elicited larger P3 amplitude. Although cues in Experiment 3 did not signal any monetary reward for an upcoming DMS task, behavioural results suggest that a conjunction DMS task was more difficult than a feature DMS task. Therefore, the larger P3 amplitude elicited by conjunction task cues might reflect more voluntary effort devoted to prepare for a conjunction DMS task. In addition, the overall preparatory activity was more positive-going over frontal scalp sites shortly before the conjunction task and more negative-going over posterior scalp sites than the feature task. The different scalp distributions might suggest processing of different types of information. The ERP activity during retention of object information is largest over frontal scalp sites while the ERP activity during retention of spatial information is largest over parietal scalp sites (Perez & Vogel, 2012; Ruchkin, Grafman, Cameron, & Berndt, 2003). As a test probe for a feature DMS task was always a black dot, the object information for the feature DMS task might be ignored by participants when they prepared for the feature DMS task. Preparatory processes for the feature DMS task involved brain activity for only spatial information while preparatory processes for a conjunction DMS task involved brain activity for spatial and object information, which spatial information in the conjunction DMS task was represented by object information. Another possible account for the overall preparatory activity is that the level of processing (LOP) might be deep in the preparatory process for the conjunction task compared to the feature task. Schott, Richardson-Klavehn, Heinze and Düzel (2002) found a frontocentral positive-going effect in the deep study condition compared to the shallow study condition and this LOP effect was independent of subsequent memory.

If the overall preparatory activity for a conjunction DMS task reflects deeper LOP or processing of object information combined with its spatial information, then a brain state conducive to successful memory formation could be induced by preparing for the conjunction DMS task. The behavioural results of recognition memory accuracy and reaction times for the LTM probes from the conjunction condition generally support this idea. As discussed before, larger P3 amplitude might reflect greater effort made on preparing for the conjunction task. A significant correlation between reaction times for the DMS task and recognition memory accuracy for the LTM probes was only found in the conjunction condition across subjects. This might indicate that the more effort made on the conjunction task, the more likely a LTM probe could be remembered. This could also explain why some participants did not show advantage on the LTM probes from the conjunction condition as they did not make sufficient effort to prepare for the conjunction DMS task, which also led to slower reaction times for the conjunction DMS task. This is not the case for the feature DMS task.

However, a good brain state for a future task might be a decrease in activation of neural networks underlying the task. Yoo et al. (2012) suggest that less activity in the PPA provides a brain state that has more processing resources for a new memory formation. Therefore, a picture presented after such brain state was more likely to be allocated resource in the PPA so that the picture could be remembered. Manelis and Reder (2013) also suggest that the neural networks underlying preparation should reflect clearing the buffer for leaving resources for future tasks. According to those proposals, it could be argued that a good brain state for successful memory formation should not resemble the neural networks underlying a conjunction DMS task. If preparation for a conjunction DMS task similarly activates the hippocampus as during the conjunction

DMS task, less resources in the hippocampus is available for encoding a new memory. This is not consistent with the behavioural results. However, this might be able to explain why smaller encoding-related activity was found for the LTM probes before a conjunction DMS task.

The activity elicited by feature task cues was more positive-going before recognised probes than forgotten probes in the feature DMS condition over extended time windows while the activity elicited by conjunction task cues was more negative-going before recognised probes than forgotten probes in the conjunction DMS condition only in an early time window. The positive-going encoding-related activity preceding probes for the feature condition resembles the positive-going pre-stimulus subsequent memory effects found in previous studies on voluntary control and emotional control (Galli et al., 2011; 2014; Gruber & Otten, 2010), which is suggested to reflect motivational processes. The effect also replicates the positive-going pre-stimulus subsequent memory effects found in Experiments 1 and 2. In contrast, negative-going encoding-related activity preceding probes for the conjunction condition was found only in an early time window. Although a negative-going pre-stimulus subsequent memory effect is suggested to reflect semantic or more elaborated preparatory processes (Galli et al., 2012; 2013; Otten et al., 2006; 2010), the negative-going encoding-related activity for the LTM probes from the conjunction condition was only found from 300 – 700 ms after cue onset, which is different from the sustained effects found in previous literature. As discussed above, it could be argued that this weak effect might be caused by less processing resources available for memory encoding as preparation for the conjunction DMS task might occupy too much resources in the hippocampus, which is critical for memory encoding. Galli et al. (2013) also suggest that pre-stimulus activity is engaged for memory encoding only when sufficient resources are available before an event. In addition, encoding-related activity after the LTM probes was larger in the feature than the conjunction condition. As mentioned in Chapter 1, the MTL activity and the PFC activity are decreased during encoding if a secondary task is performed concurrently (Anderson et al., 2000; Fletcher et al, 1998; Iidaka et al., 2000). In Experiment 3, the difference between the overall preparatory activity shortly before a conjunction task and a feature task was also found within the time windows where significant subsequent memory effects were found. The conjunction task was more difficult than the feature task. The participants also reported they prepared more thoroughly when they saw the conjunction cues as they had to combine identities of the stimuli with their specific locations. These all suggest that compared to a feature DMS task, a conjunction DMS task costs more processing resources, which could lead to reduced encoding-related activity (Chun & Turk-Browne, 2007).

Differently, Schott et al. (2002) found that in the early time window of the LOP effect, a subsequent memory effect was found in the shallow study condition. In a later time window of the LOP effect, subsequent memory effects were found for both shallow and deep study conditions. They suggested that the early subsequent memory effect found only in the shallow condition might reflect processing of perceptual level of information that could be stored in memory trace, which is not necessary for deep encoding condition. If this is true, then in the current experiment only the later encoding-related activity was critical to deeper levels of encoding. The absence of the early subsequent memory effect in the conjunction condition did not influence the recognition memory performance. As discussed above, the overall frontal positive-going preparatory activity elicited by conjunction cues could reflect deeper level of processing. Then as a secondary task to memory encoding, preparation for a conjunction DMS task might not influence memory encoding on an LTM probe as Hoffmann, von Helversen and Rieskamp (2013) suggest that performance for the main task could be improved if the strategy that is used for a secondary task is the same as the main task.

The additional frontal retrieval-related activity found in the probes for the conjunction condition also seems to support the idea that insufficient resource are available for memory encoding before a conjunction DMS task. Johnson, Nessler and Friedman (2013) found left frontal retrieval-related activity when healthy young adults tried to retrieve words that were encoded under divided attention task but not under full attention. They called this additional left frontal activity ‘compensatory’ activity. They suggested that this activity appeared only when left-parietal activity was absent and should be correlated with participants’ performance. That means the activity is a compensation for poor memory representations during encoding. Such ‘compensatory’ activity appears after a feeling of familiarity and differs across individuals. In Experiment 3, the additional frontal retrieval-related activity in the conjunction condition started from 500 ms to 800 ms and was extended in a later time window 1400 – 1700 ms where was after the memory control and monitoring processes (Wilding & Ranganath, 2012). The amplitudes of the difference between retrieval-related activity in the conjunction and feature conditions were correlated with participants’ recollection judgments in the conjunction condition. This means the degree of participants’ attempts to recollect probes in the conjunction condition contributes to their recollection of the probes for the conjunction condition. This seems to be consistent with the compensatory account to the additional frontal retrieval-related activity while attempting to retrieval some poor encoded events. However, in Experiment 3, it did not show any absence in left-parietal old-new effect in the conjunction condition. This might suggest that the memory representations of the probes in the conjunction condition were encoded elaborately enough to show the left-parietal old-new effect. A right frontal old-new effect was found from 1400 ms until the end of the epoch. The differences between the old-new effects in the conjunction condition and the feature condition were not restricted to right frontal scalp sites but the whole anterior scalp sites in the time window of 1400 – 1700 ms. In addition, the differences were correlated with the numbers of recollection judgments participants made for the LTM probes from the conjunction condition. Wilding and Rugg (1996) suggest that right frontal old-new effect sustained until the end of the epoch although in their findings the effect was maximal from 1100 ms. Larger magnitude of such frontal old-new effects over extended time windows also reflected the recollection of source judgments. The extended frontal old-new effects found in the conjunction condition may play a key role in additional attempts to recollect past events, which might contribute to the enhancement in memory performance for the conjunction condition.

One problem of the current study is that there was no baseline performance or 'brain state' for the current study like the study done by Yoo et al. (2012). The brain states were built by preparation for two different DMS tasks. But there was no neutral brain state of no preparation. The results of the current study provide some evidence that preparation for a conjunction of multiple pieces of information could build a better brain state for memory formation than preparation for an individual feature. However, there is no evidence about whether this good or not good brain state is better or worse than no preparation.

In conclusion, the behavioural results, the overall preparatory activity before DMS task onset and the results of retrieval-related activity support the idea that memory can be enhanced by a brain state that is built by preparation for a conjunction DMS task. However, the encoding-related activity before and after the probes was smaller in the conjunction condition, which is a puzzle. This seems not be able to be completely explained by insufficient available processing resource. The findings open up the opportunity for the application of brain states in educational and patient settings. Although real-time fMRI allows detecting a preparatory brain state for efficient learning more accurately (Yoo et al., 2012), the paradigm of Experiment 3 provides an easier setup. A preparatory brain state for efficient memory encoding can be induced by asking participants to prepare for a task involving the binding of multiple types of information.

Chapter 4: Does amount of advance information influence pre-stimulus encoding-related theta and alpha activity?

4.1 Experiment 1: The influence of graded perceptual preparation on pre-stimulus encoding-related theta and alpha activity

4.1.1 Introduction

As discussed in Chapter 2, in the additive model of the relationships between ERP and oscillations, ERP and oscillations capture different neural processes underlying a cognitive event. The phase-resetting view suggests that ERP and oscillations depend on each other. Therefore, analysing the same dataset in both ERP and oscillations domains is interesting to reveal the neural mechanisms represented by these two perspectives on a cognitive event. In Experiment 1, the pre-stimulus subsequent memory ERP effects did not differ as a function of amount of advance information. To complement the ERP analyses, the same dataset was re-analysed in time-frequency domain to see if pre-stimulus oscillatory brain activity is engaged in preparation for memory encoding depending on the degree of perceptual information to be prepared.

The role of oscillatory activity in theta frequency band (4-8 Hz) preceding or following an event has both been demonstrated to be critical in supporting memory encoding (Addante et al., 2011; Fell et al., 2011; Fellner et al., 2013; Gruber et al., 2013; Guderian et al., 2009). Such encoding-related theta increase effect prior to an item was found to be located in the MTL (Fell et al., 2011; Guderian et al., 2009), which suggests the functional role of such theta activity might be pre-activation of mnemonic context role. Further, Gruber et al. (2013) suggest that the encoding-related theta activity prior to an event is under voluntary control.

Compared to the role of theta activity in preparing for forming a new memory, there are not so many studies on the role of alpha activity in supporting memory encoding preceding an event. Fell et al. (2011) also found an MTL alpha enhancement before successful memory encoding. In the other cognitive domains such as perception, attention or working memory, alpha activity plays the role in gating information from dorsal visual stream (van Dijk et al., 2008; Jokisch & Jensen, 2007). Therefore, Fell et al. (2011) suggest the MTL alpha enhancement before successful memory encoding might reflect inhibitory control of contextual information, which could boost preparation for stimulus-related processing. Such findings suggest that both theta and alpha activity is important to preparing for forming a new memory.

Recently, not only synchronisation in brain oscillations but also desynchronisation in brain oscillations in memory-related processes has attracted attention. As suggested above, increase in alpha activity plays a role in gating information in brain visual areas. Therefore, decrease in alpha activity reflects increase in flow of visual information (for a review, see Jensen & Mazaheri, 2010). In memory domain, decrease in alpha activity has been found to support encoding a visual memory (Hanslmayr et al., 2009; Fellner et al., 2013; Park et al., 2014). Hanslmayr et al. (2012) suggest that when local neurons are firing in a fashion of no synchrony, the population of neurons that encode information increases. Therefore, desynchronisation in brain oscillatory activity increases the degree of information to be processed. Such an idea suggests that a decrease in alpha activity reflects the capacity of processing more information so that decreases in alpha activity can help memory-related processes. If this idea is true, then memory-related preparation for the amount of perceptual information should be associated with the degree of desynchronisation in brain oscillations. The higher degree of the amount of perceptual information to be prepared, the more desynchronised the brain oscillations should be found.

In Experiment 1, preparation for more perceptual details might have larger decrease in encoding-related alpha activity than preparation for less perceptual details. It is possible that non-informative cues also elicit an encoding-related alpha decrease activity prior to picture onset. Non-informative cues did not signal the type of an upcoming picture but signalled the presentation of either a photo or an outline. Therefore, preparation for successful encoding in an unpredictable condition might increase the gain for more visual information to pass as two types of pictures were anticipated in that condition so that pre-stimulus alpha activity would decrease. Although theta activity has been found to be important to episodic memory encoding, it is not clear how theta activity plays a role in preparing for encoding a pictorial stimulus. If theta activity plays a role in pre-activating contextual information for preparing to form a new memory then theta activity should not differ in the amount of information to be prepared.

4.1.2 Methods

Participants, stimulus material, procedure and EEG acquisition are all described in section 3.1.2

EEG time-frequency analysis. The EEGLAB toolbox (http://sccn.ucsd.edu/eeglab/) that is implemented in MATLAB (Delorme & Makeig, 2004) was used for time-frequency analyses. The continuous EEG data were high-pass filtered with a low cut-off point at 0.5 Hz for removing slow drifts, which optimized the Independent Component Analysis (ICA) (Delorme & Makeig, 2004). The EEG data was downsampled to 250 Hz to reduce the data size. The continuous EEG data were segmented into epochs of 4400 ms duration from -0.8 to 3.6 s (0 is cue onset). The reason why this length was picked is that there would be sufficient time / frequency information for the whole interval between the cue-picture (1.5 s) and the 1.5 s duration after picture onset. Therefore, it would not be affected by edge effects at the beginning and the end of an epoch as the time-frequency information was derived for each time point from cue onset until 1.5 s after picture onset. Each epoch was baseline corrected by the mean amplitude of an interval from 600 ms to 0 s before pre-stimulus cues onset in the time domain. Trials were rejected when the amplitudes exceeded more than 3 standard deviations on a single channel or more than 5 standard deviations across all channels. These two steps were both for optimizing ICA decomposition. Then ICA decomposition was carried out to remove components related to blinks, eye-movements or line noise (Delorme & Makeig, 2004). After the ICA, the trials that still included muscle artefacts and AtoD saturation were rejected manually. The data were re-referenced to linked mastoids and the online reference was reinstated. Time-frequency analyses were performed using Morlet wavelets (Percival & Walden, 1993) with 4 cycles. The computation was done in every 20 ms time window in a 0 – 3 s interval. Wavelet analyses were done in steps of 1Hz in the 4 to 12 Hz frequency range. Then power values of trials in each condition were averaged (see Table 22 for the mean trial numbers in each condition): later recognized trials in each condition; later forgotten in each condition, trials of all judgments of each condition. Here, the criteria for ‘recognized’ and ‘forgotten’ trials were the same as those used in the ERP analyses.

Table 22. Mean trial numbers in each condition in Experiment 1 time-frequency analyses (Range in brackets)

	Photo Cue Condition	Outline Cue Condition	Neutral Cue Condition
Recognized trials	39 (17 to 64)	40 (20 to 63)	39 (13 to 65)
Forgotten trials	30 (13 to 46)	26 (12 to 63)	30 (14 to 50)
Overall (regardless of memory performance)	92 (60 to 105)	92 (66 to 103)	93 (65 to 105)

Statistical analyses of time-frequency analyses. The data were collapsed into 6 time windows of 500 ms per time window for a 3 s interval for statistical analyses as mentioned in Chapter 2. The mean theta power between 4-8 Hz and the mean alpha power between 9-12 Hz were taken. Permutation tests were used to test channel clusters that showed significant effects in each comparison (Maris & Oostenveld, 2007). First, a two-tailed t-test was used to compare the means of two selected conditions, for example, mean theta power of each subject for later recognized items and forgotten items in the photo cue condition. Then, the power values for each condition from each participant were pooled across participants and assigned randomly into two pseudo conditions. A two-tailed t-test then was used to compare the means of these two pseudo conditions to check whether the effect could have been obtained by chance. This step was repeated 1000 times. This resulted in a distribution of 1000 pseudo t-values. Finally, a critical t-value was created according to the two tails of that distribution. The alpha level was 0.05 and there were 1000 permutations. As the two tails were 0.025 and 0.975 respectively, the critical t-values of this distribution should be the 25th and the 975th values of the distribution. This t-value could be used to see if the null hypothesis should be rejected. The t-value from the original data was compared to the critical t-value of the distribution. This approach was conducted for 30 scalp electrodes as there was 1 bad channel (41) for 6 subjects. For symmetric reason, the data of both channel 41 and 45 for each subject were excluded from statistical analyses. A Type I error would be expected as too many electrodes were used for comparisons (0.05 * 30 = 1.5 electrodes per time window). Therefore, only effects in two adjacent electrodes were counted into significant effects to avoid Type I error.

Permutation tests were first used to test interactions between subsequent memory effect and cue condition. The difference in power between later recognised pictures and later forgotten pictures for each cue condition was compared to see if there was any significant interaction. If any significant interaction was found, further permutation tests were conducted for each cue condition separately to understand the interaction. If no significant interaction was found, further permutation tests were done to compare the difference in power between recognised pictures and forgotten pictures regardless of cue conditions to see if any main effect of subsequent memory effect was found irrespective of cue conditions.

4.1.3 Results

Encoding-related pre-stimulus theta effect. Theta power (4-8 Hz) appeared to decrease before pictures that were later recognized than forgotten and these theta decrease subsequent memory effects prior to picture onset were especially robust in the photo cue and neutral cue conditions (Figures 21 - 23).

Permutation tests revealed significant interactions between cue conditions (Figure 24). The neutral cue condition had larger encoding-related theta desynchronisation compared to the photo cue condition over left temporal scalp electrodes, compared to the outline cue condition over left occipital-central scalp electrodes. The interactions were found 500 ms before picture onset. Permutation tests compared the power differences between recognised pictures and forgotten pictures, irrespective of cue conditions in the first two time windows (0 – 500 ms and 500 – 1000 ms) that did not reveal significant interactions between subsequent memory and cue condition. Theta power decreased significantly before recognised pictures compared to forgotten pictures in both time windows. Such encoding-related theta desynchronisation was over left temporal electrodes from cue onset to 500 ms after cue onset and over left frontocentral and right occipital scalp sites from 500 ms to 1000 ms after cue onset. A further permutation test was done to test the desynchronisation subsequent memory effect by collapsing these two time windows (0 – 1000 ms after cue onset). The theta desynchronisation subsequent memory effect regardless of cue conditions was over left scalp sites from cue onset until 1000 ms after cue onset.

Separate permutation tests were done to each cue condition to understand the interactions between subsequent memory effect and cue condition. Theta power significantly decreased before recognised pictures in both photo cue and neutral cue conditions in the time window of 1000 ms to 1500 ms after cue onset (Figures 21 - 23). Encoding-related theta desynchronisation was found over occipital scalp sites in the photo cue condition. In contrast, a left-lateralised theta power decrease subsequent memory effect was found in the neutral cue condition. No significant subsequent memory effect was found in the outline cue condition.

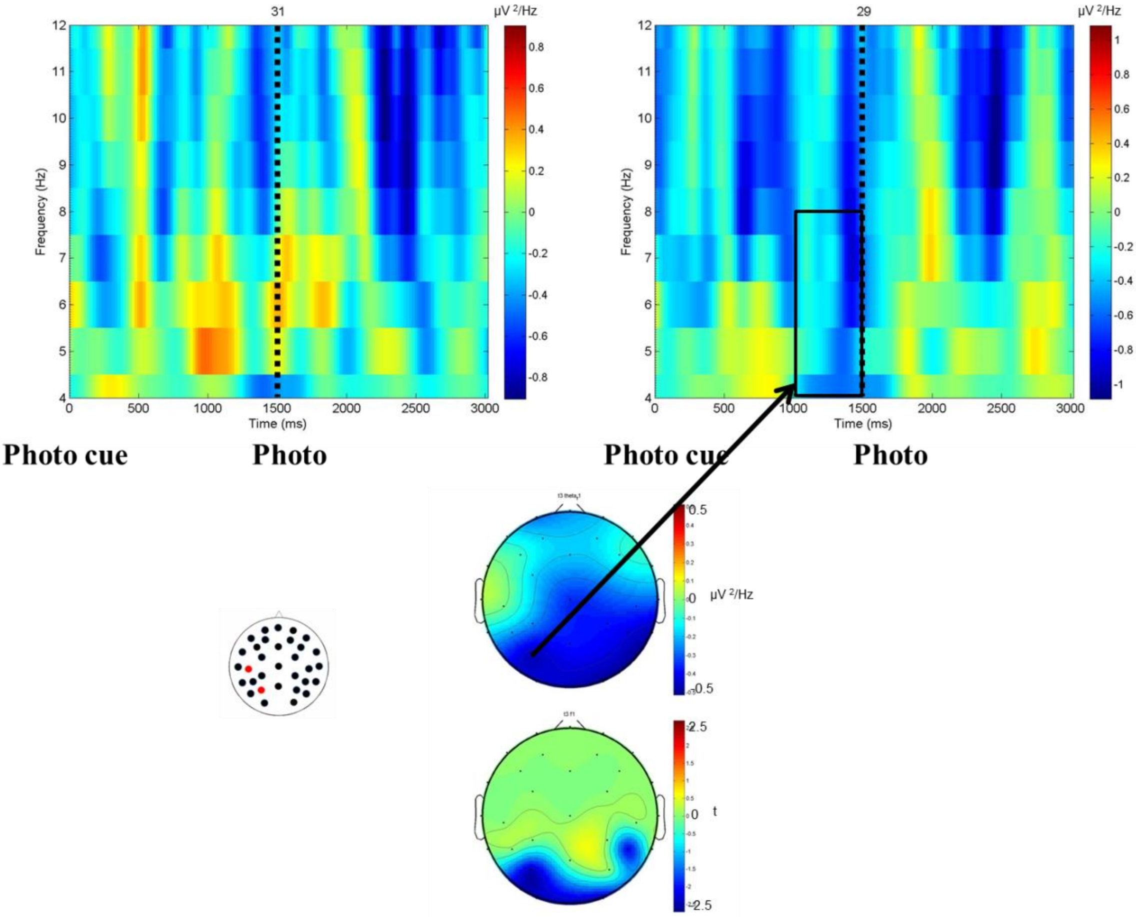


Figure 21. Pre-stimulus encoding-related theta effect in the photo cue condition

a) Top: time-frequency representations of pre-stimulus encoding-related theta activity at two electrode sites (sites 29 and 31 from montage 10). b) Top: a scalp map indicates the difference in theta power before later recognised and forgotten pictures. Bottom: a corresponding statistical map shows the significant differences in pre-stimulus theta power between later recognised and forgotten pictures. Scalp maps reflect the time window of 1000 ms to 1500 ms after cue onset.

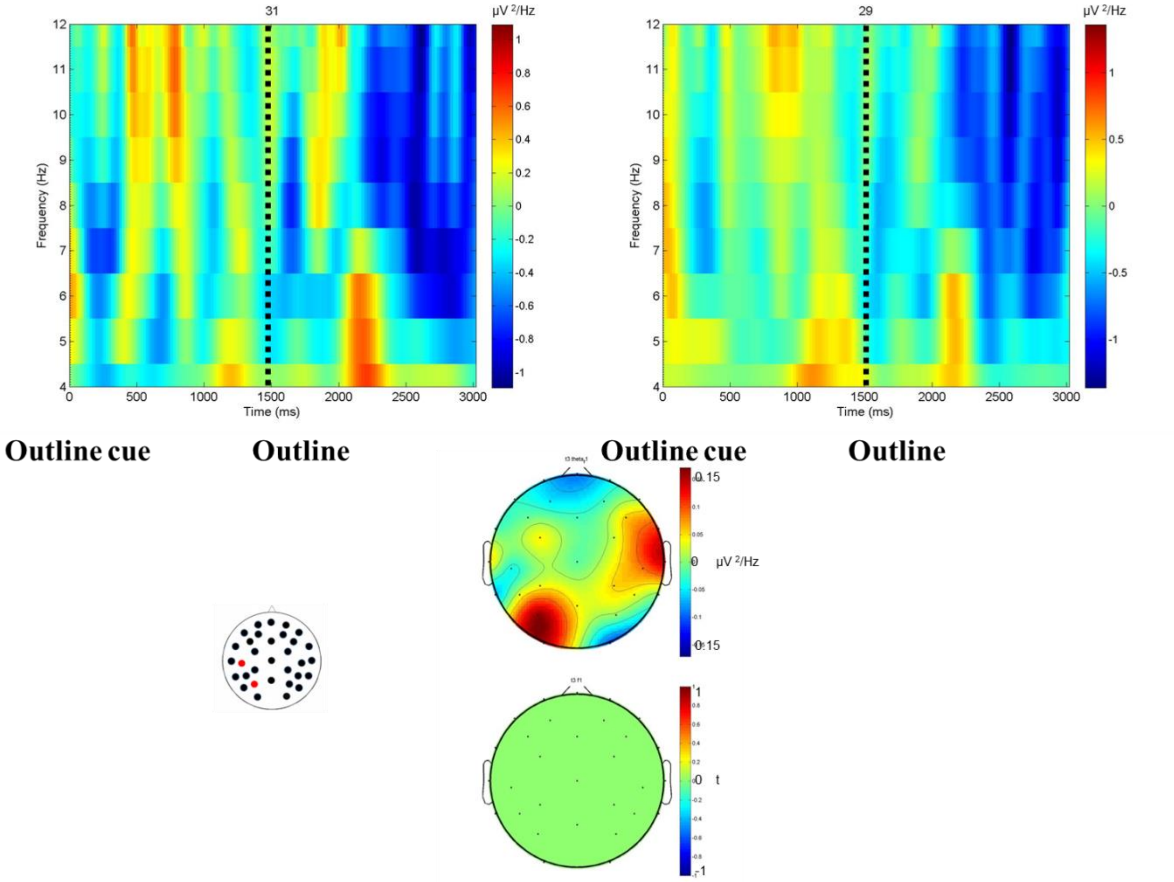


Figure 22. Pre-stimulus encoding-related theta effect in the outline cue condition

a) Top: time-frequency representations of pre-stimulus encoding-related theta activity at two electrode sites (sites 29 and 31 from montage 10). b) Top: a scalp map indicates the difference in theta power before later recognised and forgotten pictures. Bottom: a corresponding statistical map shows the significant differences in pre-stimulus theta power between later recognised and forgotten pictures. Scalp maps reflect the time window of 1000 ms to 1500 ms after cue onset.

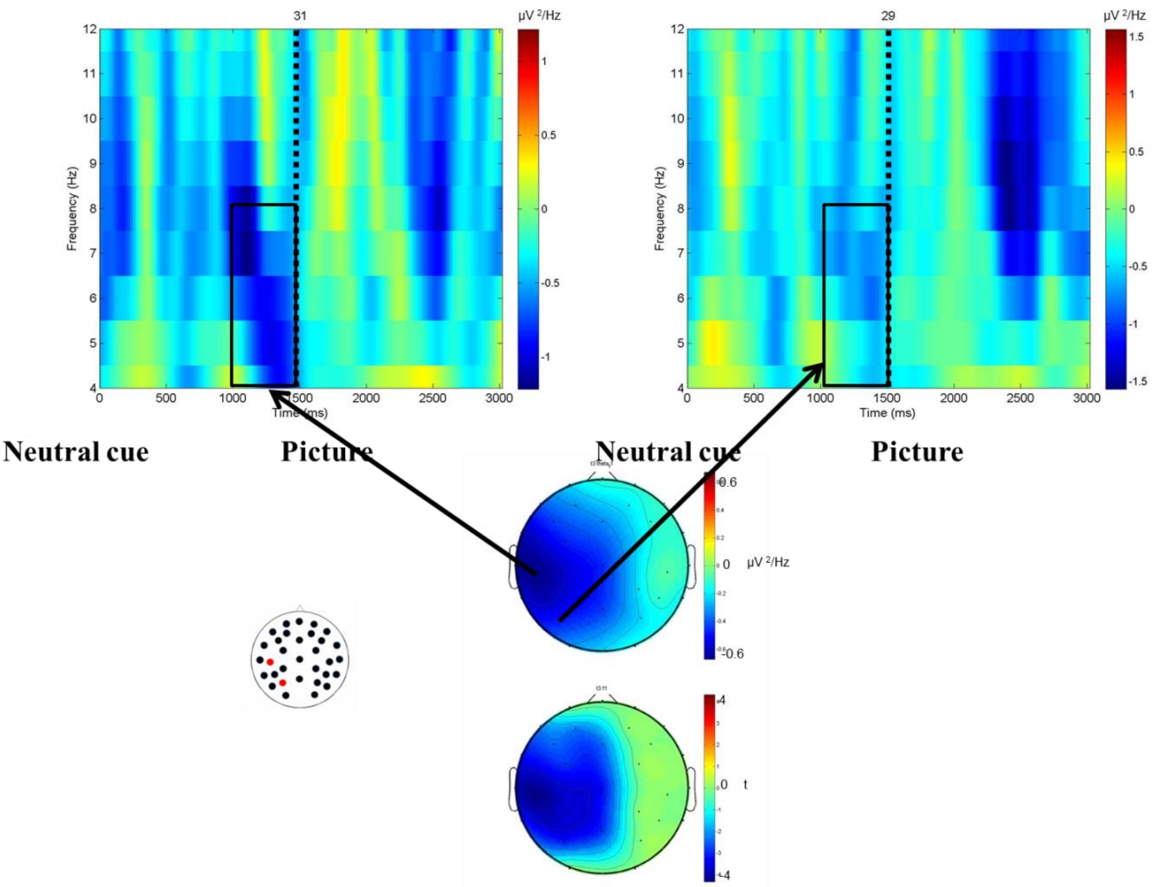


Figure 23. Pre-stimulus encoding-related theta effect in the neutral cue condition

a) Top: time-frequency representations of pre-stimulus encoding-related theta activity at two electrode sites (sites 29 and 31 from montage 10). b) Top: a scalp map indicates the difference in theta power before later recognised and forgotten pictures. Bottom: a corresponding statistical map shows the significant differences in pre-stimulus theta power between later recognised and forgotten pictures. Scalp maps reflect the time window of 1000 ms to 1500 ms after cue onset.

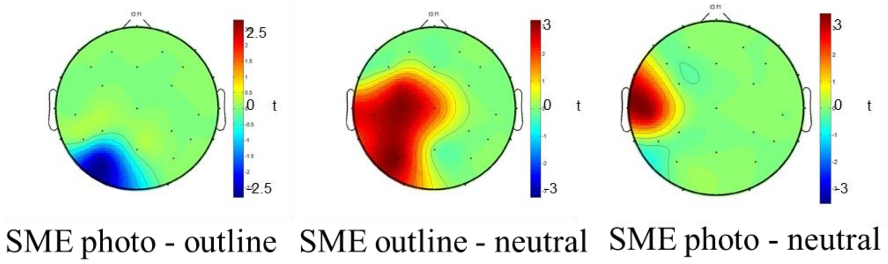


Figure 24. Differences in pre-stimulus encoding-related theta power between cue conditions in Experiment 1

Left: significant differences in pre-stimulus encoding-related theta power between photo cue and outline cue conditions. Middle: as in left, but the differences are between outline cue and neutral cue conditions. Right: as in left and middle, but the differences are between photo cue and neutral cue conditions. Scalp maps reflect the time window of 1000 ms to 1500 ms after cue onset

Encoding-related post-stimulus theta effect. The permutation tests revealed no interaction between subsequent memory and amount of perceptual details of a picture. Then permutation tests were done to test overall subsequent memory effect irrespective of picture type. Significant theta power decrease subsequent memory effects were found from 500 ms to 1500 ms after picture onset. In the time window of 500 ms to 1000 ms, theta power decreased significantly when a picture was recognised compared to forgotten over occipital scalp electrodes. In the time window of 1000 ms to 1500 ms, encoding-related theta desynchronisation was found over the whole scalp. A further permutation test revealed a widespread encoding-related theta power decrease effect from 500 ms to 1500 ms after picture onset when two time windows were collapsed.

