

# **Investigating unconscious visual episodic memory and its underlying neural substrate using fMRI and eye tracking**

---

Haleh Khoshkhouy Delshad

BSc, MSc

Department of Cognitive Science

Faculty of Medicine, Health and Human Sciences

Macquarie University, Sydney, NSW, Australia

This thesis is presented for the degree of

Doctor of Philosophy (PhD)

December 2019



# Table of contents

Table of contents.....	ii
Thesis abstract.....	vi
Statement of originality.....	ix
Acknowledgement .....	xi
Author note .....	xiii
Chapter 1- general introduction .....	1
1.1 Importance and implications of unconscious memory.....	3
1.2 Classic definition of episodic memory.....	4
1.3 Toward a memory model for unconscious episodic memory .....	5
1.4 Processing based memory model .....	8
1.5 Unconscious episodic memory according to the major memory models and frameworks .....	11
1.6 Viewing behaviour and memory .....	16
1.7 Role of viewing behaviours in reflecting memory retrieval mediated by MTL .....	19
1.8 Visual attention toward memory in the absence of conscious awareness.....	21
1.9 Brain areas that control viewing behaviour during unconscious retrieval of episodic memory.....	22
1.10 The confounding effect of attentional bias on viewing behaviour.....	25
1.11 Summary and Conclusion .....	28

1.12 Approach and overview of experimental chapters .....	29
1.13 References .....	30
Chapter 2 - What can eye tracking tell us about unconscious memory of episodically associated visual stimuli? .....	43
2.1 Abstract .....	44
2.2 Introduction .....	45
2.3 Methods .....	51
2.4 Results .....	58
2.5 Discussion .....	62
2.6 References .....	66
Chapter 3 - Investigating the unconscious encoding of episodically associated visual stimuli: an fMRI study .....	75
3.1 Abstract .....	76
3.2 Introduction .....	77
3.3 Methods .....	80
3.4 Results .....	91
3.5 Discussion .....	96
3.6 References .....	101
Chapter 4 - How does functional connectivity related to unconscious episodic memory of visual associations modulate viewing behaviour? .....	109
4.1 Abstract .....	110
4.2 Introduction .....	111



4.3 Methods .....	116
4.4 Results .....	120
4.5 Discussion .....	126
4.6 References .....	129
Chapter 5– General discussion.....	135
5.1 Overview of thesis.....	136
5.2 Implications and limitations of findings in chapter 2.....	137
<i>What can eye tracking tell us about unconscious memory of episodically associated visual stimuli?</i> .....	137
5.3 Implications and limitations of findings in chapter 3.....	148
<i>Investigating the unconscious encoding of episodically associated visual stimuli: an fMRI study.</i> .....	148
5.4 Implications and limitations of findings in chapter 4.....	158
<i>How does unconscious memory of episodically associated visual stimuli modulate viewing behaviour?</i> .....	158
5.5 Episodic memory models .....	164
5.6 Summary and conclusions.....	167
5.7 References .....	168
Appendix 1 .....	179



## **Thesis abstract**

Classically, episodic memory is considered a subcategory of declarative memory and is accessible to conscious report. But recent clinical and brain imaging findings have led to a new processing-based-memory model. According to this model episodic memory is defined as a rapidly formed memory of novel associations that can be retrieved in a flexible manner. Hypothetically, a memory with these characteristics can exist at both conscious and unconscious levels. The main aim of this thesis is to test the possibility of unconscious encoding and subsequent unconscious retrieval of complex visual associations and investigating their underlying neural correlates using fMRI.

In chapter 1, I review the literature about unconscious visual episodic memory and behavioural measures and neural mechanisms related to it. In chapter 2, using eye tracking, I test the possibility of unconscious encoding and unconscious retrieval of complex visual association according to the processing-based-memory model. This makes a foundation for chapter 3, in which I use functional magnetic resonance imaging (fMRI) to test whether the main brain areas known to be involved in conscious episodic memory are also involved in unconscious visual episodic memory. In this chapter I also used eye tracking simultaneously with fMRI to investigate the possibility of a correlation between viewing behaviour and brain activation related to unconscious episodic memory. Chapter 4, presents a functional connectivity analysis on these fMRI data to find the underlying neural mechanism for modulation of viewing behaviour by unconscious episodic memory.

Overall, the findings in this thesis provide support for the existence of a memory with the characteristics of episodic memory without conscious awareness. This memory recruits the main brain areas that are involved in conscious episodic memory and modulates viewing behaviour through interaction with bottom-up attention network. Chapter 5, presents a general

discussion about the implications of these findings, limitations and questions for future research.



## Statement of originality

*This work has not previously been submitted for a degree or diploma in any university. To the best of my knowledge and belief, the thesis contains no material previously published or written by another person except where due reference is made in the thesis itself.*

(Signed) Haleh Khoshkhoy Delshad

Date: 26/12/2019

**Candidate's name**



# Acknowledgement

I like to thank all my supervisors who supported me from the beginning of my PhD candidature at Macquarie University: Professor Mark Williams, Associate professor Anina N. Rich and Associate professor Paul F. Sowman. I'm very thankful for their supervision, time and advice that helped me improve my research. I also like to thank all the staff at the cognitive science department for their support and the pleasant environment. I am also very thankful to my family for supporting me in my educational pursuits.

I am very grateful to Macquarie University for giving me the opportunity to work in this new field of research that I was very passionate about.

This research was supported by an Australian government research training program (RTP) scholarship. I was also supported by the international Macquarie Research Excellence scholarship (iMQRES).





## **Author note**

I have prepared all the work in this thesis during my PhD candidature at Macquarie University.

This thesis is prepared under the format of “thesis by publications”.

I have conducted all the stages of each chapter including conception, designing, programming and preparing the experiments, data collection, analysis and writing.

Professor Mark Williams supervised the conception of the whole thesis. He supervised the designing, programming and preparing the experiment, data collection and analysis in chapter 2. He also gave me advice about the writing in chapter 2. He supervised the designing, programming and preparing the experiment and the data collection in chapter 3. In addition, he gave me advice about the data analysis in chapter 3.

Associate professor Anina N. Rich supervised all the aspects of chapter 2. She also gave me advice about the conception, data analysis and the writing in all the other chapters. She also performed the editing and proofreading of all the chapters.

Associate professor Paul F. Sowman gave me advice about the conception, analysis and the writing in all the chapters. He also performed the editing and proofreading of all the chapters.

The writing of the eye-tracking ethics protocol was done by Associate professor Anina N Rich.

The writing of the fMRI ethics protocol was done by Professor Mark Williams.

The MRI equipment was provided by the Macquarie Medical Imaging (MMI) and Macquarie University. Margery Pardey, the chief research facilitator and Jeffery McIntosh, the manager at the MMI gave me support in the fMRI data acquisition.

Marcus Ockenden, the “Senior Technical Research and Innovation Specialist” and Craig Richardson, the “Technical Research and Innovation Team Leader” supported me by fixing the technical issues with the eye tracker and the MRI equipment.

Lesley Mcknight, the department administrator gave me administrative support.

Due to the thesis by publication format there is a degree of repetition in some chapters. The repetition is particularly between the general introduction or the introduction of the experimental chapters and also between the general discussion and discussion of each experimental chapter. I have tried to avoid unnecessary repetition while each chapter stand on its own.



# Chapter 1- general introduction

---

Department of Cognitive science, Macquarie University, Sydney NSW 2109,  
Australia



# **General introduction**

## **1.1 Importance and implications of unconscious memory**

We have all been in situations where we could not recall a previously encountered event. But the same event could be subsequently recalled with details in the presence of an appropriate cue. One of the key questions in the literature about memory and recall is whether we need to deliberately or consciously recall an experience, or whether events can be encoded and retrieved without our consciousness (Henke 2010).

The capacity and influence of our unconscious mind is the topic of intense curiosity and study, but it is difficult to investigate. It has a vast importance in many aspects like clinical cases, social relationships, immoral behaviour in criminal cases, and economics. For example, there are studies exploring the unconscious effects of advertisements on our decisions against our will or other studies on heuristic decision making (Janiszewski 1990, Mychaskiw, Horowitz et al. 2001, Gigerenzer and Gaissmaier 2011, Kent, Mashour et al. 2013). From the clinical point of view, there are reports of conscious recall of intraoperative events under general anesthesia (Lubke, Kerssens et al. 2000, Mychaskiw, Horowitz et al. 2001, Kent, Mashour et al. 2013). Such patients are prone to distress and psychological sequelae because of the intrusive recall of the unconsciously encoded event (Kent, Mashour et al. 2013). Results from previous studies also shows that depressed patients show preferential recall of negative information at the unconscious level compared with non-depressed people (Watkins, Vache et al. 1996). Implicit emotional memory is also of dominant interest in studies of emotional disorders like post-traumatic stress disorder. For instance, in a novel study in 2013 Kuriama and his colleagues showed that suppression of conscious recall of details related to a traumatic event increases the

unconscious recall of the emotional components of that event (Kuriyama, Honma et al. 2013). Overall, these studies emphasize that unconscious encoding and retrieval of events can affect the behaviour and decisions of healthy individuals and can also contribute to psychological disorders which makes it an important area of research.

## **1.2 Classic definition of episodic memory**

Episodic memory is a special neurocognitive system through which we can remember past events (Tulving 2002). The idea of a distinction between episodic memory and semantic memory is based on the nature of the memorised material; It particularly depends on whether retrieved items are personally experienced events or general concepts and knowledge (Tulving 1972). Considering a distinct biological structure for episodic memory was initially based on the investigations in patients with brain damage or animals with experimental brain lesions. Based on his neurological investigations in 1985, Nielsen reported that there are two pathways for two different type of declarative memory, one is memory of personal experiences and the other is memory of acquired knowledge (Nielsen 1958). This was an important finding that made the way for defining episodic memory as a memory related to encoding and retrieval of events.

To provide a framework for the role of medial temporal lobe, particularly the hippocampus, in episodic memory, I will explain the anatomical organization of this region. Monkey studies using silver impregnation method (Foot and Foot 1932), have shown that the hippocampus receives converging connections from modality specific areas and also association areas (Van Hoesen, Pandya et al. 1975, Van Hoesen and Pandya 1975, Mishkin, Suzuki et al. 1997). According to these studies, neo-cortex is connected to medial temporal lobe via projections to entorhinal and parahippocampal gyrus. The anatomical connections of hippocampus with neo-



cortex makes it a suitable candidate for forming memories of different events. Early clinical findings showed that even small amount of damage confined to hippocampus is enough to produce significant amnesia (Zola-Morgan, Squire et al. 1986, Victor and Agamanolis 1990). Patients with brain lesion in hippocampus showed a deficit for episodic memory of everyday life experience (Vargha-Khadem, Gadian et al. 1997). These patients did not show any deficit in factual knowledge, literacy or language competence. These findings led to the initial idea that hippocampus mediates memory of events as opposed to facts (Mishkin, Suzuki et al. 1997, Tulving 2002).

But according to these initial definitions, episodic memory was defined as *conscious* encoding and retrieval of events (Mishkin, Suzuki et al. 1997, Tulving 2002). Most commonly, studies of patients with medial temporal lobe lesion showed a deficit in types of memory that were accessible to consciousness. In contrast, these patients performed quite normally in implicit memory tests that did not require a conscious report (Milner, Corkin et al. 1968, Knowlton, Ramus et al. 1992, Clark and Squire 1998, Levy, Stark et al. 2004). These observations contributed to a proposal that hippocampus was a hub for the formation and retrieval of the conscious (and only conscious) form of episodic memory. To study unconscious episodic memory, we need a new model that embraces both the conscious and unconscious aspects of episodic memory.

### **1.3 Toward a memory model for unconscious episodic memory**

There were other clinical observations that made our way towards a new memory model that embraced both conscious and unconscious forms of episodic memory. In 1982, Warrington and Weiskrantz reported an interesting finding on amnesic patients with medial temporal lobe damage. These patients were presented with word pairs that were semantically close or distant.

After a delay, their relational memory was tested by asking them to retrieve one of the words after they viewed the other word from each pair. Medial temporal amnesic patients showed a retrieval deficit only in word pairs that were semantically distant compared with semantically close pairs (Warrington and Weiskrantz 1982). Subsequent experiments on patient Y.R with bilateral hippocampal lesions showed specific deficits in her recognition memory for associations between items that belonged to different categories (e.g. face and sounds). Interestingly, her performance was relatively normal for the same tests on related items or intra-item associations (e.g. features of the same face). The patient's normal performance for the related items could be due to facilitation of retrieval by familiarity of the related items as a unique representation. The authors suggested that the preserved familiarity memory for related items could be produced by Y.R's intact medial temporal lobe cortices outside the hippocampus. Her bilateral hippocampal lesions could have resulted in the loss of her memory for novel relations (Mayes, Holdstock et al. 2002, Mayes, Holdstock et al. 2004). These findings suggested a revised role for the hippocampus in forming novel relations that may not be limited only to conscious mnemonic processes.

Further studies on priming effects in amnesic patients revealed more insight about the role of hippocampus in memory. In a word completion task, amnesic patients were presented with related (e.g. dog cat) and unrelated word pairs (e.g. window reason). Their memory for these items was tested indirectly by asking them to complete fragments of each word by the first word that came to their mind (e.g., rea- for reason). The words were presented in the same pair or in a new pairing of the words. Healthy subjects had better performance for the same pair condition compared with the novel pair condition. Their performance was used as a measure for unconscious relational memory. Contrary to normal subjects, amnesic patients did not show a facilitation of performance in the same pair condition for unrelated words, but their

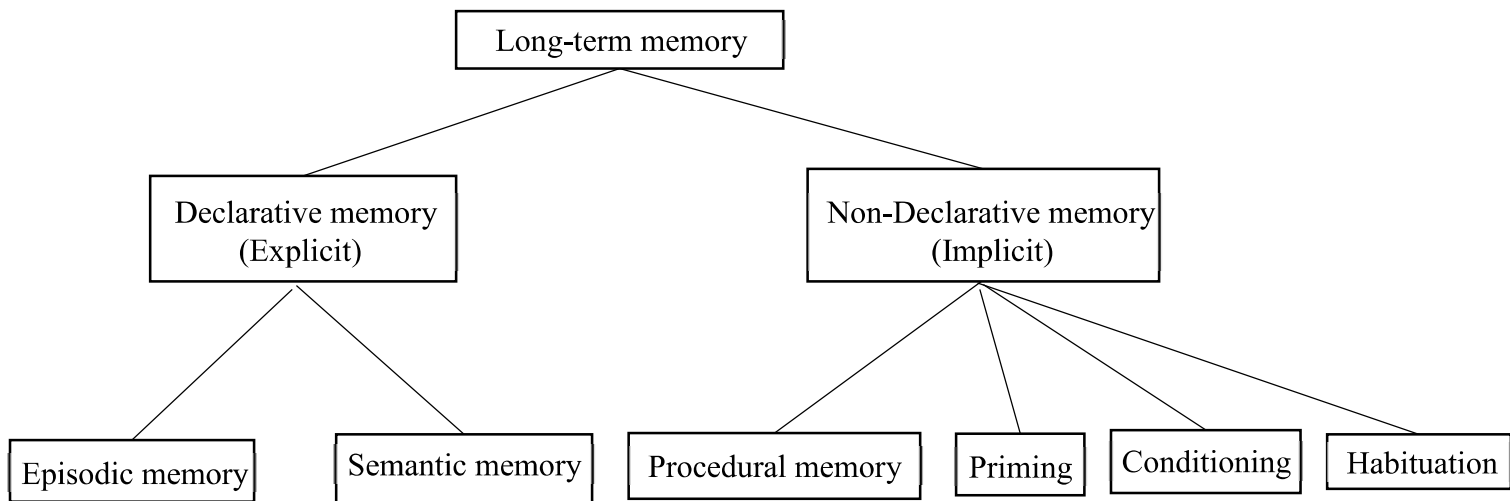


Figure 1. Traditional classification of memory based on consciousness. The memory class that includes the capacity for conscious recollection is called declarative memory (Explicit memory). The non-declarative memory (Implicit memory) refers to a class of memory that includes unconscious memory functions. Declarative memory is classified into episodic memory and semantic memory subclasses. Episodic memory encompasses the conscious encoding and recollection of personally experienced events. Semantic memory includes general knowledge that is not driven from recollection of a personal experience (Tulving 2002). Non-declarative memory involves all types of memory that manifest in behavioural changes rather than conscious recollection. These include procedural learning of skills and habits, priming, conditioning and habituation (Squire, Stark et al. 2004).

performance was normal for semantically related words in both conditions (Schacter and Graf 1986, Shimamura and Squire 1989)). Such studies provide more support for the hypothesis that the role of hippocampus in forming new relations may include unconscious mnemonic processes (Schacter and Graf 1986, Shimamura and Squire 1989).

Further evidence for the unconscious aspect of episodic memory comes from functional magnetic resonance imaging (fMRI) studies. fMRI, gives us the opportunity to make inference about changes in the activation of deep brain structures like hippocampus through changes in oxygenated blood flow while performing a cognitive task. There is accumulating evidence from fMRI studies about hippocampal activation during unconscious encoding and retrieval of associated items (Degonda, Mondadori et al. 2005, Daselaar, Fleck et al. 2006, Kirwan, Shrager et al. 2009, Reber, Luechinger et al. 2012, Duss, Reber et al. 2014, Züst, Colella et al. 2015). For example in a pioneering study by Hannula et al (Hannula, Ryan et al. 2007), novel face-scene associations were encoded consciously. One of the scenes was then presented as a cue to provoke retrieval of the associate face (target). Subsequently, the participants freely viewed the target face alongside a distractor face. The participants spent more time viewing the target face compared with the distractor face. It was shown that this modulation of viewing behaviour was absent in patients with hippocampal damage (Hannula, Ryan et al. 2007). In another experiment using the same design, hippocampal activation during viewing the cue predicted the proportion of time allocated to view the target compared with the distractor face. This correlation was also found in the absence of conscious retrieval that was tested through subjective reports (Hannula and Ranganath 2009). These findings about the role of hippocampus in unconscious memory of associations paved the way for a processing-based-memory model that included both the conscious and unconscious forms of episodic memory.

#### **1.4 Processing based memory model**

In 2010, Henke proposed a processing-based-memory model (figure 2). Instead of classifying memory based on consciousness, she defined different memory types based on their processing characteristics (Henke 2010). Some forms of memory require a large number of learning trials

and other memory types can develop with a single exposure. For example, priming and episodic memory can form with only one experience, whereas skill and habit formation require a large number of learning trials. Hence the first characteristic of episodic memory is that it can form by a single exposure to an event. The second characteristic is the cognitive complexity or the number of cognitive modules involved in memory representation. For example, priming requires fewer cognitive modules compared with episodic memory. In contrast, episodic memory is multifaceted and consists of sensory, conceptual, emotional, temporal and spatial information. The third characteristic is compositionality and flexibility of the memory representations. Elements of a compositional memory can be stored independently and be accessible separately. Therefore, these elements and their associations can be activated by many routes. This enables flexibility because of the interaction between different modules of episodic memory. Priming compared with episodic memory has less memory modules and less flexibility. According to the Henke's model, episodic memory is a flexible and multifaceted memory system that can form rapidly and depends on the MTL (medial temporal lobe), particularly the hippocampus (Henke 2010). An episodic memory with these characteristics can also form at unconscious level.

According to the processing-based-memory model, hippocampus mediates episodic memory over short or long retention times (Henke 2010). But traditionally, episodic memory is known to be a subcategory of long-term memory. This idea originated from the initial studies on amnesic patients. It was shown that amnesic patients with MTL damage achieved some retention of stimuli over short periods of time (Milner, Corkin et al. 1968). This finding led to the idea that MTL is not involved in short-term memory. But, it has been shown that when the memory load is high enough, hippocampus plays a dominant role in short-term memory formation for novel associations, and also for complex singular visual stimuli like novel faces. Such relatively difficult memory formation conditions require challenges such as long retention

times (above 7s), presence of a distractor, novel visual stimuli or formation of novel associations (Cabeza, Dolcos et al. 2002, Nichols, Kao et al. 2006, Rissman, Gazzaley et al. 2008, Jeneson, Mauldin et al. 2011). Hence, I expected that hippocampally-mediated episodic memory played a dominant role in episodic encoding and retrieval of novel and complex visual associations over long retention times (above 7s) and in the presence of distractors. I used this criteria to design all the experiments in my thesis.

To the best of my knowledge, no study so far has investigated unconscious encoding and subsequent unconscious retrieval of visual episodic memory. In this thesis I investigated the unconscious encoding and unconscious retrieval of complex visual associations in a way that was consistent with the characteristics of episodic memory according to the processing-based-memory model. According to the processing-based-memory model episodic memory is characterized by rapid encoding of associations and flexible retrieval (Henke 2010). Novel face-scene associations were masked from consciousness during encoding. After the unconscious encoding phase, there was a retention period (above 7s) in the presence of distractors (i.e. participants were distracted from the encoded items by solving different math problems). According to the model, if the face-scene memory was flexible, retrieval of one of the associate stimuli (the scene) should instigate or facilitate the unconscious retrieval of the other associate stimulus (the face). Hence, after the retention period one of the scenes was presented as a cue to provoke retrieval of the associate face (target). I used this paradigm in all of the experiments in this thesis in combination with different behavioural and brain imaging measures to investigate unconscious encoding and retrieval of visual episodic memory.

## **1.5 Unconscious episodic memory according to the major memory models and frameworks**

A question that comes to mind is whether Henke's definition of unconscious episodic memory (Henke 2010) is compatible with other major memory models and frameworks. In this section, I briefly review some of the major models and frameworks of memory and whether they are compatible with the definition of unconscious episodic memory as defined by the processing-based-memory model.

### **1.5.1 The memory models proposed by Tulving and Squire**

The processing-based-memory model suggests that episodic memory can form at both conscious and unconscious levels (Henke 2010). This idea, is contrary to Squire's model (Squire, Stark et al. 2004) and Tulving's model (Tulving 2002) in which episodic memory is confined to conscious (declarative) memory of events. But, there are also significant similarities between these models. For example, according to the processing-based-memory model, episodic memory has different processing characteristics compared with semantic memory and hence is classified as a separate memory category (Henke 2010). In this regard, the processing-based-memory model is compatible with Squire's model and Tulving's model since both consider episodic memory and semantic memory as separate categories of memory. In addition, all of these models suggest that different neural substrates mediate different categories of memory. They specifically regard the hippocampus as the main brain area involved in episodic memory (Tulving 2002, Squire, Stark et al. 2004, Henke 2010). However, even though the idea of episodic memory as a separate memory system is compatible with the original models of Tulving and Squire, extending the model to encompass unconscious memory is a new hypothesis proposed by the processing-based memory model (Henke 2010).

### **1.5.2 The memory model proposed by Atkinson and Shiffrin**

The multi-store model is the other major memory model that is proposed by Atkinson and Shiffrin in 1968 (Atkinson and Shiffrin 1968). According to the multi-store model, memory is divided into several components including sensory memory, short term memory and long term memory. Sensory information first registers in the sensory memory. The information then moves to a short term store in which it is processed by working memory and then moves to a long term store. In their model, they did not confine the long term memory only to conscious encoding and retrieval of events. The only part of the multi-store model that requires conscious attention is the intentional rehearsal required for working memory performance. According to the processing-based memory model, episodic memory can form rapidly by a single exposure to an event (Henke 2010). Hence, the intentional rehearsal of working memory (which is the only part of the multi-store model that necessarily requires conscious attention) is not a necessary component of episodic memory. In this regard, the possibility of formation of an unconscious episodic memory is not basically incompatible with the multi-store memory model. Thus, if sensory information can be processed at an unconscious level, there is a chance that this information might form a long term memory without conscious awareness. Basically, the multi-store model is not incompatible with the idea of unconscious episodic memory.

### **1.5.3 The levels of processing framework**

The levels of processing (LOP) is one of the major memory frameworks that is often used to understand episodic memory (Galli 2014). According to the LOP ( Craik and Lockhart 1972) framework, depth of processing is an important factor that determines the nature of memory processing. In this regard, for a stimulus to form a long term memory it requires deep and



elaborate processing. The LOP framework does not limit the possibility of deep encoding only to conscious events. Hence according to the LOP framework it is possible that stimuli are encoded at a deep level without conscious awareness. According to the processing-based-memory model, episodic memory is a flexible memory of associations (Henke 2010). Associative and contextual processing of stimuli induces a deeper encoding compared with processing of a single stimulus out of context. In this regard, the processing-based-memory model is compatible with the LOP framework since both of them consider deep processing as an important factor for formation of long term episodic memory. In this thesis, I investigate the possibility of associative and contextual encoding of faces in the context of scenes. In other words, I investigate the possibility of deep encoding of visual stimuli at an unconscious level that is compatible with the LOP framework.

#### **1.5.4 The process dissociation procedure framework**

The process dissociation procedure (PDP) is another major memory framework (Jacoby 1991) that was introduced by Jacoby in 1991. According to the PDP framework, recognition memory is comprised of two different processes based on the role of intention. One process is intentional memory or recollection that requires full attention, and is hampered when attention is divided. The other process is automatic memory or familiarity and not affected by manipulation of attention (e.g. using distractors to manipulate attention). Hence, the PDP framework explains the difference between familiarity and conscious recollection based on their reliance on attention.

According to the processing-based-memory model, unconscious episodic memory relies on the same neural substrate and also shares the same processing characteristics as conscious episodic memory (conscious recollection) (Henke 2010). In this regard, it is possible that unconscious

episodic memory, like conscious episodic memory, benefits from full attention during encoding. In this thesis, I design experiments such that participants can have their attention on the location where masked stimuli are presented in order to boost unconscious episodic encoding. I ensure that participants pay attention to the location of the masked stimuli by responding to direction of a bar flashing on the same location. On the other hand, the unconscious nature of the experiments in this thesis makes it impossible to have the participants' full attention on the unconscious encoding and retrieval of the stimuli. For this purpose, in my experiments, unconscious memory task is concealed within another task that participants intentionally perform (attentional task during the encoding and free-viewing during the retrieval). This reduces the possibility of conscious perception and hence conscious encoding of the stimuli. But, the lack of intentionality and full attention would hamper the unconscious memory performance in my experiments, inevitably. In this way, I propose that the unconscious memory performance in my experiments is weaker than similar tasks of conscious episodic memory that benefit from full attention. Overall, the PDP framework is not in nature, incompatible with the idea of unconscious episodic memory. In addition, it can provide insight about unconscious memory performance in my experiments.

### **1.5.5 The transfer appropriate processing framework**

The transfer appropriate processing (TAP) (Roediger, Weldon et al. 1989, Franks, Bilbrey et al. 2000), is a framework which incorporates dissociation between explicit and implicit memory. According to this framework, explicit memory (e.g. recollection) is conceptually driven while implicit memory (e.g. priming) is data driven (Roediger, Weldon et al. 1989). As they described in the TAP framework, conceptually driven memory means that variables like levels of processing or elaborative processing of stimuli enhance explicit memory performance.

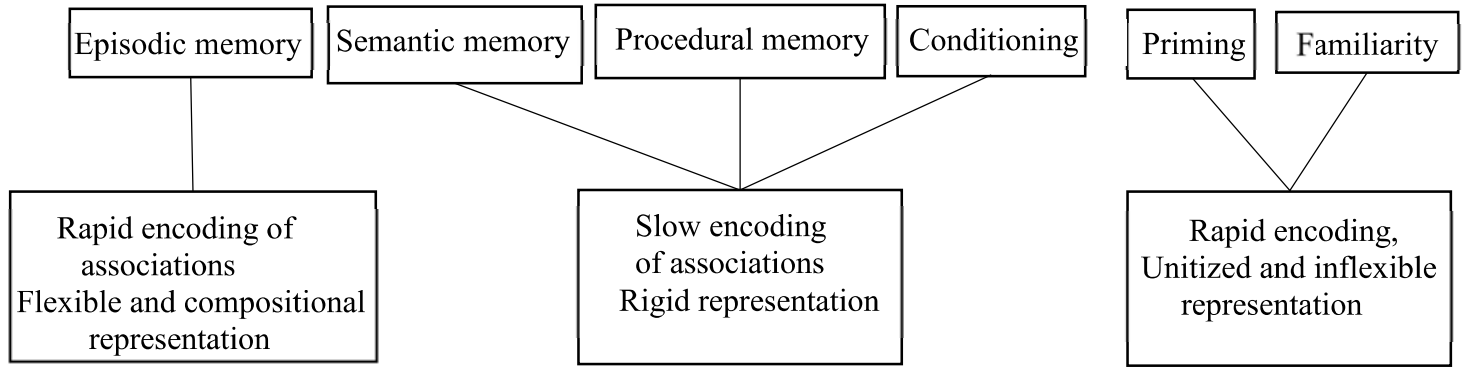
On the contrary, the data driven nature of implicit memory means that conceptual processing has little effect on implicit memory other than variation of the “*surface features*” of stimuli (e.g. words versus pictures or auditory versus visual stimuli) that affect implicit memory performance .

As mentioned earlier, according to the processing-based-memory model, the same neural substrate that mediates conscious episodic memory also mediates unconscious episodic memory (Henke 2010). In addition, both conscious and unconscious forms of episodic memory share the same processing characteristics (Henke 2010). According to the TAP framework explicit memory (e.g. conscious episodic memory) is conceptually driven (Roediger, Weldon et al. 1989). Hence, regarding the processing-based-memory model, one can expect that unconscious episodic memory like conscious episodic memory (explicit memory) is conceptually driven and hence sensitive to levels of processing. Hence, deep contextual processing of stimuli during encoding might benefit unconscious episodic memory. As mentioned earlier, this idea about deep processing is compatible with my experiments in this thesis. In this regard, the TAP framework is not incompatible with the possibility of the formation of episodic memory without conscious awareness.