Picture-related theta activity irrespective of memory performance. To be consistent with the ERP analyses, picture-related theta activity irrespective of memory performance was compared between picture types to see if theta activity was influence by amount of perceptual details of a picture. The more perceptual details a picture had the less theta power the picture elicited. Significant decrease in theta power was found after a photo compared to an outline over right frontal scalp sites in the time window of 0 to 500 ms after picture onset.

Cue-related theta activity irrespective of memory performance. To see if theta activity was also influenced by amount of perceptual information to be prepared, trials in each cue condition were collapsed regardless of memory performance. Permutation tests revealed differences in theta power between cue conditions in a time window of 1000 ms to 1500 ms after cue onset. Neutral cues elicited larger theta desynchronisation than photo cues over right posterior scalp sites, than outline cues over the whole scalp except left central electrodes. Compared to outline cues, photo cues also elicited larger theta desynchronisation over frontal scalp sites.

Encoding-related pre-stimulus alpha effect. Similarly to the encoding-related pre-stimulus theta effect, alpha power (9-12 Hz) decreased before pictures that were later recognized (Figures 23 - 25). Again, the effect was robust in the photo and neutral cue conditions.

Permutation tests revealed significant interactions between subsequent memory and cue condition in a time window of 500 ms to 1000 ms after cue onset. Similarly to the theta effects, neutral cues elicited larger encoding-related alpha desynchronisation than photo cues over right central-temporal scalp sites, than outline cues over bilateral temporal scalp sites (Figure 28). Compared to outline cues, photo cues elicited larger encoding-related alpha desynchronisation over left posterior scalp sites. Then permutation tests compared alpha power differences between recognised pictures and forgotten pictures regardless of cue conditions in the other time windows. A widespread significant encoding-related alpha decrease effect was found only in the time window before picture onset (1000 ms to 1500 ms after cue onset).

Separate permutation tests were done to each cue condition in the time window of 500 ms to 1000 ms after cue onset. Consistently with theta decrease subsequent memory effects, alpha power also significantly decreased before recognised pictures in both photo cue and neutral cue conditions (Figure 25 - 27). Alpha power decreased before recognised photos compared to forgotten photos over occipital scalp sites in the photo cue condition. Encoding-related alpha desynchronisation was found over right temporal scalp sites in the neutral cue condition.

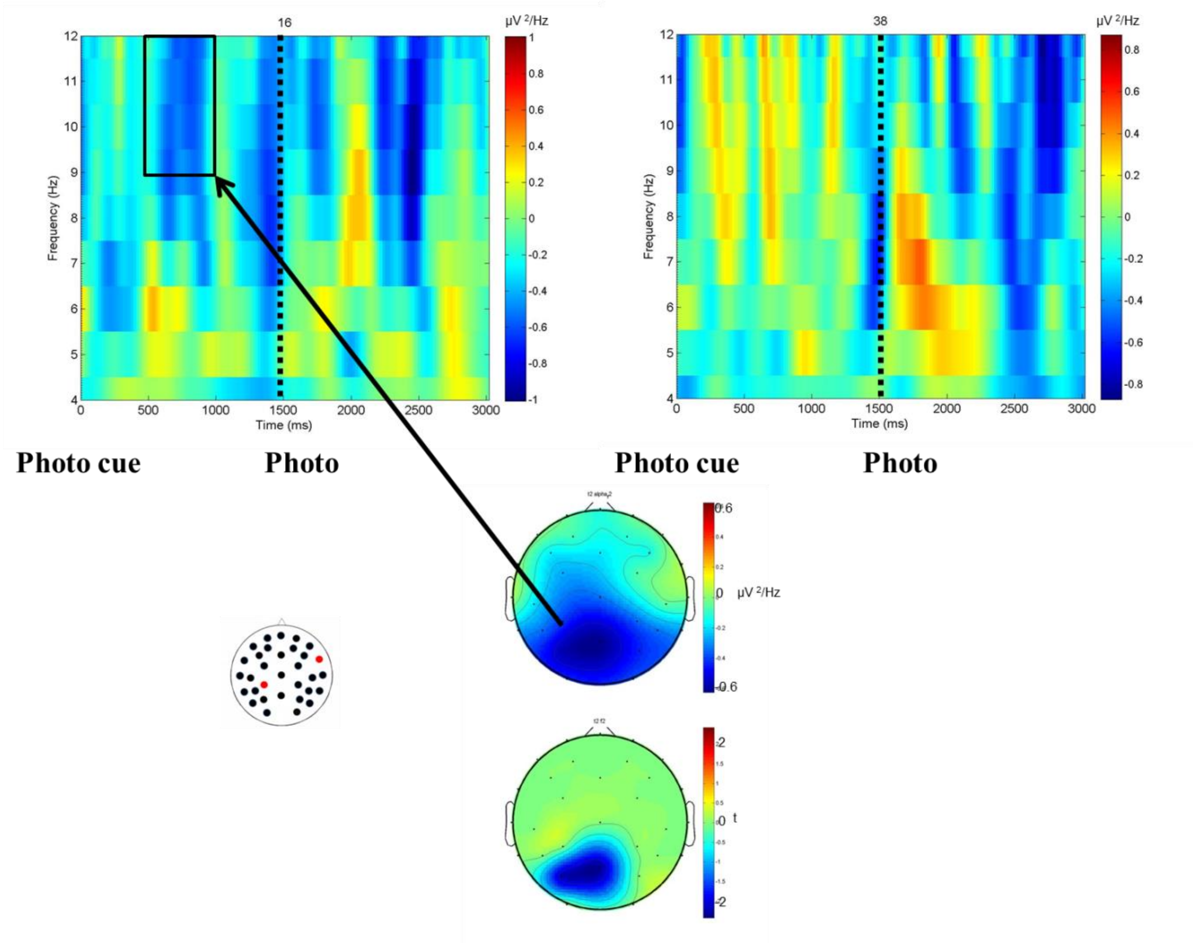


Figure 25. Pre-stimulus encoding-related alpha effect in the photo cue condition

a) Top: time-frequency representations of pre-stimulus encoding-related alpha activity at two electrode sites (sites 29 and 31 from montage 10). b) Top: a scalp map indicates the difference in alpha power before later recognised and forgotten pictures. Bottom: a corresponding statistical map shows the significant differences in pre-stimulus alpha power between later recognised and forgotten pictures. Scalp maps reflect the time window of 500 ms to 1000 ms after cue onset.

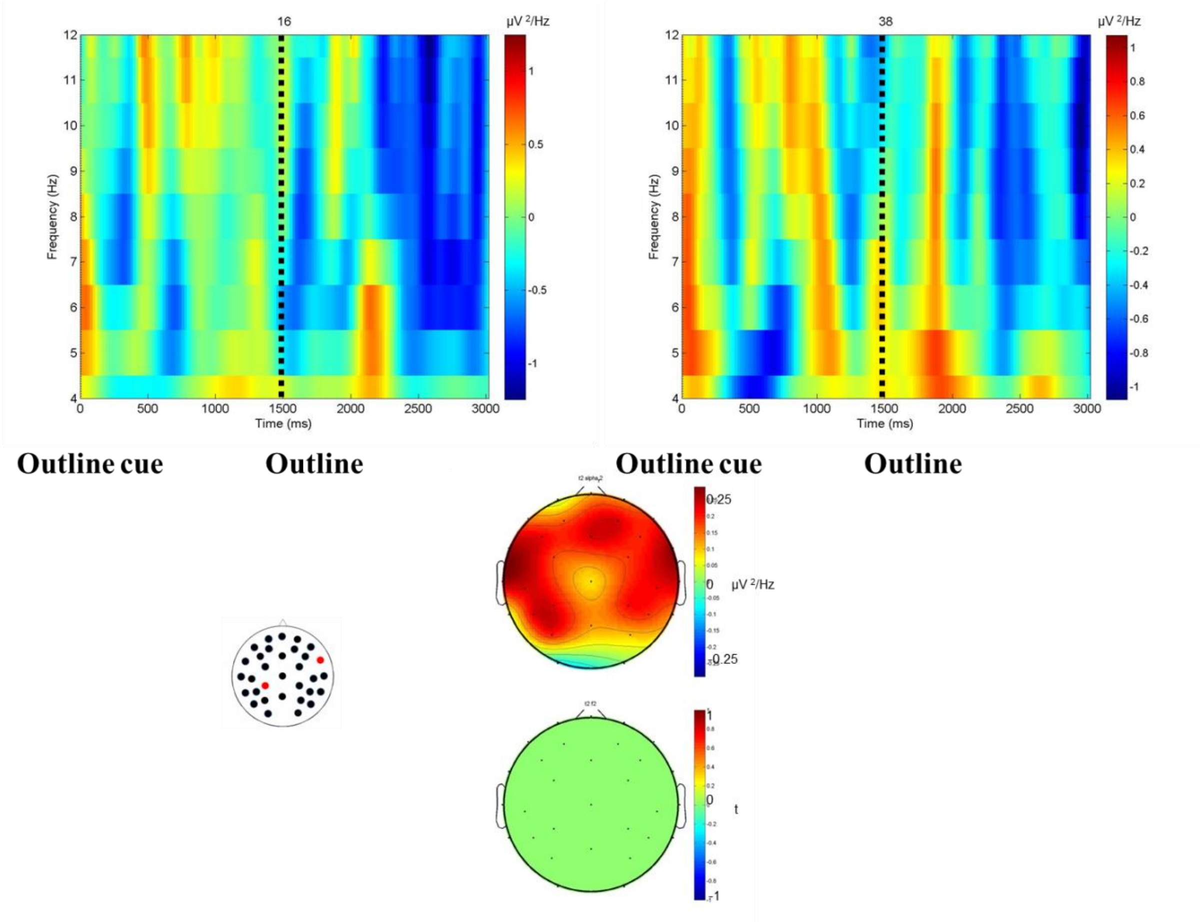


Figure 26. Pre-stimulus encoding-related alpha effect in the outline cue condition

a) Top: time-frequency representations of pre-stimulus encoding-related alpha activity at two electrode sites (sites 29 and 31 from montage 10). b) Top: a scalp map indicates the difference in alpha power before later recognised and forgotten pictures. Bottom: a corresponding statistical map shows the significant differences in pre-stimulus alpha power between later recognised and forgotten pictures. Scalp maps reflect the time window of 500 ms to 1000 ms after cue onset.

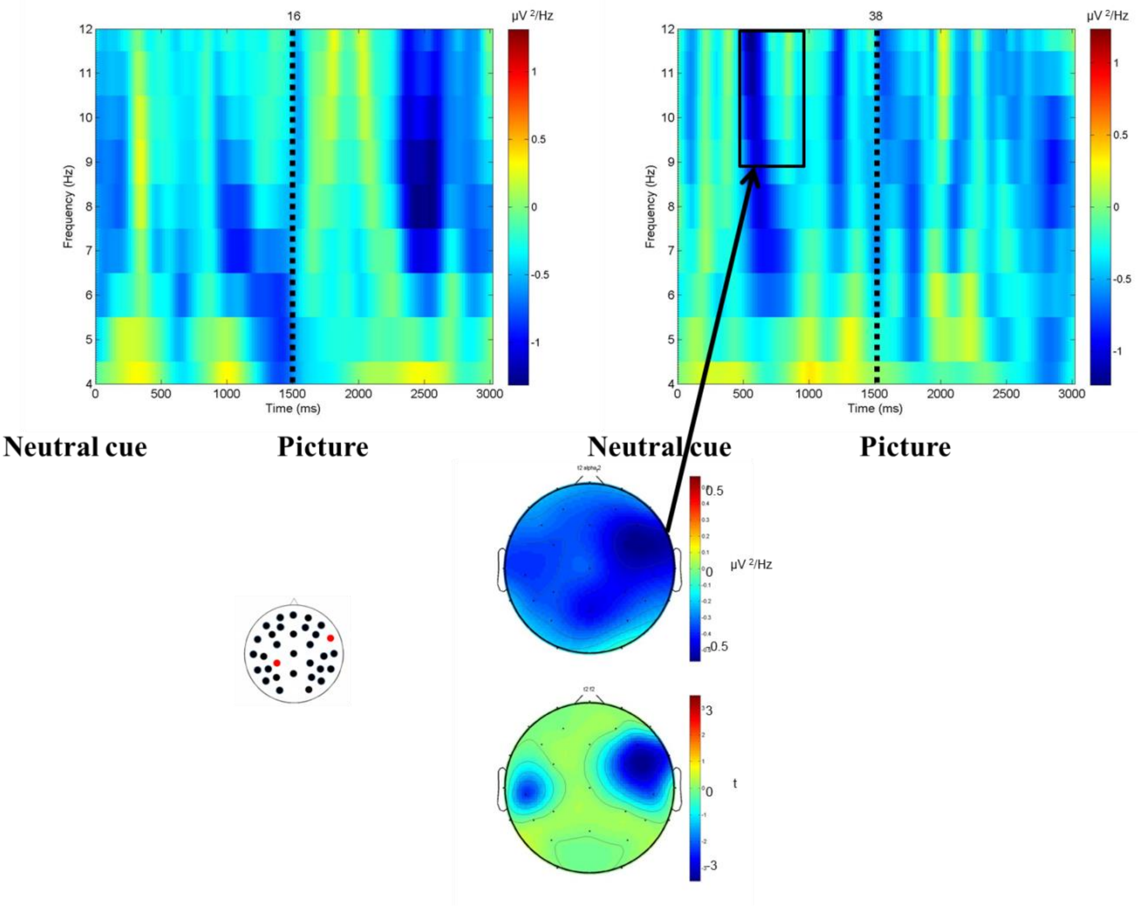
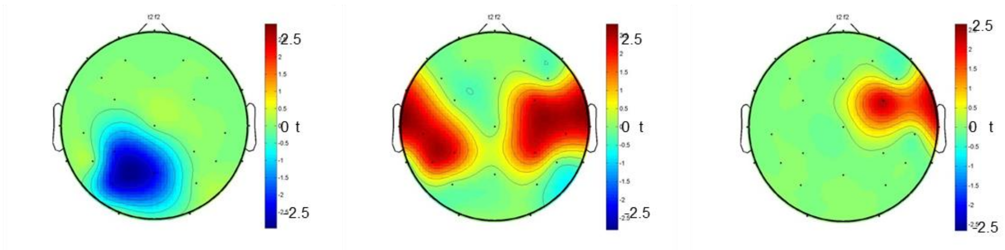


Figure 27. Pre-stimulus encoding-related alpha effect in the neutral cue condition

a) Top: time-frequency representations of pre-stimulus encoding-related alpha activity at two electrode sites (sites 29 and 31 from montage 10). b) Top: a scalp map indicates the difference in alpha power before later recognised and forgotten pictures. Bottom: a corresponding statistical map shows the significant differences in pre-stimulus alpha power between later recognised and forgotten pictures. Scalp maps reflect the time window of 500 ms to 1000 ms after cue onset.



SME photo - outline SME outline - neutral SME photo - neutral

Figure 28. Differences in pre-stimulus encoding-related alpha power between cue conditions.

Left: significant differences in pre-stimulus encoding-related alpha power between photo cue and outline cue conditions. Middle: as in left, but the differences are between outline cue and neutral cue conditions. Right: as in left and middle, but the differences are between photo cue and neutral cue conditions. Scalp maps reflect the time window of 500 ms to 1000 ms after cue onset

Encoding-related post-stimulus alpha effect. No interaction between subsequent memory and picture type was found in the permutation tests. Permutation tests on subsequent memory irrespective of picture type revealed significant subsequent memory effect in all three time windows after picture onset. In the time window of 0 to 500 ms after picture onset, the encoding-related alpha desynchronisation was over right scalp sites. After 500 ms, the alpha desynchronisation was over the whole scalp supporting memory encoding. When collapsing the three time windows into one time window from 0 to 1500 ms after picture onset, the encoding-related alpha desynchronisation was found over the whole scalp.

Picture-related alpha activity irrespective of memory performance. Picture-related alpha activity irrespective of memory performance was of interest as mentioned above, alpha activity is demonstrated to play an important role in processing visual information. Alpha activity was found to decrease after a photo compared to an outline first from picture onset to 500 ms after picture onset over right frontal scalp sites. Then alpha activity increased after a photo compared to an outline over right frontocentral and left occipital scalp sites in the time window of 1000 ms to 1500 ms after picture onset.

Cue-related alpha activity irrespective of memory performance. Alpha activity decreased when more perceptual details were to be prepared over left frontotemporal scalp sites in the time window of 500 ms to 1000 ms after cue onset. In terms of amount of advance information, alpha activity decreased 1000 ms to 1500 ms after non-informative cue onset compared to informative cues. Such alpha desynchronisation in the non-formative cue condition compared to informative cue conditions was found over occipital scalp sites.

Summary of the time-frequency analyses. The time-frequency analyses showed pre-stimulus encoding-related desynchronisation in both theta and alpha frequency bands. Such desynchronisation was found robust in the photo cue and neutral cue conditions but not in the outline cue conditions. The interactions revealed that the neutral cue conditions had the largest theta and alpha desynchronisation before recognised pictures than the other two cue conditions. In addition, both theta and alpha activity irrespective of memory performance decreased after neutral cue onset compared to the other two kinds of cues.

The direction of the effects was the same in the theta and alpha frequency bands. But different time windows and scalp distributions suggest that the two effects might be two independent effects rather than an overall low frequency band effect. The pre-stimulus encoding-related theta decrease effect occurred later than the pre-stimulus encoding-related alpha decrease effect. The post-stimulus encoding-related theta decrease effect was also later than the alpha decrease effect and less widespread than the alpha effect.

4.1.4 Discussion

Experiment 1 investigated whether encoding-related brain oscillatory activity before an event is influenced by amount of perceptual information to be prepared. Informative cues signalled the type of an upcoming picture. A greyscale photo with rich perceptual details was preceded by a photo cue and a perceptually impoverished outline was preceded by an outline. Non-informative cues did not signal the level of perceptual richness of an upcoming picture. Significant decreases in theta and alpha power was found before remembered pictures compared to forgotten pictures. Such encoding-related theta and alpha desynchronisation was influenced by the amount of perceptual information to be prepared. In a middle time window of 500 ms to 1000 ms after cue onset, encoding-related alpha desynchronisation prior to a picture onset was only found in the photo cue and non-informative (neutral) cue conditions but not in the outline cue condition. In a late time window of 1000 ms to 1500 ms after cue onset, encoding-related theta desynchronisation prior to a picture onset was found in the photo cue and neutral cue conditions but not in the outline cue condition.

The findings support the idea that desynchronisation in the alpha frequency band supports memory encoding by increasing perceptual richness of information (Hanslmayr et al., 2012). First, significant decrease in alpha power was found both preceding and following an event. The role of decrease in alpha power in efficient memory encoding has been demonstrated to be crucial in a good number of studies (for a review, see Hanslmayr et al., 2012). Especially when encoding task is a semantic processing task, decrease in alpha power is found to support successful memory encoding (e.g. Fellner et al., 2013; Hanslmayr et al., 2009). Hanslmayr and Staudigl (2013) suggest that alpha power decrease during encoding reflects semantic processing underlying the encoding task as desynchronisation allows increasing the capacity of semantic information processing.

Second, pre-stimulus encoding-related alpha desynchronisation differed in amount of perceptual information to be prepared and amount of advance information. When a cue signalled a presentation of an upcoming greyscale photo, encoding-related alpha desynchronisation was significantly larger over occipital scalp sites than when a cue signalled a presentation of an upcoming outline. The pre-stimulus occipital alpha power decrease is suggested to reflect increase in processing visual information (Park et al., 2014; van Dijk et al., 2008). Therefore, the larger encoding-related alpha desynchronisation before a photo might reflect pre-activating more visual processing for encoding a perceptually rich photo than a perceptually impoverished outline. Surprisingly, when cues did not signal the amount of perceptual details about an upcoming picture, pre-stimulus encoding-related alpha desynchronisation was larger than both informative cue conditions. Hanslmayr et al. (2012) argue that according to information theory, richness of information reflects unpredictability of an event. Then the larger encoding-related alpha desynchronisation before a picture found in the non-informative cue condition might reflect preparation for the unpredictability of an upcoming picture. Preparation under an unpredictable condition might activate more information to process as two types of pictures were anticipated so that the picture could be encoded successfully. In addition, the scalp distributions of the larger pre-stimulus encoding-related desynchronisation in the non-informative condition were different from the photo cue condition. Lateralised and bilateral differences were found when compared to the photo cue condition and compared to the outline cue condition, respectively. This suggests that compared to more perceptual preparation for encoding a photo, preparation for memory encoding in a non-informative cue condition might reflect more general preparatory processes. Previous studies indicate that different neural networks were engaged in helping successful memory encoding in an unpredictable condition compared to a predictable condition, which they suggest neural networks underlying unpredictable condition reflect bottom-up oriented memory encoding (Summerfield & Mangels, 2006; Uncapher et al., 2011). Therefore, the preparatory processes in the photo cue condition might be filtered to visual or perceptual preparation as more perceptual details were anticipated. In contrast, more information was prepared in a non-informative cue condition as either a photo or an outline was anticipated. However, such preparation for more information was not restricted to perceptual information. Pre-stimulus subsequent memory effects in separate conditions showed similar scalp distributions. Encoding-related alpha decrease effect was found over occipital scalp sites in the photo cue condition while the effect was over right temporal scalp sites in the non-informative cue condition, which further demonstrates the preparatory mechanisms differ in amount of advance information.

It is not clear why decrease in theta power before a remembered picture was found in Experiment 1. The known encoding related pre-stimulus theta effects are all increase in theta power before a remembered item (Fell et al., 2011; Fellner et al., 2013; Gruber et al., 2013; Guderian et al., 2009). The stimuli they used were all words. Whether the different direction of the effect in Experiment 1 is related to material types is not clear. Source localizations in the study by Guderian et al. and the iEEG study by Fell et al. both show that the medial temporal lobe is important for the encoding-related pre-stimulus theta increase effect. They suggest pre-stimulus theta activity helps to pre-activate contextual information in a predictable experimental series. It is not a stimulus-related process. Gruber et al. (2013) found a frontal pre-stimulus theta increase before remembered words in the high monetary reward condition. Hanslmayr and Staudigl (2013) reviewed studies that found decrease or increase in theta power supporting successful memory encoding. They suggest that the negative or positive theta subsequent memory effect depends on the underlying processes during encoding. Therefore, the theta decrease effect found in Experiment 1 might reflect different preparatory processes from the previous studies. Similarly as for the findings in the alpha frequency band, theta power decreased over the occipital scalp sites before recognised photos in the photo cue condition, which might indicate a perceptual preparation for memory formation. In the non-informative cue condition, the theta decrease effect was over the left scalp sites. This effect might be more comparable to the previous findings about the role of theta activity in pre-activating contextual information. Stimulus-related information is relatively unpredictable in this condition. Therefore, the theta decrease effect in the non-informative condition was more likely to be general or contextual preparation for memory formation. Guderian et al. (2009) also suggested that after an increase in pre-stimulus theta activity, followed will be a decrease theta activity after a remembered stimulus. This implies a relationship between encoding-related pre-stimulus and post-stimulus theta activity in combining contextual information with stimulus-related information.

Whether the theta decrease effect found in Experiment 1 is a theta-specific effect or an alpha bleeding to theta effect? According to the time windows of the two effects they seem to be two individual effects. The theta effects appeared just before pictures onset while the alpha effects appeared in a middle time window after cue onset. Of note, the post-stimulus alpha effects started also earlier than the theta effects and were more widespread than the theta effects. This might reflect the fact that the theta decrease effects were initiated by the alpha effects. However, the two effects are quite similar in terms of the direction and the two effects were shown in both the photo and neutral cue conditions but not in the outline conditions. According to Hanslmayr et al. (2012), if the mechanism of desynchronisation in oscillatory brain activity reflects more capacity of information processing then it should also apply to slower frequency bands such as theta. Therefore, encoding-related desynchronisation in theta and alpha found in Experiment 1 might both reflect memory is encoded by increase in information processing.

The post-stimulus encoding-related theta and alpha decrease effects were found in both picture types and there was no interaction between picture types. This might suggest that the need of information processing is the same during efficient memory encoding in the two picture conditions. However, differences between overall picture-related activity were found in both theta and alpha frequency bands, which suggests overall processing on the two types of pictures was different but such difference did not interacted with memory encoding. Early decreases in theta and alpha power were found right after photo onset compared to an outline, which is consistent with the information processing mechanism of desynchronisation (Hanslmayr et al., 2012). Such early decrease in theta and alpha power might reflect early processing of photos with more perceptual details than outlines. Surprisingly, an increase in alpha power was found over occipital scalp sites in a late time window after photo onset compared to an outline. This suggests that in late processes on two types of pictures, more visual information was processed on the outlines than the photos. Or more irrelevant visual information was filtered in the photos than the outlines. This leads to a question of the information processing mechanism of desynchronisation. That is, whether desynchronisation in oscillatory brain activity reflects uncertainty about an event or more pieces of information about an event? If richness of information refers to uncertainty status about an event, then a perceptually impoverished outline is more uncertain than a photo as less perceptual details are available. Thus, such late increase in alpha power after photo onset can be explained. However, the current findings in Experiment 1 favour the latter argument. Not only pre-stimulus encoding-related desynchronisation differed in the amount of perceptual information to be prepared and amount of advance information, but also the overall cue-related activity irrespective of memory performance differed in amount of advance information and perceptual information to be prepared. Non-informative cues elicited the largest theta and alpha desynchronisation than the other two kinds of cues just before picture onset. Photo cues elicited larger theta desynchronisation than outline cues before picture onset and larger alpha desynchronisation in a middle time window. Non-informative cues were followed by either photos or outlines thus two kinds of pictures were required to prepare. The degree of desynchronisation is a function of amount of information to be prepared. Nevertheless, Experiment 1 still cannot completely answer the question as a non-informative cue also represents unpredictability about a future event. The functional role of desynchronisation in oscillatory brain activity needs more understanding.

In summary, encoding-related pre-stimulus oscillatory activity in theta and alpha frequency bands is influenced by degree of perceptual preparation. The more perceptual details are available to guide preparation, the more likely it is that pre-stimulus desynchronisation influences encoding. When amount of perceptual details to be prepared is not available, more pre-stimulus desynchronisation engages in memory encoding, which might reflect a bottom-up preparation for memory encoding. The findings suggest that encoding-related pre-stimulus oscillatory brain activity can be engaged strategically depending on the amount of information to be encoded.

4.2 Experiment 2: The influence of amount of time available before an event on pre-stimulus encoding-related theta and alpha activity

4.2.1 Introduction

In Experiment 1, significant decreases in theta and power were found to support successful memory encoding. Such encoding-related desynchronisation in brain oscillations was only found when preparing for more perceptual details or more than one kind of pictures but was absent when preparing for less perceptual details, which suggests that encoding-related desynchronisation in theta and alpha prior to an item is a function of the degree of perceptual preparation. Experiment 2 addressed question about whether such encoding-related desynchronisation is influenced by amount of time available to prepare before an event.

The ERP evidence of Experiment 2 and a study done by Galli et al. (2013) both suggest that the engagement of pre-stimulus activity in memory encoding does not only depend on voluntary control (Gruber & Otten, 2010) but also depends on whether there is opportunity before an event. If pre-stimulus encoding-related theta activity is also under voluntary control (Gruber & Otten, 2010), then when there is more opportunity to engage such preparatory activity in memory encoding pre-stimulus encoding-related theta activity should be larger. In Experiment 2, the opportunity to engage encoding-relate preparatory activity was manipulated by amount of preparation time before an event. The results from Experiment 1 suggest that encoding-related desynchronisation was larger when more perceptual details were available to guide preparation than when preparing for a perceptually impoverished outline. In Experiment 2, experimental stimuli were always perceptually rich greyscale photos. If longer preparation time provides more opportunity to engage such perceptual preparation, encoding-related desynchronisation should be larger when longer preparation time is available than shorter preparation time.

In Experiment 1, larger encoding-related desynchronisation before recognised pictures was found when a cue was non-informative than other two kinds of informative cues. Non-informative cues were followed by either a photo or an outline. Thus, such larger encoding-related desynchronisation might reflect preparation for encoding more than one type of pictures. However, such larger encoding-related desynchronisation in an unpredictable cue condition might also reflect uncertainty about a future event. Alpha and theta power increase when a stimulus is expected after a predictable interval (Cravo, Rohenkohl, Wyart, & Nobre, 2011; Min et al., 2008; Zanto et al., 2011). Synchronisation in oscillatory activity found in an expected interval before a stimulus might reflect preparation for processing the stimulus by suppressing irrelevant information and tuning the temporal precision (Klimesch, 2012). Therefore, larger encoding-related desynchronisation was expected to be found in unpredictable conditions as in Experiment 1.

To further investigate whether encoding-related theta and alpha activity is influenced by the degree of preparation before an event, the data from Experiment 2 was re-analysed in the time-frequency domain. In Experiment 2, advance information was about the preparation time available before an event to manipulate the opportunity to engage perceptual preparatory activity for encoding a greyscale photo. The analyses focused on theta (4-8 Hz) and alpha frequency band (9-12 Hz) as was done in Experiment 1. As the same material type was used in the photo cue condition in Experiment 1, encoding-related desynchronisation was expected to be found in Experiment 2. If longer preparation time provides more opportunity to engage perceptual preparation for encoding a photo, larger and more sustained encoding-related desynchronisation was expected to be found in long cue conditions than short cue conditions. If increases in pre-stimulus power reflect inhibiting irrelevant information and preparation for processing stimulus-related information in a predictable interval, then larger encoding-related desynchronisation should be found in unpredictable conditions than predictable conditions.

4.2.2 Methods

Participants. The participants used for the time-frequency analyses were a subset of 24 participants used for the ERP analyses in Experiment 2 (see section 3.2.2). In Experiment 1, robust theta and alpha power decrease subsequent memory effects were found for the confident old judgments. To be consistent with Experiment 1, the analyses were done for 18 participants (mean age 22.1 years, range 18 – 29 years, all right handed, 11 females) who had at least 11 artefact-free trials for confident old judgments.

Stimulus material, procedure and EEG acquisition are all described in section 3.2.2

EEG time-frequency analyses. The continuous EEG data were segmented into epochs of 5600 ms duration from -0.6 to 5 s (0 is cue onset). This length of epochs left sufficient time / frequency information for a pre-stimulus cue period in both cue lengths (1.5 s or 3 s) to avoid edge effects at the beginning and the end of the epoch. The other information on EEG time-frequency analyses can be found in section 4.1.2 (See Table 23 for the mean trial numbers in each condition). The criteria for ‘recognized’ and ‘forgotten’ trials were the same as those used in the analyses for Experiment 1.

Table 23. Mean trial numbers in each condition Experiment 2 time-frequency analyses (Range in brackets)

	Predictable short	Predictable long	Unpredictable short	Unpredictable long
Recognized trials	27 (13-49)	29 (18-52)	29 (15-47)	27 (11-45)
Forgotten trials	24 (13-37)	23 (14-42)	24 (16-35)	26 (15-42)
Overall (regardless of memory performance)	68 (42-81)	69 (46-77)	68 (55-75)	69 (51-78)

Statistical analyses of time-frequency analyses. The approach of statistical analyses of time-frequency analyses can be found in section 4.1.2. The only difference is the approach was conducted for all 37 scalp electrodes used in Experiment 2. Therefore this leads to a Type I error of 1.85 electrodes (37*0.05) for each time window. Again, only when significant differences were found from at least two neighbouring electrodes effects would be considered.

As two cue lengths (1.5 s and 3 s) were used in Experiment 2, permutation tests were first done for a 1.5 s interval to test interactions between subsequent memory and amount of advance information. Trials in predictable cue conditions and unpredictable cue conditions were collapsed respectively, irrespective of amount of preparation time. The difference in power between later recognised pictures and later forgotten pictures for predictable and unpredictable conditions was compared to see if there was any significant interaction. If any significant interaction was found, further permutation tests were conducted for the unpredictable condition separately to see if any significant subsequent memory effect was found before in the 1.5 s interval. For the predictable condition, additional permutation tests were done to compare differences in subsequent memory and amount of preparation time. Permutation tests were conducted to test subsequent memory in predictable short and predictable long conditions if any interaction between subsequent memory and amount of preparation time was found. If no significant interaction was found between subsequent memory and amount of preparation time, further permutation tests were done for the predictable condition regardless of amount of preparation time as were done for the unpredictable condition to see if any significant subsequent memory effect was found regardless of amount of preparation time before 1.5s. If no significant interaction between subsequent memory and amount of advance information was found, further permutation tests were conducted to compare the difference in power between recognised pictures and forgotten pictures regardless of cue conditions to see if any main effect of subsequent memory effect was found irrespective of cue conditions.

Between 1.5 s until picture onset, as there were only predictable long and unpredictable long cue conditions permutation tests were done to compare subsequent memory differences between predictable long and unpredictable long conditions. If any interaction was significant, further permutation tests were conducted to test subsequent memory effect in separate conditions. If no interaction was found, subsequent memory irrespective of cue conditions was tested by permutation tests.

4.2.3 Results

Task Performance

Study. Performance for the study phase for the 18 participants used in the time-frequency analyses is summarized in Table 24. The results were consistent with the results for the 24 participants except that no significant difference was found between when categorising reaction times of the size judgment task by subsequent old sure and subsequent new (collapsing new sure and new unsure) judgments (see section 3.2.3 for the full patterns of 24 participants).

Table 24. Study task performance for 18 participants in Experiment 2 time-frequency analyses

		Predictable short	Predictable long	Unpredictable short	Unpredictable long
Accuracy	M	0.81	0.79	0.81	0.83
(proportion)	SD	0.06	0.06	0.06	0.06
Response	M	801	802	819	821
times (ms)	SD	161	161	161	167

Values are across-subject means. n=18.

Test. Recognition memory performance for the 18 participants used in the time-frequency analyses is summarized in Table 25. The analyses showed consistent results as shown for the 24 participants (see Section 3.2.3 for the full patterns). Additional ANOVAs were conducted for Pr and Br values that only included confident old judgments to be consistent with the criteria used for the response category in the time-frequency analyses. No significant difference was revealed. Pr in the predictable short condition was 0.30, in the predictable long condition 0.31, in the unpredictable short condition 0.31, and in the unpredictable long condition 0.29 (all *p*s > 0.15). For Br, the corresponding values were 0.16, 0.17, 0.17, and 0.16 respectively (all pairwise *p*s > 0.095).

Table 25. Recognition memory performance for 18 participants in Experiment 2 time-frequency analyses

Condition	Recognition Type			
	Confident old	Unconfident old	Unconfident new	Confident New
Proportion of responses				
Old				
Predictable short	0.41 (0.14)	0.23 (0.15)	0.19 (0.09)	0.17 (0.13)
Predictable long	0.42 (0.14)	0.23 (0.15)	0.20 (0.09)	0.15 (0.13)
Unpredictable short	0.43 (0.13)	0.22 (0.13)	0.19 (0.08)	0.16 (0.09)
Unpredictable long	0.40 (0.12)	0.23 (0.13)	0.20 (0.09)	0.16 (0.12)
New	0.11 (0.08)	0.18 (0.09)	0.34 (0.16)	0.37 (0.19)
Mean reaction time (ms)				
Old				
Predictable short	1003 (116)	1281 (285)	1320 (370)	1146 (264)
Predictable long	1035 (131)	1279 (286)	1311 (301)	1155 (268)
Unpredictable short	1013 (114)	1324 (309)	1296 (341)	1133 (260)
Unpredictable long	1018 (120)	1302 (292)	1323 (341)	1175 (234)
New	1103 (217)	1316 (335)	1293 (301)	1144 (217)

Values are across-subject means (SD). n=18. The reaction times shown above are based on 18 participants except predictable long unconfident old judgments, unpredictable long unconfident old judgments, and new pictures unconfident old judgments, which are based on 17 participants as one participant did not have any trials for each condition mentioned above.

Encoding-related pre-stimulus theta effect. In a 1.5 s interval, time-frequency representations showed theta power decreased before recognised pictures compared to forgotten pictures especially in the predictable cue conditions (Figures 29 and 30).

Permutation tests revealed significant interactions between subsequent memory and cue predictability over frontocentral scalp sites across all the time windows (0 – 500 ms, 500 – 1000 ms and 1000 – 1500 ms after cue onset). Predictable cue, conditions irrespective of amount of preparation time that they signalled, elicited larger encoding-related theta desynchronisation than unpredictable cues. A further permutation test was done to test the interaction when collapsing three time windows into a time window from cue onset until 1500 ms after cue onset. Predictable cues elicited significant larger encoding-related theta desynchronisation than unpredictable cues over frontocentral scalp sites from cue onset until 1500 ms after cue onset. No significant subsequent memory effect was found in the unpredictable cue condition in any time window. A further permutation test was done within predictable cue conditions to test the interaction between subsequent memory and cue length. A larger encoding-related theta desynchronisation was found over left temporal-occipital scalp sites in a time window of 1000 ms to 1500 ms after predictable long cue onset than predictable short cue. Then, permutation tests compared the power differences between recognised pictures and forgotten pictures in the predictable cue condition, irrespective of cue lengths in the first two time windows (0 – 500 ms and 500 – 1000 ms) that did not reveal significant interactions between subsequent memory and cue length. Theta power decreased significantly before recognised pictures compared to forgotten pictures in both time windows. Such encoding-related theta desynchronisation was over frontocentral electrodes from cue onset to 500 ms after cue onset and over left frontal scalp sites from 500 ms to 1000 ms after cue onset. A further permutation test was done to test the desynchronisation subsequent memory effect by collapsing these two time windows (0

– 1000 ms after cue onset). The theta desynchronisation subsequent memory effect regardless of cue conditions was over frontocentral sites from cue onset until 1000 ms after cue onset.

Separate permutation tests were done to predictable short and predictable long cue conditions separately to understand the interactions between subsequent memory effect and cue length. No significant subsequent memory effect was found in the predictable short cue condition from 1000 ms to 1500 ms after cue onset. Theta power significantly decreased before recognised pictures in the predictable long condition over right frontocentral and left occipital scalp sites in the time window of 1000 ms to 1500 ms after cue onset (Figure 30).

After 1500 ms, permutation tests revealed a significant interaction between cue predictability and subsequent memory 500 ms before picture onset. Significant larger encoding-related theta desynchronisation was found in the unpredictable long cue condition than the predictable long cue condition over right frontocentral scalp sites. Then permutation tests were conducted to test subsequent memory differences irrespective of cue predictability in the other two time windows to see if absence of interactions in these two time windows was caused by significant subsequent memory effects regardless of cue predictability. A frontal significant theta power decrease subsequent memory effect was only found in the time window of 1500 to 2000 ms after cue onset.

Separate permutation tests were done to predictable long and unpredictable long cue conditions separately, to understand the interactions between subsequent memory effect and cue predictability 500 ms before picture onset. No significant subsequent memory effect was found in the predictable long cue condition from 2500 ms to 3000 ms after cue onset. Theta power significantly decreased before recognised pictures in the unpredictable long condition over frontocentral scalp sites 500 ms before picture onset (Figure 30).

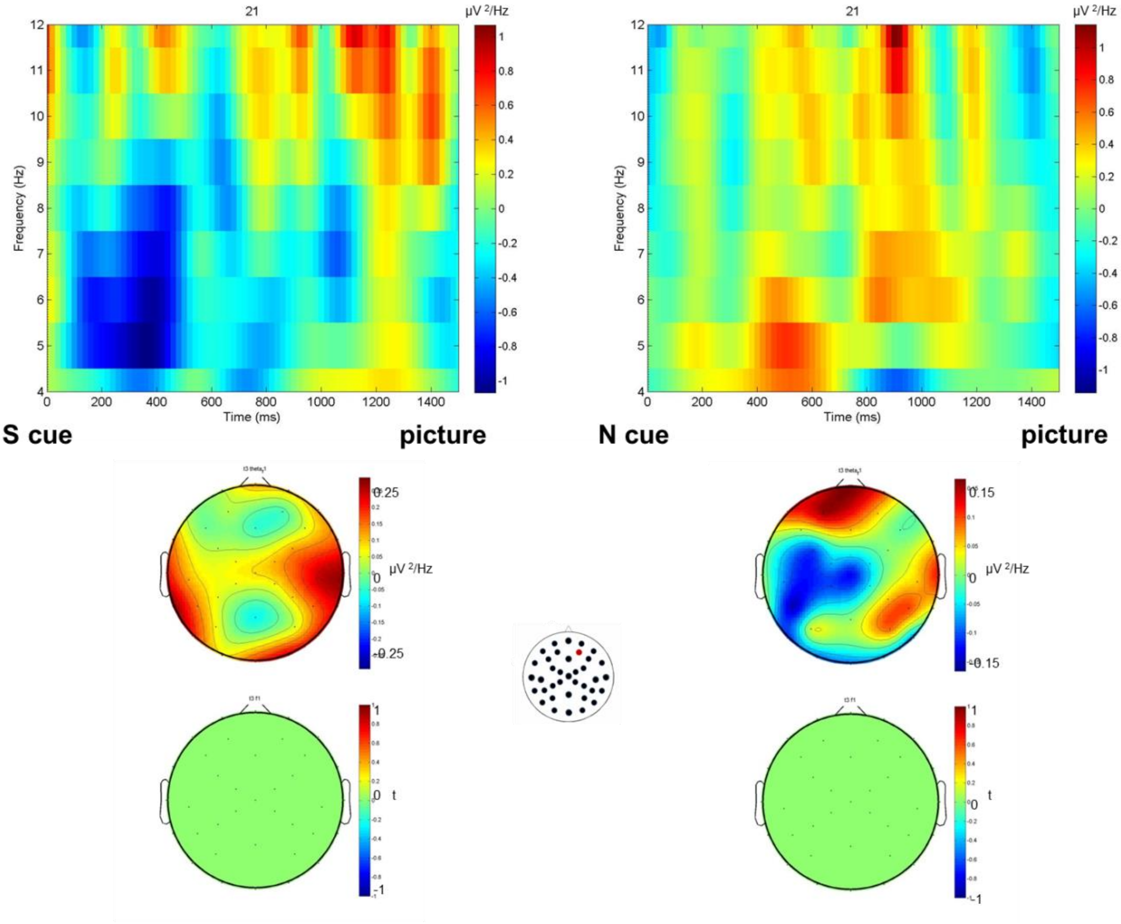


Figure 29. Pre-stimulus encoding-related theta power in the predictable short cue and unpredictable short cue conditions

Top: time-frequency representations of pre-stimulus encoding-related theta activity at one representative frontal electrode site (site 21 from montage 10). Middle: scalp maps indicate the difference in theta power before later recognised and forgotten pictures. Bottom: corresponding statistical scalp maps show the significant differences between later recognised and forgotten pictures. Left: predictable short cue condition. Right: unpredictable short cue condition. Scalp maps reflect the time window of 1000 ms to 1500 ms after cue onset.

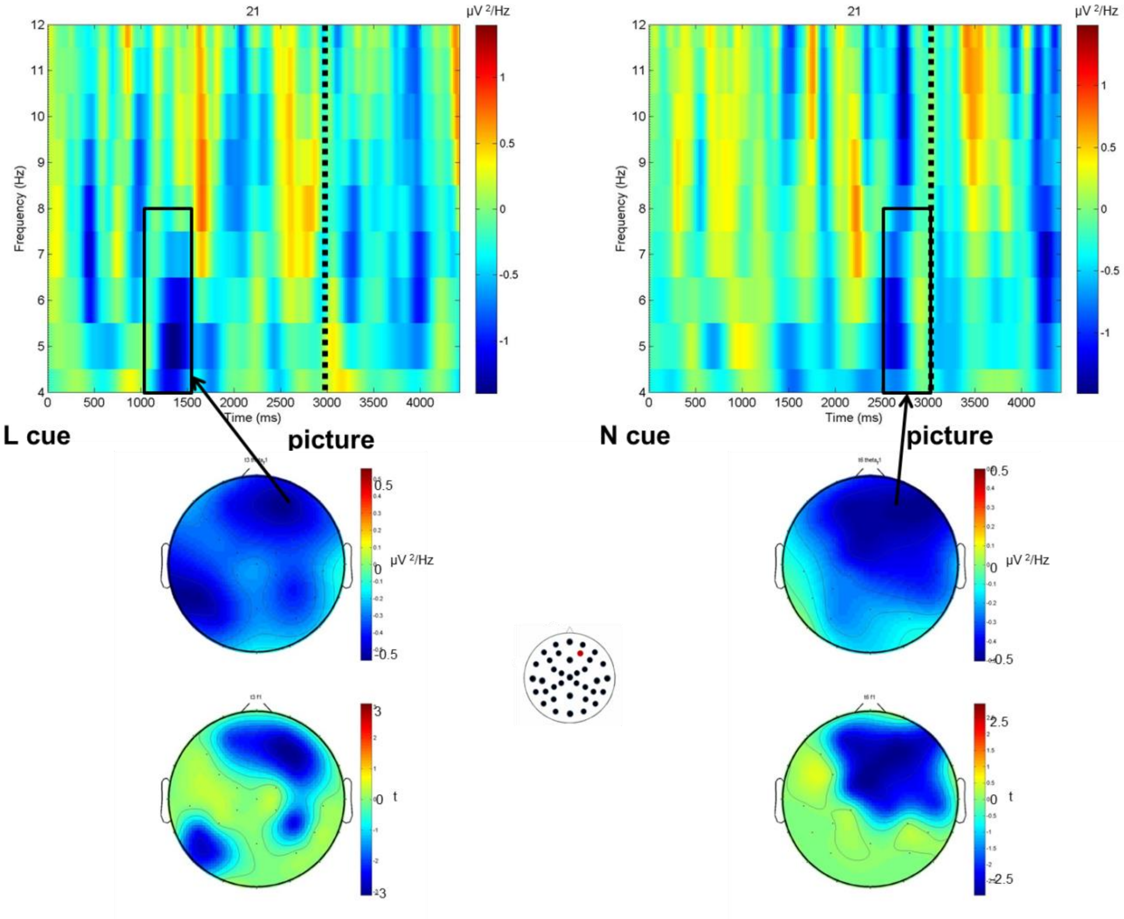


Figure 30. Pre-stimulus encoding-related theta power in the predictable long cue and unpredictable long cue conditions

Top: time-frequency representations of pre-stimulus encoding-related theta activity at one representative frontal electrode site (site 21 from montage 10). Middle: scalp maps indicate the difference in theta power before later recognised and forgotten pictures. Bottom: corresponding statistical scalp maps show the significant differences between later recognised and forgotten pictures. Left: predictable long cue condition. Right: unpredictable long cue condition. Scalp maps reflect the time window of 1000 ms to 1500 ms after cue onset in the predictable long cue condition. Scalp maps of the unpredictable long cue condition reflect the time window of 2500 ms to 3000 ms after cue onset.

Cue-related pre-stimulus theta activity irrespective of memory performance. As mentioned above, theta activity plays an important role in anticipating presentation of a target in an expected interval. Therefore overall theta activity elicited by cues regardless of memory performance was compared in terms of cue predictability and cue length, to see how much time is critical for theta activity playing a role in anticipation. Trials in each cue condition were collapsed regardless of memory performance (for means trial numbers, see Table 23).

First, permutation tests were done in 1.5 s intervals to see theta power differences between predictable and unpredictable short cue conditions. Theta power increased over right occipital scalp sites 500 ms to 1000 ms after cue onset in the predictable short cue condition compared to the unpredictable short cue condition. In an earlier time window (0 to 500 ms after cue onset), permutation tests revealed a widespread significant increase in theta power in the predictable short cue condition compared to the predictable long cue condition. In the same time window, permutation tests showed a significant decrease in theta power in the predictable long cue condition over left frontotemporal scalp sites compared to the unpredictable long cue condition. No significant difference in theta power between the predictable long cue condition and the unpredictable long cue condition was found after 1.5 s. The findings suggest in a short cue interval (1.5 s), theta power increased when the cue interval was predictable than unpredictable. In contrast, if a long cue interval (3 s) was expected, theta power decreased compared to when a short cue interval was expected or a cue length was not informative.

Encoding-related pre-stimulus alpha effect. In a 1.5 s interval, time-frequency representation showed alpha power decreased before recognised pictures in the predictable cue conditions but increased in the unpredictable cue conditions (Figures 31 and 32).

Permutation tests on the interactions between subsequent memory and cue predictability demonstrated this observation. Predictable cues irrespective of cue lengths elicited larger encoding-related alpha desynchronisation than unpredictable cues over frontocentral scalp sites in the time window of 500 to 1000 ms after cue onset. A significant increase in alpha power was found before recognised pictures over left frontal scalp sites 500 to 1000 ms after cue onset in the unpredictable cue condition irrespective of cue lengths. No significant overall subsequent memory effect in alpha was found regardless of cue predictability. A further permutation test was done within predictable cue conditions to test the interaction between subsequent memory and cue length. A larger encoding-related alpha desynchronisation was found over left temporal-central scalp sites in time windows of 0 to 500 ms and 1000 ms to 1500 ms after predictable long cue onset than predictable short cue. Then, permutation tests compared the alpha power differences between recognised pictures and forgotten pictures in the predictable cue condition, irrespective of cue lengths in the middle time windows (500 – 1000 ms) that did not reveal significant interactions between subsequent memory and cue length. No significant subsequent memory effect was found in that time window.

Separate permutation tests were done to predictable short and predictable long cue conditions separately to understand the interactions between subsequent memory effect and cue length. Alpha power significantly decreased before recognised pictures in the predictable long condition over left temporal-central scalp sites after cue onset until 500 ms after cue onset (Figure 32). In contrast, an increase in alpha power was found

500 ms before recognised picture onset over left temporal-occipital scalp sites in the predictable short condition (Figure 31).

After 1500 ms, permutation tests revealed a significant interaction between cue predictability and subsequent memory 500 ms before picture onset. Widespread significant larger encoding-related alpha desynchronisation was found in the unpredictable long cue condition than the predictable long cue condition. Then permutation tests were conducted to test subsequent memory differences irrespective of cue predictability in the other two time windows to see if absence of interactions in these two time windows was caused by significant subsequent memory effects regardless of cue predictability. No significant subsequent memory effect was found in any time window.

Separate permutation tests were done to predictable long and unpredictable long cue conditions separately to understand the interactions between subsequent memory effect and cue predictability 500 ms before picture onset. No significant subsequent memory effect was found in the predictable long cue condition. Alpha power significantly decreased before recognised pictures in the unpredictable long condition over frontocentral and right temporal-occipital scalp sites 500 ms before picture onset (Figure 32).

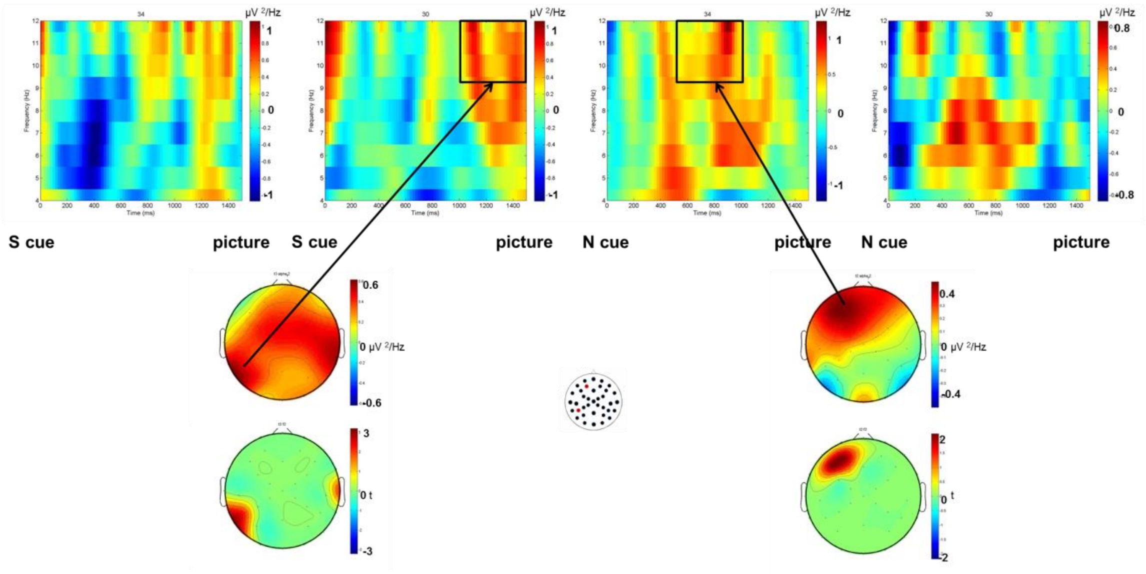


Figure 31. Pre-stimulus encoding-related alpha power in the predictable short cue and unpredictable short cue conditions

Top: time-frequency representations of pre-stimulus encoding-related alpha activity at two representative frontal electrode sites (sites 34 and 30 from montage 10). Middle: scalp maps indicate the difference in alpha power before later recognised and forgotten pictures. Bottom: corresponding statistical scalp maps show the significant differences between later recognised and forgotten pictures. Left: predictable short cue condition. Right: unpredictable short cue condition. Scalp maps of the predictable short cue condition reflect the time window of 1000 ms to 1500 ms after cue onset. Scalp maps of the unpredictable short cue condition reflect the time window of 500 ms to 1000 ms after cue onset.

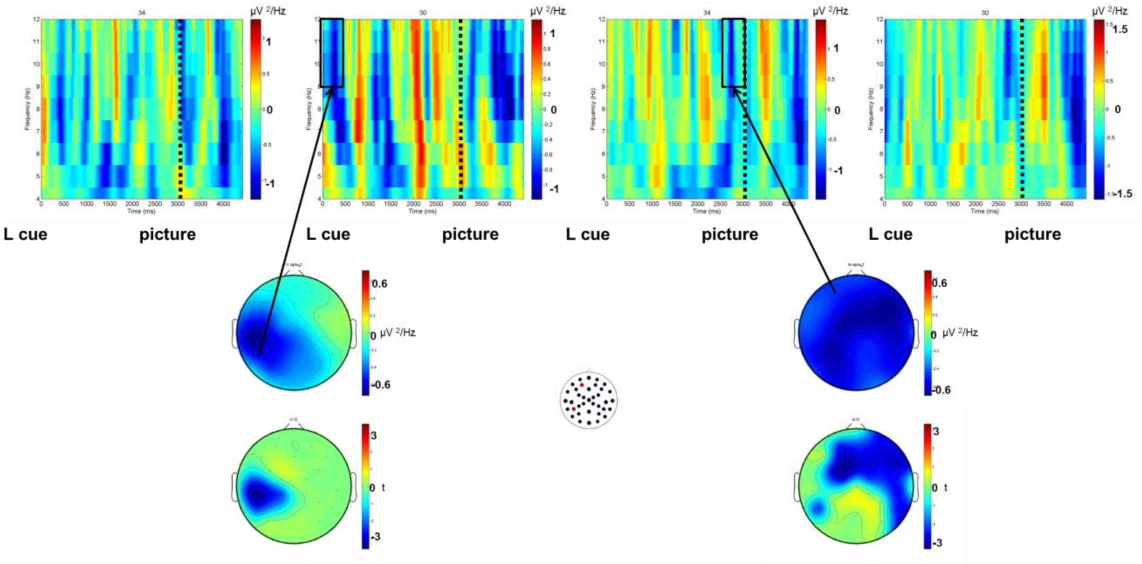


Figure 32. Pre-stimulus encoding-related alpha power in the predictable long cue and unpredictable long cue conditions

Top: time-frequency representations of pre-stimulus encoding-related alpha activity at two representative frontal electrode sites (sites 34 and 30 from montage 10). Middle: scalp maps indicate the difference in alpha power before later recognised and forgotten pictures. Bottom: corresponding statistical scalp maps show the significant differences between later recognised and forgotten pictures. Left: predictable long cue condition. Right: unpredictable long cue condition. Scalp maps of the predictable long cue condition reflect the time window of 0 to 500 ms after cue onset. Scalp maps of the unpredictable long cue condition reflect the time window of 2500 ms to 3000 ms after cue onset.

Cue-related pre-stimulus alpha activity irrespective of memory performance. As mentioned above, alpha activity is engaged flexibly in preparing for processing a stimulus when the stimulus is expected to be presented after a short interval. To investigate if alpha activity can be still engaged in preparing for a more complex stimulus (a greyscale object) in a predictable interval and how long the interval should be, trials in each cue condition were collapsed regardless of the memory performance. When an interval was short (1.5 s), a significant increase in alpha power was found over right temporal-occipital scalp sites 500 ms after cue onset until 1000 ms after cue onset in a predictable condition compared to an unpredictable condition. When an interval was long (3 s), significant decrease in alpha power was found over left temporal scalp sites in the first two time windows after cue onset (0 – 500 ms and 500 – 1000 ms) in a predictable condition compared to an unpredictable condition. Then a permutation test was done to compare the alpha power difference between predictable long and unpredictable long conditions when collapsing the two time windows into one time window from 0 to 1000 ms after cue onset. Left temporal alpha power significantly decreased in the predictable long condition compared to the unpredictable long condition.

Summary of the time-frequency analyses. The time-frequency analyses showed that both theta and alpha power decreased to support preparation for encoding an upcoming picture successfully. From cue onset until 1.5 s after cue onset, a short cue signalled a presentation of a picture after this interval. A long cue indicated another 1.5 s until picture onset after this interval. A non-informative cue was either followed by a 1.5 s interval or a 3 s interval. In the first 1.5 s interval, predictable cues elicited larger theta and alpha encoding-related desynchronisation than unpredictable cues. Within predictable cues, a cue signalled longer preparation time elicited larger encoding-related theta and alpha encoding-related desynchronisation than a cue signalled shorter preparation time. After 1.5 s, larger encoding-related theta and alpha desynchronisation was found before picture onset in an unpredictable long interval than when a long interval was predictable to be 3 s.

Although the findings from theta and alpha were consistent, different time windows showed that the findings from different frequency bands might suggest separate effects from each other. First, in the first 1.5 s, predictable cues elicited larger encoding-related theta desynchronisation than unpredictable cues in the whole interval from cue onset until 1.5 s after cue onset. Such larger theta desynchronisation was caused by larger decreases in theta power before recognised pictures in the predictable cue conditions. In contrast, larger encoding-related alpha desynchronisation was found in the predictable cue conditions than the unpredictable cue conditions only in the time window of 500 to 1000 ms after cue onset. In addition, such alpha desynchronisation was not caused by larger encoding-related desynchronisation in the predictable cue conditions but increases in alpha power before recognised pictures in the unpredictable cue conditions. Second, larger encoding-related theta desynchronisation was found in the predictable long condition than the predictable short condition in a middle time window (1000 to 1500 ms after cue onset). In contrast, larger encoding-related alpha desynchronisation was found in the predictable long condition in an earlier time window (0 – 500 ms after cue onset). Third, larger encoding-related alpha desynchronisation in the unpredictable long condition was more widespread than larger encoding-related theta desynchronisation in the unpredictable long condition after 1.5 s.

When a cue interval was predicted to be long, alpha and theta activity regardless of subsequent memory performance decreased compared to an unpredictable cue. In contrast, alpha activity increased in the predictable cue condition compared to the unpredictable cue condition if the cue interval was short. When a cue interval was short and predictable, theta activity increased than both the unpredictable cue condition and a predictable long cue condition.

4.2.4 Discussion

Experiment 2 manipulated the opportunity to engage preparatory activity for memory encoding by changing amount of preparation time. Informative cues (‘S’ and ‘L’) indicated the amount of preparation time. Non-informative cues (‘N’) did not signal the amount of preparation time, which could be short (1.5 s) or long (3 s). Decreases in theta and alpha power before picture onset supported efficient memory encoding. Alpha power decrease effects were found only when a cue interval was long (3 s). When cues were informative, pre-stimulus encoding-related alpha desynchronisation was found before 1.5 s. In contrast, pre-stimulus encoding-related alpha desynchronisation was only found when cues were non-informative after 1.5 s. Theta power decrease effects were found in both long and short intervals. Same as the effects in alpha, theta effects were found before 1.5 s when cues were informative but after 1.5 s when cues were non-informative. When cues were informative, larger encoding-related desynchronisation was found when cues signalled longer preparation time than shorter preparation time. The findings suggest encoding-related desynchronisation was influenced by amount of preparation time. The more preparation time is available before picture onset, the more likely it is that pre-stimulus theta and alpha activity can be engaged to influence encoding. In addition, encoding-related desynchronisation was also influenced by amount of advance information. The more informative a cue is, the earlier it is that pre-stimulus desynchronisation predicts successful encoding.

Theta power decreased before recognised pictures compared to forgotten pictures, which replicated the findings from Experiment 1. In Experiment 1, occipital theta power decrease was found before recognised greyscale photos, which might suggest a perceptual preparation for encoding a photo. Differently from the findings from Experiment 1, mainly frontocentral theta desynchronisation was found to support preparation for successful memory encoding in Experiment 2. Frontocentral theta power is related to episodic memory encoding (for a review, see Hsieh & Ranganath, 2013) especially frontocentral theta power is found to be increased when contextual information is successfully encoded into episodic memory (Staudigl & Hanslmayr, 2013). In contrast, when item memory is failed to bind with contextual information, theta power decreased to support successful item memory encoding (Staudigl & Hanslmayr, 2013). Frontal theta power is also thought help strengthen the link between item and context but suppress irrelative information such as competing source or item-specific information (Hanslmayr et al., 2009; Hsieh & Ranganath, 2013; Staudigl & Hanslmayr, 2013). Therefore, frontal theta desynchronisation in Experiment 2 might help to prepare for encoding more item-specific information thus later a greyscale photo of an object could be successfully retrieved.