The major memory models and frameworks discussed above can provide precious insight about unconscious episodic memory. The idea that episodic memory is a separate memory category that is mainly mediated by hippocampus was initially proposed by the Tulving model and the Squire model and is also compatible the processing-based-memory model. Memory frameworks like the TAP, PDP or the LOP, are not incompatible with the notion of unconscious episodic memory and can give us further insight about performance of unconscious episodic memory in different conditions.

## **1.6 Viewing behaviour and memory**

In this section I explain why viewing behaviour is the most important behavioural measure to reflect unconscious episodic memory. Vision is primate's most dominant sensory modality. This can be illustrated by the fact that monkeys do not need any training or reward for viewing pictures and they naturally prefer pictures to blank screens (Humphrey 1972, Wilson and Goldman-Rakic 1994). Primates view their environment through fixations and saccades. Saccades are rapid and ballistic eye movements between fixations. Saccades can be initiated voluntarily but they also happen automatically when we are looking at a target (Purves, Augustine et al. 2001). During each fixation the high acuity part of retina receives visual information from a small area of environment (about two degrees of visual angle from the centre of gaze) (Meister and Buffalo 2016). Hence our uniform visual perception is made of discrete bits of information received from the fixations that we make between saccades. Viewing behaviour has been the most important behaviour measure in the field of unconscious visual episodic memory. To the best of my knowledge, all the studies in this field have relied on the modulation of viewing behaviour as an indication of unconscious retrieval (Ryan, Althoff et al. 2000, Ryan and Cohen 2004, Hannula, Ryan et al. 2007, Hannula and Ranganath 2009, Wuethrich, Hannula et al. 2018). Viewing behaviour can be used to investigate memory when verbal reports or introspective judgements are not reliable (e.g. young children, elderly people, severely amnesic patients or unconscious retrieval).



**Figure 2.** The processing-based-memory model. This model classifies memory based on different processing modes including the speed of encoding, formation of associations, flexibility and compositionality of the encoded associations. According to this model, episodic memory includes rapid encoding of associations that forms a flexible and compositional representation. Semantic memory, procedural memory and conditioning share similar processing characteristics including slow encoding of associations that leads to a rigid and inflexible representation. Priming and familiarity include rapid encoding of a single item or a unitized item as a whole without flexibility of its parts (Henke 2010).

It has been suggested that, number of fixations is the most important eye tracking measure that can predict the strength of subsequent retrieval (Meister and Buffalo 2016). Successful encoding drops drastically when fixations are more than two visual degrees distant from the position of critical details of a picture that should be retrieved later (Nelson and Loftus 1980). This means that fixating directly on a target is very important for successful encoding and subsequent retrieval. When a picture is viewed for a fixed amount of time, a higher number of fixations on the picture during encoding predicts a better performance during retrieval (Loftus 1972). Duration of fixations or total viewing time may not be as crucial as number of fixations in predicting memory performance. In the same experiment, Loftus found that the total viewing

time with the same number of fixations did not predict the strength of retrieval. One may conclude that relatively high number of fixations with short duration on many parts of a picture could strengthen memory more than few fixations with long duration on few parts of the same image. Hence parts of an image that have higher number of fixations are more likely to be retrieved later (Pertsov, Avidan et al. 2009). Even though both of the number of fixations and the total viewing time are used in previous studies as an index of memory, these findings can provide support for the idea that number of fixations can be a better predictor of retrieval compared with total viewing time. Pupil size is another eye tracking measure that has been reported to accompany memory retrieval. Pupil dilation has been reported during the recognition of old items compared with new items (Heaver and Hutton 2011, Otero, Weekes et al. 2011, Kucewicz, Dolezal et al. 2018). Overall, these findings emphasise that viewing behaviour provides a reliable measure of memory. In this thesis, I used different eye tracking measures (i.e. number of fixations, total viewing time and pupil size) as a reflective of unconscious retrieval of episodic memory.

One of the paradigms that is commonly used to investigate viewing behaviour during memory retrieval is free-viewing (Meister and Buffalo 2016). The position of fixations during viewing a picture is not random. Fixations are guided by visual characteristics of a picture (brightness, contrast, hue, etc.) and also by viewer's memory or previous knowledge of the picture. For example, viewers fixate more and with longer duration on unusual parts of images that violate their expectations based on previous knowledge (e.g. an octopus in a yard) (Mackworth and Morandi 1967, Loftus and Mackworth 1978). Participants fixate less and also spend less viewing time on the repeated images that do not have novelty and new information compared with new images (Smith and Squire 2008, Crutcher, Calhoun-Haney et al. 2009). These findings suggest that viewing behaviour during free-viewing can reflect memory retrieval. In this thesis, I investigated different eye tracking measures during the free viewing of the target

and the distractor. I expected to see a modulation in the eye tracking measures on the unconsciously retrieved items (target) compared with the distractors.

## **1.7 Role of viewing behaviours in reflecting memory retrieval mediated by MTL**

Clinical studies have provided evidence for the role of medial temporal lobe (MTL) structures in modulation of viewing behaviour during memory retrieval. It has been shown that contrary to normal participants, patients with MTL damage do not show a significant modulation in number of fixations or total viewing time while looking at old associations compared with new associations (McKee and Squire 1993, Smith and Squire 2008). One of the principle symptoms of patients with Alzheimer's disease is deficit in episodic memory that has been related to pathological changes in hippocampus and entorhinal cortices. It has also been shown that patients with Alzheimer's disease show diminished modulation of pupil size and fixation numbers during the retrieval of objects in scenes compared with healthy individuals (Dragan, Leonard et al. 2017). In another study, amnesic patients with MTL damage freely viewed novel and repeated scenes (Smith and Squire 2008). Patients with MTL damage, contrary to healthy adults, failed to show any decrement in their number of fixations on the repeated images compared with novel images (Smith and Squire 2008). It was consistent with the findings of the study by Hannula et al in which the modulation of viewing behaviour on the target compared with the distractor was absent in patients with MTL damage (Hannula, Ryan et al. 2007). More evidence come from animal studies. For example the firing rate of hippocampal neurons shows a significant correlation with the total viewing time during memory retrieval (Jutras and Buffalo 2010). These findings provide evidence for the important role of viewing behaviour in reflecting episodic memory mediated by MTL at conscious level.

Viewing behaviour has also been used to reflect unconscious visual episodic memory. The hippocampal activation during viewing the cue predicted the proportion of time allocated to view the target compared with the distractor face. This correlation was also found in the absence of conscious retrieval (Hannula and Ranganath 2009). The other example comes from a study by Ryan et al (2000). During this study, participants freely viewed novel scenes and the same scenes with manipulations (e.g. a part of image was deleted, added or changed position). Participants showed an increment in the number of fixations on, and the total time viewing, the manipulated part of the image compared with the same part of the original image, while they were unaware of the change (Ryan, Althoff et al. 2000). Since the manipulation occurred through changing one part of the scene in relation to other parts, the unconscious retrieval of associative memory played a dominant role in modulation of viewing behaviour. They showed that amnesic patients did not show any modulation in viewing behaviour during the free viewing of the manipulated scenes compared with the novel scenes. But it is worth considering that in their experiment, size and area of brain damage was not reported (Ryan, Althoff et al. 2000). These findings provide support for the dominant role of viewing behaviour in reflecting unconscious episodic memory mediated by MTL.

In chapter 3, I used different eye tracking measures in combination with fMRI to test whether the MTL, particularly the hippocampus, is involved in unconscious encoding and subsequent unconscious retrieval of visual episodic memory. Since both of the MTL activation and viewing behaviour reflect unconscious episodic memory, I also expected to see a correlation between these measures provoked by unconscious episodic memory.



## **1.8 Visual attention toward memory in the absence of conscious awareness**

The idea that viewing behaviour can be modulated in the absence of consciousness comes from attention literature. For example it has been shown that task irrelevant stimuli that appear suddenly can trigger eye movements toward their location. This oculomotor capture happens even when the participants make volitional effort to prevent them and in the absence of conscious awareness (Kramer, Hahn et al. 2000, Belopolsky, Kramer et al. 2008). Studying literature about modulation of visual attention in the absence of consciousness can be very beneficial in understanding the mechanism for modulation of viewing behaviour by unconscious episodic memory retrieval.

Some studies in the field of attention show that previous memory can guide visual attention in the absence of conscious awareness. For example, in priming of pop-out, participants are faster to find a target when either the feature or the location is repeated, even if they are not aware of having seen it previously (Maljkovic and Nakayama 2000). The participants also make quicker and more accurate saccades on an odd target with similar colour as previous trials (McPeck, Maljkovic et al. 1999). The context in which an object is once viewed can also guide the deployment of visual attention and saccadic eye movements. During visual search for a target among distractors, repetition of the same configuration of the distractors and the target in the same position facilitates performance. This is known as ‘contextual cueing’ and facilitates visual search even when participants are not instructed to memorize the context (Chun and Jiang 1998). In another contextual cueing experiment, the participants were asked whether they recognized the contextual configurations. The participants’ performance was at chance level during this recognition test. The authors concluded that modulation of visual attention by the repetition of the context does not require the conscious retrieval of the context and was driven

by implicit (unconscious) memory (Chun and Jiang 1998). Overall, these studies indicate that modulation of visual attention by memory can lead to modulation of viewing behaviour.

Contextual cueing demonstrates an effect of memory on attention and eye movements in the absence of conscious retrieval. It does not, however, test the flexibility of the memory, which the processing-based-memory model posits is a key feature of episodic memory. Other studies in the field of unconscious episodic memory have shown that unconscious retrieval of a flexible memory can modulate eye movements (Ryan and Cohen 2004, Hannula, Ryan et al. 2007, Hannula and Ranganath 2009). As described earlier, in the study by Ryan et al, participants showed a modulation in viewing the manipulated parts of the scenes compared with the same parts in the original scenes without conscious awareness of the manipulation (Ryan, Althoff et al. 2000). Unconscious change detection in a scene means that the stored memory of that scene is used to guide the viewing behaviour. During free viewing of a previously encoded image, visual information is compared with the stored memory of that image. The result of this comparison then affects the visual attention and the viewing behaviour. These processes can occur without being accessible to consciousness and verbal report. These findings suggest that episodic memory retrieval can modulate visual attention and hence viewing behaviour without conscious awareness.

## **1.9 Brain areas that control viewing behaviour during unconscious retrieval of episodic memory**

Decades of research have revealed that where we look is modulated by what we remember. The models of oculomotor guidance acknowledge two mechanisms for guidance of saccade

during viewing. According to these models, the selection of saccades is based on characteristics of the stimuli (colour, luminance etc.) combined on previous knowledge and expectations about the behavioural saliency of the stimuli. The final selection of a spatial location for a saccade is determined by the outcome of the competition between these two forces (Findlay and Walker 1999, Itti and Koch 2000, Hamker 2006).

The underlying neural network through which the hippocampus-mediated memory modulates viewing behaviour, however, is a matter of debate (Meister and Buffalo 2016, Ryan, Shen et al. 2019). There are many brain areas that are involved in controlling eye movements in primates. Different oculomotor areas are involved in different aspects of control of viewing behaviour. In 2019, Ryan and her colleagues reviewed the literature with a focus on the relationship between oculomotor control and hippocampal memory (Ryan, Shen et al. 2019). According to their review, frontal eye field (FEF), superior colliculus (SC) and intra-parietal area are mostly involved in tasks that provoke eye movements based on the visual saliency of the stimuli. In contrast, dorsolateral prefrontal cortex, anterior cingulate cortex and supplementary eye field are mostly reported in tasks that involve goal driven, cognitive control of saccades via top-down modulation of FEF and SC (Ryan, Shen et al. 2019). They concluded in their review that there are many brain areas that could be possible candidates for receiving input from the hippocampus for oculomotor control. The question that limits my search is which brain area is functionally relevant for the modulation of viewing behaviour by unconscious episodic memory.

To investigate modulation of viewing behaviour toward an unconsciously retrieved image, one needs to be able to rule out saliency of the visual characteristics of that image (e.g. color, contrast etc.) as an alternative explanation. In addition, unconscious retrieval during free-viewing means that the retrieval is not driven by any goal for retrieval and happens involuntarily in the presence of a cue. This way the neural networks involved in saliency of

stimuli or top-down control based on goal of the task should not be involved in modulation of viewing behaviour by unconscious episodic memory.

As mentioned in previous section modulation of visual attention by memory can lead to modulation of viewing behaviour. In their attention-to-memory model, Cabeza et al described how episodic memory modulates visual attention and viewing behaviour (Cabeza, Ciaramelli et al. 2008). According to this model, involuntary episodic memory retrieval generates internal information that interacts with bottom-up visual attention (Cabeza, Ciaramelli et al. 2008). It may seem a bit confusing since bottom-up attention is known to be involved in guiding visual attention based on the saliency of visual stimuli (Katsuki and Constantinidis 2014). As discussed before the saliency of visual stimuli should not have a dominant role in guiding visual attention by unconscious retrieval. But as Cabeza et al described in their model *“if one defines bottom-up attention as attention driven by incoming information, regardless of its source”* then involvement of bottom-up attention in modulation of attention by unconscious episodic memory will be clear.

It is well established that there are two cortical pathways of visual attention toward visual stimuli: the dorsal frontoparietal network and the ventral frontoparietal network (Corbetta and Shulman 2002). The dorsal frontoparietal attentional network is considered to mediate top-down control of attention toward visual stimuli based on current goals and expectations. It has been proposed that FEF, IPS, and dorsal frontal cortex are part of this network (Corbetta, Patel et al. 2008). The ventral frontoparietal network instead responds to the salient stimuli that suddenly grab attention in a bottom-up fashion, without previous expectation. This ventral frontoparietal network mostly involves the inferior parietal areas, inferior frontal areas and also parts of temporal gyrus (Corbetta and Shulman 2002, Corbetta, Patel et al. 2008). According to the attention-to-memory model during involuntary retrieval hippocampus interacts with ventral parietal areas (part of the ventral frontoparietal network) to modulate visual attention

(Cabeza, Ciaramelli et al. 2008) . As Cabeza et al mentioned in their review, ventral parietal cortex, especially the supra-marginal gyrus, is considered an interface between episodic memory and bottom-up attention (Cabeza, Ciaramelli et al. 2008). They also suggest that it is plausible that the ventral frontal cortex that is a part of the ventral frontoparietal network, plays a part in attention to involuntary retrieval of episodic memory but this requires more evidence (Corbetta, Patel et al. 2008). In this regard previous literature suggests a dominant role for the interaction between hippocampus and ventral parietal cortex in modulation of visual attention by unconscious episodic retrieval.

To the best of my knowledge, the attention-to-memory model is the only model that suggests a neural mechanism for modulation of visual attention and hence viewing behaviour by unconscious episodic memory retrieval. In chapter 4, using a functional connectivity method, I tested whether unconscious retrieval of episodic memory influences the interaction between the main brain areas involved in episodic memory (hippocampus) and bottom-up attention (ventral frontoparietal network particularly ventral parietal area). I also investigated whether such an interaction modulates viewing behaviour during unconscious retrieval.