It seems that theta activity plays similar role in preparation for memory encoding as alpha activity, namely, gating information from encoding system. As expected, larger encoding-related theta and alpha desynchronisation was found when preparation time was long. Although in a later time window, larger encoding-related theta and alpha desynchronisation was found right before picture onset when a long interval was unpredicted, which was as expected. In an early time window, larger encoding-related theta and alpha desynchronisation was found only when cues were informative. The findings might suggest that theta and alpha activity can be engaged flexibly by using cue information. Longer preparation time enables more opportunity to engage theta and alpha activity for influencing memory encoding before picture onset. Informative cues prioritise such engagement while in an unpredictable long interval, encoding-related desynchronisation can only play a role in the last stage prior to picture onset to help memory encoding. The findings might also be able to answer the remained question from Experiment 1, that is, whether larger desynchronisation in the non-informative cue condition in Experiment 1 reflects preparation for more kinds of pictures or preparation for uncertainty (Hanslmayr et al., 2012). The findings from Experiment 2 might suggest the former interpretation. First, in the first 1.5 s interval, predictable cues rather than unpredictable cues elicited larger encoding-related desynchronisation, which is against that desynchronisation means more uncertainty. Second, although larger encoding-related desynchronisation was found in the later 1.5s interval, at that time, an unpredictable long interval could be known how much time was until picture onset. Therefore, such larger desynchronisation might reflect more preparation for encoding item-specific information. The difference between the non-informative cues in Experiments 1 and 2 is whether the cue is non-informative about an upcoming stimulus. As the non-informative cue in Experiment 1 did not signal the physical form of an upcoming picture, preparation under such condition might be preparing for both physical forms of the picture, which might lead to larger desynchronisation. The larger desynchronisation in Experiment 2 reflects more opportunity to engage the pre-stimulus encoding-related theta and alpha activity, which suggests that pre-stimulus desynchronisation does not reflect preparation for an uncertain status but preparation for encoding more information.

Another difference between the findings from Experiment 2 and the findings from Experiment 1 is that increases in alpha power were found before recognised pictures. First, alpha power increased right before recognised picture onset when a cue interval was predictable to be short. If larger theta power decreases in the predictable conditions reflect preparation for encoding more item-specific information, such increase in alpha power might reflect inhibition of irrelevant information (Fell et al., 2011). Second, alpha power also increased in a middle time window before recognised picture onset in unpredictable conditions before 1.5 s, irrespective of cue length. The finding is consistent with the ERP findings, which suggests that participants might treat non-informative cues strategically same as a short cue since once 1.5 s elapsed, an unpredictable interval could also be predictable to have 1.5 s until picture onset. In addition, compared to a predictable short condition, more information such as unpredictable temporal information should compete with preparation for encoding in unpredictable conditions. Therefore, alpha power increases occurred in an earlier time window to suppress more memory-irrelevant information. However, it is not clear why such alpha synchronisation was not found when preparation time was long. There might be different preparatory mechanisms in a longer preparation time that such alpha synchronisation was not necessarily engaged to prepare for memory encoding.

The overall theta and alpha activity irrespective of memory performance elicited by predictable cues increased than unpredictable cues only when a cue interval was short. When a cue interval was long, opposite patters were found. In addition, overall theta activity elicited by predictable short cues was higher in power than predictable long cues. Such findings replicated the findings from previous literature (Babiloni et al., 2004; Cravo et al., 2011; Min et al, 2008; Zanto et al., 2011). First, a widespread theta-specific difference was found between the predictable short cue condition and the predictable long cue condition. Predictable short cues elicited higher power in theta activity than the theta activity elicited by predictable long cues. Babiloni et al. (2004) found a lower alpha band (6-8 Hz) specific effect in comparing Event-related Synchronisation (ERS) values of short foreperiod to long foreperiod in a detection task. A stronger ERS was found in short foreperiod than long foreperiod in lower alpha band (6-8 Hz) but not in other alpha bands (8-10 Hz and 10 – 12 Hz). This also happened in a large range scalp distribution. The findings suggest that a faster modulation of temporal attention rather than a motor preparation in short foreperiod than long foreperiod. Of note, the lower alpha band in their study is actually within the range of theta band (4-8 Hz) in Experiment 2. Also, the theta power increase effect between predictable short and long conditions was band-specific and not found in alpha band (9-12 Hz). This might suggest that the role of temporal attentional modulation in theta activity can also be engaged in a 1.5 s interval before a more complex stimulus such as a greyscale photo of an object. Second, occipital power increases in the predictable short condition compared to the unpredictable short conditions was found in both theta and alpha frequency bands. The power increases in theta and alpha activity in a predictable condition of timing compared to an unpredictable condition is found before target onset in a few studies (e.g. Cravo et al., 2011; Zanto et al., 2011). Such power increases were suggested to be a top-down control in motor and perception of expectation to upcoming events rather than expectations in visual features before target onset. Third, different patterns, namely, decreases in theta and alpha power decreases were found after predictable long cues compared to unpredictable long cues. Some studies suggest that the temporal preparation mechanism is only engaged when a short interval is predictable as after the short time passed, the unpredictable long interval is obviously predictable (Miniussi et al., 1999; Zanto et al., 2011). Therefore, the opposite patterns might suggest no engagement of temporal modulation in long intervals. However, the theta and alpha power decreases in the predictable long condition were over left temporal scalp sites. This scalp distribution might indicate that cue information enables a time estimation process (Fraisse, 1984). In conclusion, the results of overall oscillatory activity regardless of memory performance indicate a dynamic role of temporal expectation. A predictable short cue could enable a faster temporal modulation than a predictable long cue. In a middle time window, the power increases in theta and alpha frequency bands were found in the predictable short cue condition relatively to the unpredictable short cue condition, which suggests the role of top-down control in preparation in a short time before target onset. The findings suggest temporal preparatory mechanisms can also be engaged in a relatively long period (1.5 s) for a more complex target (a greyscale photo of an object).

In summary, encoding-related theta and alpha desynchronisation also depends on the opportunity to engage pre-stimulus theta and alpha activity in preparation for memory encoding. The longer preparation time is available before picture onset, the more likely it is that decreases in theta and alpha power influence encoding a picture. Further, the more information a cue signals, the earlier encoding-related desynchronisation occurs. The findings suggest preparatory mechanisms for memory may reflect the beneficial effect of active processes engaged prior to stimulus onset.

4.3 Experiment 3: Probing memory before a delayed match-to-sample task influences memory-related oscillatory brain activity

4.3.1 Introduction

Experiments 1 and 2 demonstrated decreases in pre-stimulus theta and alpha power predict effective memory encoding for an item presented 1.5 s or 3 s after pre-stimulus cue onset. Such findings suggest that the brain state of decreases in theta and alpha power is important for successfully encoding a picture with rich perceptual details (Guderian et al., 2009; Hanslmayr et al., 2012; Yoo et al., 2012). Differently from previous studies (Fell et al., 2011; Gruber et al., 2013; Guderian et al., 2009), decreased rather than increased pre-stimulus theta and alpha power predicted successful memory encoding in Experiments 1 and 2. Such decreases in theta and alpha power might reflect preparation for encoding more perceptual information of a picture as the decreases were only shown when preparing for more perceptual details (Experiment 1) or when more opportunity was available before encoding (Experiment 2). In addition, Hanslmayr and Staudigl (2013) suggest that the positive (increase in power) or negative (decrease in power) subsequent memory effects in brain oscillations might reflect different cognitive and perceptual processes underlying encoding. Desynchronisation is thought to be related to deep processing during encoding (Hanslmayr et al., 2009; Fellner et al., 2013; Klimesch, 1999). Therefore, the brain state of pre-stimulus decreases in theta and alpha power that supports successful memory encoding might be able to be induced by a concurrent cognitive task that involves similar neural processes as episodic memory encoding.

To investigate if the brain state of decreases in theta and alpha power can be induced by a cognitive task that involves similar neural mechanisms as episodic memory encoding, the EEG data from Experiment 3 was re-analysed in the time-frequency domain. In experiment 3, participants were asked to prepare for different

DMS tasks. If participants saw a ‘C’ cue, they needed to prepare for remembering a conjunction of an object and its specific location in a short delay, which the task is known to involve the hippocampus (Olson et al., 2006). If an ‘L’ cue was presented, participants needed to prepare for remembering only a feature (here, a location) of an object in a short delay, which does not necessarily involve the hippocampus. Memory-related theta state is found to be located at the MTL (Fell et al., 2011; Guderian et al., 2009). Therefore, if preparation for a conjunction DMS task can also pre-activate the hippocampus, then the underlying preparatory processes should be same as preparation for memory encoding. To enable sufficient preparation time to develop the brain state of decrease in theta and alpha power, a colour photo of an object (long-term memory probe) was inserted 3 s after DMS task cue onset. If preparation for a conjunction DMS task has similar underlying perceptual and cognitive processes as preparation for memory encoding, similar direction of the oscillatory activity should be found in task-related activity as found in memory-related activity. Namely, higher decreases in theta and alpha power should be found when preparing for a conjunction DMS task compared to preparing for a feature DMS task. Such decreases can induce a brain state for effective memory encoding, which might lead to larger encoding-related theta and alpha desynchronisation for the long-term memory (LTM) probes presented after conjunction DMS task cues in contrast to the LTM probes presented after feature DMS task cues.

4.3.2 Methods

Participants, stimulus material, procedure and EEG acquisition are described in section 3.3.2

EEG time-frequency analyses. The continuous EEG data of the DMS tasks were segmented into epochs of 6200 ms duration from -0.6 to 5.6 s (0 is cue onset) as this length of epochs contained sufficient time/ frequency information in the whole cue period (5 s), which was not affected by edge effects. The continuous EEG data of recognition test were segmented into epochs of 3400 ms duration from -0.8 to 2.6 s (0 is LTM probe onset). In the time domain, -0.8 s to -0.2 s was subtracted as baseline for each epoch. It still ensured an epoch to include -0.2 s to 2 s after calculating time-frequency information to avoid edge effects. In the frequency domain, -0.2 s to 0 was used as baseline to see power changes compared to the baseline as no pre-stimulus information was of interest in the retrieval stage. The other information of EEG time-frequency analyses can be found in the previous two experiments. See Table 26 for the mean trial numbers in each condition. The criteria for 'recognized' and 'forgotten' trials were the same as was used in the ERP analyses.

Table 26. Mean trial numbers in each condition in Experiment 3 time-frequency analyses (Range in brackets)

	DMS task (N=24)	Recognised (N=18)	Forgotten (N=18)	Confident Hits (N=18)	Correct Rejections (N= 18)
Conjunction	91 (73-110)	22 (11-40)	24 (11-39)	24 (17-40)	48 (37-57)
Feature	98 (80-117)	22 (13-36)	27 (10-40)	24 (13-38)	

Statistical analyses of time-frequency analyses. The approach of statistical analyses of time-frequency analyses can be found in sections 4.1.2 and 4.2.2. The permutation tests were conducted for 37 scalp electrodes as were used in section 4.2.2. A Type I error of 1.85 electrodes (37*0.05) for each time window was produced. Only when significant differences were found from at least two neighbouring electrodes effects would be considered.

Permutation tests first tested the comparison between overall preparatory activity for a conjunction DMS task and a feature DMS task before 3 s. After 3 s, as an

LTM probe was presented in half the trials, permutation tests tested the difference in the task-related theta and alpha power differences when an LTM probe was presented and when no LTM probe was presented. If any difference in task-related power differences was found between with and without the LTM probe, permutation tests were used to test individual power differences in the conjunction DMS task and the feature DMS task. If no difference was found, permutation tests were used to test the difference between overall preparatory activity after 3 s, regardless of whether there was or not the LTM probe.

Then permutation tests were used to test interactions between encoding-related activity and DMS task condition. The difference in power between later remembered LTM probes and later forgotten LTM probes from each DMS task condition was compared. If any difference was found, further permutation tests were conducted for each DMS task condition separately to understand the interaction. If no difference was found, further permutation tests were conducted to compare the overall subsequent memory effect regardless of DMS task condition.

A similar procedure was used to test retrieval-related activity. Permutation tests tested interactions between old-new effect and DMS task condition. If any difference was found, further permutation tests were used to test the old-new effects from each DMS task condition individually. If no difference was found, further permutation tests were conducted to compare the overall old-new effect irrespective of DMS task condition.

4.3.3 Results

Overall preparatory theta activity preceding DMS task onset. Time-frequency representations showed that theta power increased in early time windows and then decreased in middle time windows prior to a conjunction DMS task compared to a feature DMS task (Figure 33).

Permutation tests confirmed this observation. Conjunction cues elicited larger theta power than feature cues over frontocentral scalp sites in the first time window after cue onset (0 – 500 ms). Decreases in theta power were found in two middle windows prior to the conjunction DMS task compared to the feature DMS task. In the time window of 1000 to 1500 ms after cue onset, the decrease in theta power was over parietocentral scalp sites. In the later time window of 1500 – 2000 ms, the decrease in theta power was over right temporal-parietal and left scalp sites. Further permutation tests revealed a widespread decrease in theta power from 1000 to 2000 ms after conjunction cue onset when collapsing two time windows.

When an LTM probe was presented 3 s after task cue onset, the difference between preparatory activity for the conjunction task and the feature task increased compared to when no LTM probe was presented. The difference was over parietal scalp sites and in a time window of 3000 to 3500 ms after task cue onset (or 0 to 500 ms after the LTM probe onset). Permutation tests showed theta power increased over parietal scalp sites prior to the conjunction task only when an LTM probe was presented. After 3500 ms, no difference was found between when an LTM probe was presented and when no LTM probe was presented. Therefore, permutation tests were tested the difference between the overall preparatory activity regardless of the presence of an LTM probe. A decrease in theta power was found over frontal scalp sites 500 ms before conjunction task onset compared to feature task onset.

Encoding-related theta activity before LTM probes. The time-frequency representations showed that theta power decreased before remembered LTM probes compared to forgotten LTM probes especially in the feature condition (Figure 34).

The permutation tests revealed encoding-related theta effects increased from 1000 to 3000 ms after conjunction task cue onset. The increase in the encoding-related theta power difference was over central scalp sites in the time window of 1000 to 1500 ms and over parietocentral scalp sites in both time windows of 1500 to 2000 ms and 2000 to 2500 ms. The increase was found over right temporal scalp sites right before LTM probe onset. Then permutation tests tested the difference when collapsing four time windows into a time window from 1000 to 3000 ms after task cue onset. A widespread increase in theta power was found.

This increase in theta power in the conjunction condition compared to the feature condition was caused by encoding-related theta desynchronisation found only in the feature condition but not in the conjunction condition. Permutation tests were conducted to test the encoding-related theta effect separately on each condition. Theta power decreased before remembered LTM probes over left frontal scalp sites in the time window of 1000 ms to 1500 ms after feature task cue onset. In the time window of 2000 to 2500 ms after feature cue onset, the decrease in theta power was found over right temporal-occipital scalp sites. Such encoding-related theta power decrease was over right scalp sites right before LTM probe onset in the feature condition. The effects in the later consecutive time windows were tested again by permutation tests when collapsing the two time windows into a time window of 2000 to 3000 ms after feature cue onset. A significant theta power decrease effect was found over right scalp sites for before LTM probe onset in the feature condition. No subsequent memory effect was found in the conjunction condition before LTM probe onset. In addition, no overall subsequent memory effect was found irrespective of DMS task condition in the first two time windows after task cue onset where no interaction was found.

Encoding-related theta activity after LTM probes. Similarly, significant differences in encoding-related theta activity were found after LTM probe onset between the DMS task conditions (Figure 34). LTM probes from the conjunction condition elicited larger encoding-related theta power than LTM probes from the feature condition over right occipital scalp sites from LTM probe onset until 500 ms after LTM probe onset. In a later time window of 1000 to 1500 ms after LTM probe onset, such difference was found over left frontotemporal scalp sites. In the following time window of 1500 to 2000 ms after LTM probe onset, such difference was widespread over the scalp. Then permutation tests were conducted for collapsing the two consecutive time windows. A significant difference in encoding-related theta activity between the DMS task conditions was found over left parietocentral scalp sites.

Such differences were caused by early encoding-related theta desynchronisation in the feature condition and late encoding-related synchronisation in the conjunction condition (Figure 34). Follow-up permutation tests on separate DMS conditions confirmed this observation. In the time window of 0 – 500 ms after LTM probe onset, a significant decrease in theta power was found over left temporal-parietal scalp sites after remembered LTM probes in the feature condition. In the later time windows of 1000 to 1500 ms and 1500 to 2000 ms after LTM probe onset, encoding-related theta synchronisation was found over left temporal scalp sites from 1000 to 1500 ms and over bilateral temporal and central scalp sites from 1500 to 2000 ms. A further permutation test revealed a left temporal encoding-related theta power increase effect from 1000 ms to 2000 ms after LTM probe onset when two time windows were collapsed. In addition, in the time window of 500 to 1000 ms after LTM probe onset where no interaction was found, an overall encoding-related theta power decrease effect was found over occipital scalp sites irrespective of DMS task condition.

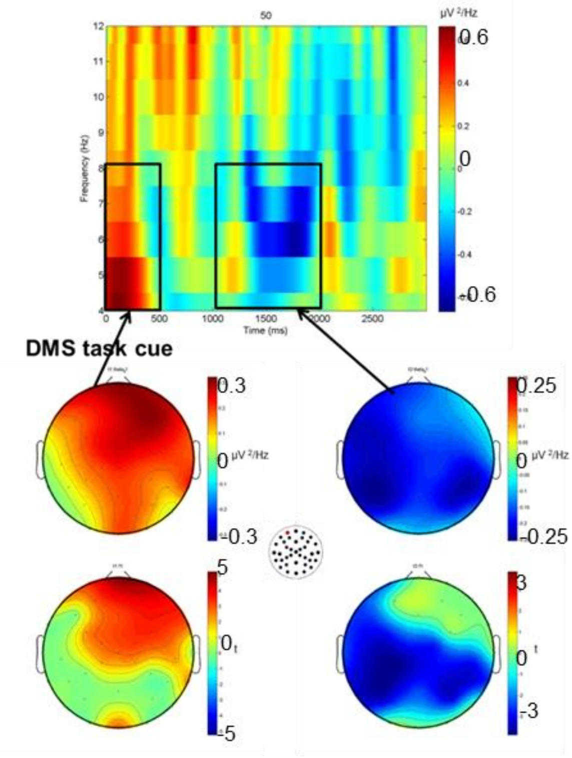


Figure 33. Difference in theta activity before DMS task onset

Top: time-frequency representations of power difference in theta activity between two DMS task conditions at a representative frontal electrode site (site 50 from montage 10). Middle: scalp maps indicate the power difference in theta activity between two DMS task conditions. From left to right: theta activity before the conjunction DMS task minus the theta activity before the feature DMS task from cue onset until 500 ms after cue onset, theta activity before the conjunction DMS task minus the theta activity before the feature DMS task from 1000 ms to 2000 ms after cue onset. Bottom: corresponding statistical scalp maps show the significant differences between two DMS task conditions. From left to right: theta activity before the conjunction DMS task minus the theta activity before the feature DMS task from cue onset until 500 ms after cue onset, theta activity before the conjunction DMS task minus the theta activity before the feature DMS task from 1000 ms to 2000 ms after cue onset.

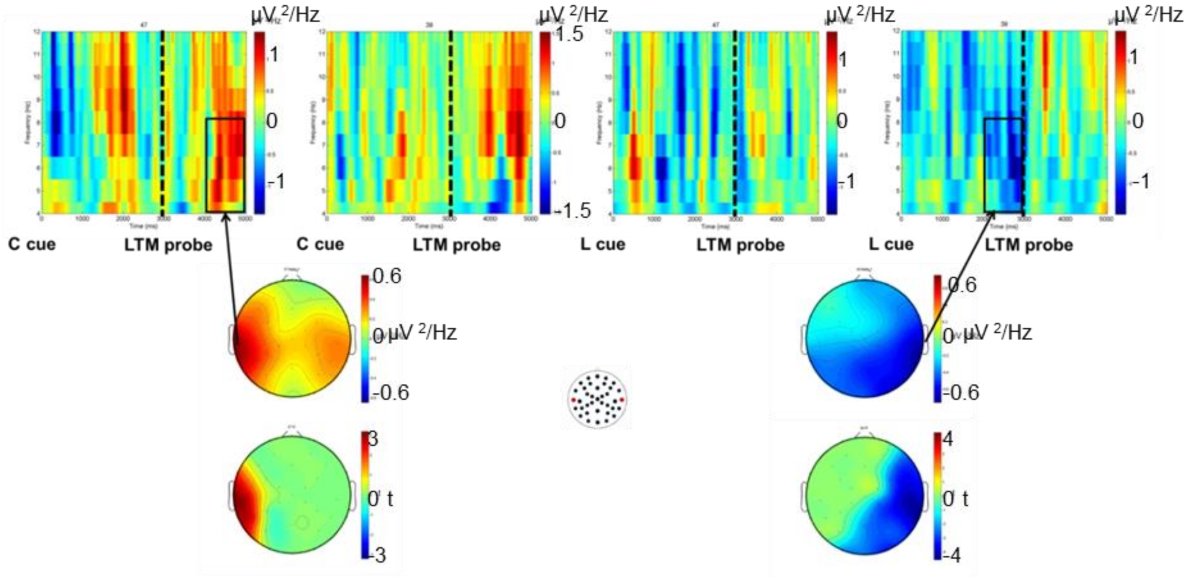


Figure 34. Encoding-related theta effects in Experiment 3

Top: time-frequency representations of encoding-related theta activity at two representative temporal electrode sites (sites 47 and 39 from montage 10). From left to right: overall encoding-related theta activity irrespective of DMS task condition, encoding-related theta activity for the conjunction DMS condition, encoding-related theta activity for the feature DMS task condition. Middle: scalp maps indicate the difference in theta power before later recognised and forgotten LTM probes. From left to right: overall difference in theta power before recognised and forgotten LTM probes from the conjunction condition in the time window of 4000 ms to 5000 ms after task cue onset, the difference in theta power before recognised and forgotten LTM probes from the feature DMS task condition in the time window of 2000 – 3000 ms after task cue onset. Bottom: corresponding statistical scalp maps show the significant differences between later recognized and forgotten trials.

Retrieval-related theta activity. The time-frequency representations showed that theta power decreased after LTM probes that attracted remember (remember and confidently recognised) judgments compared to the new pictures that attracted new (unconfidently recognised, unconfident new and confident new) judgments (Figure 35).

A significant difference in old-new theta effects between DMS conditions was found over right frontal scalp sites from picture onset until 500 ms after picture onset. The remembered LTM probes from the conjunction condition elicited larger theta power than the remembered LTM probes from the feature condition (Figure 35). Permutation tests were conducted to test the old-new effects separately for both conjunction and feature conditions. No significant old-new effect was found in either conjunction or feature conditions in this time window.

Permutation tests were used to test the overall old-new effect irrespective of DMS task conditions after 500 ms as no interaction was found after 500 ms. Significant theta decrease old-new effects were found from 500 ms until 2000 ms after picture onset. The old-new effect was over left temporal scalp sites from 500 ms to 1000 ms. In the latter two time windows, the old-new effects were widespread over the posterior scalp sites. Then permutation tests were conducted for collapsing the three consecutive time windows. A widespread posterior old-new effect was found from 500 ms to 2000 ms after picture onset irrespective of DMS task conditions.

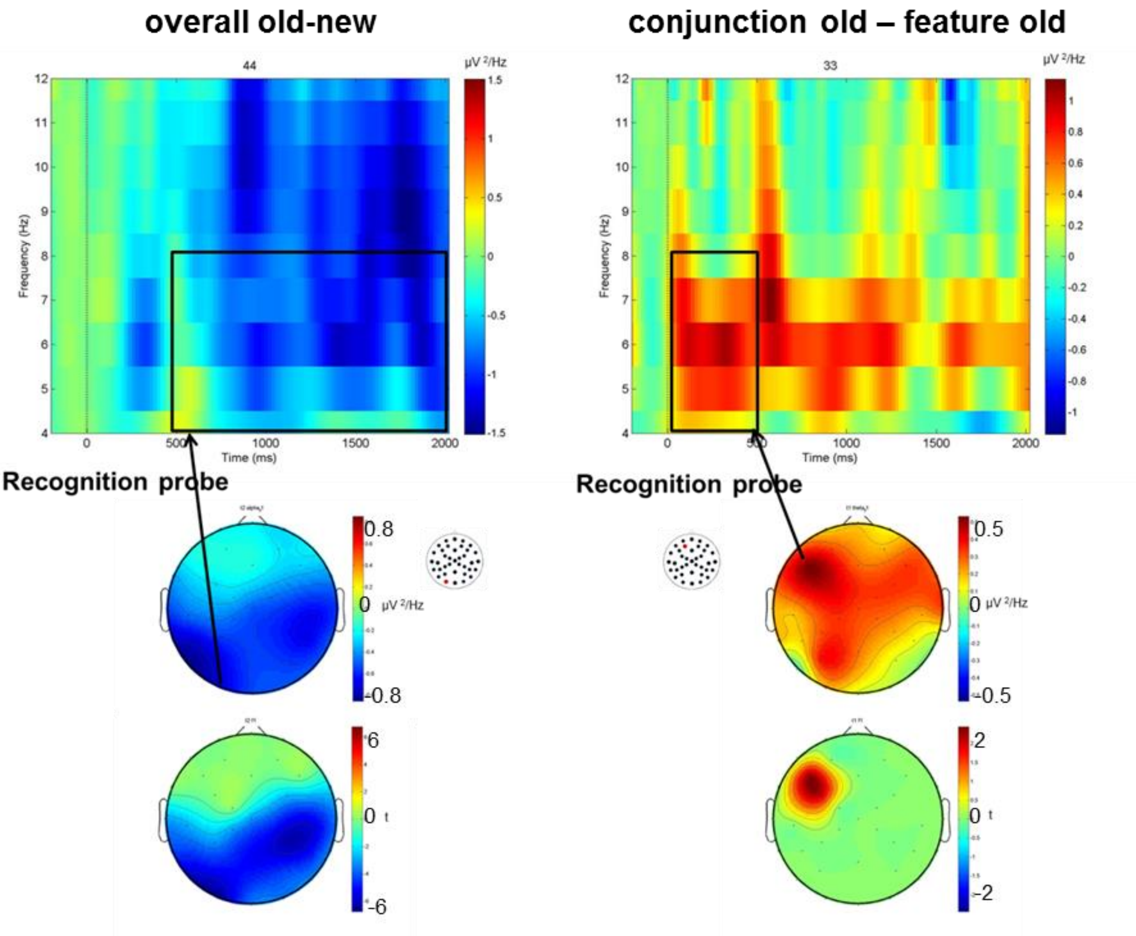


Figure 35. Retrieval-related theta effects in Experiment 3

Top: time-frequency representations of retrieval-related theta activity two electrode sites (sites 44 and 33 from montage 10). Left: retrieval-related theta activity for the recognition probes irrespective of DMS task conditions. Right: Differences in retrieval-related theta activity between the conjunction and feature conditions. Middle: scalp maps indicate the difference in theta power in correct judged old items and new items. From left to right: retrieval-related theta activity irrespective of DMS task conditions in the time window of 500 ms to 2000 ms after picture onset, difference between conjunction and feature conditions in the time window of 0 to 500 ms after picture onset. Bottom: Corresponding statistical scalp maps show the significant differences.

Overall preparatory alpha activity preceding DMS task onset. Time-frequency representations showed that alpha power increased after conjunction cue onset compared to feature cue onset (Figure 36).

Permutation tests showed alpha power increase over frontal and occipital scalp sites after conjunction cue onset until 500 ms after cue onset compared to feature cue onset. After 3 s, when an LTM probe was presented, the difference between overall preparatory activity prior to a conjunction task and a feature task increased than the difference when no LTM probe was presented from 3500 to 4000 ms after cue onset. Permutation tests revealed that this difference was caused by that alpha power decreased prior to the conjunction task compared to the feature task when no LTM probe was presented. Permutation tests on the overall preparatory activity irrespective of whether there was or not an LTM probe showed no difference in the overall preparatory activity in the time windows where no interaction was found.

Encoding-related alpha activity before LTM probes. The time-frequency representations showed that alpha power decreased before remembered LTM probes compared to forgotten LTM probes in the feature condition (Figure 37). In contrast, alpha power increased before remembered LTM probes in the conjunction condition.

The permutation tests revealed significant interactions between encoding-related alpha effect and DMS task condition. Compared to the encoding-related alpha effect in the feature condition, conjunction task cues elicited larger encoding-related alpha activity in the time windows of 0 – 500 ms, 1000 – 1500 ms, 1500 – 2000 ms and 2000 – 2500 ms. Further permutation tests were done for collapsing the latter three consecutive time windows. A widespread increase in alpha power was found from 1000 to 2500 ms after task cue onset.

Follow-up permutation tests on each DMS task condition revealed that the differences were caused by encoding-related alpha desynchronisation in the feature condition and encoding-related alpha synchronisation in the conjunction condition. In the early time window of 0 – 500 ms after task cue onset, alpha power decreased over right temporal scalp sites when an LTM probe was remembered in the feature condition. In two middle time windows, alpha power increased over occipital scalp sites before remembered LTM probes in the conjunction condition. The occipital alpha power increase effect was still significant from 1000 to 2000 ms after task cue onset when testing the collapsed two time windows in the conjunction condition. In contrast, a widespread alpha power decrease subsequent memory effect was found in the time window of 1500 to 2000 ms after feature cue onset. In the following time window, the alpha power decrease effect was found over right posterior scalp sites in the feature condition. A further permutation test was conducted for collapsing two time windows and revealed a significant alpha power decrease effect over right posterior scalp sites from 1500 ms to 2500 ms after feature cue onset.

In the two time windows where no interaction was found, significant decreases in alpha power were found before remembered LTM probes regardless of DMS task conditions. In the time window of 500 to 1000 ms after task cue onset, the effect was over central scalp sites. In the time window of 2500 to 3000 ms after cue onset, the effect was over right temporal scalp sites.

Encoding-related alpha activity after LTM probes. Alpha power decreased after remembered LTM probes in the feature condition while alpha power increased after remembered LTM probes in the conjunction condition (Figure 37).

A significant interaction was found between DMS task conditions. In the time window of 1000 to 1500 ms after LTM probe onset, LTM probes from the conjunction condition elicited larger encoding-related alpha activity over frontal scalp sites than probes from the feature condition. Permutation tests on each DMS task condition revealed a frontal encoding-related alpha decrease effect in the feature condition and a bilateral encoding-related alpha increase effect in the conjunction condition in this time window.

Further permutation tests were conducted to compare the overall differences in alpha power between remembered LTM probes and forgotten LTM probes irrespective of DMS task conditions in the time windows where no interaction was found. In the time window of 500 to 1000 ms after LTM probe onset an overall encoding-related alpha power decrease effect was found over occipital scalp sites. In the time window of 1500 to 2000 ms after LTM probe onset, alpha power increased over frontal and right scalp sites when an LTM probe was remembered irrespective of DMS task condition.

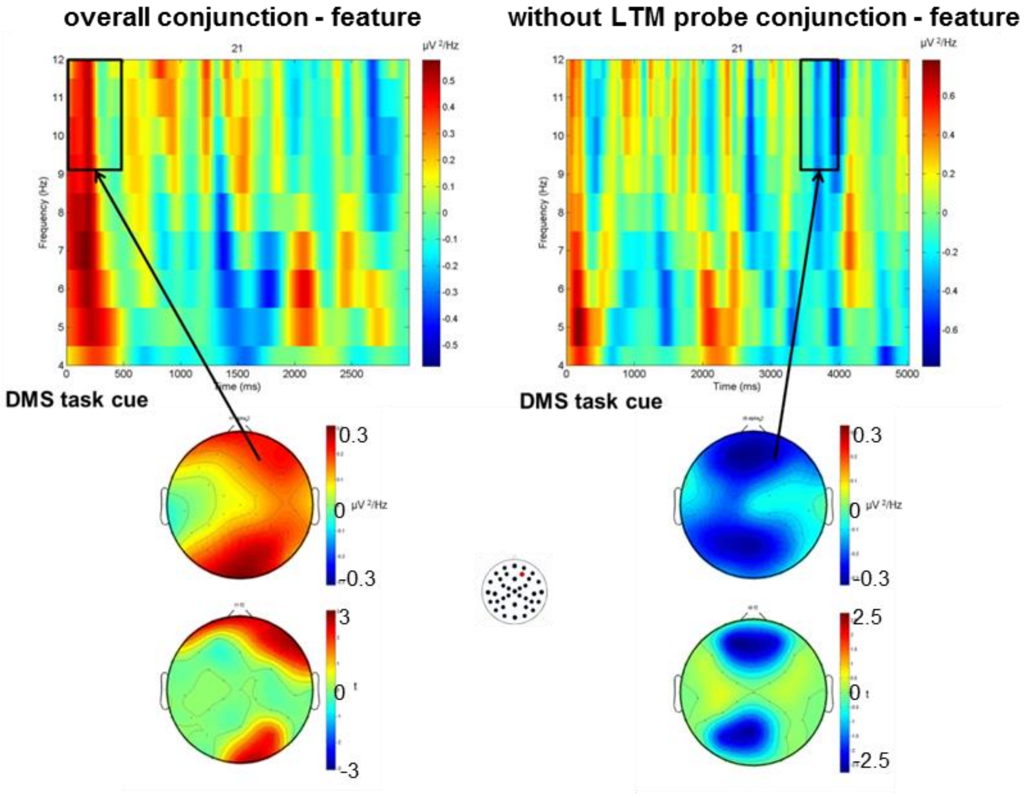


Figure 36. Difference in alpha activity before DMS task onset

Top: time-frequency representations of power difference in alpha activity between two DMS task conditions at a frontal representative electrode site (site 21). Left: difference in alpha power between two DMS task conditions irrespective whether there was or not an LTM probe. Right: as in left but the difference is between two DMS task conditions when there was no LTM probe. Middle: scalp maps indicate the power difference in alpha activity between two DMS task conditions. Left: difference in alpha power between two DMS task conditions irrespective of whether there was or not an LTM probe in the time window of 0 – 500 ms after DMS task cue onset. Right: as in left, but the difference is between two DMS task conditions when there was no LTM probe in the time window of 3500 ms to 4000 ms after DMS task cue onset. Bottom: corresponding statistical scalp maps show the significant differences between two DMS task conditions.

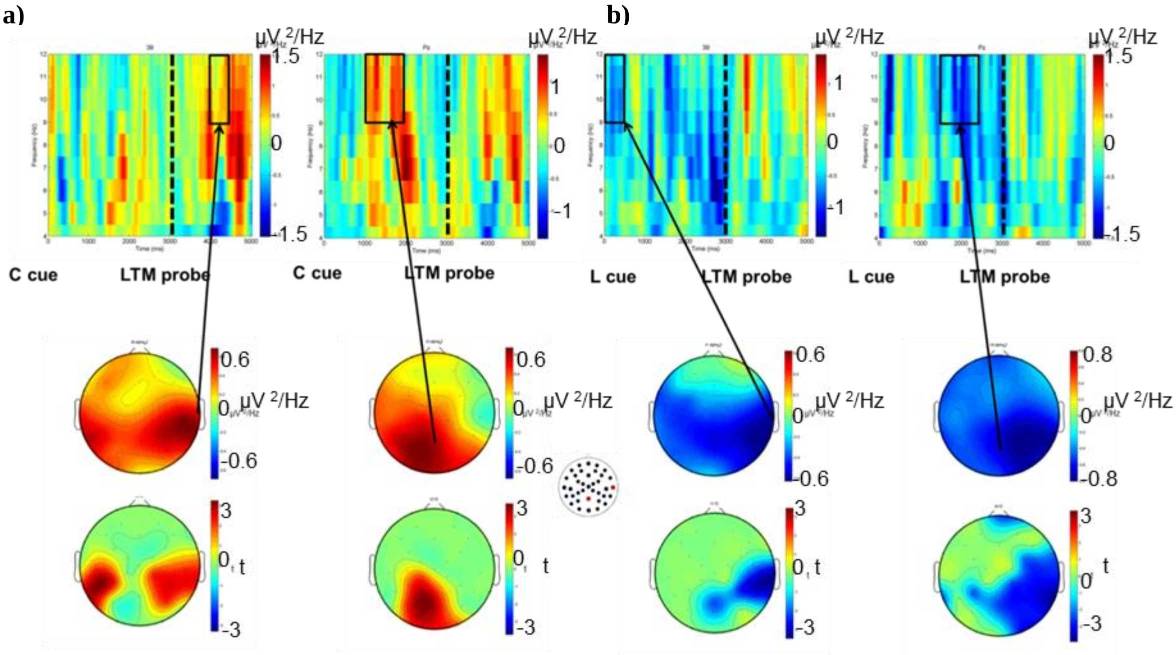


Figure 37. Encoding-related alpha effects before and after LTM probe onset

a) Top: time-frequency representations of encoding-related alpha activity for the LTM probes from the conjunction condition at two electrode sites (sites 39 and Pz from montage 10). Middle: scalp maps indicate the difference in alpha power before later recognised and forgotten LTM probes from the conjunction condition. Left: the difference of the 4000 ms to 4500 ms after conjunction cue onset. Right: as in left, but in the time window of 1000 ms to 2000 ms after conjunction cue onset. Bottom: corresponding statistical scalp maps show the significant differences between later recognized and forgotten trials. b) Same as a, but the effects are from the feature DMS task conditions. Middle: as in a, but the difference is for the probes from the feature condition in the 0 – 500 ms time window (left) and 1500 ms to 2500 ms time window (right). Bottom: corresponding statistical scalp maps for the feature condition.

Retrieval-related alpha activity. Alpha power decreased after LTM probes that attracted old judgments compared to the new pictures that attracted new judgments (Figure 38).

No significant difference was found between old-new effects in different DMS task conditions. Overall old-new effects were found over posterior scalp sites from 500 ms after picture onset until 2000 ms after picture onset, irrespective of DMS task conditions. Then permutation tests were conducted for collapsing the three consecutive time windows. A widespread posterior old-new effect was found from 500 ms to 2000 ms after picture onset irrespective of DMS task conditions.

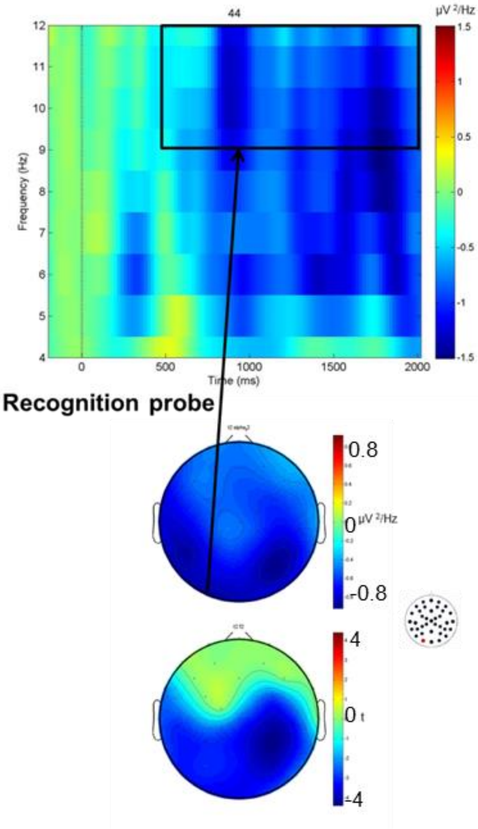


Figure 38. Retrieval-related alpha effects in Experiment 3

Top: time-frequency representations of retrieval-related alpha activity irrespective of DMS task conditions at one representative parietal electrode site (site 44 from montage 10). Middle: scalp maps indicate the difference in alpha power in correct judged old items and new items in the time window of 500 ms to 2000 ms after picture onset. Bottom: corresponding statistical scalp maps show the significant differences between old and new items that attracted correct judgments.

Summary of the time-frequency analyses. The time-frequency analyses showed that conjunction task cues elicited larger theta power than feature task cues over frontocentral scalp sites right after task cue onset. In middle time windows from 1000 to 2000 ms after task cue onset, theta power decreased prior to a conjunction DMS task. However, no significant encoding-related effect was found in the conjunction condition before LTM probe onset. In contrast, significant encoding-related theta desynchronisation was found in the feature condition.

After LTM probe onset, theta power increased prior to conjunction DMS task onset only when there was an LTM probe presented. A significant decrease in theta power was found 500 ms before conjunction DMS task onset compared to feature DMS task onset. However, a larger encoding-related theta decrease effect was found in the feature condition not in the conjunction condition. Encoding-related theta activity was also found for the LTM probes from the conjunction condition, but in opposite pattern. Theta activity increased in power when an LTM probe from the conjunction condition was subsequently remembered compared to forgotten.

During retrieval, correctly remembered old pictures from the conjunction condition elicited larger theta power than pictures from the feature condition right after picture onset until 500 ms. After 500 ms, significant retrieval-related theta desynchronisation was found widespread until 2000 ms irrespective of DMS task conditions.

Alpha power increased in the conjunction cue condition compared to the feature cue condition from cue onset until 500 ms after cue onset. Encoding-related alpha synchronisation was found from 1000 ms to 2000 ms after cue onset in the conjunction condition. In contrast, encoding-related alpha desynchronisation was found in the feature condition.

After 3 s, a decrease in alpha power was found prior to conjunction task cue onset compared to feature task cue onset from 3500 ms to 4000 ms after cue onset. Similarly to the encoding-related effects before LTM onset, significant encoding-related alpha desynchronisation was only found for the LTM probes from the feature condition. In the conjunction condition, alpha power increased after remembered LTM probes.

No difference in retrieval-related alpha activity between DMS conditions was found. Alpha activity decreased after correctly remembered pictures compared to correctly judged new pictures from 500 to 2000 ms after picture onset.

4.3.4 Discussion

In Experiment 3, participants started to prepare for a conjunction DMS task when they saw a conjunction cue 5 s before DMS task onset or prepare for a feature DMS task when they saw a feature cue. An LTM probe was inserted 3 s after cue onset in half the trials. Participants' memory on the LTM probe was tested in a later recognition memory test. Early increases in both theta and alpha power were found after conjunction cue onset compared to feature cue onset. Conjunction cues also elicited decreases in theta and alpha power in later time windows compared to feature cues. However, larger encoding-related desynchronisation in theta and alpha activity was found for the LTM probes from the feature condition. The LTM probes from the conjunction condition elicited an opposite pattern, that is, increases in theta and alpha power were found for remembered probes compared to forgotten LTM probes. Such findings seemed to be against the idea that preparing for a conjunction DMS task can induced larger theta and alpha desynchronisation states for successful memory encoding. However, the findings suggest that preparation for two different types of DMS task might influence the underlying cognitive processes during encoding.

Compared to the overall preparatory activity elicited by feature cues, conjunction cues elicited increases in theta and alpha right after cue onset. In the early time window after cue onset, participants got the information of preparing for a combination of two pieces of information or just one feature. Frontal midline theta is suggested to be increased in its magnitude when working memory load is increased (Gevins, Smith, McEvoy, & Yu, 1997; Hsieh & Ranganath; 2013). The difference in the early overall preparatory activity might reflect an evaluation of the working memory load in each DMS task. The frontocentral theta power increase elicited by conjunction cues might indicate preparation for an increase in working memory load of a conjunction DMS task. An increase in theta power in the conjunction condition compared to the feature condition was also found right after LTM probe onset. Such increase was not found when no LTM probe was presented. According to the occipital scalp distribution of this theta increase, such theta increase might reflect similar functional role of occipital alpha activity that is, protecting preparation for the DMS conjunction task from distract information (Jensen & Mazaheri, 2010).

Alpha power increases have been associated with updating or increasing working memory load when maintaining information (Manza, Hau, & Leung, 2014; Nenert, Viswanathan, Dubuc, & Visscher, 2012; Sauseng et al., 2005). The frontal alpha is especially related to top-down control in allocating visual processing resource for increased working memory load (Sauseng et al., 2005). Therefore, frontal alpha is thought to be accompanied with a decrease in occipital alpha power. However, an increase rather than a decrease in occipital alpha power was found right after conjunction cue onset. Such occipital alpha power increase is suggested to reflect a role of gating irrelevant information from the visual stream (Bonnefond & Jensen, 2012). The early preparatory theta and alpha activity elicited by conjunction cues suggests that early preparation for a conjunction task might engage more processing resource than preparation for a feature task.

A decrease in theta power was found in a middle time window (1000 to 2000 ms after cue onset) and a late time window (4500 to 5000 ms after cue onset) before conjunction DMS task onset. The middle effect was widespread over the scalp. Such theta desynchronisation replicates the findings from Experiments 1 and 2 that when preparing for more perceptual information or more opportunity for preparation was available, theta power decreased. The middle effect occurred after processing the cue information and before LTM probe onset. The effect might reflect pre-activation in the neural networks of processing a combination of an object and its location. The preparatory processes might be similar to the preparatory processes for episodic encoding. Therefore if a LTM probe inserted after this preparatory state, memory encoding for the probe should be enhanced. However, a significant encoding-related theta desynchronisation preceding LTM probes was not found in the conjunction condition but the feature condition within the same time window (1000 to 2000 ms after cue onset) where the decrease in the overall preparatory theta activity was found in the conjunction condition. This finding is against the better preparatory theta decrease state in the conjunction condition as well as the behavioural performance in the Section 3.3.3. One possible reason is that although the overall preparatory activity for a conjunction task decreased than the activity for a feature task, the activity for the forgotten probes from the feature task was significantly larger than the activity for the remembered probes from feature task, which led to larger encoding-related desynchronisation. Additional permutation test confirmed this idea. The theta power before the forgotten LTM probes from the feature condition was significantly larger than the theta power before the forgotten LTM probes from the conjunction condition. But there was no difference between theta power before the recognised LTM probes from the two conditions. The overall preparatory theta decrease state in the conjunction condition might enhance the preparatory processes for encoding an LTM probe inserted, which also led to better memory performance. However, in contrast to this idea, an increase in theta power was found after LTM probe onset when the LTM probe was remembered and this increase was within the same time window (4500 to 5000 ms after cue onset) where a frontal decrease in theta power was found prior to a conjunction DMS task compared to a feature DMS task. If the theta decrease state can enhance memory encoding, the theta activity elicited by a subsequently remembered probe should not be significantly larger in power than a subsequently forgotten probe. Increases and decreases in oscillatory activity power during successful memory encoding are suggested to reflect different cognitive and perceptual processes underlying encoding processes (Hanslmayr & Staudigl, 2013). Decreases in theta and alpha power might reflect elaborated encoding for item-specific information (Hanslmayr et al., 2009). Increases in theta power are usually suggested to be related to encoding item-context binding information (Guderian et al., 2009; Hanslmayr et al., 2009; Staudigl & Hanslmayr, 2013). The functional role of increases in theta power is consistent with the idea that preparation for a task of binding an object with its location can induce a brain state conducive to episodic memory encoding, which stresses memory of binding item and its contextual information.

A decrease in alpha power was also found before conjunction task onset compared to feature task onset, but only when no LTM probe was presented. This might be caused by that an increase in alpha power was found for the remembered LTM probes, in contrast to the forgotten LTM probes from the conjunction condition. Alpha power increased before and after an LTM probe when preparing for a conjunction DMS task. Both pre and post LTM probe alpha power increases were over posterior scalp sits. The pre-stimulus alpha activity is suggested to be related to preparation for stimulus-related information and inhibit irrelevant information, which reflects a top-down control role of alpha in preparing for memory encoding (Fell et al., 2011). Post-stimulus alpha is found to be increased over posterior scalp sites during maintaining a sequence of items in a working memory paradigm when the sequence is subsequently remembered in a recognition test (Khader, Jost, Ranganath, & Rösler, 2010; Meeuwissen, Takashima, Fernández, & Jensen, 2011). Meeuwissen et al. (2011) suggest that retention during the working memory task increased parietal alpha power compared to presentation of the sequence, which built an optimal brain state for long-term memory encoding to inhibit external irrelevant visual information. In Experiment 3, when no LTM probe was inserted, a decrease in frontal and parietal alpha power was found prior to a conjunction task compared to a feature task, which suggests compared to a feature task, preparation for a conjunction task activates more visual processing. However, such decrease state did not provide an optimal brain state for long-term memory encoding as no such decrease was shown when an LTM probe was presented. In contrast, the encoding-related alpha synchronisation for the LTM probes from the conjunction condition might reflect the interaction between underlying preparatory processes for the conjunction task and long-term memory encoding. Therefore, synchronisation rather than desynchronisation in alpha was found as the cognitive process underlying encoding processes for an LTM probe might share similar systems with preparation for a conjunction DMS task, which increased alpha activity can protect memory encoding from interference with preparation for the conjunction task. In contrast, the overall preparatory alpha activity showed that preparation for a feature DMS task might not need to be engaged as much processing resources as a conjunction DMS task. Therefore, encoding-related alpha desynchronisation could be engaged to support elaborated encoding for stimulus-specific information. The underlying cognitive processes during encoding for the LTM probes from the feature condition might be traditional semantic encoding (Hanslmayr et al., 2009).

Previous studies suggest that theta power increases when an old item was remembered, in contrast to a new item was correctly judged as new (Guderian & Düzel, 2005; Klimesch et al., 2001; Osipova et al., 2006). In Experiment 3, decreases in both theta and alpha were found after corrected judged old items compared new items, in contrast to a pre-stimulus baseline for the LTM probes from both the conjunction and feature conditions. The power decrease old-new effects seemed to be across low frequency band effects, not restricted to theta or alpha as the latency and scalp distributions were similar in both frequency bands. Hanslmayr et al. (2012) suggests that alpha desynchronisation does not only play a role in efficient memory encoding but also retrieval. Alpha power decrease old-new effects might suggest a re-activation of perceptual information about an old item. Compared to a new item, an old item holds more information related to a formed memory representation. Therefore, alpha desynchronisation can help restore the related information for an old item. The colour photographs of daily objects used in Experiment 3 might cause re-activation of more perceptual information than verbal material. Hence, a retrieval-related alpha desynchronisation effect was found over a widespread scalp distribution and might bleed-into the theta frequency band. Although there was no difference in the retrieval-related theta and alpha desynchronisation, an early difference in retrieval-related activity between the probes from the conjunction and feature conditions exclusively to the theta frequency band was found. The remembered old probes from the conjunction condition elicited a larger theta activity than the remembered old probes from the feature condition over left frontal scalp sites from probe onset until 500 ms after probe onset. A previous study showed that larger theta power was associated with old items that were given ‘Know’ judgment during an early time window (Klimesch et al., 2001). This indicates that early frontal theta power increase might reflect an early familiarity judgment to the probes. The probes from the conjunction condition might be more familiar than the probes from the feature condition. Unfortunately, there were insufficient items given ‘R’ and ‘know sure’ judgments to consider each category separately. Therefore, it is difficult to demonstrate whether correct ‘R’ judgments mainly contributed to the increase in theta power, as was done in previous studies that suggest that theta activity reflects item-source binding (Gruber et al., 2008; Jensen & Lisman, 1996; Staudigl & Hanslmayr, 2013).

In conclusion, the overall preparatory theta and alpha activity for the conjunction DMS task generally supports the idea that preparation for binding an object with its location can induce a theta and alpha state conducive to encoding. Although such state did not enhance encoding-related desynchronisation for the LTM probes from the conjunction condition, encoding-related synchronisation in alpha and theta for the LTM probes from the conjunction condition might suggest that successful encoding for an LTM probe depends on the concurrent cognitive processes underlying encoding processes. Retrieval-related desynchronisation was found for the LTM probes from both the conjunction and feature condition. Such retrieval-related desynchronisations might reflect a re-activation of more perceptual information for the old probes. The remembered old probes from the conjunction condition elicited larger frontal theta power than the remembered old probes from the feature conditions, which might suggest that the probes from the conjunction condition were more familiar than the probes from the feature condition during the retrieval processes.

Chapter 5: The relationship between encoding-related preparatory processes and overall memory performance

This chapter includes two behavioural experiments: Experiment 4 and Experiment 5. Elena Entesarian who was an undergraduate intern in the Cognitive Electrophysiology Group collected a large part of the data in Experiment 4, which was her summer internship project.

Introduction

Pre-stimulus activity has been widely demonstrated to influence the efficiency with which information presented on individual trials is encoded into long-term memory. The encoding-related pre-stimulus activity is suggested to reflect active preparatory processes (Galli et al., 2013). However, it is not clear whether such active preparatory processes influence overall subsequent memory performance. For example, Galli et al. (2011) found when a cue signalled presentation of an unpleasant picture, pre-stimulus activity predicted successful memory formation but only in females not males. However, the overall memory performance did not differ by sex. In addition, Galli et al. (2013) showed when processing resources before an item were shared with a secondary task, pre-stimulus activity predicted successful encoding on the item only when the secondary task was easy. No overall memory performance difference was found between the easy secondary task condition and the difficult secondary task condition. In Experiment 2 of this doctoral thesis, although longer preparation time has been demonstrated to provide more opportunity to engage pre-stimulus activity in preparing for efficient memory encoding, no better overall memory performance was found compared to shorter preparation time.

In contrast, a few studies show evidence that pre-stimulus neural activity predicts overall memory performance enhancement. In one study, Bollinger et al. (2010)

used category cues to signal that the category of an upcoming picture was a face or a scene, in contrast to neutral cues that did not signal the category of the upcoming picture. The results showed that when a cue predicted presentation of a face, the FFA was more activated even before picture onset compared to a neutral cue. Most importantly, the overall memory performance for the faces after a predictable cue was better than the overall memory performance for the faces after a neutral cue. Another study used spatial cues to indicate one of two locations where an upcoming object was presented (Uncapher et al., 2011). The results showed that preparatory activity in the cue period was positively correlated with later memory success only when a cue validly signalled the location of the object. The overall memory performance was also found to be significantly better for the objects after valid spatial cues than the objects after invalid spatial cues. These two studies do not show that pre-stimulus activity predicts later memory success on individual trials but both studies show that pre-stimulus activity predicts overall memory enhancement. The findings suggest that similar ‘Posner cueing effect’ (Posner, 1980) can be also found in long-term memory. Memory performance can be enhanced by preparation in predictable conditions.

In two experiments of this doctoral thesis, amount of advance information was manipulated. However, no such overall memory enhancement was found when a cue validly signalled the physical form of an upcoming picture in Experiment 1. The reason for the absence of the overall memory enhancement might be encoding-related pre-stimulus ERP activity did not differ in the amount of advance information. In addition, encoding-related pre-stimulus theta and alpha desynchronisation was larger after a neutral cue compared to the activity after informative cues. Even when a cue did not signal the physical form of the picture, preparatory oscillatory activity could also influence later memory success. Therefore, the overall memory performance might not differ as non-informative cues might guide additional preparatory mechanisms. In

Experiment 2, preparatory ERP activity for memory encoding was found in a long preparatory interval regardless of cue predictability. Encoding-related theta and alpha desynchronisation was larger in earlier time windows for a predictable long interval whilst desynchronisation for an unpredictable long interval was larger in a later time window right before picture onset. The findings further support the absence of overall memory enhancement in a cued or predictable cue condition might be caused by additional preparatory mechanisms for efficient memory encoding in unpredictable conditions.

However, overall memory performance was not either enhanced when preparation time was longer (irrespective of cue predictability) compared to shorter preparation time which no pre-stimulus subsequent memory effect was found in Experiment 2. Summerfield and Mangels (2006) suggested that longer preparation time prior to an event could help to enhance the overall memory performance. In their study, different numbers of intervals between items were used. The number of intervals could be zero, one and two. The time length of each interval was equalled. Therefore, when an item was preceded by two intervals participants had longer and predictable time to prepare. The results showed that words following 2 intervals were more likely to be remembered than the other two interval conditions. Further, Galli et al. (2013) showed that when participants had to do a perceptual discrimination task before encoding a word, the reaction times on the perceptual discrimination task predicted later memory performance for auditory words. The faster a discrimination task decision was made, the more likely an upcoming auditory word could be recalled. The findings indirectly demonstrated that when more preparation time remains before encoding a word, the word is more likely to be encoded successfully.

One possible explanation about the absence of the overall memory performance enhancement when longer preparation time was available is that other memory-related processes help to compensate poor memory representations during the encoding stage (Galli et al., 2013). As mentioned in Chapter 1, whether an event can be remembered or forgotten depends on encoding, consolidation and retrieval stages or the interaction between these stages. Therefore, if failing to engage preparatory processes in memory encoding leads to a poor memory representation, additional compensatory processes in the other memory stages might be engaged in making the memory representation more likely to be remembered. For example, in Experiment 3 of this doctoral thesis, the overall memory performance for the LTM probes from the conjunction condition was better than the memory performance for the LTM probes from the feature condition although smaller encoding-related activity was found for the probes from the conjunction condition. Retrieval-related activity elicited by the probes from the conjunction condition was larger than retrieval-related activity elicited by the probes from the feature condition, which suggests that compensatory processes in the retrieval stage might help probes from the conjunction condition to be more likely to be remembered ultimately, even though memory representations might be weaker during the encoding stage.

To investigate if this compensation hypothesis is true to explain the relationship between preparatory processes for long-term memory encoding and overall memory performance, Experiments 4 and 5 used secondary tasks to prevent retrieval from engaging compensatory processes. If the compensation idea is true, the overall memory performance should differ in amount of preparation time when there is less opportunity to engage compensatory processes during retrieval. As mentioned in Chapter 1, overall memory performance is interfered when a secondary task was conducted during encoding (Anderson et al., 2000; Craik et al., 1996; Craik et al., 2010; Fernandes & Moscovitch, 2000; Iidaka et al., 2000; Naveh-Benjamin et al., 1998; Naveh-Benjamin & Craik, 2000). However, only certain secondary tasks during the retrieval stage have been demonstrated to impair memory performance (Fernandes & Moscovitch, 2000). Therefore, to prevent retrieval from engaging compensatory processes that can help a poor memory representation to be ultimately remembered to the greatest extent, semantic secondary tasks that are demonstrated by Fernandes and Moscovitch (2000) to impair memory performance significantly were used in Experiments 4 and 5.

Experiment 4

5.1.1 Introduction

In Experiment 4, the same encoding paradigm was used as in Experiment 2. As significant pre-stimulus subsequent memory effects were found only when preparation time was long, more preparatory processes were engaged in helping forming a stronger memory representation. Therefore, if a secondary task during retrieval prevents compensatory processes for a poor memory representation, the memory performance from the long preparation time conditions should be less interfered than the memory performance from the short preparation time conditions. Participants were asked to perform a secondary task of semantic judgment on an auditory word while doing a recognition memory test for pictures.

In Experiment 2, encoding-related pre-stimulus ERP activity had different scalp distributions in a middle time window when a long interval was predictable, in contrast to an unpredictable interval. In addition, encoding-related pre-stimulus oscillatory desynchronisation occurred in different time windows. It is not clear how different kinds or latency of preparatory activity for memory encoding influence the strength of a memory representation. As mentioned in Chapter 1, different scalp distributions or latency of encoding-related activity after an event seem not to influence how likely the event can be remembered. The different scalp distributions or latency of preparatory activity before an event might not either influence the strength of a memory representation.

5.1.2 Methods

Participants. The experimental procedures were approved by the University College London Research Ethics Committee. 24 healthy adults were paid at a rate of £7.50/h to take part. Their mean age was 22 years (range of 18 - 28 years) and 13 of them were female. They met all criteria described in Experiment 1. In addition, participants reported that they had normal hearing.

Stimulus Material. Stimuli for memory task were the same as the stimuli used in Experiment 2. Stimuli for the secondary task consisted of 264 words (concrete nouns, 2 – 11 letters, Kučera-Francis written frequency: 1 – 377 per million (Kučera & Francis, 1967)). Three sets of 84 words were pseudo-randomly selected to create a secondary test list. 72 of them pertain to living things. The remaining 12 filler items were used for practice. 4 of them pertain to living things. The words were pre-checked to make sure that no identical greyscale photos of objects were presented.

Stimulus presentations were the same as in Experiment 2. During the test phase, the procedure was generally the same as in Experiment 2 except that participants were asked to listen to an auditory word while doing the confidence recognition memory test to a picture in three out of six test blocks. The order to present a block with or without a secondary task was altered across subjects. An auditory word was presented at the same time as a picture was presented. The recordings were in a British adult male voice and 113 ms mean duration. From the picture onset until next exclamation mark onset, there was a variable period randomly lasting from 2.5 to 4 s. This inter-trial-interval (ITI) was 500 ms longer than Experiment 2 as pilot work showed that the original ITI was not sufficient for participants to be able to perform the recognition test and the secondary task concurrently. Therefore, a longer ITI was opted to ensure that participants did not ignore either task.

Procedure. The experiment procedure was generally the same as in Experiment 2. The procedure of study phase was exactly the same as in Experiment 2. In the test phase, pictures that were presented in the study phase appeared again along with new pictures (Figure 39). Each test picture was presented with an auditory word in 3 out of 6 blocks. To be as consistent as possible with Experiment 2, both key responses and reaction times for each picture in the recognition test were recorded. In that case, recording the key responses and reaction times for each auditory word from another task concurrently was not possible. Therefore, participants were asked to count how many living things they heard through the block. They were asked to give their answers at the end of each block. Half of the participants started with a block with the secondary task while half of the participants started with a block without the secondary task. A block without the secondary task always followed a block with the secondary task. Participants could take a break after each block ended. They were told both the recognition test and the secondary task were important to ensure that they shared attention equally to each task. They were given a practice phase before the real experiment to get used to the task.

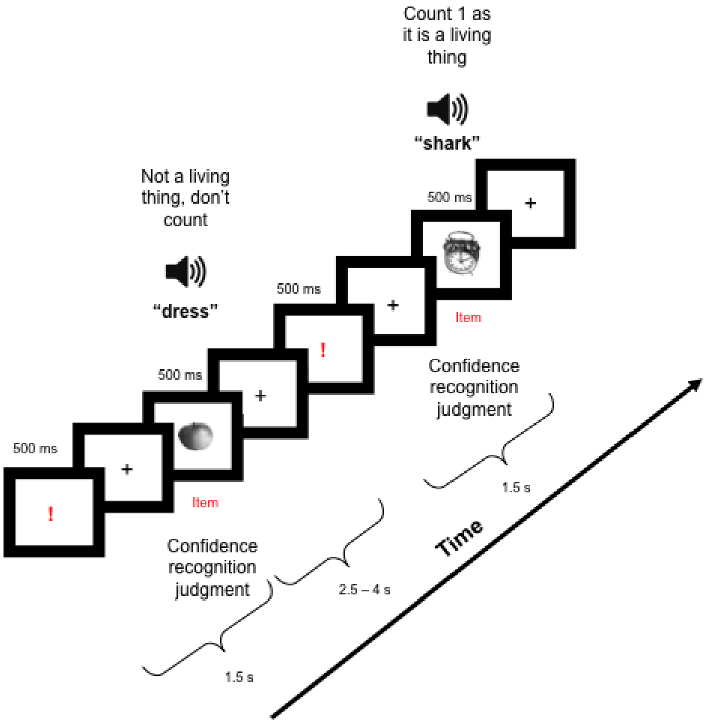


Figure 39. An example series of the block with the secondary task in test phase in Experiment 4

5.1.3 Results

Study. Performance for the study phase is summarized in Table 27. The analyses were done in the same way as were done in Experiment 2. The analyses used ANOVA with repeated measure factors of amount of advance information (informative, non-informative) and amount of preparation time (short 1.5s, long 3s). No significant difference was found between either amount of advance information or amount of preparation time (all *p*s > 0.2). Reaction times of the size judgment task were also categorised by subsequent memory performance. 'Confident old' and 'unconfident old' were collapsed into 'recognised' category and 'confident new' and 'unconfident new' were collapsed into 'forgotten' category to be consistent with Experiment 2. No significant difference was found between later old and new judgments (all *p*s > 0.3).