### **1.10 The confounding effect of attentional bias on viewing behaviour**

Apart from memory, visual attention can be modulated by an inherent bias in our attention system toward the left visual field (Siman-Tov, Mendelsohn et al. 2007, Newman, Loughnane et al. 2017). The initial observations that supported this idea came from unilateral neglect syndrome. Patients with unilateral neglect are not able to attend to the stimuli contralateral to the side of their brain lesion. This syndrome is more common and severe when the lesion is in the right compared with left hemisphere (Stone, Halligan et al. 1993). This has since been backed up by research in healthy participants showing that they pay more attention to the

stimuli in the left visual hemi-field than on the right, which can manifest in better performance and faster response times for targets in the left compared with the right hemi-field (Nicholls, Bradshaw et al. 1999, Nicholls, Hobson et al. 2017). Hence it is important to investigate the possible influence of attentional bias in modulation of viewing behaviour during unconscious retrieval.

Leftward attentional bias is related to the dominance of the right hemisphere over the left hemisphere in processing of visuospatial attention (de Schotten, Dell'Acqua et al. 2011, Nicholls, Hobson et al. 2017). In a study using diffusion imaging tractography, De schotten at al (de Schotten, Dell'Acqua et al. 2011) showed a higher volume of tracts in the frontoparietal network of attention in the right hemisphere compared with the left hemisphere. Human frontoparietal connections include three components including dorsal, middle and ventral superior longitudinal fasciculus (SLF) (de Schotten, Dell'Acqua et al. 2011). In their study, this right lateralized distribution of tracts was seen specifically in the ventral SLF. They saw a trend of small right laterality in the middle SLF and the distribution of tracts was bilateral in the dorsal SLF (de Schotten, Dell'Acqua et al. 2011). The size of this structural asymmetry in attentional network also correlated with the degree of the attentional bias in visuospatial tasks (de Schotten, Dell'Acqua et al. 2011). As mentioned earlier ventral frontoparietal network is involved in bottom-up attentional processing (Corbetta, Patel et al. 2008). Hence the tractography findings show that ventral frontoparietal network that is responsible for bottom-up attention is largely right lateralized. Regarding the important role of bottom up attention in modulation of viewing behaviour by unconscious retrieval during free-viewing, the attentional bias can be an important confounding factor in my experiments.

The size of the leftward attentional bias is not constant in each individual. It has been shown that experimental variables that increase the right hemisphere dominance over the left hemisphere can increase the size of leftward attentional bias (Cattaneo, Silvanto et al. 2009,

Ricci, Salatino et al. 2012, Petitet, Noonan et al. 2015). Trans-cranial magnetic stimulation over the right inferior parietal areas, including the angular gyrus or the supramarginal gyrus, reduces or inverts the leftward attentional bias (Cattaneo, Silvanto et al. 2009, Ricci, Salatino et al. 2012, Petitet, Noonan et al. 2015). Similarly, a reduction in right hemisphere dominance/resources in attentional processing with aging has also been proposed to explain a reduction in the leftward bias with age (Benwell, Thut et al. 2014). It has also been shown that engagement in tasks that enhance the right hemisphere dominance over the left hemisphere can increase the leftward visual bias. For example using the left hand (Sampaio and Chokron 1992, McCourt, Freeman et al. 2001) or the left eye (McCourt, Garlinghouse et al. 2001) or presentation of the stimuli in the left visual field (Bultitude and Aimola Davies 2006) increases the leftward attentional bias. These findings suggest that engagement in tasks that increase the right hemisphere dominance over the left hemisphere could increase the leftward attentional bias.

A growing body of evidence suggests that right hemisphere is specialized for face processing (Kim, Andreasen et al. 1999, Nakamura, Kawashima et al. 2000, Schweinberger, Huddy et al. 2004, Kloth, Dobel et al. 2006, Yovel, Tambini et al. 2008, Gainotti 2013). This specialization has been used to explain why participants perform face recognition tasks with higher speed and accuracy when the faces are presented in the left visual hemi-field compared with the right hemifield (Rizzolatti, Umiltà et al. 1971, Hilliard 1973, Leehey and Cahn 1979, Gainotti 2013). According to brain imaging studies memory of novel faces is dominantly mediated by right MTL structures (Ranganath and D'Esposito 2001, Taylor, Mills et al. 2011, Von Der Heide, Skipper et al. 2013). Clinical studies also show that patients with right MTL lesions have a more severe deficit in retention of novel faces compared with patients with left MTL lesion (Crane and Milner 2002, Milner 2003). The face stimuli that were used in this thesis were novel to the participants. Hence, I assumed that interaction between right dominant facial memory of

the target and right dominant bottom-up attention during the free-viewing in my experiments could increase leftward attentional bias. Thus, if the target is in the left visual field this increment in the leftward attentional bias could increase the overall visual attention toward the target in the left. This idea was used in chapter 4, to investigate the correlation between the viewing behaviour on the target and the functional connectivity between the main brain areas involved in episodic memory and bottom-up attention.

## **1.11 Summary and Conclusion**

Despite its importance, very little is known about unconscious episodic memory of visual stimuli. The main focus of this thesis is investigating unconscious encoding and subsequent unconscious retrieval of complex visual associations. When verbal reports are not available or appropriate, eye tracking measures can be very beneficial in investigating unconscious episodic memory. Regarding the previous literature in this field I considered that modulation of different eye tracking measures during free-viewing can be a behavioural index of unconscious retrieval.

The MTL, particularly the hippocampus, are the main structures involved in conscious episodic memory. The processing-based-memory model posits that the same brain structures that mediate episodic memory at a conscious level also mediate episodic memory at an unconscious level. Whether these important structures mediate the unconscious encoding of episodically associated visual stimuli and their subsequent unconscious retrieval is yet to be tested.

Viewing behaviour has been the most important behavioural measure to investigate unconscious visual episodic memory. Despite its importance the underlying neural mechanism that modulates eye movements by unconscious episodic memory is not yet known. Regarding the attention-to-memory model, I hypothesized that modulation of visual attention by unconscious episodic memory is mediated by the interaction of MTL with the attentional



network involved in bottom-up attention especially inferior parietal regions. It is also important to consider that interaction between right dominant facial memory of the target and right dominant bottom-up attention can increase the leftward attentional bias.

Studying the possibility of unconscious encoding and the subsequent unconscious retrieval of complex visual associations using eye tracking measures can shed light on the capacity of unconscious episodic memory at an unconscious level. Investigating the main brain areas that mediate this unconscious memory and how these areas interact with visual attention areas to modulate viewing behaviour can be beneficial in better understanding of unconscious episodic memory. This understanding can also help us in developing clinical and non-invasive tools in future for disorders related to unconscious episodic memory.

## **1.12 Approach and overview of experimental chapters**

The main focus of this thesis is on unconscious encoding and subsequent unconscious retrieval of visual associations in a way that complies with the characteristics of episodic memory according to the processing-based-memory model. According to this model episodic memory is characterised by rapid encoding of associations and flexible retrieval. I used eye tracking, fMRI and functional connectivity methods to test for the existence of such a memory and to explore its behavioural and neural attributes.

**Chapter 2.** In chapter 2, I investigated whether an episodic memory of complex visual associations can be encoded and retrieved at unconscious level. For this purpose, face-scene associations were masked from conscious awareness during encoding. During retrieval, the viewing behaviour of the participants was investigated using different eye tracking measures.

**Chapter 3.** In chapter 3, I investigated whether the main brain areas known to be involved in conscious episodic memory are also involved in unconscious encoding and subsequent

unconscious retrieval of episodic associations. I used fMRI to test my hypothesis about the involvement of deep brain structures like MTL and hippocampus in unconscious visual episodic memory. I also used eye tracking measures to investigate the relationship between viewing behaviour and MTL activation provoked by unconscious retrieval following unconscious encoding.

**Chapter 4.** In this chapter, I investigated the underlying neural mechanism for modulation of viewing behaviours by unconscious visual episodic memory. I tested whether the interaction between the main areas involved in episodic memory and bottom-up attentional had a dominant role in modulation of viewing behaviour during the unconscious retrieval of episodic associations. I performed a functional connectivity analyses on the fMRI data from chapter 3 to investigate functional connectivity between MTL and inferior parietal regions and its relationship with viewing behaviour during unconscious retrieval.

**Chapter 5.** In my final chapter, I presented an overview of the main findings of each chapter and discussed their implications. I also discussed the limitations and challenges of the research in each chapter and proposed future directions.

## 1.13 References

Atkinson, R. C. and R. M. Shiffrin (1968). Human Memory: A Proposed System and its Control Processes. Psychology of Learning and Motivation. K. W. Spence and J. T. Spence, Academic Press. **2**: 89-195.

Belopolsky, A. V., A. F. Kramer and J. Theeuwes (2008). "The role of awareness in processing of oculomotor capture: evidence from event-related potentials." J Cogn Neurosci **20**(12): 2285-2297.

Benwell, C. S., G. Thut, A. Grant and M. Harvey (2014). "A rightward shift in the visuospatial attention vector with healthy aging." Front Aging Neurosci **6**: 113.

Bultitude, J. H. and A. M. Aimola Davies (2006). "Putting attention on the line: investigating the activation-orientation hypothesis of pseudoneglect." Neuropsychologia **44**(10): 1849-1858.

Cabeza, R., E. Ciaramelli, I. R. Olson and M. Moscovitch (2008). "The parietal cortex and episodic memory: an attentional account." Nat Rev Neurosci **9**(8): 613-625.

Cabeza, R., E. Ciaramelli, I. R. Olson and M. Moscovitch (2008). "The parietal cortex and episodic memory: an attentional account." Nature reviews. Neuroscience **9**(8): 613-625.

Cabeza, R., F. Dolcos, R. Graham and L. Nyberg (2002). "Similarities and differences in the neural correlates of episodic memory retrieval and working memory." Neuroimage **16**(2): 317-330.

Cattaneo, Z., J. Silvanto, A. Pascual-Leone and L. Battelli (2009). "The role of the angular gyrus in the modulation of visuospatial attention by the mental number line." Neuroimage **44**(2): 563-568.

Chun, M. M. and Y. Jiang (1998). "Contextual Cueing: Implicit Learning and Memory of Visual Context Guides Spatial Attention." Cognitive Psychology **36**(1): 28-71.

Clark, R. E. and L. R. Squire (1998). "Classical conditioning and brain systems: the role of awareness." Science **280**(5360): 77-81.

Corbetta, M., G. Patel and G. L. Shulman (2008). "The reorienting system of the human brain: from environment to theory of mind." Neuron **58**(3): 306-324.

Corbetta, M. and G. L. Shulman (2002). "Control of goal-directed and stimulus-driven attention in the brain." Nat Rev Neurosci **3**(3): 201-215.

Craik, F. I. M. and R. S. Lockhart (1972). "Levels of processing: A framework for memory research." Journal of Verbal Learning and Verbal Behavior **11**(6): 671-684.

Crane, J. and B. Milner (2002). "Do I know you? Face perception and memory in patients with selective amygdalo-hippocampectomy." Neuropsychologia **40**(5): 530-538.

Crutcher, M. D., R. Calhoun-Haney, C. M. Manzanares, J. J. Lah, A. I. Levey and S. M. Zola (2009). "Eye tracking during a visual paired comparison task as a predictor of early dementia." Am J Alzheimers Dis Other Demen **24**(3): 258-266.

Daselaar, S. M., M. S. Fleck, S. E. Prince and R. Cabeza (2006). "The medial temporal lobe distinguishes old from new independently of consciousness." J Neurosci **26**(21): 5835-5839.

de Schotten, M. T., F. Dell'Acqua, S. J. Forkel, A. Simmons, F. Vergani, D. G. M. Murphy and M. Catani (2011). "A lateralized brain network for visuospatial attention." Nature Neuroscience **14**(10): 1245-1246.

Degonda, N., C. R. Mondadori, S. Bosshardt, C. F. Schmidt, P. Boesiger, R. M. Nitsch, C. Hock and K. Henke (2005). "Implicit associative learning engages the hippocampus and interacts with explicit associative learning." Neuron **46**(3): 505-520.

Dragan, M. C., T. K. Leonard, A. M. Lozano, M. P. McAndrews, K. Ng, J. D. Ryan, D. F. Tang-Wai, J. S. Wynn and K. L. Hoffman (2017). "Pupillary responses and memory-guided visual search reveal age-related and Alzheimer's-related memory decline." Behavioural Brain Research **322**: 351-361.

Duss, S. B., T. P. Reber, J. Hanggi, S. Schwab, R. Wiest, R. M. Muri, P. Brugger, K. Gutbrod and K. Henke (2014). "Unconscious relational encoding depends on hippocampus." Brain **137**(Pt 12): 3355-3370.

Findlay, J. M. and R. Walker (1999). "A model of saccade generation based on parallel processing and competitive inhibition." Behav Brain Sci **22**(4): 661-674; discussion 674-721.

Foot, N. C. and E. B. Foot (1932). "A Technique of Silver Impregnation for General Laboratory Purposes." The American journal of pathology **8**(2): 245-254.241.

Franks, J. J., C. W. Bilbrey, K. G. Lien and T. P. McNamara (2000). "Transfer-appropriate processing (TAP) and repetition priming." Mem Cognit **28**(7): 1140-1151.

Gainotti, G. (2013). "Laterality effects in normal subjects' recognition of familiar faces, voices and names. Perceptual and representational components." Neuropsychologia **51**(7): 1151-1160.

Galli, G. (2014). "What makes deeply encoded items memorable? Insights into the levels of processing framework from neuroimaging and neuromodulation." Frontiers in psychiatry **5**: 61-61.

Gigerenzer, G. and W. Gaissmaier (2011). "Heuristic decision making." Annu Rev Psychol **62**: 451-482.

Hamker, F. H. (2006). "Modeling feature-based attention as an active top-down inference process." Biosystems **86**(1-3): 91-99.

Hannula, D. E. and C. Ranganath (2009). "The eyes have it: hippocampal activity predicts expression of memory in eye movements." Neuron **63**(5): 592-599.

Hannula, D. E., J. D. Ryan, D. Tranel and N. J. Cohen (2007). "Rapid onset relational memory effects are evident in eye movement behavior, but not in hippocampal amnesia." J Cogn Neurosci **19**(10): 1690-1705.

Heaver, B. and S. B. Hutton (2011). "Keeping an eye on the truth? Pupil size changes associated with recognition memory." Memory **19**(4): 398-405.

Henke, K. (2010). "A model for memory systems based on processing modes rather than consciousness." Nat Rev Neurosci **11**(7): 523-532.

Hilliard, R. D. (1973). "Hemispheric Laterality Effects on a Facial Recognition Task in Normal Subjects." Cortex **9**(3): 246-258.

Humphrey, N. K. (1972). "'Interest' and 'pleasure': two determinants of a monkey's visual preferences." Perception **1**(4): 395-416.