Table 27. Study task performance in Experiment 4

	Predictable short	Predictable long	Unpredictable short	Unpredictable long
Accuracy M	0.84	0.86	0.85	0.85
(proportion) SD	0.06	0.04	0.05	0.05
Response M	863	869	862	858
times (ms) SD	152	153	151	155

Values are across-subject means. n=24.

Animacy counting task. The mean accuracy of the secondary task (animacy counting) was 0.91 (range: 0.78 – 0.99). The values are across-subject means (N = 24).

Recognition Test. Recognition memory performance is summarized in Tables 28 and 29. Pr and Br values collapsed across confident and unconfident responses were analysed with ANOVAs with repeated measure factors of amount of advance information (informative, non-informative), amount of preparation time (short 1.5 s, long 3s) and secondary task during retrieval [full attention (FA), divided attention (DA)]. The ANOVAs revealed a main effect of secondary task for Pr. Pr under the divided attention (DA) condition was significantly poorer than Pr under the full attention (FA) condition, $F(1, 23) = 7.451$, $p = 0.012$.

Significant interactions were found between amount of preparation time and secondary task for both Pr and Br, $F(1, 23) = 10.382$ and 6.169, respectively, $p = 0.004$ and 0.021. Subsidiary analyses were done for FA and DA conditions separately to understand the interaction. No effect was found in the FA condition for either Pr or Br. In the DA condition, both Pr and Br were significantly larger when the preparation time was long than, irrespective of cue predictability, $F(1, 23) = 4.281$ and 4.975, respectively, $p < 0.05$, $p = 0.036$ (see Figure 40). When subsidiary analyses were done for the cue conditions with short and long preparation times separately, a significant effect of secondary task was found for Pr only when preparation time was short, $F(1, 23) = 13.712$, $p = 0.001$. No effect emerged when preparation time was long, $p = 0.126$. This suggests that the ability to discriminate old from new items was impaired by a secondary task only when preparation time during encoding was short. For confident hits, the discriminations between old and new items were significantly greater than zero, all p values ≤ 0.001.

Another ANOVA with the same factors was performed for the reaction times when collapsing reaction times for confident and unconfident hits. A main effect of secondary task was found, $F(1, 23) = 47.208$, $p < 0.001$. Reaction times for confident old and unconfident old responses were significantly slower under DA than under FA conditions. A significant interaction was found between amount of preparation time and secondary task, $F(1, 23) = 6.926$, $p = 0.015$. Subsidiary analyses were conducted for FA and DA conditions separately to understand the interaction. A significant effect of amount of preparation time was found under the DA condition, $F(1, 23) = 6.621$, $p = 0.017$. Reaction times for the pictures from the long preparation time conditions were significantly slower than reaction times for the pictures from the short preparation time conditions when participants performed the recognition test concurrently with a secondary task. No significant effect of amount of preparation time was found in the FA condition, $p = 0.147$. When subsidiary analyses were done for short cue conditions and long cue conditions separately, significant effects of secondary task were both found when preparation time was short and long. Reaction times for the pictures from long preparation time conditions were slowed down by the secondary task, $F(1, 23) = 48.971$, $p < 0.001$, more robustly than reaction times for the pictures from short preparation time conditions, $F(1, 23) = 37.009$, $p < 0.001$.

Table 28. Mean proportion of recognition memory responses in Experiment 4

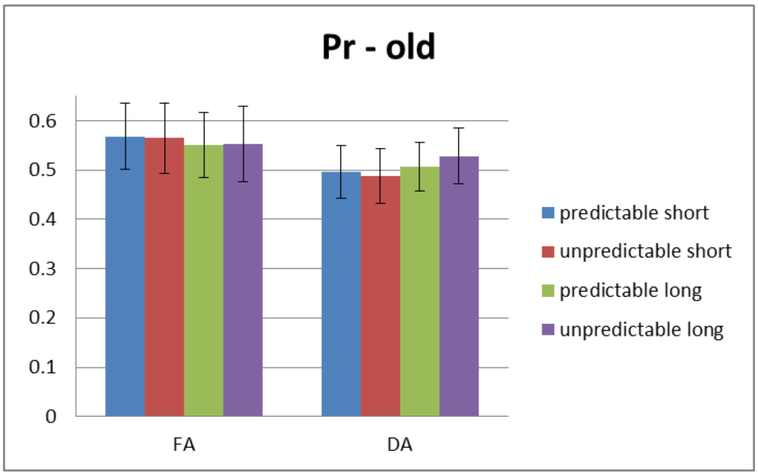
Condition			Recognition Type			
			Confident old	Unconfident old	Unconfident new	Confident New
Full Attention	Informative cue	short	0.70 (0.15)	0.12 (0.10)	0.09 (0.08)	0.09 (0.08)
		long	0.68 (0.14)	0.13 (0.11)	0.09 (0.06)	0.10 (0.10)
	Non-informative cue	short	0.70 (0.15)	0.11 (0.10)	0.08 (0.08)	0.10 (0.09)
		long	0.70 (0.17)	0.10 (0.09)	0.09 (0.08)	0.09 (0.08)
	New		0.14 (0.11)	0.11 (0.08)	0.30 (0.16)	0.45 (0.20)
Divided Attention	Informative cue	short	0.64 (0.16)	0.12 (0.12)	0.13 (0.09)	0.11 (0.12)
		long	0.65 (0.17)	0.12 (0.12)	0.11 (0.09)	0.11 (0.13)
	Non-informative cue	short	0.64 (0.18)	0.11 (0.11)	0.11 (0.10)	0.14 (0.12)
		long	0.67 (0.20)	0.12 (0.12)	0.10 (0.10)	0.10 (0.10)
	New		0.16 (0.11)	0.11 (0.08)	0.30 (0.18)	0.43 (0.21)

Values are across-subject means (SD). n=24.

Table 29. Mean RTs (ms) for collapsing confident and unconfident hits in Experiment 4

Full Attention				Divided Attention			
Informative cue		Non-informative cue		Informative cue		Non-informative cue	
short	long	short	long	short	long	short	long
1029 (177)	1009 (160)	1035 (195)	1004 (169)	1285 (301)	1338 (332)	1277 (298)	1309 (305)

Values are across-subject means (SD). n=24.



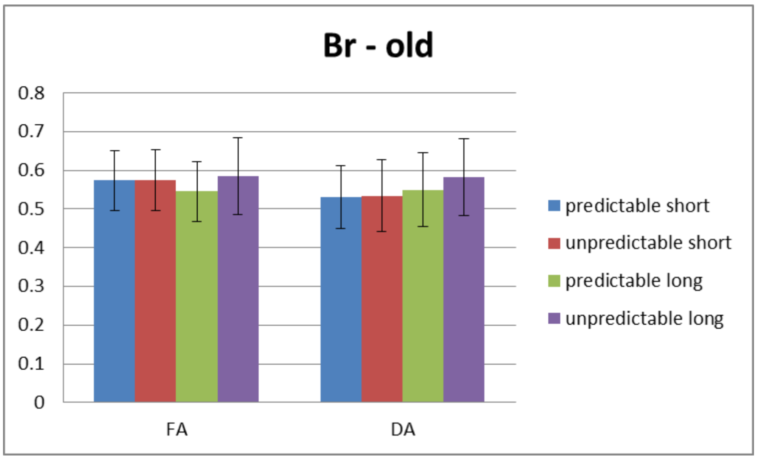


Figure 40. Pr and Br for confident and unconfident responses in each cue condition under FA and DA conditions during retrieval.

5.1.4 Discussion

In Experiment 4, the question was addressed whether preparatory processes for long-term memory encoding can enhance overall memory performance when less opportunity is available for engaging compensatory processes during retrieval. The same encoding paradigm was used as in Experiment 2. Informative cues indicated amount of preparation time was short (1.5 s) or long (3 s). Non-informative cues could be followed by either a short preparation time or long preparation time. The only difference between Experiments 4 and 2 was in the test phase. In Experiment 4, participants were asked to count the animacy things that they heard from a series of auditory words presented concurrently with pictures for a recognition memory test. Such manipulation was in order to prevent the engagement of compensatory processes during retrieval. The results suggest that the overall recognition memory accuracy was impaired by the secondary task especially when preparation time was short during encoding. When retrieval was interfered by the secondary task, pictures were more likely to be recognised if longer preparation time was available in the encoding stage. The findings demonstrated that overall memory performance might be able to be enhanced when longer preparation time is available for memory encoding, if the engagement of compensatory processes during retrieval was prevented.

However, some patterns of the results from Experiment 4 seemed to be insufficient to support the compensation hypothesis. First, the memory advantages from longer preparation time under the DA condition seem to be a trade-off between memory performance and reaction time for the recognition test. In the DA condition during retrieval, reaction times for giving ‘old’ (confident and unconfident) judgments were significantly slower for the pictures from longer preparation time conditions than short preparation time conditions. Fernandes and Moscovitch (2000) suggest that there are two processes underlying long-term memory retrieval. One is reactivation of a memory trace from the past, which is suggested to rely on neocortical representation system. Therefore, if a secondary task shared the neocortical resources with this process, such as retrieval of semantic knowledge, the reactivation of the memory trace will be interfered so that memory will be impaired. The other process is setting up and maintaining a retrieval mode, which mainly depends on the PFC. Craik et al. (1996) suggest that this process was a resource-demanding process. Therefore, if a retrieval mode is successfully set up and maintained, there must be a cost to delay performing the secondary task, that is, a cost on reaction times for the secondary task. Experiment 4 used an animacy word counting task to avoid conflicts with key pressing for the recognition test, which is different from most dividend attention studies on memory, where the focus is on recording RTs for secondary tasks. Although there was no need to press keys for the secondary task, the PFC resources were still competing between building and maintaining a retrieval mode and animacy counting. Such resource competition might lead to a cost on reaction times for recognition judgments. The reaction time costs under the DA condition were found for pictures from all the cue conditions. The larger reaction time cost under the DA condition for the pictures from long preparation time conditions might suggest a retrieval mode was more difficult to build and maintain for the pictures from the long preparation time conditions than the pictures from the short preparation time. This probably reflects a compensatory process for poorer memory representations from short preparation time during encoding. To compensate a poor memory representation due to less engagement of preparatory processes during encoding, a retrieval mode is quicker to be established during retrieval.

Second, no cueing effect was found for the encoding task as in previous studies (e.g. Miniussi et al., 1999; Zanto et al., 2011) and in Experiment 2. Both the behavioural results and cue-related neural activity in Experiment 2 showed that participants used cue information to prepare for responses for size judgments in study phase. When cues signalled the length of a preparatory period before item onset, reaction times for size judgments were significantly faster than when cues did not signal the length in Experiment 2. However, reaction times for size judgments did not differ in cue conditions in Experiment 4. One possible reason for the absence of cueing effect for size judgments in Experiment 4 might be that preparatory processes for memory encoding and for responses for size judgments might be two separate preparatory mechanisms. First, the reaction times for size judgments in Experiment 4 did not differ as a function of subsequent memory performance, which suggests that successful encoding and memory enhancement did not depend on processing on the size judgment task for a picture. Further, the reaction times for size judgment task in Experiment 4 were slower than in Experiment 2. In contrast, the overall memory performance was better in Experiment 4 than Experiment 2, even when retrieval was under the DA condition. This indicates that participants in Experiment 4 might allocate more processing resources on preparing for memory encoding than participants in Experiment 2. The two preparatory processes might compete with each other.

In addition, no cueing effect was found in recognition memory performance, which is different from previous studies (Bollinger et al., 2010; Summerfield & Mangels, 2006; Uncapher et al., 2011). Amount of advance information during encoding did not show any difference in later recognition memory performance under either FA or DA conditions. Interestingly, the predictable interval condition in Summerfield and Mangels's study is actually more comparable to the unpredictable long preparatory foreperiod in Experiment 4. In Summerfield and Mangels's study, if a second interval was presented, participants were able to tell another 1 s remained until next word onset, which is why they named this condition as the predictable condition. The largest memory enhancement was found for words after the second interval. Similarly, participants were able to tell another 1.5 s remained for preparation until picture onset in an unpredictable long condition in Experiment 4, which is predictable at some time point. The memory enhancement in long preparation time conditions irrespective of cue predictability under the DA condition resembles Summerfield and Mangels's findings on memory enhancement for the predictable condition. The reason why no cueing effect in overall memory performance was found in Experiment 4 might be caused by the information that cues signalled. Cues in previous studies signalled the information about upcoming stimulus such as stimulus category or location (Bollinger et al., 2010; Uncapher et al., 2011). Experiment 4 cued the time to prepare before stimulus onset. Previous studies suggest that cue information about the stimulus can evoke top-down expectation on the stimulus. The information about preparation time might be only able to guide amount of preparation but not the way to prepare. When more time is predicted to be available for preparation at some time point, such as the situation in the unpredictable long condition, there might be no difference in the amount of advance information. However, if cue information about an upcoming stimulus helps the way to prepare, informative cues that signalled the physical form of an upcoming picture in Experiment 1 should enhance later memory performance, which makes it still not clear whether the amount of advance information about an upcoming stimulus can enhance overall memory performance.

An interesting finding is that only the discrimination index (Pr) was found to be affected by the secondary task. The bias index (Br) was not affected, which suggests that participants’ criteria to judge an item as old were not stricter when retrieval resources were limited by a semantic secondary task. However, a similar interaction between amount of preparation time and secondary task was found for Br as Pr. When retrieval resources were limited by a secondary task, participants tended to make significantly more old judgments following a long preparation time during encoding. One thing that should be noted is that the false alarm rates were the same within the secondary task condition. This means that the higher Br in the long preparation time conditions was caused by higher hits. The reactivation of a memory trace might be impaired by the semantic secondary task. A longer preparation time might make the memory trace stronger such that even resources are limited, the representations can be reactivated.

In conclusion, the findings from Experiment 4 generally support the idea that memory advantages from more preparatory processes for encoding a more elaborated memory representation can be shown if the engagement of compensatory processes in retrieval is prevented. However, the absence of cueing effect in study phase did not replicate the findings from Experiment 2. Also, the reaction time cost in retrieval makes the effect to be vulnerable. To further investigate the relationship between preparatory processes for long-term memory and overall memory performance and the compensation hypothesis, Experiment 5 used secondary tasks with different degree of difficulty to manipulate resources to engage the compensatory processes in retrieval.

Experiment 5

5.2.1 Introduction

Experiment 4 used a secondary task to interfere with the retrieval processes. Compared to the full attention condition during retrieval, memory enhancement from longer preparation time during encoding was evident when the secondary task prevented the engagement of compensatory processes in retrieval. The findings support the idea that the relationship between preparatory processes for memory encoding and overall memory performance can be explained by the compensation hypothesis.

If a secondary task can prevent the engagement of compensatory processes during retrieval, such compensatory processes should be sensitive to processing resources during retrieval. The opportunity to engage the compensatory processes during encoding should depend on the processing resources available during retrieval. The less processing resources are available during retrieval, the more evident it is that memory advantages from better preparatory processes during encoding should be shown. Therefore, in Experiment 5, processing resources for the opportunity to engage compensatory processes during retrieval were manipulated by varying the difficulty of the secondary task during retrieval. In 3 out of 6 blocks, the secondary task was an easy task like the one used in Experiment 4. In the other half of blocks, the secondary task was a difficult task that consisted of two semantic judgments to an auditory word. In the difficult secondary task, participants were asked to count both living things and outdoor things that they heard from the series of auditory words.

Fernandes and Moscovitch (2000) suggested that during retrieval, memory competes with a concurrent task that shares similar representational systems. Therefore, the overall memory performance costs under DA condition in Experiment 4 is suggested to reflect that retrieval of a recent episodic memory also includes the process of retrieving semantic features of an event. If more than one semantic judgment is made concurrently during retrieval, more neocortical resources will be shared with the concurrent task, which should lead to more interference with retrieval of a memory trace. If the effect in Experiment 4 is reliable it should be replicated in the easy DA condition of Experiment 5. The more difficult secondary task might cause a more dramatic decrease in memory performance due to the larger interference with retrieval. If the larger interference causes less opportunity to engage compensatory processes during retrieval for poorer memory representations, then the poor memory representations should be impaired more than the stronger memory representations that are encoded by better preparation. If the compensation hypothesis is able to explain the relationship between the preparatory processes for memory encoding and the overall memory performance, the overall memory performance in Experiment 5 should show an enhancement for the pictures from longer preparation time conditions compared to short preparation time conditions regardless of difficulty of a secondary task as in both cases less opportunity was available to engage compensatory processes during retrieval.

5.2.2 Methods

Participants. The experimental procedures were approved by the University College London Research Ethics Committee. 25 healthy adults were paid at a rate of £7.50/h to take part. One participant was excluded as the participant said 1/3 auditory words were too difficult to understand thus he got lost in the secondary tasks. Mean age of the remaining 24 participants was 22 years (range of 18 - 26 years) and 17 of them were female. They met all criteria described in Experiment 4.

Stimulus Material. Stimuli for memory task were the same as were used in Experiments 2 and 3. Stimuli for the secondary task consisted of 528 words (concrete nouns, 3 – 12 letters, Kučera-Francis written frequency: 1 – 431 per million (Kučera & Francis, 1967)). Six sets of 84 words were pseudo-randomly selected to create a secondary test list. 208 words pertain to living things. The remaining 24 filler items were used for practice. 7 filler words pertain to living things. The words were pre-checked to ensure that no word was presented with the identical greyscale photo of objects.

Stimulus presentations were the same as in Experiment 4. During the test phase, the procedure was generally the same as in Experiment 4 except that participants were asked to listen to an auditory word while doing the confident recognition memory test to each picture in all six blocks. The auditory word was presented at the same time as the picture was presented. The recordings were generated by AT&T Natural Voices (AT&T Labs, Inc. – Research) in British adult male voice and the mean duration was 994 ms. Other details were the same as in Experiment 4.

Procedure. The experimental procedure was generally the same as in Experiment 4. In the test phase of Experiment 5, pictures that were presented in the study phase appeared again along with new pictures (Figure 41). Each test picture was presented with an auditory word in all 6 blocks. Participants were asked to count how many living things that they heard through 3 out of 6 blocks. In the other half blocks, participants needed to count both living things and outdoor things. They were asked their answers at the end of each block. Half of the participants started with a block with the secondary task of only counting living things while half of the participants started with a block with the secondary task of counting both living and outdoor things. A block with only one counting secondary task always followed a block with two counting secondary task. The instructions about which secondary task to do were presented before each block. Other details of the procedure were the same as in Experiment 4.

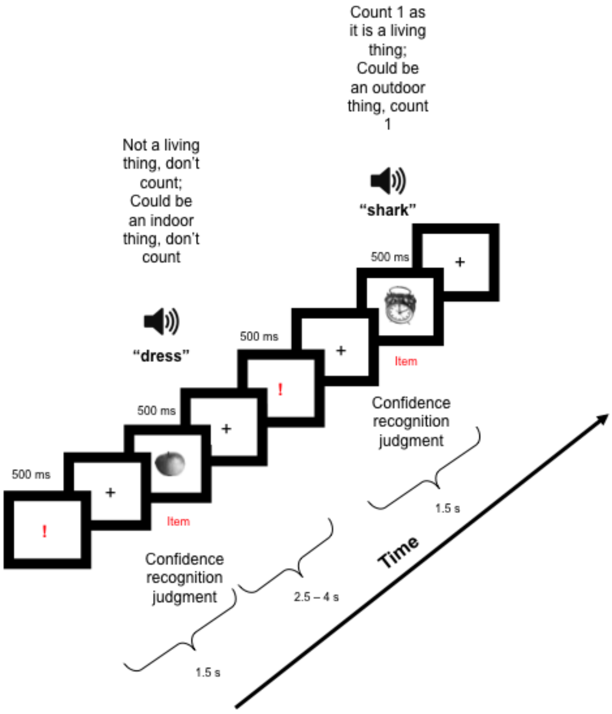


Figure 41. An example series of the block with the secondary task of 2 counting tasks in test phase in Experiment 5

5.2.3 Results

Study. Performance for the study phase is summarized in Table 30. The analyses were done by the same way as were done in Experiments 2 and 4. An ANOVA was used with repeated measure factors of amount of advance information (informative, non-informative) and amount of preparation time (short 1.5s, long 3s). No significant difference was found between either amount of advance information or amount of preparation time (all *p*s > 0.1). Reaction times for the size judgment task were also categorised by subsequent memory performance. 'Confident old' and 'unconfident old' judgments were collapsed into 'recognised' category and 'confident new' and 'unconfident new' judgments were collapsed into 'forgotten' category to be consistent with Experiments 2 and 4. No significant difference was found between later recognised and forgotten judgments (all *p*s > 0.3).

Table 30. Study task performance in Experiment 5

		Predictable short	Predictable long	Unpredictable short	Unpredictable long
Accuracy	M	0.84	0.84	0.85	0.85
(proportion)	SD	0.05	0.07	0.06	0.04
Response	M	820	838	834	838
times (ms)	SD	140	149	152	140

Values are across-subject means. n=24.

Secondary task. The mean accuracy proportion of the easy secondary task (animacy counting only) was 0.86 (range: 0.66 – 0.97). The mean accuracy proportion of the animacy counting task in the difficult secondary task was 0.85 (range: 0.72 – 0.98). The accuracy proportion of the outdoor things counting was not considered due to the nature of too many subjective judgments on the indoor/outdoor task. There was no significant difference between the accuracy proportion of the animacy counting tasks in the easy and difficult tasks, $t(23) = 0.366$, $p = 0.718$.

An ANOVA was done to compare the performance for the animacy counting task in Experiment 4, the easy condition of Experiment 5 and the difficult condition of Experiment 5 to see if the performance varies in the condition of different experiments. A main effect of condition was found after Greenhouse-Geisser correction, $F(1.917, 42.172) = 4.834$, $p = 0.014$. Pairwise comparisons showed that no difference between the performance for the animacy counting task in the easy condition in Experiment 5 and the animacy counting task in Experiment 4 was found. A significant difference was found between the accuracy proportion of the animacy counting task in the difficult condition in Experiment 5 and the animacy counting task in Experiment 4, $p = 0.013$. This finding suggests that the condition of the animacy counting task in Experiment 5 might be more difficult than the condition of the animacy counting task in Experiment 4 especially when the other semantic judgments were needed to be made.

Recognition test. Recognition memory performance is summarized in Table 31 and 32. Pr and Br for collapsed confident and unconfident responses were analysed with

ANOVAs with repeated measure factors of amount of advance information (informative, non-informative), amount of preparation time (short 1.5 s, long 3s) and secondary task difficulty during retrieval (easy, difficult). The ANOVA showed a main effect of secondary task difficulty for Pr, $F(1, 23) = 12.603$, $p = 0.002$. The Pr in the difficulty secondary task condition was significantly lower than the Pr in the easy secondary task condition. Although compared to short preparation time conditions, long preparation time conditions showed slight memory enhancement in Pr regardless of secondary task difficulty, statistically this enhancement was not significant, $F(1, 23) = 2.328$, $p = 0.141$.

Surprisingly, significant interactions were found between amount of advance information and secondary task difficulty for both Pr and Br, Pr, $F(1, 23) = 7.048$ and 7.946, respectively, $p = 0.014$ and 0.010. Subsidiary analyses were done for easy and difficult conditions separately to understand the interaction. In the easy condition, both Pr and Br for the unpredictable cue conditions were significantly higher than the Pr and Br for the predictable cue conditions, irrespective of amount of preparation time, Pr, $F(1, 23) = 6.287$ and 6.990, respectively, $p = 0.02$ and 0.015 (see Figure 40). No effect of amount of advance information was found in the difficult condition, although the Pr and Br for the predictable cue conditions were slightly higher than those in the unpredictable conditions. When subsidiary analyses were done for predictable cue conditions and unpredictable cue conditions individually, significant effects of secondary task difficulty were found for Pr in both degrees of cue predictability (predictable, $F(1, 23) = 5.326$, $p = 0.030$, unpredictable, $F(1, 23) = 17.557$, $p < 0.001$), which suggests that although the unpredictable cue conditions showed memory enhancement in Pr in the easy secondary task condition, the ability to discriminate old and new items was also impaired by the difficult secondary task. For confident hits, the discriminations between old and new items were significantly greater than zero, all p values ≤ 0.001.

Another ANOVA with same factors was performed for the reaction times when collapsing reaction times for confident and unconfident hits. A main effect of secondary task difficulty was found, $F(1, 23) = 52.127$, $p < 0.001$. Reaction times for confident old and unconfident old responses were significantly slower in the difficult condition than in the easy condition. No significant interactions were found for reaction times.

Between-experiments comparisons. ANOVAs with a between-subjects factor of experiment (Experiment 4, Experiment 5) were done to understand the similarity and difference in the two experiments. First, no any significant difference was found for the study phase across two experiments. Second, the ANOVAs were done to compare memory performance in the animacy counting task condition in both experiments. Main effects of amount of advance information in both Pr and Br were found across the two experiments, $F(1, 46) = 9.741$ and 7.211, respectively, $p = 0.003$ and 0.010.Pr and Br were significantly larger in the unpredictable than predictable cue conditions across the two experiments. A significant interaction between amount of preparation time and experiment in reaction times for collapsing confident and unconfident old judgments were also found, $F(1, 46) = 6.918$, $p = 0.012$, which suggests that reaction time cost on long preparation time conditions was only found in Experiment 4.

Table 31. Mean proportion of recognition memory responses in Experiment 5

Condition			Recognition Type			
			Confident old	Unconfident old	Unconfident new	Confident New
Easy	Informative cue	short	0.58 (0.15)	0.20 (0.13)	0.13 (0.09)	0.09 (0.09)
		long	0.59 (0.17)	0.19 (0.13)	0.13 (0.08)	0.09 (0.10)
	Non-informative cue	short	0.63 (0.17)	0.18 (0.13)	0.12 (0.08)	0.08 (0.09)
		long	0.63 (0.18)	0.18 (0.15)	0.12 (0.08)	0.08 (0.07)
	New		0.11 (0.10)	0.13 (0.09)	0.35 (0.18)	0.41 (0.23)
Difficult	Informative cue	short	0.56 (0.19)	0.19 (0.18)	0.14 (0.09)	0.09 (0.12)
		long	0.55 (0.17)	0.22 (0.20)	0.10 (0.08)	0.11 (0.17)
	Non-informative cue	short	0.53 (0.20)	0.20 (0.18)	0.13 (0.11)	0.11 (0.14)
		long	0.55 (0.19)	0.20 (0.17)	0.13 (0.11)	0.09 (0.12)
	New		0.13 (0.13)	0.14 (0.12)	0.33 (0.23)	0.37 (0.23)

Values are across-subject means (SD). n=24.

Table 32. Mean RTs (ms) for collapsing confident and unconfident hits in Experiment 5

Easy				Difficult			
Informative cue		Non-informative cue		Informative cue		Non-informative cue	
short	long	short	long	short	long	short	long
1302 (232)	1484 (304)	1274 (217)	1451 (280)	1281 (228)	1449 (274)	1262 (221)	1443 (294)

Values are across-subject means (SD). n=24.

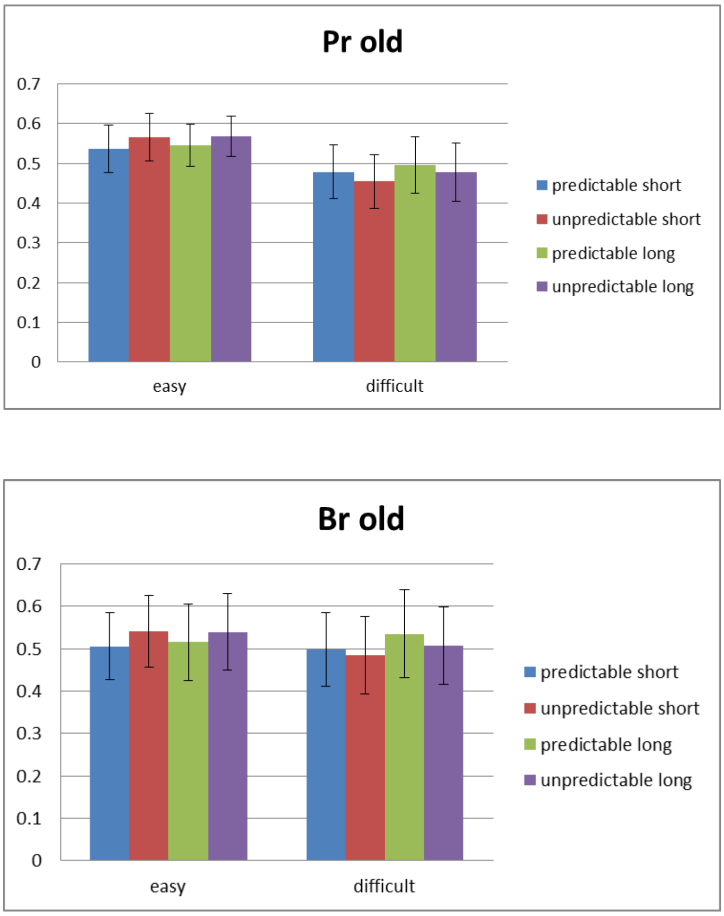


Figure 42. Pr and Br for confident and unconfident responses in each cue condition under easy and difficult conditions during retrieval.

5.2.4 Discussion

The current experiment further addressed the relationship between preparatory processes for long-term memory encoding and overall memory performance by manipulating the degree to which processing resources are available to engage compensatory processes during retrieval. Participants prepared for encoding a picture over a short time (1.5 s) or long time (3 s). Informative cues signalled the amount of preparation time while non-informative cues did not signal whether the preparation time was short or long. In test phase, participants were asked to do a recognition test concurrently with counting how many living things were there in a series of auditory words, which was the easy secondary task condition. In the difficult secondary task condition, participants were asked to count both living things and outdoor things while doing the recognition test. The results in the easy secondary task condition did not replicate the findings from Experiment 4. Pictures from the non-informative cue conditions rather than the long preparation time conditions showed memory enhancement. In the difficult secondary task, overall memory performance was impaired in all the cue conditions. Neither of the cue conditions showed memory enhancement. Again, only the discrimination index (Pr) was affected by the secondary task condition. The bias index (Br) was not affected, which suggests that the findings cannot be explained by changes in criteria between the easy and difficult task conditions. Br only differed within secondary task condition, with false alarms remaining the same. This indicates that the significant differences were caused by differences in hit rates across encoding conditions.

One possible explanation for the null finding is that the auditory stimulus material was different from the one used in Experiment 4. The auditory words used for the secondary task in Experiment 5 were generated by software that could morph human’s voices. Participants might need to get used to the non-human voices. The difficult secondary task performance did not differ from the easy secondary task performance within Experiment 5 but was significantly worse than the secondary task performance in Experiment 4, which might suggest that the synthesised voices caused difficulty to recognise the words. This is more like a perceptual rather than semantic interference to the main recognition test. Compared to the secondary task in Experiment 4, the secondary task in Experiment 5 might increase the degree of conflict in the perceptual processing resources between the reactivation of a memory trace and the understanding of an auditory word.