Itti, L. and C. Koch (2000). "A saliency-based search mechanism for overt and covert shifts of visual attention." Vision Research **40**(10): 1489-1506.

Jacoby, L. L. (1991). "A process dissociation framework: Separating automatic from intentional uses of memory." Journal of Memory and Language **30**(5): 513-541.

Janiszewski, C. (1990). "The Influence of Print Advertisement Organization on Affect Toward a Brand Name." Journal of Consumer Research **17**(1): 53-65.

Jeneson, A., K. N. Mauldin, R. O. Hopkins and L. R. Squire (2011). "The role of the hippocampus in retaining relational information across short delays: the importance of memory load." Learning & memory (Cold Spring Harbor, N.Y.) **18**(5): 301-305.

Jutras, M. J. and E. A. Buffalo (2010). "Recognition memory signals in the macaque hippocampus." Proceedings of the National Academy of Sciences **107**(1): 401-406.

Katsuki, F. and C. Constantinidis (2014). "Bottom-up and top-down attention: different processes and overlapping neural systems." Neuroscientist **20**(5): 509-521.

Kent, C. D., G. A. Mashour, N. A. Metzger, K. L. Posner and K. B. Domino (2013). "Psychological impact of unexpected explicit recall of events occurring during surgery performed under sedation, regional anaesthesia, and general anaesthesia: data from the Anesthesia Awareness Registry." Br J Anaesth **110**(3): 381-387.

Kim, J. J., N. C. Andreasen, D. S. O'Leary, A. K. Wiser, L. L. B. Ponto, G. L. Watkins and R. D. Hichwa (1999). "Direct comparison of the neural substrates of recognition memory for words and faces." Brain **122**(6): 1069-1083.

Kirwan, C. B., Y. Shrager and L. R. Squire (2009). "Medial temporal lobe activity can distinguish between old and new stimuli independently of overt behavioral choice." Proc Natl Acad Sci U S A **106**(34): 14617-14621.

Kloth, N., C. Döbel, S. R. Schweinberger, P. Zwitserlood, J. Bolte and M. Junghofer (2006). "Effects of personal familiarity on early neuromagnetic correlates of face perception." Eur J Neurosci **24**(11): 3317-3321.

Knowlton, B. J., S. J. Ramus and L. R. Squire (1992). "Intact Artificial Grammar Learning in Amnesia: Dissociation of Classification Learning and Explicit Memory for Specific Instances." Psychological Science **3**(3): 172-179.

Kramer, A. F., S. Hahn, D. E. Irwin and J. Theeuwes (2000). "Age differences in the control of looking behavior: do you know where your eyes have been?" Psychol Sci **11**(3): 210-217.

Kucewicz, M. T., J. Dolezal, V. Kremen, B. M. Berry, L. R. Miller, A. L. Magee, V. Fabian and G. A. Worrell (2018). "Pupil size reflects successful encoding and recall of memory in humans." Scientific Reports **8**(1): 4949.

Kuriyama, K., M. Honma, T. Yoshiike and Y. Kim (2013). "Memory suppression trades prolonged fear and sleep-dependent fear plasticity for the avoidance of current fear." Scientific Reports **3**: 2227.

Leehey, S. C. and A. Cahn (1979). "Lateral asymmetries in the recognition of words, familiar faces and unfamiliar faces." Neuropsychologia **17**(6): 619-628.

Levy, D. A., C. E. L. Stark and L. R. Squire (2004). "Intact Conceptual Priming in the Absence of Declarative Memory." Psychological science **15**(10): 680-686.

Loftus, G. R. (1972). "Eye fixations and recognition memory for pictures." Cognitive Psychology **3**(4): 525-551.

Loftus, G. R. and N. H. Mackworth (1978). "Cognitive determinants of fixation location during picture viewing." J Exp Psychol Hum Percept Perform **4**(4): 565-572.

Lubke, G. H., C. Kerssens, R. Y. Gershon and P. S. Sebel (2000). "Memory formation during general anesthesia for emergency cesarean sections." Anesthesiology **92**(4): 1029-1034.

Mackworth, N. H. and A. J. Morandi (1967). "The gaze selects informative details within pictures." Perception & Psychophysics **2**(11): 547-552.

Maljkovic, V. and K. Nakayama (2000). "Priming of popout: III. A short-term implicit memory system beneficial for rapid target selection." Visual Cognition **7**(5): 571-595.

Mayes, A. R., J. S. Holdstock, C. L. Isaac, N. M. Hunkin and N. Roberts (2002). "Relative sparing of item recognition memory in a patient with adult-onset damage limited to the hippocampus." Hippocampus **12**(3): 325-340.

Mayes, A. R., J. S. Holdstock, C. L. Isaac, D. Montaldi, J. Grigor, A. Gummer, P. Cariga, J. J. Downes, D. Tsivilis, D. Gaffan, Q. Gong and K. A. Norman (2004). "Associative recognition in a patient with selective hippocampal lesions and relatively normal item recognition." Hippocampus **14**(6): 763-784.

McCourt, M. E., P. Freeman, C. Tahmahkera-Stevens and M. Chaussee (2001). "The influence of unimanual response on pseudoneglect magnitude." Brain Cogn **45**(1): 52-63.

McCourt, M. E., M. Garlinghouse and J. Butler (2001). "The influence of viewing eye on pseudoneglect magnitude." J Int Neuropsychol Soc **7**(3): 391-395.

McKee, R. D. and L. R. Squire (1993). "On the development of declarative memory." J Exp Psychol Learn Mem Cogn **19**(2): 397-404.

McPeck, R. M., V. Maljkovic and K. Nakayama (1999). "Saccades require focal attention and are facilitated by a short-term memory system." Vision Res **39**(8): 1555-1566.

Meister, M. L. R. and E. A. Buffalo (2016). "Getting directions from the hippocampus: The neural connection between looking and memory." Neurobiol Learn Mem **134 Pt A**: 135-144.

Milner, B. (2003). "Visual recognition and recall after right temporal-lobe excision in man." Epilepsy Behav **4**(6): 799-812.

Milner, B., S. Corkin and H. L. Teuber (1968). "Further analysis of the hippocampal amnesic syndrome: 14-year follow-up study of H.M." Neuropsychologia **6**(3): 215-234.



Mishkin, M., W. Suzuki, D. Gadian and V.-K. F (1997). "Hierarchical organization of cognitive memory. ." Philos Trans R Soc Lond B Biol Sci **352**(1360): 1461–1467.

Mychaskiw, G., 2nd, M. Horowitz, V. Sachdev and B. J. Heath (2001). "Explicit intraoperative recall at a Bispectral Index of 47." Anesth Analg **92**(4): 808-809.

Nakamura, K., R. Kawashima, N. Sato, A. Nakamura, M. Sugiura, T. Kato, K. Hatano, K. Ito, H. Fukuda, T. Schormann and K. Zilles (2000). "Functional delineation of the human occipito-temporal areas related to face and scene processing. A PET study." Brain **123** ( Pt 9): 1903-1912.

Nelson, W. W. and G. R. Loftus (1980). "The functional visual field during picture viewing." J Exp Psychol Hum Learn **6**(4): 391-399.

Newman, D. P., G. M. Loughnane, S. P. Kelly, R. G. O'Connell and M. A. Bellgrove (2017). "Visuospatial Asymmetries Arise from Differences in the Onset Time of Perceptual Evidence Accumulation." J Neurosci **37**(12): 3378-3385.

Nicholls, M. E., J. L. Bradshaw and J. B. Mattingley (1999). "Free-viewing perceptual asymmetries for the judgement of brightness, numerosity and size." Neuropsychologia **37**(3): 307-314.

Nicholls, M. E., A. Hobson, J. Petty, O. Churches and N. A. Thomas (2017). "The effect of cerebral asymmetries and eye scanning on pseudoneglect for a visual search task." Brain Cogn **111**: 134-143.

Nichols, E. A., Y.-C. Kao, M. Verfaellie and J. D. E. Gabrieli (2006). "Working memory and long-term memory for faces: Evidence from fMRI and global amnesia for involvement of the medial temporal lobes." Hippocampus **16**(7): 604-616.

Nielsen, J. (1958). Memory and Amnesia. Los Angeles, San Lucas.

Otero, S. C., B. S. Weekes and S. B. Hutton (2011). "Pupil size changes during recognition memory." Psychophysiology **48**(10): 1346-1353.

Pertsov, Y., G. Avidan and E. Zohary (2009). "Accumulation of visual information across multiple fixations." J Vis **9**(10): 2.1-12.

Petitot, P., M. P. Noonan, H. Bridge, J. X. O'Reilly and J. O'Shea (2015). "Testing the inter-hemispheric competition account of visual extinction with combined TMS/fMRI." Neuropsychologia **74**: 63-73.

Purves, D., G. Augustine and D. Fitzpatrick (2001). Neuroscience. Sunderland Sinauer Associates.

Ranganath, C. and M. D'Esposito (2001). "Medial temporal lobe activity associated with active maintenance of novel information." Neuron **31**(5): 865-873.

Reber, T. P., R. Luechinger, P. Boesiger and K. Henke (2012). "Unconscious relational inference recruits the hippocampus." J Neurosci **32**(18): 6138-6148.

Ricci, R., A. Salatino, X. Li, A. P. Funk, S. L. Logan, Q. Mu, K. A. Johnson, D. E. Bohning and M. S. George (2012). "Imaging the neural mechanisms of TMS neglect-like bias in healthy volunteers with the interleaved TMS/fMRI technique: preliminary evidence." Front Hum Neurosci **6**: 326.

Rissman, J., A. Gazzaley and M. D'Esposito (2008). "Dynamic adjustments in prefrontal, hippocampal, and inferior temporal interactions with increasing visual working memory load." Cereb Cortex **18**(7): 1618-1629.

Rizzolatti, G., C. Umiltà and G. Berlucchi (1971). "Opposite superiorities of the right and left cerebral hemispheres in discriminative reaction time to physiognomical and alphabetical material." Brain **94**(3): 431-442.

Roediger, H. L., M. S. Weldon and B. H. Challis (1989). Varieties of memory and consciousness: Essays in honour of Endel Tulving. Hillsdale, NJ, US, Lawrence Erlbaum Associates, Inc.

- Ryan, J. D., R. R. Althoff, S. Whitlow and N. J. Cohen (2000). "Amnesia is a deficit in relational memory." Psychol Sci **11**(6): 454-461.
- Ryan, J. D. and N. J. Cohen (2004). "The nature of change detection and online representations of scenes." J Exp Psychol Hum Percept Perform **30**(5): 988-1015.
- Ryan, J. D., K. Shen and Z. X. Liu (2019). "The intersection between the oculomotor and hippocampal memory systems: empirical developments and clinical implications." Ann N Y Acad Sci.
- Sampaio, E. and S. Chokron (1992). "Pseudoneglect and reversed pseudoneglect among left-handers and right-handers." Neuropsychologia **30**(9): 797-805.
- Schacter, D. L. and P. Graf (1986). "Preserved learning in amnesic patients: perspectives from research on direct priming." J Clin Exp Neuropsychol **8**(6): 727-743.
- Schweinberger, S. R., V. Huddy and A. M. Burton (2004). "N250r: a face-selective brain response to stimulus repetitions." Neuroreport **15**(9): 1501-1505.
- Shimamura, A. P. and L. R. Squire (1989). "Impaired priming of new associations in amnesia." J Exp Psychol Learn Mem Cogn **15**(4): 721-728.
- Siman-Tov, T., A. Mendelsohn, T. Schonberg, G. Avidan, I. Podlipsky, L. Pessoa, N. Gadoth, L. G. Ungerleider and T. Hendler (2007). "Bihemispheric Leftward Bias in a Visuospatial Attention-Related Network." The Journal of Neuroscience **27**(42): 11271-11278.
- Smith, C. N. and L. R. Squire (2008). "Experience-dependent eye movements reflect hippocampus-dependent (aware) memory." The Journal of neuroscience : the official journal of the Society for Neuroscience **28**(48): 12825-12833.
- Squire, L. R., C. E. Stark and R. E. Clark (2004). "The medial temporal lobe." Annu Rev Neurosci **27**: 279-306.

- Stone, S. P., P. W. Halligan and R. J. Greenwood (1993). "The Incidence of Neglect Phenomena and Related Disorders in Patients with an Acute Right or Left Hemisphere Stroke." Age and Ageing **22**(1): 46-52.
- Taylor, M. J., T. Mills and E. W. Pang (2011). "The development of face recognition; hippocampal and frontal lobe contributions determined with MEG." Brain Topogr **24**(3-4): 261-270.
- Tulving, E. (1972). Episodic and semantic memory. Organization of memory. Oxford, England, Academic Press: xiii, 423-xiii, 423.
- Tulving, E. (2002). "Episodic Memory: From Mind to Brain." Annual Review of Psychology **53**(1): 1-25.
- Tulving, E. (2002). "Episodic memory: from mind to brain." Annu Rev Psychol **53**: 1-25.
- Van Hoesen, G., D. N. Pandya and N. Butters (1975). "Some connections of the entorhinal (area 28) and perirhinal (area 35) cortices of the rhesus monkey. II. Frontal lobe afferents." Brain Res **95**(1): 25-38.
- Van Hoesen, G. W. and D. N. Pandya (1975). "Some connections of the entorhinal (area 28) and perirhinal (area 35) cortices of the rhesus monkey. III. Efferent connections." Brain Res **95**(1): 39-59.
- Vargha-Khadem, F., D. G. Gadian, K. E. Watkins, A. Connelly, W. Van Paesschen and M. Mishkin (1997). "Differential effects of early hippocampal pathology on episodic and semantic memory." Science **277**(5324): 376-380.
- Victor, M. and D. Agamanolis (1990). "Amnesia due to Lesions Confined to the Hippocampus: A Clinical-Pathologic Study." J Cogn Neurosci **2**(3): 246-257.
- Von Der Heide, R. J., L. M. Skipper and I. R. Olson (2013). "Anterior temporal face patches: a meta-analysis and empirical study." Front Hum Neurosci **7**: 17.

- Warrington, E. K. and L. Weiskrantz (1982). "Amnesia: a disconnection syndrome?" Neuropsychologia **20**(3): 233-248.
- Watkins, P. C., K. Vache, S. P. Verney, S. Muller and A. Mathews (1996). "Unconscious mood-congruent memory bias in depression." J Abnorm Psychol **105**(1): 34-41.
- Wilson, F. A. and P. S. Goldman-Rakic (1994). "Viewing preferences of rhesus monkeys related to memory for complex pictures, colours and faces." Behav Brain Res **60**(1): 79-89.
- Wuethrich, S., D. E. Hannula, F. W. Mast and K. Henke (2018). "Subliminal encoding and flexible retrieval of objects in scenes." Hippocampus **28**(9): 633-643.
- Yovel, G., A. Tambini and T. Brandman (2008). "The asymmetry of the fusiform face area is a stable individual characteristic that underlies the left-visual-field superiority for faces." Neuropsychologia **46**(13): 3061-3068.
- Zola-Morgan, S., L. R. Squire and D. G. Amaral (1986). "Human amnesia and the medial temporal region: enduring memory impairment following a bilateral lesion limited to field CA1 of the hippocampus." J Neurosci **6**(10): 2950-2967.
- Zust, M. A., P. Colella, T. P. Reber, P. Vuilleumier, M. Hauf, S. Ruch and K. Henke (2015). "Hippocampus is place of interaction between unconscious and conscious memories." PLoS One **10**(3): e0122459.



## **Chapter 2 - What can eye tracking tell us about unconscious memory of episodically associated visual stimuli?**

---

Department of Cognitive Science, Faculty of Human Sciences, Macquarie University, Sydney NSW 2109, Australia

## **What can eye tracking tell us about unconscious memory of episodically associated visual stimuli?**

### **2.1 Abstract**

According to the processing-based-memory model proposed by Henke, episodic memory is defined as rapid and flexible memory of associations over short or long retention times (Henke 2010). This model proposes that a memory with these characteristics can exist at both conscious and unconscious levels. In this study, I investigated whether unconscious encoding and retrieval of novel and complex visual associations complies with the processing-based-memory model. 32 healthy volunteers viewed novel face-scene associations that were masked from awareness during encoding. Subsequently, one of the encoded scenes was presented as a cue to provoke retrieval of its associated face. The participants then freely viewed two faces: the associated face (the ‘target’) and a face that had been presented with a different scene (the ‘distractor’). I excluded 12 participants who showed any sign of conscious perception of the masked face stimuli based on a separate awareness test, leaving 20 participants for the unconscious memory analysis. Because of the inherent bias toward left visual field in visuospatial processing and facial memory, I had a condition with target in the left and distractor in the right and a condition with target in the right and distractor in the left. I compared eye tracking measures on the targets and the distractors in each visual field separately. In the left visual field, participants fixated more on the target compared to the distractor, and had larger pupil sizes when looking at the target compared to the distractor. In the right visual field, there were no significant differences in the number of fixations or pupil size between the target and the distractor. The laterality of these effects is consistent with previous literature demonstrating a bias for visuospatial processing and memory for faces in



the left visual field. These findings support the view that encoding and retrieval of episodically associated visual stimuli can occur at an unconscious level.

## **2.2 Introduction**

In 2010, Henke proposed a processing-based-memory model which, instead of classifying memory based on consciousness, defined different memory types based on their processing characteristics (Henke 2010). This way a memory with characteristics of episodic memory could exist at both conscious and unconscious levels. This opened a new field of research in the unconscious encoding and unconscious retrieval of episodically associated stimuli (Degonda, Mondadori et al. 2005, Daselaar, Fleck et al. 2006, Kirwan, Shrager et al. 2009, Reber, Luechinger et al. 2012, Duss, Reber et al. 2014, Züst, Colella et al. 2015). Most of the studies in this field are focused on verbal associations. To the best of my knowledge, most of the studies on episodically associated visual stimuli have been limited to unconscious retrieval after conscious encoding (Ryan, Althoff et al. 2000, Ryan and Cohen 2004, Hannula, Ryan et al. 2007, Hannula and Ranganath 2009).

According to the processing-based-memory model, episodic memory is a compositional and flexible type of memory between associations that can form rapidly. A memory with these characteristics can be maintained for short or long retention times (Henke 2010). Compositionality of episodic memory means that individual elements and their associations that make the entire memory are stored independently. As a result, viewing separate elements of the memory as a cue can reactivate the whole memory of its associations, giving flexibility to the memory.

In a series of experiments, Hannula et al showed that unconscious retrieval of visual associations after their conscious encoding leads to modulation of viewing behaviour on the

target compared with the distractor (Hannula, Ryan et al. 2007, Hannula and Ranganath 2009). In their experiment participant consciously encoded complex visual associations (i.e. face-scene). During the retrieval phase they were cued by a scene before viewing the associate face (target) alongside a distractor face. They were instructed to choose the face that was associated with the scene. They found that in trials that the participants gave a wrong response, they still preferentially viewed the target face compared with the distractor. These findings provided support for the possibility of unconscious retrieval of complex visual associations after their conscious encoding.

In 2018, Wuethrich et al. investigated the possibility of unconscious encoding of spatial position of simple objects in grids inside scenes. In their study simple objects in grids were masked from consciousness during encoding. During the retrieval phase the unconsciously encoded object was presented outside the grid and the participants were instructed to put it inside the grid. Even though the participants' performance in this task was at chance level, the eye tracking data showed that they preferentially viewed the empty position of the objects in grids without conscious retrieval of its spatial position (Wuethrich, Hannula et al. 2018). Overall, their study provided evidence for the unconscious encoding of simple objects' position.

Episodic memory can include different types of associations including item-item associations, temporal ordering and spatial arrangement of items. To my knowledge, no study so far has investigated the possibility of unconscious encoding of complex visual associations (faces in scenes), nor whether such an item-item association can be retrieved in a way that complies with the characteristics of episodic memory according to the processing-based-memory model. In this experiment, novel face-scene associations were presented rapidly and masked from consciousness during the encoding. I then tested whether these unconsciously encoded stimuli could be retrieved unconsciously in a way that demonstrated flexibility of retrieval. If the

unconscious memory of the face-scene associations exists, and it is flexible, then viewing the cue scene should re-activate the entire memory of the face-scene association. I tested this by presenting the face that had been presented on that cue scene during the masked encoding (the target face) along with a distractor face that had not been presented with the cue scene in that trial, but had been presented on another scene during that trial. I investigated the viewing behaviour for the target compared with the distractor as a measure of unconscious retrieval of the target face after its unconscious encoding. In order to make sure that both encoding and retrieval of the face-scene associations were not conscious, I conducted two separate awareness tests. During the subjective test of awareness, after the experiment the participants reported whether they consciously saw any face during the encoding. During the objective awareness test, I evaluated the participants' performance in conscious recognition of the masked faces using the same masking protocol as the main experiment. The participants who were able to consciously perceive the masked faces were excluded from the experiment. This way the experiment was designed to test the existence of unconscious visual episodic memory according to the processing-based-memory model.

There is good evidence that viewing behaviour, as measured by various eye-tracking parameters, can be modulated by memory retrieval (Meister and Buffalo 2016). This is particularly useful when addressing questions of unconscious retrieval of associations, as conscious reports of memory will not necessarily reflect an unconscious level of memory (Ryan, Althoff et al. 2000, Ryan and Cohen 2004, Hannula, Ryan et al. 2007, Hannula and Ranganath 2009). The number of times we fixate on an image has been considered the most important eye-tracking measure that reflects recognition memory or episodic memory (Loftus 1972, Kafkas and Montaldi 2011, Molitor, Ko et al. 2014, Meister and Buffalo 2016, Liu, Shen et al. 2017). Higher number of fixations on manipulated parts of scenes have been reported without participants' conscious retrieval (Ryan, Althoff et al. 2000, Ryan and Cohen 2004).

According to a review of eye tracking-based memory studies by Meiser et al. in 2016, the other important eye-tracking measure that has been related to memory retrieval is pupil size (Meister and Buffalo 2016). Recent studies have shown that pupil size can also reflect recognition memory (Heaver and Hutton 2011, Kafkas and Montaldi 2011, Otero, Weekes et al. 2011, Naber, Frassle et al. 2013, Kucewicz, Dolezal et al. 2018). This modulation of pupil size while viewing primed objects can also happen in the absence of conscious recognition (Gomes, Montaldi et al. 2015), and although the underlying neural mechanism is not yet known, it is probably different from the mechanism that modulates the number of fixations by memory retrieval. Finally, total viewing time has been reported to be modulated as a result of memory retrieval (Hannula, Althoff et al. 2010, Meister and Buffalo 2016). The importance of total viewing time in reflecting memory retrieval has been controversial and has not been completely supported according to some important reports (Loftus 1972, Meister and Buffalo 2016). Fixation duration can be a reflective of memory load and overall intensity of information processing (Meghanathan, van Leeuwen et al. 2014). The current study was based on that of Hannula et al in 2007, except that in current experiment I used unconscious encoding instead of conscious encoding (Hannula, Ryan et al. 2007). They found that viewing the cue was accompanied by an increment in the total viewing time on the target compared with the distractor within 500-750 ms after the beginning of the free-viewing and this effect decreased after that time window. Thus, I used the eye-tracking indices of number of fixations, pupil diameter and total viewing time as separate measures to reflect unconscious retrieval of the target. I expected that unconscious retrieval of episodic associations after their unconscious encoding modulates these eye tracking measures on the target compared with the distractor.

In this experiment I assumed that, unconscious memory of the target could capture visual attention and hence modulate viewing behaviour without conscious awareness. This idea was proposed by Cabeza and his colleagues as in their attention-to-memory model (Cabeza,

Ciaramelli et al. 2008). This model postulates that involuntary episodic memory captures visual attention through interaction with bottom-up attention system. It has also been shown that visuospatial attention is biased toward the left visual hemifield (Siman-Tov, Mendelsohn et al. 2007, Newman, Loughnane et al. 2017). Healthy subjects respond to the stimuli in their left hemifield with higher speed and accuracy (Nicholls, Bradshaw et al. 1999, Nicholls, Hobson et al. 2017). Hence in this experiment, I compared the eye tracking measures between the target and the distractor within fields (The target in the left visual field was compared with the distractor in the left visual field and the target in the right visual field was compared with the distractor in the right visual field).

In addition, the leftward attentional bias is not constant in each individual. The leftward attentional bias has been related to the dominance of the right hemisphere in processing of visuospatial attention (de Schotten, Dell'Acqua et al. 2011, Nicholls, Hobson et al. 2017). Experimental variables that increase this right hemisphere dominance for attention have also been shown to increase this leftward attentional bias (Cattaneo, Silvanto et al. 2009, Szczepanski and Kastner 2013, Benwell, Thut et al. 2014, Petitet, Noonan et al. 2015). For example, presentation of stimuli in the left visual field, using one's left hand or left eye increases the leftward attentional bias compared with presentation of stimuli in the right visual field, using the right hand or the right eye respectively (Sampaio and Chokron 1992, McCourt, Garlinghouse et al. 2001, Bultitude and Aimola Davies 2006). Hence if unconscious retrieval of the target during the free-viewing in current study increases the right hemisphere dominance it can increase the leftward attentional bias. It has been shown that face recognition is performed with higher speed and accuracy when the faces are presented in the left visual field compared with the right visual field (Rizzolatti, Umiltà et al. 1971, Hilliard 1973, Leehey and Cahn 1979, Gainotti 2013). This has also been related to the right hemisphere dominance of facial processing (Kim, Andreasen et al. 1999, Nakamura, Kawashima et al. 2000,

Schweinberger, Huddy et al. 2004, Kloth, Dobel et al. 2006, Yovel, Tambini et al. 2008). Brain imaging (Ranganath and D'Esposito 2001, Taylor, Mills et al. 2011, Von Der Heide, Skipper et al. 2013) and clinical studies (Crane and Milner 2002, Milner 2003) have also shown a dominant role for right hemisphere in memory of novel faces. In this context the right dominant facial memory of the target may interact with the right dominant visual attention during the free viewing of the target and enhance the size of the leftward attentional bias. When target is in the left visual field the memory-guided attention toward the target and the leftward attentional bias both increase the visual attention toward the left visual field. But when target is in the right visual field, the enhancement in the leftward attentional bias provoked by the retrieval of the target could weaken or negate the memory-guided-attention toward the target in the right. This way I expected to see an enhancement of visual attention toward the target in the left but I did not have a prior hypothesis about modulation of visual attention on the target in the right visual field.

As mentioned earlier, the unconscious episodic memory can modulate viewing behaviour by modulating visual attention. As above, I expected that unconscious retrieval of the target would be accompanied by a higher allocation of visual attention on the target compared with the distractor in the left visual field. Regarding the close relationship between visual attention and saccadic eye movements (Hannula 2018) I expected a higher number of saccades and as a result a higher number of fixations between saccades toward the target compared with the distractor in the left during the free-viewing. Pupil dilation has also been reported during enhancement of visual attention (Binda, Pereverzeva et al. 2013, Brocher, Harbecke et al. 2018). In addition to pupil size, duration of fixations is an important factor that reflects visual attention to an image (Henderson 2007). Total viewing time is the total duration of fixations on an object. Hence I also expected to see a modulation of pupil size and total viewing time on the target compared with the distractor in the left visual field. In addition to the left visual field, I also

explored the modulation of all of these three eye tracking measures (number of fixations, pupil size and total viewing time) on the target in the right compared with the distractor in the right but I did not have any prior prediction.

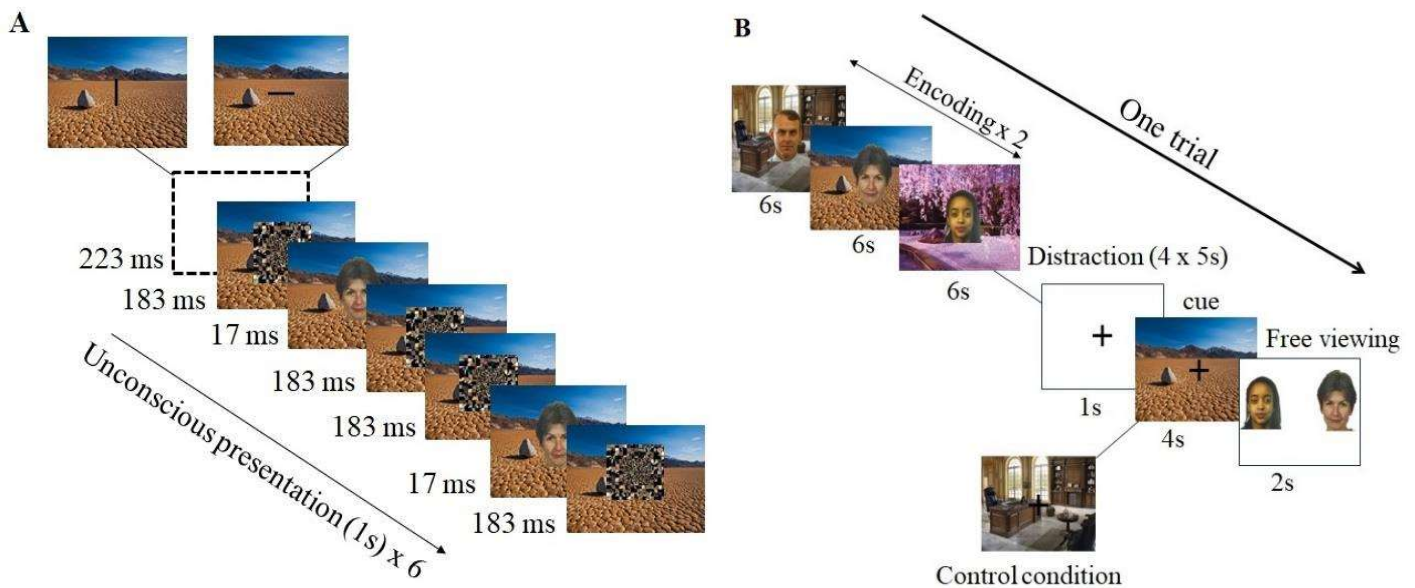
## **2.3 Methods**

### **2.3.1 Participants**

32 right-handed volunteers (28 female, 4 male) participated in this study (age range: 19-30 years, Mean: 21.87, SD: 3.16). The participants reported no neurological, psychiatric or oculomotor disorders. They also reported no current consumption of illegal or prescribed drugs. 12 participants' data were excluded based on our awareness test criteria, leaving 20 participants for unconscious memory analysis (see awareness test section). The participants gave informed consent. The study was approved by the Human Research Ethics Committee at Macquarie University (MQ; reference number: 5201200035).