In addition, the findings from Experiment 4 might not reflect reliable effects. The between-experiments analyses suggest that no difference in reaction times for the recognition tests between Experiments 4 and 5 was found. This might mean that the recognition test in Experiment 5 did not cost more processing resources. The difficulty for doing a recognition test and an animacy counting task concurrently was not affected by the synthesised voices. The significant interaction in reaction times between amount of preparation time and experiment suggests that the memory advantages from longer preparation time conditions in Experiment 4 might be attributed to a trade-off between recognition accuracy and reaction time. Surprisingly, recognition memory accuracy was consistently better for the pictures from the non-informative cue conditions across the two experiments. One possible explanation is that unpredictability of preparation time might raise participants' attention levels. As discussed in sections 3.2.4 and 4.2.4, participants might treat a non-informative cue the same as a predictable short cue before 1.5 s elapsed. Some of the participants also reported that they were more alert when they saw the 'N' cues. This might lead to more attention to upcoming pictures following 'N' cues, which results in stronger memory representations that might show memory enhancement when the engagement of compensatory processes was prevented by a secondary task. However, if this is true, the reaction times for the encoding task (size judgment task) in the non-informative conditions should be significantly faster, which was not shown in either Experiments 4 or 5.

The von Restorff effect (von Restorff, 1933) suggests that a distinctive stimulus can be memorised better than other stimuli. A distinctive stimulus usually means a salient stimulus that is unpredictable from its context. If an unpredictable cue preparatory interval before an event could make the event more distinctive from the events after a predictable preparatory interval, then the event might be more likely to be remembered even when less opportunity was available to engage compensatory processes in retrieval. However, the von Restorff effect emphasised the perceptual distinctiveness of a stimulus and some studies suggest that this effect was only found in shallow levels of encoding not deep encoding (Fabiani et al., 1990). Therefore, the effect from the non-informative cue conditions in Experiment 5 cannot simply be accounted for by the von Restorff effect.

The ERP findings in Experiment 2 suggest that even when a cue was less informative, preparatory processes are able to be engaged for encoding. In the oscillatory analyses in Experiment 2, the contrast was focused on confident hits and forgotten. A larger encoding-related theta and alpha desynchronisation was found right before picture onset when a preparatory interval was long and unpredictable. A larger encoding-related alpha synchronisation was found before 1.5 s in the non-informative cue conditions. Such alpha synchronisation was also found in a predictable short preparatory interval. The findings suggest that preparatory mechanisms in the non-informative cue conditions resemble the preparatory mechanisms for a short preparatory period before 1.5 s, which might be associated with preparation for encoding stimulus-related information (Fell et al., 2011). When 1.5 s elapsed, preparatory processes for encoding more information were engaged (Hanslmayr et al., 2012). The recognition accuracy for confident responses were consistent with collapsing confident and unconfident responses in Experiment 5, which suggests that the engagement of oscillatory preparatory activity in encoding after an unpredictable preparatory interval might lead to encoding a stronger memory representation.

Nevertheless, if the stronger memory representations that were encoded after unpredictable preparatory intervals can show evident memory enhancement when the engagement of compensatory processes were prevented by an easy secondary task in retrieval, memory advantages should be more evident when more processing resources were deprived by a difficult secondary task in retrieval. That was not the case in Experiment 5. Moreover, the memory performance in the informative cue conditions was slightly better although it was not statistically significant, which is consistent with previous studies (Bollinger et al., 2010; Summerfield & Mangels, 2006; Uncapher et al., 2011) that predictable cues enhance memory encoding by top-down preparation. However, no consistent findings across Experiments 4 and 5 suggest that the effects might be vulnerable and varied by certain conditions such as a trade-off between RTs and recognition memory accuracy.

In conclusion, Experiment 5 did not replicate the findings from Experiment 4. Pictures from unpredictable cue conditions, rather than long preparation time conditions were more likely to be recognised when an easy secondary task interfered with retrieval processes. Overall memory performance costs were found in the difficult secondary task condition but no memory advantages were shown in any cue conditions. The findings suggest the memory enhancement found when less processing resources were available in retrieval processes might be unreliable and varied by experimental conditions. Whether the role of compensatory processes during retrieval can explain the relationship between preparatory processes for memory encoding and overall memory performance is still not clear. Recording neural activity during preparation for memory encoding might be able to help understand the role of compensatory processes during retrieval. If pre-stimulus subsequent memory effects and memory enhancement when a secondary task interfere with retrieval processes are both found, the conclusion would be thus preparatory processes support encoding a stronger memory representation that is not influenced by less opportunity to engage compensatory processes during retrieval.

Chapter 6: General Discussion

Increasing numbers of studies support the idea that not only brain activity after an event, but also activity before an event, is important for memory encoding. Previous studies on investigating the functional roles of encoding-related pre-stimulus activity have focused on how the type of advance information influences pre-stimulus encoding-related activity (e.g. Galli et al., 2011; 2014; Gruber & Otten, 2010; Gruber et al., 2013; Otten et al., 2006; 2010). This doctoral thesis addressed the question of how the amount of advance information influences pre-stimulus encoding-related activity. The General Discussion section will summarise the findings of all experiments and place them into broader context with the literature. Then the implications of the findings will be discussed. The section will close with a discussion of possible future research.

6.1 Summary and broader context of the findings

6.1.1 Is pre-stimulus encoding-related activity influenced by amount of advance information?

In the first three experiments, scalp EEG was recorded while participants performed incidental encoding tasks. Amount of perceptual details of an object was manipulated. Informative cues indicated the amount of perceptual information about an upcoming picture of the object. A photo cue signalled presentation of a detailed photograph. An outline cue indicated an upcoming picture was a perceptually impoverished outline. A non-informative cue was followed by either a photo or an outline. In Experiment 1, the research question was whether encoding-related pre-stimulus activity is influenced by the amount of information to be prepared. It was expected that perceptual preparation would increase when a picture with more perceptual details was cued. Thus, pre-stimulus encoding-related activity might also be graded depending on the degree of perceptual preparation. Event-related potentials elicited by cues predicted later memory success but did not differ according to advance information provided by cues. This suggests that, at least based on the current study, there is insufficient evidence demonstrating that pre-stimulus encoding-related activity is influenced by advance information about the physical form of a picture. However, a positive-going pre-stimulus subsequent memory effect was found regardless of cue conditions. Pre-stimulus activity seemed to enhance memory encoding no matter how much advance information was available. Such widespread positive-going pre-stimulus subsequent memory effects were also shown in previous studies using monetary rewards and advance information about the valence of a picture scene (Galli et al., 2011; Gruber & Otten, 2010). The positive-going pre-stimulus encoding-related activity is suggested to reflect motivational processes, which means such pre-stimulus activity can be flexibly and strategically used to benefit encoding of an upcoming event (Gruber & Otten, 2010). Engagement of the positive-going pre-stimulus activity may reflect that participants actively prepared for the encoding of an upcoming picture. However, the absence of a significant interaction between the pre-stimulus subsequent memory effect and cue condition suggests that the pre-stimulus activity might not be influenced by the amount of perceptual information to be prepared. This argues against the idea that positive-going pre-stimulus activity is under strategic control.

An informative cue that indicates the category of an upcoming object (e.g. faces or scenes) guides expectation and elicits pre-stimulus activation in corresponding sensory areas such as the fusiform face area (FFA) (Bollinger et al., 2010; Driver & Frith, 2000). In long-term memory domain, Bollinger et al. (2010) showed that pre-stimulus functional connectivity between FFA and medial frontal gyrus was positively correlated with subsequent long-term memory performance only when a face was predictable to be seen. If such baseline shifts in sensory cortex can influence long-term memory encoding, then expectation to an object might also be able to pre-active sensory cortex to support encoding for the object. In Experiment 1, participants always expected to see a picture of an object no matter how much perceptual details were in the picture. Kourtz and Kanwisher (2000) suggest that the activity in the occipital cortex did not differ in shape processing of an object between greyscale photo and line drawing formats. This could be one of the reasons why encoding-related activity prior to a picture did not differ in the amount of perceptual details to be expected. Perceptual preparation associated with primary visual areas might be similar for photographs and outlines. Such preparation might help encoding for an object but might not influence encoding-related pre-stimulus activity as the neural correlates of processing the structure of an object do not differ in the physical form of the object.

The findings from post-stimulus encoding-related activity also support this notion. Post-stimulus subsequent memory effects in Experiment 1 did not differ in the physical form of pictures, which suggest that encoding processes on an object might be independent of the amount of perceptual information. Alternatively, the post-stimulus subsequent memory effects for the photos and outlines were both frontally distributed, which resembles the effect for verbal material in semantic encoding condition (e.g. Otten & Rugg, 2001). As discussed in Section 3.1.4, the post-stimulus subsequent memory effects in Experiment 1 reflect that the encoding processes for photos and outlines might depend on the meaning of the object portrayed in the image. If more perceptual processes were involved, the subsequent memory effects might be more over posterior scalp distribution (Gonsalves & Paller, 2000). The encoding processes for photos and outlines might differ if more perceptual processes are involved as photos are associated with more perceptual details than outlines. Therefore, an encoding task that stresses the processing of perceptual details or a memory test incorporated recollection of perceptual details may influence the engagement of perceptual processes during encoding. In both cases, encoding-related activity may differ in amount of perceptual information. Accordingly, preparatory activity for encoding may also differ in the amount of perceptual information to be prepared.

Another possible reason for the lack of differences of pre-stimulus encoding-related activity in amount of perceptual information to be prepared is that there was no need to switch between cue types. As discussed above, participants expected to see an object all the time even in a non-informative cue condition. The post-experiment questionnaires showed that fifteen participants treated all three kinds of cues the same while nine participants prepared differently according to the cue information. This variability was also shown in the grand average waveforms. The ‘prepared’ group showed a larger and earlier subsequent memory effect in the photo cue condition, which suggests that encoding-related pre-stimulus activity might be influenced by the degree of perceptual preparation. The ‘non-prepared’ group showed a smaller and later pre-stimulus subsequent memory effect in the photo cue condition, which might mainly contribute to the absence of interaction between pre-stimulus subsequent memory effect and cue condition. The individual differences in the pre-stimulus activity might suggest that the engagement of such activity is under strategic control. However, the low number of subjects made it difficult to investigate this idea statistically. Collapsing the two groups did not reveal a significant interaction between pre-stimulus subsequent memory effect and amount of perceptual information, which might only reflect general preparatory signals in both groups that are not specific to strategic control (Haynes et al., 2007).

Experiment 1 raises a question about the amount of what kind of advance information can influence encoding-related preparatory activity. Experiment 2 aimed to answer whether advance information about amount of preparation time available before an event influences pre-stimulus encoding-related activity. In Experiment 2, informative cues indicated the amount of preparation time available before a greyscale photo. A short cue meant 1.5 s was available for preparation before the photo. A long cue signalled a 3 s preparation time before photo onset. Non-informative cues were followed by either a 1.5 s or a 3 s preparation time. Positive-going pre-stimulus subsequent memory effects were shown again, but only after 1.5 s and when preparation times were 3 s regardless of the amount of advance information. In an early time window after 1.5 s, the positive-going pre-stimulus subsequent memory effect was over frontal scalp sites when the cue was informative and over posterior scalp sites when the cue was non-informative. The pre-stimulus subsequent memory effects did not differ in the amount of advance information around 1 s before picture onset. The effect was widespread over the scalp, which resembled the positive-going pre-stimulus ERP effects found in Experiment 1 and previous studies using reward and emotional valence cues (Galli et al., 2011; 2012; Gruber & Otten, 2010). The findings suggest that the engagement of the pre-stimulus activity in preparing for memory encoding might not only depend on voluntary or emotional control but also depend on the opportunity to engage such activity.

Previous studies on how temporal expectation modulates attention suggest that predictability of a cue optimises behaviour and brain activity only when the cue interval is short (Zanto et al., 2011; Miniussi et al., 1999). In an unpredictable cue condition, participants will know how much time to expect until stimulus onset when the short time elapses. In that case, an informative cue that indicates a long interval cannot benefit performance or neural activity as there is no need to use the cue information (Miniussi et al., 1999). Compared to simple detection tasks used in attention research, the encoding task in Experiment 2 was a semantic judgment that required deep processing of a target. Preparing for such task might take more time, which makes the predictability to be important for a long interval as well. In an unpredictable condition, participants had to re-focus their attention if no target was presented after a short interval, which might affect later performance on semantic tasks. It is worth noting that although behaviourally task performance for predictable conditions was significantly faster than unpredictable conditions regardless of cue lengths, no pre-stimulus encoding-related activity was found in the predictable short condition. This suggests that the engagement of pre-stimulus encoding-related activity does not depend on how easy that attention can be directed to a target, but whether there is an opportunity for the engagement of the pre-stimulus activity before encoding. This could also link to the findings in Experiment 1 that there might be insufficient opportunity (i.e. time) to establish pre-stimulus activity for encoding a photo of an object, which resulted in a pre-stimulus subsequent memory effect that did not differ in the degree of perceptual preparation.

Although overall pre-stimulus activity in the long preparation time conditions showed a slow negative deflection before picture onset, the encoding-related pre-stimulus activity could not be explained by CNV. Magnitude of CNV amplitudes are often linked with reaction times on targets. The more negative the CNV is, the faster the reaction times for the targets are (Brunia & Vingerhoets, 1980; Hillyard, 1969). The pre-stimulus subsequent memory effects in Experiment 2 were positive-going, which means the more negative the amplitudes were, the more likely items were forgotten. Reaction times for the semantic encoding task differed between subsequently remembered and forgotten judgments. Reaction times for pictures subsequently remembered were significantly faster than reaction times for subsequently forgotten pictures. This indirectly suggests that the more negative the amplitudes were the slower reaction times were. CNV is a component that reflects attention and motor preparation for an upcoming stimulus. The pre-stimulus activity in Experiment 2 might reflect strategic control processes by using advance information. First, it resembled the positive-going pre-stimulus subsequent memory effects found to be related to motivational processes (Galli et al., 2011; 2012; Gruber & Otten, 2010). Second, such effects were only evident when preparation times were 3 s but not 1.5 s. Third, the different scalp distribution in the early effects between the predictable long and the unpredictable long conditions suggests that participants could flexibly engage the preparatory mechanisms in memory encoding by using the advance information.

Interestingly, the amount of advance information even influenced post-stimulus encoding-related activity. Although 1.5 s was not sufficient to establish pre-stimulus encoding-related activity, earlier post-stimulus subsequent memory effects were found to be more widespread over the scalp in predictable conditions regardless of the amount of preparation time. As mentioned in Chapter 1, earlier subsequent memory effect was found when an incidental but deep encoding task was utilised compared to intentional encoding without a consistent encoding strategy (Fabiani et al., 1990; Friedman, 1990; Karis et al., 1984; Munte et al; 1988; Paller, 1990). Informative cues might help to direct attention to an upcoming stimulus and get ready for the deep encoding task quicker. In conclusion, advance information about amount of preparation time before stimulus onset guides preparation for optimising later behaviour and post-stimulus encoding-related activity. Engagement of pre-stimulus encoding-related activity depends on the opportunity before an event and is under strategic control by using the advance information.

In Experiment 3, it was asked whether a brain state conducive to effective encoding could be induced by asking participants to prepare for a delayed match-to-sample task involving the hippocampus. Experiment 2 showed that preparation for encoding a new picture needed sufficient time. Such sustained pre-stimulus activity may reflect a brain state related to successful encoding (Fernández et al., 1999; Otten et al., 2002; Yoo et al., 2012). Such pre-stimulus activity could benefit memory encoding on a trial-by-trial basis when participants adjust their strategies of preparation according to advance information. In Experiment 3, the advance information was what kind of DMS task participants needed to do. One task was remembering three object-location conjunctions after 3 s delay. Olson et al. (2006) suggested that this task crucially depends on the hippocampus. The other task was remembering three locations after 3 s delay, which they (Olson et al., 2006) claimed does not involve the hippocampus. The hippocampus is also crucial for episodic memory encoding (Wagner et al., 1999). Therefore, brain activity during the conjunction task may also support episodic encoding. The advance information about the two tasks was used to aim to induce preparatory brain states that involved different degrees of episodic encoding. ERP waveforms were more positive-going over frontal scalp sites prior to the conjunction task compared to the feature task. In addition, this preparatory activity for the DMS tasks enhanced recognition memory performance for probes inserted 3 s into the preparatory phase. The probes also elicited larger retrieval-related activity over frontocentral scalp sites over an extended time period. The findings suggest that advance information about a DMS task can lead to a preparatory brain state conducive to efficient memory formation. Memory can be enhanced by asking individuals to prepare for a task involving the binding of multiple types of information.

Although it is still not clear about whether preparation for a conjunction task activated the hippocampus more than a feature task, the positive-going preparatory activity for the conjunction task had a similar polarity as pre-stimulus encoding-related activity found in Experiments 1 and 2 and previous studies using monetary cues and valence cues (Galli et al., 2011; 2014; Gruber & Otten, 2010). Further, pre-stimulus activity in the anterior hippocampus predicts successful memory formation when cues signalled the higher reward to a remembered word or cues signalled a presentation of an upcoming negative picture (Adcock et al., 2006; Mackiewicz et al., 2006). Considering that similar paradigm was used in the fMRI studies as was used in the ERP studies, it can be inferred that the positive-going pre-stimulus encoding-related activity might have some relationship with the hippocampal networks. Hence, positive-going preparatory activity prior to the conjunction task might be a neural predictor for more efficient episodic encoding. Memory performance was therefore better for the probes inserted after such activity.

However, encoding-related activity for the probes at study was larger in the feature than conjunction condition. The LTM probes from the feature condition rather than the conjunction condition elicited larger and earlier encoding-related activity, which was contrary to the idea that preparation for the conjunction task enhances memory encoding processes. The behavioural performance for the DMS tasks showed that the conjunction task was significantly more difficult than the feature task, which suggests that preparation for a conjunction task might need more processing resources than a feature task. The engagement of encoding-related activity might compete more with preparatory processes for the conjunction task. Encoding-related activity is suggested to be smaller when processing resources are not sufficient (e.g. Galli et al., 2013; Mangels et al., 2001). This might be one of the possible reasons why encoding-related activity for the LTM probes from the conjunction condition was smaller than the feature condition.

Another possible reason why smaller encoding-related pre-stimulus activity was shown for the probes before the conjunction task may be that the pre-stimulus activity in the conjunction condition might be more sensitive to recollection judgments than collapsing recollection and know judgments. The pre-stimulus activity found in the hippocampus was sensitive to recollection (Park & Rugg, 2010). The preparation for the conjunction task aimed to activate the hippocampus to induce an episodic brain state. In addition, the retrieval-related activity elicited by the probes in the conjunction condition was larger than the activity elicited by the probes in the location condition. The difference in the retrieval-related activity between the conjunction condition and the feature condition was positively correlated with numbers of recollection judgments from the conjunction condition across subjects. This means when participants' retrieval-related activity from the conjunction condition was larger than the activity from the feature condition, the more the difference was, the more recollection judgments were that a participant made for the probes from the conjunction condition. The retrieval-related activity elicited by the probes from the conjunction condition might be associated with episodic retrieval, which supports the idea that the probes inserted into a preparatory phase for a conjunction task was encoded in a better episodic brain state. Unfortunately, there were not enough trials to look at recollection-related activity during encoding and retrieval separately. Therefore it is difficult to give an answer to whether the brain state induced by preparation for a conjunction task is only sensitive to recollection.

Another reason why memory performance was better for the probes before the conjunction task but encoding-related activity was smaller could be that the episodic brain state might not only be activated during the preparatory phase but also during the DMS task. The involvement of the hippocampal activity was observed in an fMRI study only when maintaining a conjunction of object and location but not an individual feature (Piekema et al., 2006). This suggests that in a conjunction task, the activity during retention might also play a role in supporting more efficient episodic encoding. One future direction could be analysing the data during the maintenance period of DMS tasks to see if there is any difference between a conjunction task and a location task and whether this difference has the same polarity as the preparatory activity.

The aim of Experiment 3 was to generate a brain state conducive of episodic encoding by asking participants to prepare to perform a task involving the hippocampus. The inverse problem of EEG makes it unclear whether the preparatory processes indeed involve the hippocampus. It is possible that the overall preparatory activity elicited by conjunction cues reflect overall higher level of attention caused by the difficulty of the task. As discussed above, both reaction time and the encoding-related activity suggest that the conjunction task was more difficult and resource consuming than the feature task. However, a raised overall attention level due to higher level of difficulty cannot explain the enhanced memory performance for the conjunction task. If difficulty level influences the efficiency of episodic information encoding, memory performance should be better when difficulty level is higher. However, a positive correlation was found between reaction time for the conjunction task and memory performance across participants in Experiment 3. The faster decisions were made during the conjunction task, the better memory performance was for the probes in the conjunction task. This finding suggests that the preparatory processes for the conjunction task might not compete with the simultaneous encoding processes for the probes. In contrast, the benefits of preparation for the conjunction task could also enhance encoding for incidental information inserted into the preparatory phase. Instead of prioritising attentional resources and compromising preparation for the DMS task, encoding and task preparation more likely take advantage of similar underlying processes.

Nevertheless, the probability that the overall preparatory activity reflects preparation for the different difficulty levels exists. First, reaction times for the encoding tasks under different cue conditions did show that when less perceptual or advance information was available, decisions for the encoding tasks were more difficult. Second, overall preparatory activity irrespective of memory performance showed larger attention-related effects for the more difficult cue conditions. It might be tempting to conclude that the overall preparatory processes reflect different levels of difficulty rather than cognitive control processes. However, it should be noted that difficulty level did not affect encoding-related preparatory processes. Encoding-related pre-stimulus oscillatory activity was graded by the amount of information available to prepare for encoding. Both pre-stimulus ERP and oscillatory activity were engaged in supporting effective memory formation depending on the amount of preparation time. It was not the most difficult condition, but the condition that was needed most, elicited the largest encoding-related pre-stimulus activity. Although the findings from Experiment 3 might in part reflect difficulty levels, the main aim was to induce a brain state for efficient episodic memory encoding by preparing for an ongoing task involving similar elements as episodic memory formation. Such preparatory processes might include attentional processes caused by estimation of the difficulty level. However, the encoding processes given to inserted incidental information may not be separable from ongoing preparatory processes. In combination, they may affect encoding efficacy. This is not in contradiction to the hypothesis that preparation for tasks of involving binding of information induces a brain state conducive to episodic encodings.

In addition, in Experiment 3 larger encoding-related activity was elicited by probes from the feature condition, but memory was better for probes from the conjunction condition. This might indicate that state-related activity supports episodic memory encoding in a way that is opposite to how item-related activity supports efficient memory encoding. Otten et al. (2002) found an overlap between item-related activity and state-related activity supporting later memory in inferior prefrontal cortex with opposite patterns of effect. The transient item-related activity was larger when subsequent memory was better, while the sustained state-related activity was negatively correlated with successful memory. This suggests that the two kinds of brain activity might reflect a competition or trade-off between each other. In Experiment 3, it was unfortunately not possible to look at sustained overall preparatory activity depending on subsequent memory performance because too many artefacts occurred in the 5 s epoch. Overall preparatory activity irrespective of subsequent memory performance was larger for the conjunction task than feature task over frontal scalp sites. However, robust positive-going encoding-related activity was observed for probes from the feature condition. In contrast, encoding-related activity was smaller or even of opposite polarity for probes from the conjunction condition. If the overall preparatory activity elicited by conjunction cues reflect better episodic encoding, then the item-related activity should be larger when the item is subsequently remembered. The overall preparatory activity for the conjunction task might reflect preparation for combining an object with its location. Such preparation might help to bind the incidental probe with the contextual information, which is important for episodic memory formation. The item-related activity might reflect both item-specific encoding and item-context binding. The reduced item-related activity might reflect that item-context binding processes were replaced by preparatory processes for the conjunction task. Although the number of remember judgments did not differ across DMS task conditions, the magnitude of retrieval-related activity that reflects recollection positively correlated with the number of remember judgments for probes from the conjunction condition. This supports the idea that a preparatory brain state for combining information may enhance episodic encoding for incidental information presented during that state.

Preparatory brain states are found in many other cognitive domains including attention, memory retrieval, and task switching. For example, Düzel et al. (1999) used DC recordings to show that EEG activity was more positive-going over right frontal scalp sites when participants tried to retrieve episodic information about an item relative to when participants tried to retrieve semantic information about an item. The changes were slow and developed in a 10 s epoch. This slow task-related activity was suggested to reflect a retrieval mode, a cognitive set when someone attempts to remember episodic information that happened before or episodic information that might not have happened (Tulving, 2002). The term “retrieval mode” stresses two points. First, retrieval mode refers to episodic retrieval in contrast to episodic encoding or other kinds of retrieval (e.g. semantic retrieval). Second, retrieval mode can happen whether or not information is successfully retrieved. Therefore, the brain areas that define retrieval mode do not have to overlap with the brain areas that are activated by retrieval success (Donaldson, Petersen, Ollinger, & Buckner, 2001). The task-related preparatory activity found in Experiment 3 might reflect a similar cognitive set of “encoding mode”. Such an encoding mode might be a cognitive set when episodic information is attempted to be encoded. Thus, such a mode can be elicited by preparation for episodic information such as an object and its associated location, even though the information is not necessary to be retrieved in the future. In addition, such a preparatory set might not have to relate with retrieval success. On this account, the reduced encoding-related activity for the probes from the conjunction condition might reflect that some item-non-specific episodic information might be encoded such that activity elicited by forgotten items does not differ much from activity elicited by remembered items.

It should be noted that regardless of encoding or retrieval, sustained state-related activity needs to be developed over a long period of time. Wilding and Nobre (2001) used two different retrieval tasks and manipulated whether the retrieval processes were in separate blocks or within the same blocks. They found that the task-related activity elicited by correct rejections differed significantly in retrieval tasks when the two tasks were separated by blocks. The finding suggests that maintaining a set of which specific information is retrieved (retrieval orientation) needs sufficient time. The findings from Experiment 2 suggest that the preparatory processes related to encoding success also depend on sufficient time. The encoding-related preparatory activity might in part reflect sustained control processes of task-switching. For example, the encoding-related pre-stimulus activity did not differ in the degree of perceptual preparation in Experiment 1, which might indicate that establishing a new preparatory mechanism for encoding different amounts of perceptual information might take too many resources compared to just maintaining similar preparatory processes across conditions. The findings in Experiment 2 demonstrated that developing preparatory activity for encoding perceptual details need more time and the 1.5 s used in Experiment 1 might not be sufficient. However, this idea cannot be directly tested by data in this doctoral thesis because there were insufficient numbers of trials that could be categorised into stay and switch conditions. Otten et al. (2010) demonstrated that the encoding-related preparatory processes for semantic encoding in both auditory and visual items can be set up flexibly on a trial-by-trial basis, and that these processes do not differ across stay and switch trials. Nevertheless, the data in this doctoral thesis cannot completely exclude the probability that control processes in task switching play a role in encoding-related preparatory processes for pictures.

Another possible interpretation of the preparatory mechanism is a baseline shift due to attentional set (Driver & Frith, 2000). This view suggests that background activity is enhanced in relevant sensory brain areas when a stimulus is expected. For example, if a face is expected, the brain areas related to face processing might be activated before the face is presented. This may help stimulus-related activity to be engaged more rapidly. Driver and Frith (2000) suggested that the baseline shifts serve as a template for a later target to be fitted in more efficiently. The encoding-related preparatory processes found in this doctoral thesis cannot merely be explained by attentional baseline shifts, however. First, if the encoding-related pre-stimulus activity reflects that a sensory target template is formed successfully before stimulus onset, the pre-stimulus activity should be maximal over posterior scalp sites. Second, the baseline shifts suggest that the background activity increases in relevant sensory areas to support later enhanced activity related to stimulus processing (Chawla, Rees, & Friston, 1999). Many studies of encoding-related pre-stimulus activity have demonstrated that pre-stimulus activity and post-stimulus activity are dissociable (Otten et al., 2006; 2010). In this doctoral thesis, the pre-stimulus activity and post-stimulus activity also did not necessarily occur at the same time to support efficient encoding. Additionally, enhanced post-stimulus encoding-related activity was found when encoding-related pre-stimulus activity was absent in Experiment 2, which more likely reflects compensatory mechanisms related to memory rather than attentional baseline shifts.

In conclusion, although there are remaining questions, the three experiments generally support that brain activity preceding an event could influence successful memory encoding. In Experiment 1, the preparatory activity did not differ in the amount of information to be prepared for encoding, which might reflect that preparatory signals were not specific to the preparatory processes or general preparation. In Experiment 2, the preparatory processes were only engaged in aiding successful memory encoding when sufficient preparation time was available. This suggests that such preparatory processes can be engaged strategically depending on the opportunity for the activity to support successful memory formation. In Experiment 3, a brain state conducive to efficient episodic memory encoding was built by preparing for an episodic DMS task. The preparatory activity for the episodic DMS task, in contrast with the preparatory activity for the non-episodic DMS task, resembled the positive-going pre-stimulus subsequent memory effect that reflects motivational processes. The engagement of such preparatory activity is also under strategic control depending on that participants used the pre-stimulus cue information to monitor the control.

6.1.2 Is pre-stimulus encoding-related theta and alpha activity influenced by amount of advance information?

Recently, a few studies have shown that pre-stimulus oscillatory brain activity can also predict later memory success. To investigate functional roles of the encoding-related pre-stimulus oscillatory brain activity, the EEG data from Experiments 1, 2 and 3 was re-analysed in the frequency domain. The analyses focused on power in oscillatory activity of lower frequency bands (theta, 4-8 Hz and alpha, 9-12 Hz). A consistent finding across three experiments is that decreases rather than increases in theta and alpha power were found before remembered pictures, in contrast to forgotten pictures. Such encoding-related desynchronisation in brain oscillations prior to an event was modulated by amount of advance information.

In Experiment 1, encoding-related theta and alpha desynchronisation was found after pictures, regardless of amount of perceptual information of a picture. Crucially, decreases in theta and alpha power predicted efficient memory encoding even before picture onset. However, the pre-stimulus encoding-related theta and alpha desynchronisation was shown only when a cue signalled a presentation of a perceptually rich photo. Surprisingly, such encoding-related desynchronisation was also found after non-informative cues. In Experiment 2, decreases in pre-stimulus theta power predicted later memory success before short cue intervals (1.5 s) elapsed only when cues were informative. In addition, larger pre-stimulus encoding-related theta desynchronisation was found when a cue indicated a long preparation time before 1.5 s. In the alpha frequency band, the pre-stimulus encoding-related desynchronisation before 1.5 s was only found when a cue signalled a long preparation time. After 1.5 s, decreases in both theta and alpha power were found to support efficient memory encoding only when cues were, again surprisingly, non-informative. In Experiment 3, although the overall preparatory activity in theta and alpha frequency bands elicited by conjunction cues reduced, in contrast to the activity elicited by feature cues, encoding-related theta and alpha desynchronisation was only found for the LTM probes from the feature condition. During retrieval, decreases in theta and alpha power were also found when old probes attracting correct judgments compared to new pictures attracting correct judgments, which suggests a crucial role of theta and alpha desynchronisation in memory retrieval.

What is the functional role of power decreases (i.e. desynchronisation) in oscillatory activity? First, item-related encoding-related alpha desynchronisation was found in Experiments 1 regardless of amount of perceptual information that a picture contains (photos or outlines). Hanslmayr and Staudigl (2013) reviewed studies that found increases and decreases in power of encoding-related oscillatory activity. They found that when an encoding task is a semantic task, decreases in alpha and beta power predict memory formation. Hanslmayr et al. (2012) suggested that desynchronisation in brain oscillations increases the capacity of information encoding in local firing neurons. If spikes of two groups of neurons were the same, the more desynchronised the neurons fired, the more information the group of neurons encode. According to this account, Hanslmayr and Staudigl (2013) suggested that the encoding-related desynchronisation in the semantic encoding task may reflect the increase in capacity of semantic information processing by decreasing the synchrony of local firing neurons. In Experiment 1, a semantic judgment had to be made on each picture. The encoding-related desynchronisation was found regardless of amount of perceptual information that a picture contains may reflect participants' semantic processing rather than perceptual processing on each picture during encoding processes.