### **2.3.2 Stimuli**

253 naturally coloured face images (127 male and 126 female) were selected from the FERET data base (Phillips, Wechsler et al. 1998, Phillips, Hyeonjoon et al. 2000) and the Face Database of the Bonn-Rhein-Sieg University of Applied Sciences (<http://isf.h-brs.de/en/skin-db/>) (Steiner, Sporrer et al. 2016). 181 coloured scene images (90 indoor and 91 outdoor) were also used in this study. Each face was resized to 225 X 225 pixels and each scene was resized to 800 X 600 pixels. For each participant, 166 face images (83 male, 83 female) were randomly superimposed on 166 scenes (83 outdoor, 83 indoor) to make the novel face-scene pairs



**Figure 1.** Experimental design. A) Illustration of the unconscious presentation of face-scene associations. Each face was sandwiched between forward and backward masks. For each association, the unconscious presentation (1s) depicted above was repeated six times and began with the presentation of a bar as the attention task stimulus. The participants responded to the direction of the bar (vertical or horizontal) by pressing a button while they were encoding the background scene. B) Illustration of the main experiment. Each trial began with an encoding part that consisted of the unconscious presentation of three novel face-scene associations as explained in part A. The whole encoding part was repeated (two presentations of the same stimuli). During the subsequent distraction period of 20 seconds, participants solved 5 math problems. The cue then appeared, which was either one of the encoded scenes with a fixation cross in the centre. The participants were instructed to retrieve the cue scene in their mind while keeping their gaze on the centre. Finally, two faces were presented, a target face and a distractor face, which the participants freely viewed for 2 seconds. I analysed eye movements in this final free-viewing stage to test for evidence that a face-scene association could be retrieved after only unconscious encoding.



presented in the main experiment. 15 face images (8 male, 7 female) were randomly superimposed on 15 scenes (8 outdoor, 7 indoor) for the training experiment. 72 faces were assigned to awareness test. The faces were randomly assigned to the awareness test and the main experiment for each participant.

A mask to ensure the stimuli were not perceived was constructed in two steps. First, a scrambled mask was made by shuffling 5 x 5 pixel squares of a selected face and resizing it to 106 x 106 pixels. This was then superimposed on a bigger mask of 250 x 250 pixels which resulted from the shuffling of 15 x 15 pixel squares of the same face.

### **2.3.3 Unconscious stimulus presentation**

I adopted the unconscious presentation of stimuli parameters of Henke et al. (Henke, Mondadori et al. 2003). During the unconscious encoding of the face-scene associations, the faces were masked and the scenes were visible. This way the association between faces and scenes was not perceivable at the conscious level, but the cue scene could be encoded consciously. In this protocol, the unconscious presentation of stimuli is embedded in an attention task in which participants report the orientation of a bar (vertical or horizontal) by pressing a button. This ensures that gaze is directed to the position where the faces were being presented without participants being directed to attend to the faces. Participants performed the attention task whilst trying to memorize the background scene, without the main purpose of the experiment being obvious. During unconscious encoding, each masked stimulus was presented twelve times within 6s. The presentation duration was 17 ms for the stimuli (S), 183 ms for the masks (M), and 233 ms for the fixation bars for the attention task (B). Each stimulus was presented in the following sequence B-M-S-M-M-S-M-B-M-S-M-M-S-M-B-M-S-M-M-S-M-B-M-S-M-M-S-M-B-M-S-M-M-S-M-B-M-S-M-M-S-M. The sequence

of the presentation of stimuli for 1s (this was repeated 6 times within 6s) is depicted in figure 1.

#### **2.3.4 Procedure**

Each experiment started with practice during which the task instructions were explained to the participants. During the practice, participants tried the experiment with a different set of stimuli. They then started the main experimental block. The experimental paradigm (illustrated in Figure 1) consisted of 55 trials. Each trial included encoding, distraction and free-viewing. During the encoding part, three novel face-scene associations were presented as outlined in Figure 1. The encoding part of each trial was repeated twice. The distraction part lasted 20 seconds during which participants solved 5 math problems. In the distraction period of the trial, 5 sets of three random digits appeared on the screen, each set for 4 seconds. Participants reported, via button press, whether the largest digit was equal to the sum of the other two digits (yes vs no). Even though the delay between the encoding and retrieval was a few seconds, I wanted the episodic memory to be the main type of memory involved in this experiment. It has been shown that memory of novel associations over short delays is mediated by hippocampally mediated episodic memory when the memory load is high. This high load of memory can be manifested in relatively long delay between the encoding and retrieval (above 7s), presence of distractors during the delay and novelty of stimuli (Cabeza, Dolcos et al. 2002, Nichols, Kao et al. 2006, Rissman, Gazzaley et al. 2008, Jenson, Mauldin et al. 2011). In order to reach a high load of memory I had three novel and complex visual associations in each trial that should be retained over 20s in the presence of distractors. Hence the experiment was designed in a way that episodic memory had a dominant role in the experiment. Then a fixation cross was presented for one second followed by the presentation of the cue scene for 4 seconds followed by the faces. The cue scene was selected from the scenes displayed in the encoding part of that

trial and a fixation cross was superimposed on its centre. In each case, a fixation cross was superimposed on its centre and participants were instructed to try to remember the cue scene while maintaining fixation. Subsequently, two faces were presented, one target and one distractor. Participants freely viewed the two faces. In the experimental (left target) condition, the target face that was superimposed on the cue scene during the encoding phase of the same trial was presented in the left visual field during the free-viewing. In the experimental (right target) condition, the target face that was superimposed on the cue scene during the encoding phase of the same trial was presented in the right visual field during the free-viewing. The distractor face was chosen from the faces presented in the same trial but not on the cued scene. In the control condition, none of the faces that were freely viewed were superimposed on the cue scene during encoding. Hence, there is no actual target or a distractor in this control condition; the ‘target’ and ‘distractor’ faces were chosen randomly from one of the three face-scene associations presented during the encoding part of that trial. The experimental and the control trials were interleaved randomly throughout the experiment. This experiment had, 18 experimental trials with the target on the right, 18 experimental trials with the target on the left and 18 control trials.

### **2.3.5 Awareness test**

In the end of the main experimental session, participants were asked whether they had consciously perceived a face during the encoding phase of the experiment. Data from participants who responded positively to this question were excluded from the analysis. The next stage was an objective awareness test consisting of 36 trials. In each trial, one novel face was presented unconsciously using the same method outlined in Figure 1(i.e. identical to the main experiment). As in the main experiment, they responded to the attention task (orientation of the bar), but in addition, on each trial, they were presented with a forced choice decision

about which face was presented in the masked section of the trial. This ensured that the attentional demands of the awareness task were equated with those of the main experiment. During the forced choice section of 4s, the face that had been masked was presented alongside a novel face which had never been presented before, randomly allocated to the left or right position. I used a binomial test to compare the participants' performance with chance. The participants who had more than 22 correct choices (binomial test  $p < 0.05$ ) were considered to respond above chance level and excluded from the rest of analysis.

### **2.3.6 Eye tracking acquisition and analysis**

Eye tracking measures were recorded with an Eyelink1000 tracker (SR Research, Ontario, Canada) at a sampling rate of 500 Hz. Calibration was performed using the built-in Eyelink 9-point calibration procedure every 9 trials. Event timing was controlled by Presentation software (Neurobehavioral Systems, Berkeley, CA).

The Data viewer software from SR Research was used to analyse the eye tracking measures during the free-viewing phase of each trial. I defined left and right interest areas (IA) for the left faces and the right faces. The average viewing time, average fixation number and the average pupil size (area) were calculated during the free-viewing for each IA in each condition.

The eye-tracking data were categorised into: target on left, target on right, distractor on left, distractor on right, control face on left and control face on right. The eye tracking measures when participants were freely viewing these faces were then averaged across trials for each participant. During the cue, the participants fixated on the centre of the screen to ensure the free-viewing analyses started with an estimate of the actual centre of the screen. I defined the Interest areas (IA) for the faces in left and the right interest areas with respect to this value. In

a few trials, participants did not fixate on the centre of screen during the cue. For these trials, there was not a clear way to define the IAs, so were excluded from the analysis. Trials with more than 15% of the free-viewing time as blinks were also excluded. On average 1% of the trials were excluded for each participant.

Pupil size changes largely with variables other than memory including level of alertness or fatigue, and also colour and contrast of visual stimuli (Morad, Lemberg et al. 2000, Lobato-Rincón, Cabanillas-Campos et al. 2014). The pupil size change in exposure to light also varies largely between individuals (Higuchi, Ishibashi et al. 2008). There is no consensus for baseline correction in pupillometry (Mathot, Fabius et al. 2018). I considered the average of average pupil size on left and right IAs as an estimation of baseline for each participant. I then calculated the average pupil size ratio by dividing the average pupil size for each IA by this baseline.

Pupil size (area) was measured as the number of camera pixels occupied by the pupil. The eye tracker used in this experiment was head mounted and the distance and the angle between the camera and the right eye varied while the participants were looking at the left and the right IAs. To compensate for this, I only compared the different conditions within the same IA (left or right). This correction has the beneficial effect of also avoiding influences of the inherent bias toward the left visual field outlined before (Siman-Tov, Mendelsohn et al. 2007).

Regarding my *a priori* hypothesis I expected to see a modulation in each of the eye tracking measures on the target compared with the distractor in the left visual field. But I did not have a prior hypothesis about the right visual field. I conducted a paired t-test to compare each eye tracking measure between the target and the distractor in the left visual field. As an exploratory analysis, I also performed a paired t-test to compare the eye tracking measures between the target and the distractor in the right visual field without a prior prediction. I used SPSS, version 25.0 to conduct the analyses. Cohen's d was calculated by dividing the mean of paired differences by the standard deviation (SD) of paired differences. All the graphs of the paired t

tests, were produced according to the Cousineau-Morey method (Cousineau 2005, Morey 2008). According to this method, just for visualization purpose, the data was normalized and the error bars showed the within subject 95% confidence interval of the normalized data (Cousineau 2005, Morey 2008).

## 2.4 Results

### 2.4.1 Awareness test

In total, 12 participants were excluded from the experiment either because they reported seeing a face during encoding or they performed above chance in the awareness test. This left 20 participants for the unconscious episodic memory analysis.

### 2.4.2 Evidence of unconscious encoding of face-scene associations in the left visual field

*Number of fixations:* On average, for experimental trials, participants made more fixations per trial on target faces in the left IA ( $mean=2.35$ ;  $SD=0.43$ ) compared to distractors in the left IA when the target was on the right; ( $mean=2.26$ ;  $SD=0.49$ ); *paired samples* ( $mean\ of\ paired\ differences=0.124$ ;  $SD\ of\ paired\ differences=0.184$ ;  $t(19)=3.002$ ,  $p=0.007$ ,  $Cohen's\ d=0.67$ )).

There was not a significant difference between the average number of fixations on the target in the right IA ( $mean=2.27$ ;  $SD=0.44$ ) and the distractors in the right IA, ( $mean=2.26$ ;  $SD=0.37$ ); *paired samples* ( $mean\ of\ paired\ differences=0.023$ ;  $SD\ of\ paired\ differences=0.382$ ;  $t(19)=0.263$ ,  $p=0.79$ ). The comparison between the number of fixations on the target and the distractor in each IA is depicted in Figure 2. In the control condition, there were 2.23 ( $SD=0.5$ ) fixations in the left IA and 2.27 ( $SD=0.52$ ) fixations in the right IA.

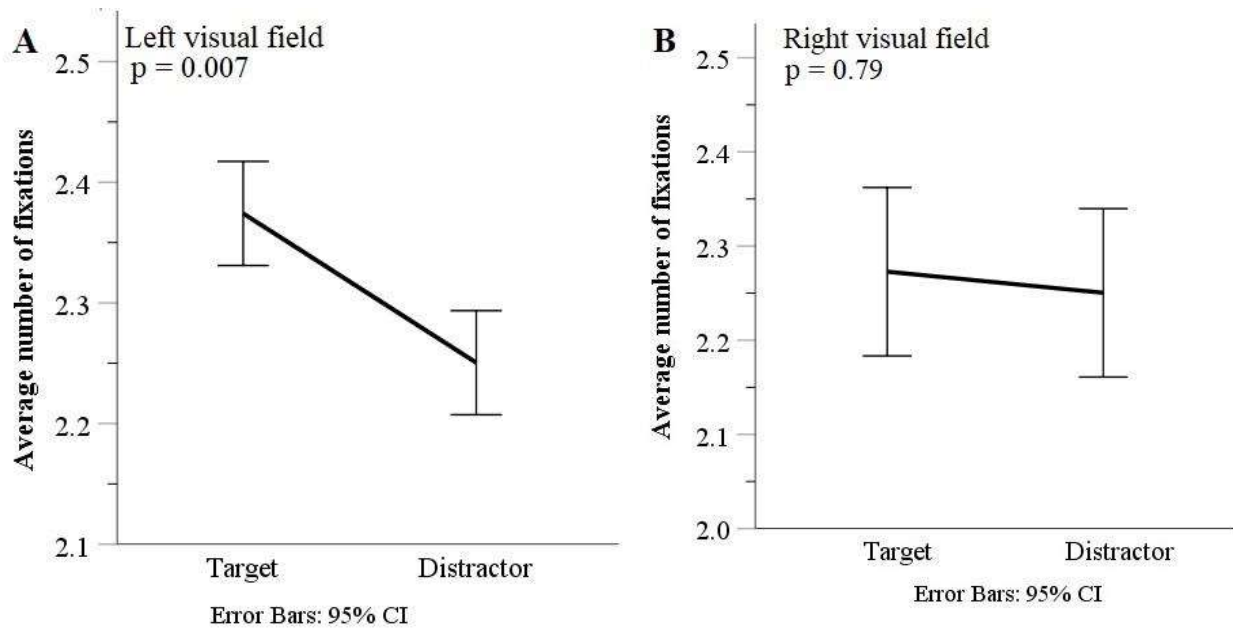


Figure 2. The average number of fixations on the target and distractor faces in the left and the right visual fields. A) The average number of fixations was significantly higher on the target compared with the distractor in the left interest area. B) There was no significant difference in the average number of fixations between the target and the distractor in the right IA. Error bars represent within subject 95% confidence interval (Cousineau 2005, Morey 2008).