Why were decreases in theta power also found in Experiment 1? First, the theta power decreases might be a 'bleed-in' from alpha decreases effects as the frequency bands are sometimes categorised arbitrarily (Lisman & Jensen, 2013). The theta decreases might just be an alpha decrease or 'bleed-in' effect as the theta effect started later and the scalp distributions had the same scalp distribution as the alpha effect. However, a broad theta decrease subsequent memory effect was shown in a free recall task, which means that theta power decrease can also support memory encoding when there is no semantic encoding task (Long et al., 2014). Encoding-related desynchronisation may not be restricted to frequency bands or encoding tasks.

In Experiment 3, desynchronisation was found in later time windows when participants prepared a conjunction DMS task compared to a feature DMS task, which is consistent with the account that desynchronisation reflects the increase in the capacity of information processing. However, no encoding-related desynchronisation was found when an LTM probe was inserted into a preparatory phase for the conjunction task. In contrast, encoding-related theta and alpha desynchronisation was evident for the LTM probes from the feature condition. Surprisingly, encoding-related theta and alpha synchronisation was shown for the LTM probes from the conjunction condition. If the decreases in theta and alpha power for the overall preparatory activity elicited by conjunction cues reflect preparation for increasing the capacity of information processing, encoding-related activity should be also decreased in oscillatory power to predict later memory success. Hanslmayr and Staudigl (2013) suggested that increases and decreases in oscillatory power may reflect the underlying cognitive and perceptual processes during encoding. That is, the ongoing cognitive processes can influence the increases or decreases in oscillatory power during encoding. Encoding-related increases in theta power are thought to be associated with encoding item binding with its contextual information (Guderian et al., 2009; Staudigl & Hanslmayr, 2013). A possible mechanism to support episodic memory encoding in the conjunction could be that preparation for the conjunction task might elicit larger desynchronisation in oscillations to enable more information to be processed. Such increase in capacity of information processing can induce a brain state for an item to be encoded with more contextual information. However, in order to encode an episode more precisely, only contextual information specific to the item can be encoded. Such processes of encoding item-specific contextual information may be accomplished by increases in theta power. Due to the limitation of scalp EEG, the theta-gamma amplitude-phase coupling idea could not be tested in this doctoral thesis. Thus, the data cannot provide sufficient evidence about the computational model that suggests individual feature information is encoded by increasing gamma amplitude and binding together by ongoing theta phase changes (Jensen & Lisman, 1996). In addition, encoding-related alpha synchronisation was found in studies that used a working memory paradigm (Khader et al., 2010; Meeuwissen et al., 2011). Alpha activity increased to support successful encoding of words while the words were maintained in a working memory sequence. The increase in alpha power while the sequence of words was maintained was suggested to reflect remembering the relations between the words (Meeuwissen et al., 2011). Such explanation might also apply to the findings from Experiment 3. The encoding processes of LTM probes were influence by preparatory processes for the DMS tasks. The increases in alpha power for the remembered LTM probes from the conjunction condition might reflect creating relations between an LTM probe and its contextual information. Preparation for the conjunction task was preparing for creating associations between an object and its location. Only one piece of information was needed to be prepared for a feature DMS task. Therefore, in the feature condition, encoding the LTM probe might decrease power in theta and alpha activity to increase the capacity of item-related semantic information processing without restrictions in building relationships with item-specific contextual information.

Decreases in theta and alpha activity were also found when items were successfully retrieved compared to new items in Experiment 3. Such decreases old / new effects were evident in both theta and alpha frequency bands, which shared similar latencies and scalp distributions. Decreases old/new effects in alpha power have been demonstrated in a number of studies (for a review, see Hanslmayr et al., 2012). Alpha desynchronisation during retrieval is related to a recovery of multiple sensory features of a memory representation (Hanslmayr et al., 2012). Therefore, functional roles of alpha activity in retrieval are similar to the roles in encoding. Decreases in alpha power enable more information to be processed. In contrast, theta activity is usually found to be increased in power when an old item is retrieved compared to a new item (for a review, see Nyhus & Curran, 2010). In Experiment 3, from the time-frequency representations of each electrode, the decreases old/ new effect in theta power seemed to be a ‘bleed-in’ from alpha activity as the effect showed similar scalp distributions and latencies as the alpha effect. Theta activity might play a similar role in retrieval as alpha activity. Theta activity increased in power during a selective retrieval phase compared to a re-exposure phase of old items, which suggests that theta activity plays a role in inhibiting unwanted memory trace (Staudigl, Hanslmayr, & Bäuml, 2010). In another study that used a similar paradigm, a decrease in theta power was found when an item was not practiced compared to when an item was selectively retrieved during a recognition test phase (Spitzer, Hanslmayr, Opitz, Mecklinger, & Bäuml, 2009). When an inhibited memory trace is being attempted to be recovered, more decreases in theta power were found to support the retrieval. Therefore, the decrease old/ new effect in theta power in Experiment 3 might reflect reactivation of more information of a stored memory trace as same as the role of alpha activity.

If desynchronisation in oscillations reflects more degrees of richness of information processing in memory-related processes then it should vary as a function of amount of advance information. In Experiment 1, pre-stimulus oscillatory activity predicted successful memory formation in a 1.5 s cue interval. Decreases in pre-stimulus theta and alpha power were associated with successfully encoding a photo when a cue indicated the physical form of an upcoming picture. Such pre-stimulus encoding-related theta and alpha desynchronisation was also found before 1.5 s when the preparation time was predictable and long in Experiment 2, which replicated findings in Experiment 1. The findings suggest that when more perceptual information was expected, or when more preparation opportunity was expected, desynchronisation in theta and alpha activity was engaged in preparation for memory encoding, which is consistent with the hypothesis that desynchronisation reflects more information processing.

Desynchronisation in oscillatory brain activity is caused by random firing of neurons. Decreases in power reflect desynchronisation of local neurons, which can ultimately result in a chaotic brain state that cannot optimise for our behaviour (Friston, 2010; Hanslmayr et al., 2012). In that case, decreases in oscillatory power should be evident when a target is not predictable. Encoding-related desynchronisation in theta and alpha activity also predicted successful memory formation when a cue was non-informative in Experiments 1 and 2. The findings suggest that when the status of a future event is relatively unpredictable (Experiment 1, the amount of perceptual information, Experiment 2, the preparation time), desynchronisation in oscillatory brain activity can also be engaged in preparing for forming a new memory. However, such pre-stimulus encoding-related desynchronisation might be engaged corresponding to the amount of advance information as they showed different scalp distributions (Experiment 1) or different latency (Experiment 2) from the effects in the predictable conditions. In Experiment 1, both theta and alpha encoding-related desynchronisation showed lateralised effects when a cue did not indicate the physical form of an upcoming picture while the decrease effects were over posterior scalp sites when an upcoming picture was known to be a photo. The encoding-related decreases in oscillatory power in the non-informative cue condition might reflect preparation for encoding a picture that could be either a photo or an outline, which information processing was not restricted to sensory or perceptual processes. While the preparation for encoding a greyscale photo that was known to be with more perceptual details may be more likely to be specific to perceptual processes. In Experiment 2, encoding-related decreases in pre-stimulus theta and alpha power occurred before 1.5 s when a preparation time was predictable and long while the encoding-related desynchronisation was evident right before picture onset when a preparation time was unpredictable and long. The findings suggest that when a cue was informative to indicate the preparation time was long decreases in pre-stimulus theta and alpha power were engaged more quickly to support memory encoding. In summary, desynchronisation in theta and alpha activity can be engaged to support preparation for memory encoding when more perceptual information or more opportunity was available to guide preparation. Such pre-stimulus encoding-related desynchronisation was also found in unpredictable cue conditions due to unstable status in the conditions. However, informative cues can guide more efficient preparation to engage the pre-stimulus desynchronisation in memory encoding.

If synchronisation or desynchronisation of ongoing EEG activity in specific frequency bands reflects active cognitive processes, pre-stimulus power of brain oscillations should also influence processing on an upcoming event. For example, pre-stimulus alpha power has been demonstrated to play roles in perceptual processes and visual discrimination and visual working memory (de Lange, Rahnev, Donner, & Lau, 2013; Nenert et al., 2012; van Dijk et al., 2008). Increases in alpha power are suggested to play an active inhibitory role prior to an event and usually reflect higher levels of attention to the upcoming event. Decreases in pre-stimulus alpha power are thought to be associated with more accurate visual perception, which suggests an endogenous preparatory process before a stimulus. If oscillatory activity is actively involved in anticipating a new event pre-stimulus power should vary depending on amount of advance information. In Experiment 1, non-informative cues elicited the largest decrease in theta and alpha power among three kinds of cues. Outline cues elicited the smallest decrease in theta and alpha power among three kinds of cues. Larger decreases in pre-stimulus theta and alpha power in the non-informative cue condition may reflect expectation to two kinds of pictures. Within the informative cues, photo cues elicited more alpha desynchronisation than outline cues. This is consistent with the explanation that increased alpha activity would ‘gate’ the information from the visual stream (Jokisch & Jensen, 2007). Therefore, expectation for a stimulus with more perceptual information should reduce alpha power to allow more visual information passing.

In Experiment 2, increases in alpha and theta power were elicited by predictable short cues. This is consistent with a previous study, which suggests that when the time before a stimulus is short and predictable, increased alpha activity reflects top-down control on expectation to the upcoming stimulus (Zanto et al., 2011). However, this is not the case for long intervals. Decreases in theta and alpha power were found after predictable long cue onset compared to unpredictable long cue onset. Participants might pay more attention to unpredictable intervals compared to a predictable long interval as an unpredictable interval could be as short as 1.5 s, which suggests that participants were able to engage their theta and alpha activity flexibly to prepare according to the cue information.

In Experiment 3, the overall preparatory oscillatory activity before two DMS tasks showed similar patterns as previous findings in the maintenance period of visual working memory task (e.g. Bastiaansen, Posthuma, Groot, & de Geus, 2002; Nenert et al., 2012; Sauseng et al., 2005). Sustained theta power decreases were found before a conjunction DMS task compared to before a location DMS task. Frontal alpha power increases were found before the conjunction DMS task compared to before the location DMS task. Similar findings in the preparatory phase as the maintenance phase suggest that the preparatory mechanisms for the DMS tasks might involve similar neural networks of maintaining information in a short period, which reflects an active role of pre-stimulus neural activity in preparation. Decreases in theta power were found during the maintenance period that targets were not shown, in contrast to the period that targets were always presented, which suggests that decreases in theta power reflect a working memory-specific role (Bastiaansen et al., 2002). In Experiment 3, sustained decreases in theta power were also found before a conjunction DMS compared to a location task. This suggests that preparation for a conjunction DMS task might involve in the similar visual-spatial working memory-specific component by decreasing theta power. Future direction can be analysing the EEG data during the maintenance phase in frequency domain to see if activity during two phases has any relationship and whether preparatory mechanisms are similar to maintenance information thus cause a brain state that involves the hippocampus (Olson et al., 2006).

In summary, the overall preparatory oscillatory activity was actively engaged depending on advance information. Desynchronisation in theta and alpha activity was found to support preparation for memory encoding when more perceptual information and more opportunity were available before a picture to guide preparation. When a cue was non-informative, such desynchronisation could also be engaged prior to a picture to support memory encoding. However, the preparation in a non-informative cue condition was less specific or slower than the preparatory mechanisms engaged in the informative cue conditions. The findings suggest that participants used the advance information as an external guide to strategically select when and how preparatory processes were engaged to support efficient memory encoding. The findings from Experiment 3 suggest that increases and decrease in theta and alpha encoding-related activity might reflect the different ongoing cognitive processes during encoding.

It is noted that many effects found in oscillations were not shown in a similar ERP patterns. It could be that ERP and oscillations reflect different underlying processes to support memory processes or anticipatory processes as suggested in Chapter 2. Oscillations reflect rhythmic ongoing neural activity while ERPs are sensitive to stimulus and have to be phase-locked to stimulus. The effects captured by time-frequency analyses were around 4 Hz to 12 Hz, which might not be able to show in slow ERP effects. Although oscillatory power sometimes can be correlated with ERP components such as evoked visual responses and alpha power increases (Bastiaansen et al., 2012), the findings from the oscillatory analyses were not consistent from the ERP analyses. It is still unclear about the relationship between oscillations and ERPs (for a review, see Sauseng et al., 2007). The reason why there is still no consistent view in the relationship between oscillations and ERPs might be that the index or measure to dissociate or associate the two things is not convincing. Neither phase synchronisation nor amplitude concentration can completely support one view over the other (Mazaheri & Picton, 2005). However, either phase resetting or additive / shared generators suggest that ongoing oscillations should not be treated as background noise to ERPs anymore. Brain oscillations do provide insights about the relationship between the brain and information processing.

This doctoral thesis mainly focused on induced oscillatory power averaged across experimental manipulations, which complements the ERP analyses that focused on phase-locked EEG activity. As discussed in Chapter 2, some previous studies on pre-stimulus oscillatory activity seem to suggest that the functional roles of pre-stimulus theta power are different from pre-stimulus ERP activity (Guderian et al., 2009; Otten et al., 2006). This might be caused by pre-stimulus theta power reflecting different cognitive functions. Guderian et al. (2009) refer to this interpretation as an activation of mnemonic context. Encoding-related pre-stimulus ERP activity, in contrast, may reflect semantic elaboration for to-be-encoded items (Otten et al., 2006). However, a recent study that compared pre-stimulus theta power and pre-stimulus ERP activity used the same experimental manipulations and showed that both are under voluntary control (Gruber & Otten, 2010; Gruber et al., 2013). This doctoral thesis also offers an opportunity to compare the cognitive functions of encoding-related pre-stimulus oscillatory activity and ERP activity within the same experimental setups. There are both consistencies and inconsistencies between ERPs and oscillations within each experiment. As discussed above, decreases in pre-stimulus theta and alpha power were mainly found to support successful memory encoding. Such decreases in pre-stimulus theta and alpha power were engaged in helping encoding only when preparation time was sufficient, which is consistent with the findings in the encoding-related pre-stimulus ERP activity. In addition, overall preparatory theta activity decreased in power before a conjunction DMS task compared to a feature task. An additional increase in theta power was found for correctly recognised items compared to correctly judged new items only for the conjunction probes. However, encoding-related desynchronisation was only found for the probes before the feature task, not the conjunction task. The findings are all consistent with the ERP findings, which suggests that oscillatory activity and ERPs might reflect similar underlying cognitive processes that can support effective memory encoding.

In contrast, time-frequency analyses showed significant effects that were not revealed by the ERP analyses. Encoding-related pre-stimulus ERP activity did not differ according to amount of perceptual information to prepare. Significant decreases in both pre-stimulus theta and alpha power were found to predict later memory success, only when preparing for encoding more perceptual details. Moreover, pre-stimulus alpha activity was found to reflect strategic processes in preparation for memory encoding. Predictable long cues elicited encoding-related alpha desynchronisation while encoding-related pre-stimulus alpha synchronisation was found after predictable short cues. No significant pre-stimulus subsequent memory effect was shown when preparation time was predicted to be short in the ERP analyses. In addition, ERP analyses did not reveal significant difference of encoding-related pre-stimulus activity in amount of advance information. Time-frequency analyses showed larger encoding-related pre-stimulus desynchronisation when a non-informative cue indicated an upcoming picture could be either a photo or an outline. When preparation time was not predictable, increases in pre-stimulus alpha power played a role in supporting subsequent memory formation. The findings suggest that oscillatory analyses might show some underlying cognitive functions that could not be revealed by ERPs. It is noted that, in this doctoral thesis, the effects missed by ERPs were most found in a relatively short interval, 1.5 s, which might suggest that pre-stimulus activity in a short interval in serving for forming a new memory representation of a picture object might be dynamic neural correlates that could only be captured by ongoing theta and alpha activity but not slow ERP shifts that are both time and phase-locked to the pre-stimulus cues.

The ongoing oscillations might be able to perturb the random phases to be concentrated to pre-stimulus cues when there is sufficient time to develop sustained phase-locked activity to be ready for encoding new memory (Guderian et al., 2009). The preparatory processes in short intervals might be only able to be reflected by induced power of the ongoing oscillation as the neural generators of phase-locked activity might not have chance to support such dynamic changes related to subsequent memory success. The findings suggest that both induced oscillatory activity and phase-locked ERP activity can support preparatory processes in long preparatory intervals. This supports the phase-resetting view that ERP might be generated from phase concentration of the ongoing oscillations. However, the data is not against the additive view or shared generators because only induced preparatory activity supported later efficient memory encoding in short intervals when ERP effects were absent. The neural generators might only be able to generate induced activity when preparation time was limited. When preparation time was sufficient, both evoked and induced components can be generated or the ongoing activity will be phase-locked at the same time while induced components are generated. Therefore, the data of this doctoral thesis did not support one specific model over the others but can be explained by all three views.

6.1.3 Does memory performance benefit from more opportunity to prepare for encoding?

Experiments 4 and 5 used behavioural measures to address the relationship between encoding-related anticipatory processes and overall memory performance. So far, a good number of studies show that pre-stimulus activity predicts later memory performance on a trial-by-trial basis and a few studies show a positive relationship between magnitudes of pre-stimulus encoding-related activity and the number of remembered items (Adcock et al., 2006; Guderian et al., 2009; Mackiewicz et al., 2006). If pre-stimulus encoding-related activity reflects active preparatory processes for encoding a new memory then it can be engaged to improve later overall memory performance. Such encoding-related activity was evident when there was sufficient time to prepare before encoding a picture in Experiment 2. However, no evidence was found about whether longer preparation time also enhanced later overall memory performance. One possible reason is that memory performance does not only depend on encoding but all the memory-related processes that can influence memory such as consolidation, retrieval or the interaction between them (Godden & Baddeley, 1975; Morris et al., 1977; Nadel & Moscovitch, 1997; Tulving & Thomson, 1973; Tulving, 1974). Therefore, poor preparatory processes could be compensated by later memory processes to form a stronger memory representation. If the opportunity to engage such compensatory processes is less available then it would be possible to show the advantages by better preparatory processes on memory performance.

To test this idea, semantic tasks were used as secondary tasks during retrieval in Experiments 4 and 5. The designs during encoding were stage kept the same as in Experiment 2 in order to see if longer preparation time during encoding would benefit later memory performance when retrieval resources were limited. Memory performance was better in long cue interval conditions regardless of cue predictability when retrieval was interfered by a secondary task. Such finding was not replicated in Experiment 5 that compared retrieval under same secondary task condition as used in Experiment 4. Experiment 5 contrasted retrieval under the same secondary task as used in Experiment 4 and a difficult secondary task that used two semantic tasks. Instead, memory performance was better in unpredictable cue interval conditions regardless of cue lengths when retrieval was interfered by the same secondary task.

Although inconsistent findings were found between Experiments 4 and 5, when collapsing the data from Experiments 4 and 5, a consistent finding was that unpredictable cue interval conditions led to better memory performance when retrieval resources were limited by one semantic task. It is noted that in time-frequency analyses of Experiment 2, the unpredictable cue conditions showed pre-stimulus frontal increases in alpha power in association with later memory success, which increases in pre-stimulus alpha power suggested to be related to top-down control processes for preparing for encoding stimulus-related information (Fell et al., 2011). Such pre-stimulus alpha power might support a better memory representation in unpredictable cue conditions. In previous literature on attention, working memory or long-term memory, Predictable cue condition always showed a better performance (Schmidt, Vogel, Woodman, & Luck, 2002; Uncapher et al., 2011; Zanto et al., 2011). However, predictable cues were suggested to elicit more attention-related activity to enable more elaborated processing on an upcoming item (Uncapher et al., 2011). If unpredictable cues can also elicited attention-related activity, such as increases in alpha power, it might be possible to explain the memory performance advantage in unpredictable cue conditions across Experiments 4 and 5. Nevertheless, Experiments 4 and 5 showed inconsistent results from Experiment 2 in the encoding task. Neither Experiments 4 nor 5 showed faster reaction times after predictable cue intervals. Therefore, it is difficult to explain the results of Experiments 4 and 5 by the enhancement of preparatory brain activity for memory encoding in Experiment 2.

In summary, memory performance was better following longer preparation time during encoding when retrieval resources were limited by a secondary task in Experiment 4. This supports the compensatory roles that memory related processes play in forming a strong memory representation due to poor preparation for encoding. Unfortunately, this finding was not replicated in Experiment 5. The relationships between preparatory processes for encoding and overall memory performance need more research to be understood. Experiments 4 and 5 are not able to give a consistent conclusion about whether the relationships could be well understood by decreasing the opportunity for the compensatory process during retrieval. However, it could be one future direction if neuroimaging method is also incorporated. It enables to look at the neural correlates of compensatory memory encoding processes when later retrieval is limited in processing resources.

6.2 Implications and future research

Previous research on pre-stimulus encoding-related activity has indicated that the current memory theory on encoding needs to be updated, which means activity preceding an event is as important to memory encoding as activity after the event (Otten et al., 2006; 2010). So far, at least two kinds of such activity have been found. One is frontal negative-going pre-stimulus encoding-related activity, which is suggested to reflect semantic preparation (Galli et al., 2012; 2013; Otten et al., 2006; 2010). The other one is widespread positive-going pre-stimulus encoding-related activity, which reflects motivational preparatory processes (Galli et al., 2011; 2014; Gruber & Otten, 2010). Those studies indicate that pre-stimulus activity is not a random fluctuation before an event. It helps later memory formation in certain circumstances. Therefore, appropriate preparation for an upcoming event can lead to better memory.

However, the real world is full of certainty and uncertainty. In this doctoral thesis, a series of experiments showed that pre-stimulus encoding-related activity was not only found before a predictable event but was also found before an unpredictable event. Positive-going pre-stimulus encoding-related activity and desynchronisation in oscillatory activity (4 – 12 Hz) were both evident before predictable and unpredictable events but they differed in latency and scalp distributions. Encoding-related anticipatory processes before predictable and unpredictable events seemed to reflect different cognitive processes, which suggests that how to prepare for encoding a new event appropriately depends on the information given by the pre-stimulus cues. Our brain can be optimised for remembering a future event by external cues.

Around 40 years ago, Craik and Lockhart (1972) has proposed that our memory is a function of levels of processing, which means more conceptual or meaningful aspects of an items is analysed during encoding, later memory trace will be more endurable. More recently, EEG studies showed that fronto-central positive-going subsequent memory effect and encoding-related alpha desynchronisation play crucial roles in forming an endurable memory trace via deep levels of processing. In this doctoral thesis, such fronto-central positive-going subsequent memory effect and encoding-related alpha desynchronisation was found across experiments, which indicates that memory encoding processes in these studies mainly were products of deep meaningful analyses of an item. It should be noted that activity before the item also played a role in supporting such endurable memory trace. Although the stimuli were pictures, the processing focused on their conceptual meaning rather than perceptual aspects. Therefore, to support such deep levels of processing, preparatory processes might contribute to increase capacity of deeper levels of processing to enable an upcoming item to be more likely to receive elaborate processing (Hanslmayr & Staudigl, 2013; Otten et al., 2006; 2010). However, the polarity of the pre-stimulus subsequent memory effects found in this doctoral thesis was different from the polarity of the pre-stimulus subsequent memory effect of semantic preparation. The preparatory processes in this doctoral thesis might not only reflect semantic preparation but many simultaneous cognitive processes such as attention, sensory preparation, and strategic control processes, which actually is reflected by positive-going pre-stimulus subsequent memory effect (Gruber & Otten, 2010). As constructive processes, encoding a memory representation includes processing perceptual attributes and analysing them in a deeper level to construct meaningful experience (Schacter, Norman, & Koutstaal, 1998). Such constructive processes reflect that episodic memory formation is actively building connections between features or gist rather than video-recording everything. Now brain activity has been demonstrated to support the constructive processes even beforehand. The processes beforehand are sensitive to semantic processing and under voluntary control for encoding verbal materials, which might suggest preparatory processes are also active and related to the opportunity of semantic analyses of physical features. More importantly, the findings from this doctoral thesis suggest that the active preparatory processes also supported encoding pictorial stimuli. Pictorial stimuli contain more perceptual processing to modulate substantial attributes in deeper analysing. The active preparatory processes played a crucial role in forming memory representations for pictorial stimuli when there was more need, or more opportunity to increase capacity of analysing new physical features.

One puzzle is that if pre-stimulus encoding-related activity reflects active control processes in preparing for forming endurable memory trace, why memory performance was not enhanced when such preparatory activity was shown compared to not shown? As discussed before, encoding processes might be reflected by a combination of state-related and item-related activity (Donaldson, et al., 2001; Otten et al., 2002), such state might not differ in later retrieval success but help to enter into attempts to encode episodic information. Also, memory success depends on encoding, retrieval, consolation processes and the interactions between them. The additional encoding-related post-stimulus activity and retrieval-related activity found in the conditions that did not show robust pre-stimulus encoding-related activity support this idea.

Experiment 2 showed amount of preparation time before encoding was crucial to pre-stimulus encoding-related ERP activity. It indicates that deficits in memory might be related to insufficient preparation time beforehand. A recent study by Galli et al. (2013) suggests that encoding-related anticipatory processes can only be engaged when sufficient resources are available before event onset. Therefore, not only the will to prepare but also the opportunity to prepare is important to the engagement of encoding-related anticipatory processes. An interesting future direction could be to investigate the relationship between available preparation time and available cognitive resources for preparation. When resources of preparatory phase are limited by a difficult secondary task, more preparation time might enable anticipatory processes to be recruited for encoding. Such findings could be useful for the populations that lack cognitive resources such as the elderly. It might be helpful for them to prepare longer when learning something.

Although Experiments 4 and 5 did not show consistent behavioural results for the benefits of longer preparation time, it could be a potential direction to see when other memory-related processes are impaired, how preparatory processes work for overall memory performance. For example, using Transcranial Magnetic Stimulation (TMS) to stimulate prefrontal cortex during encoding can cause poorer memory performance compared to no stimulation (Machizawa et al., 2010). If longer preparation time is available before encoding, a decrease in overall memory performance caused by TMS to prefrontal cortex might be reduced compared to less preparation time. In Experiment 3, the overall memory performance was enhanced marginally significantly by manipulating preparation for an episodic task before encoding a picture. This finding suggests that a better brain state for memory encoding can be predicted by other cognitive tasks an individual is going to do. It is possible to apply the paradigm to educational and patient settings. If individuals are in a mood of being ready for a task, including episodic components such as binding of multiple types of information, learning can be enhanced. Yoo et al. (2012) used real-time fMRI to induce a good brain state for memory by comparing real-time BOLD signals with reference BOLD signals. Such methods might be more accurate to induce a good brain state for memory but less ecology-friendly for application. However, more future work should be done to understand more about the paradigm of Experiment 3 thus be able to develop an efficient tool for application. For example, which brain areas are involved in preparatory phase for a conjunction DMS task compared to a feature DMS task? If it is the hippocampus, then what kind of hippocampal activity is involved and what kind of the relationships exist between encoding-related activities? A positive correlation was found between DMS task performance and recognition accuracy in the conjunction condition. Pilots for Experiment 3 showed that the more difficult the DMS tasks were, the more advantage the conjunction condition showed in memory performance. These results indicate that if preparation for later DMS tasks is required more, later memory formation for the probes during preparatory phase is more efficient. It would be interesting to see the relationships between overall preparatory activity and later DMS task-related activity, as well as the relationships between later DMS task-related activity and the memory performance. In addition, future work can be done to increase the need to prepare for DMS tasks, such as difficulty, to see if the conjunction condition shows more advantages in memory performance.

It is noted that time-frequency analyses showed different effects from ERP analyses. It would be sensible to look at oscillations as a supplement of ERP analyses as they reflect non-phase-locked ongoing EEG activity. If preparatory processes for later memory encoding are not random fluctuations pre-stimulus oscillatory activity should vary in its magnitude to the degree of preparation. In this doctoral thesis, mainly encoding-related desynchronisation was found before event onset. In Experiment 1, lateralised encoding-related desynchronisation was found after a cue indicating an upcoming picture could be either a photo or an outline while posterior encoding-related desynchronisations was found after a cue indicating an upcoming picture was a photo. The findings basically supported the information theory accounts of desynchronisation in alpha activity (Hanslmayr et al., 2012). Photo cues guided perceptual preparation for encoding a photo with more perceptual details. Non-informative cues guided a general preparation for encoding two kinds of pictures, which might reflect an uncertain brain state for a future event. Future work might be of interest in differing two kinds of encoding-related desynchronisation. First, large-scale phase synchrony can be investigated to see whether local desynchronisations found in two cue conditions reflect same large-scale brain networks (Bastiaansen et al., 2012). For example, if a predictable cue indicating an upcoming picture was a photo guided perceptual preparation then phase synchronisations between frontal areas and posterior areas should be enhanced. In contrast, phase desynchronisation should be found after a non-informative cue if the preparation the non-informative cue guides is for unknown types of pictures (Varela, Lachaux, Rodriguez, & Martinerie, 2001). Second, the desynchronisations found in the non-informative cue condition could reflect unpredictability about a future event or preparation for more pieces of information than predictable condition. Although the findings from Experiment 2 did not favour the former notion, it is still unclear whether more desynchronisation can be elicited by an unpredictable cue or a predictable cue that informs more stimulus-related information to be prepared. Therefore, future works can be done on comparing unpredictability and types of information. For example, a picture of an object that is consisted of half photo and half outline can be created as the third type of picture. There are three kinds of pictures: photo, outline, half photo and half outline. There can be three kind of pre-stimulus cues: 100% informative cues indicate an upcoming picture is half photo and half outline, 50% informative cues indicate an upcoming picture can be either a photo or an outline, 33% informative cues indicate an upcoming picture can be one of three types of pictures. If desynchronisation found in the non-informative cue condition more reflect preparation for two kinds of information, then the levels of desynchronisation should not differ in cue types as they all indicate preparing for two pieces of information. Whilst desynchronisation found in the non-informative cue condition reflect uncertainty about future events, then the levels of desynchronisation should vary as a function of cue predictability, which 1/3 informative cues elicited the greatest desynchronisation and 100% informative cues elicited the least desynchronisation.

In conclusion, research on pre-stimulus activity that contributes to efficient memory encoding is an important direction to reveal the relationships between brain activity and successful memory formation. It demonstrates flexibility of our brain activity in supporting an endurable memory trace. It might be a predictor for our future behaviour. Incorporation with latest methods such as neurofeedback or neural decoding on pre-stimulus activity can have wide applications on education, clinic and business. For example, Yoo et al. (2012) used real-time fMRI to define when the best time is to learn new things. Similar techniques can be applied to EEG as EEG has higher temporal resolution, which is more sensitive to detect the exact time when a new thing should be learnt. The neural decoding or MVPA analyses can predict whether memory can be remembered on a trial-by-trial basis, which might be of interest to business area, for example, advertisement, or marketing. Clinically, Experiments 2 and 3 suggest that maybe longer preparation time or a state that also involves binding of episodic information might help to compensate encoding processes. Cognitive training that involves learning while preparing for other tasks of binding information can be used for people who have deficits in encoding.

6.3 Final conclusion

This doctoral thesis addressed the role of amount of advance information in encoding a pictorial event into long-term memory. The findings of three EEG experiments and two behavioural experiments suggest that the more advance information is available to guide preparation, the more likely it is that pre-stimulus activity influences encoding. However, there seems to be more general preparatory processes when the advance information is less informative. Encoding-related pre-stimulus activity is under strategic control and influenced by the opportunity to engage such activity.

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