*Pupil size:* The average pupil size ratio on the target in the left IA ( $mean=1.018$ ;  $SD=0.015$ ) was bigger than a distractor in the left IA ( $mean=1.013$ ;  $SD=0.014$ ); paired samples ( $mean\ of\ paired\ differences=0.005$ ;  $SD\ of\ paired\ differences=0.01$ ;  $t(19) = 2.13$ ,  $p = 0.045$ , Cohen's  $d = 0.5$ ). The average of pupil size ratio during viewing the target in the right IA ( $mean=0.986$ ;  $SD=0.015$ ) was not different from the average pupil size on the distractor in the right IA

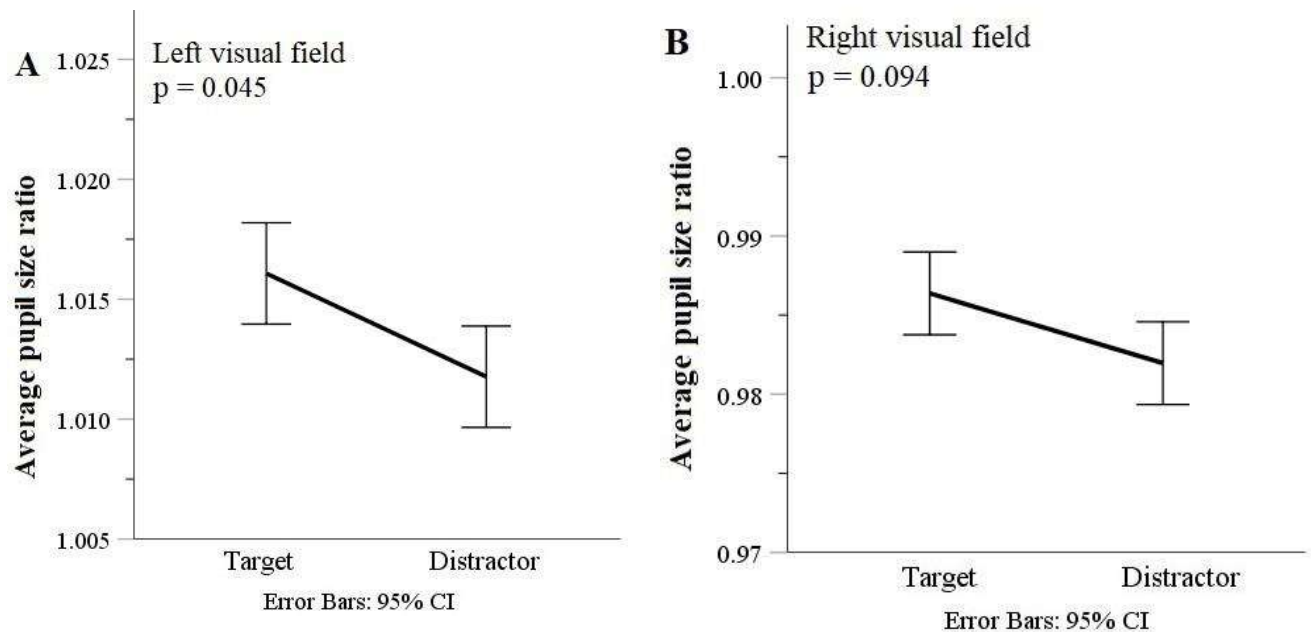


Figure 3. The average pupil size ratio on the target and the distractors in the left and the right visual fields. Pupil size ratio was calculated by dividing the average pupil size in each IA by the average of pupil size in both interest areas as baseline. A) The average pupil size ratio was significantly higher on the target compared with the distractor in the left interest area. B) There was no significant difference in the average pupil size ratio between the target and the distractor in the right IA. Error bars represent within subject 95% confidence interval (Cousineau 2005, Morey 2008).

( $mean=0.982$ ;  $SD=0.015$ ); paired samples ( $mean\ of\ paired\ differences=0.004$ ;  $SD\ of\ paired\ differences=0.11$ ;  $t(19)=1.76$ ,  $p=0.094$ ). The comparison between the average pupil size ratio on the target and the distractor in each visual field is depicted in Figure 3. During the control condition, the average pupil size ratio was 1.018 ( $SD=0.018$ ) in the left IA and 0.982 ( $SD=0.018$ ) in the right IA.



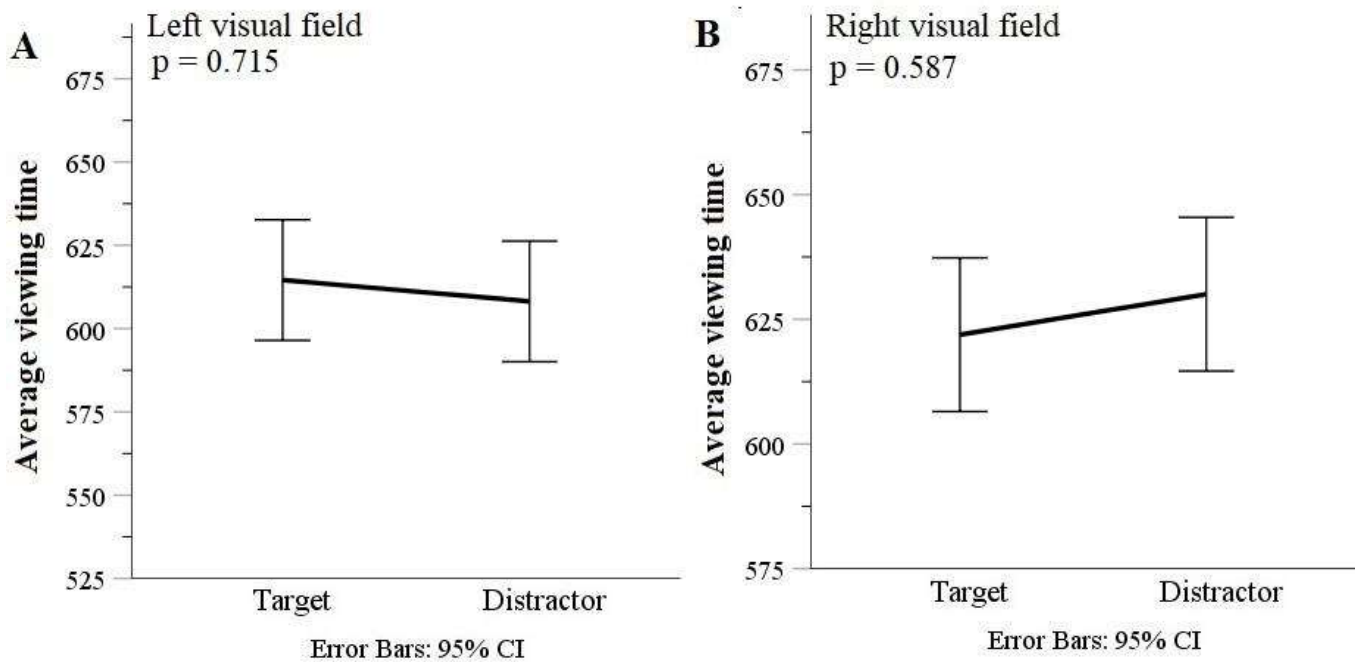


Figure 4. The average viewing time on the target and the distractor in the left (left graph) and the right (right graph) visual fields. A) There was no significant difference in the average viewing time between the target and the distractor in the left IA. B) There was no significant difference in the average viewing time between the target and the distractor in the right IA. Error bars represent within subject 95% confidence interval (Cousineau 2005, Morey 2008).

*Viewing time:* The average viewing time on the target face in the left IA ( $mean=615ms$ ;  $SD=113$ ) was not significantly different from the average viewing time on the distractor in the left IA ( $mean=608ms$ ;  $SD=128$ ); paired samples ( $mean\ of\ paired\ differences=6.401$ ;  $SD\ of\ paired\ differences=77.368$ ;  $t(19) = 0.370$ ,  $p = 0.715$ ). The average viewing time of the target in the right IA ( $mean=621ms$ ;  $SD=69$ ) was not significantly different for the distractor in the right ( $mean=630ms$ ;  $SD=80$ ); paired samples ( $mean\ of\ paired\ differences=0.022$ ;  $SD\ of\ paired\ differences=0.382$ ;  $t(19) = 0.553$ ,  $p = 0.587$ ). The comparison between the average viewing time on the target and the distractor in each visual field is depicted in Figure 4. During the

control condition the average viewing time in the left IA was  $621ms$  ( $SD=117$ ) and for the right IA it was  $626ms$  ( $SD=54$ ).

## 2.5 Discussion

In this study, I investigated the possibility of unconscious encoding and subsequent unconscious retrieval of episodically associated complex visual stimuli. According to the processing-based-memory model, if the episodic memory network is involved in encoding of masked face-scene associations, the rapid encoding of these novel and complex visual associations should lead to the formation of a flexible memory that can last over short (as well as long) retention times (Henke 2010). The experiment was designed such that the total time for the unconscious presentation of each face-scene association was very short (less than a second). If this rapid presentation of visual associations resulted in the formation of a flexible memory, retrieval of the scene stimulus should trigger or assist retrieval of the associated face stimulus. I tested for this unconscious retrieval using eye tracking measures. The average number of fixations and the average pupil size ratio was significantly higher on the target in the left visual field compared with the distractor in the left visual field. There were no such effects in the right visual field. The left visual field results are consistent with the formation of a rapid and flexible memory of complex visual stimuli at unconscious level. The lack of effects for targets in the right visual field could be due to an interaction between attentional bias toward left and the memory-guided attention toward the target on right. There was no modulation in the total viewing time between the target and the distractor.

The modulation of fixations and pupil size during the free viewing of the target compared with the distractor cannot be simply explained by the familiarity of the stimuli. The target and the distractor in each trial were randomly chosen from the faces previously presented in the encoding part of the same trial. Hence, the target and the distractor were equally familiar. The

only difference was that the target face was previously superimposed on the cue scene during the encoding, whereas the distractor face was presented on a different scene. As a result any difference between the experimental free-viewing and the control free-viewing should be the result of unconscious retrieval of the association between the cue scene and the target. Unconscious retrieval of face-scene associations would not be possible without a successful unconscious encoding. Hence these findings provide support for both unconscious encoding and unconscious retrieval of face-scene associations in my experiment.

Pupil size changes can also occur as a result of task difficulty, in addition to memory retrieval (Kahneman and Beatty 1966, Otero, Weekes et al. 2011). In this experiment the participant were instructed to freely look at the target and the distractor and the task demands were equal across conditions. Hence modulation of pupil size between the experimental and the control free-viewing could not be due to the difference in the task difficulty between these conditions.

I did not see any significant change in the total viewing time spent on the target compared with the distractor. In the study by Hannula and her colleagues [8], participants consciously encoded face-scene associations. They found that the participants' total viewing time was longer on the target compared with the distractor without conscious awareness of the target (Hannula and Ranganath 2009). In their study, the effect of unconscious retrieval on total viewing time emerged within 500-750 ms after the beginning of the free-viewing phase and faded away after that time window. I assume that the participants in their experiment were able to fixate on the presented faces within 500-750 ms from the beginning of the free-viewing phase. Hence it was possible to compare the total viewing time spent on different faces within that time window. My results show an average of total viewing time on each face of more than 600 ms. Within 750 ms from the beginning of the free-viewing phase, in many trials, my participants had not even looked yet at the second face. Hence, calculating the total viewing time for the two faces

within that time window was not feasible for my data. The above mentioned studies by Hannula et al were about modulation of total viewing time by unconscious retrieval of face-scene associations after conscious encoding (Hannula, Ryan et al. 2007, Hannula and Ranganath 2009). As a result during the viewing of the target and the distractor, these faces were familiar. In my experiment, during the free-viewing, the target and the distractor were still novel at conscious level. It was because the target and the distractor were only unconsciously presented during the encoding. It has been shown that participants fixate less and also spend less time viewing the repeated images compared with new images (Smith and Squire 2008, Crutcher, Calhoun-Haney et al. 2009). Hence, it seems plausible that in my experiment viewing the target and the distractor took more time compared with their experiment. This could explain why I was not able to compare the total viewing time spent on the target and the distractor in the time window of 500-750 ms. In this regard, lack of a significant effect of unconscious retrieval on total viewing time is not surprising.

Previous experiments on the relationship between the eye-tracking measures and unconscious retrieval of associations have been mixed, with some positive results being unable to be replicated (Ryan, Althoff et al. 2000, Smith, Hopkins et al. 2006, Smith and Squire 2008). For example, in the studies by Smith et al. (Smith, Hopkins et al. 2006, Smith and Squire 2008), there was no significant change in eye movement measures to show unconscious retrieval of manipulated parts of images after their conscious encoding. An important limitation of the studies by Smith et al was the low number of trials assigned to investigate the unconscious retrieval effect. This low number of trials were then divided to conscious and unconscious trials based on subjective awareness reports. A trial was considered unconscious only when the participants were not able to consciously recognize the manipulated part of a scene, even after they were informed about it (Smith, Hopkins et al. 2006, Smith and Squire 2008). This conservative approach may lead to the exclusion of many potential unconscious trials, in which

the participants were able to describe the manipulations only after being informed of them. In current experiment, I had much higher number of trials for each condition compared with their experiment. The combination of the two awareness tests that I used eliminated the need to exclude some trials based on subjective reports. During the subjective awareness test, participants who reported that they saw even one face during the unconscious encoding were excluded from the rest of the experiment. The objective awareness test further excluded the participants who might have seen the masked faces by excluding those who identified the masked faces above chance in the awareness test. This conservative method ensured I had higher number of trials and lower possibility of contamination of the results by conscious encoding. Hence the low number of trials in the studies by Smith et al could explain why they did not see a significant effect of unconscious retrieval on viewing behaviour (Smith, Hopkins et al. 2006, Smith and Squire 2008).

A further potential issue in previous studies (Wuethrich, Hannula et al. 2018) could be not considering the confounding effect of leftward attentional bias in modulation of viewing behaviour during the free-viewing by unconscious episodic retrieval. Regarding the leftward attentional bias in processing visuospatial information, if the unconscious memory effect on viewing behaviour is left lateralized, collapsing the viewing behaviour in the right and the left visual fields might eliminate the effect. In our study, I controlled the spatial position of the targets and the distractors and analysed the data from each visual field separately to avoid the potential influence of such general effects.

Overall, the current study has provided support for the prediction of the processing-based-memory model that encoding and retrieval of episodically associated, complex visual stimuli are not limited by consciousness. The participants' fixations and pupil dilation reflected the unconscious retrieval of episodically associated visual stimuli after their unconscious

encoding. Our data also suggests that eye tracking is a powerful technique in investigating unconscious memories.

In current experiment I found a behavioural index of unconscious episodic memory. The next step in testing the hypothesis that episodic memory can be unconscious could be to explore the role of classic memory structures such as the hippocampus in this function. Functional magnetic resonance imaging (fMRI) is a powerful technique that can reveal the role of deep brain structures (e.g. medial temporal lobe) in different cognitive functions. I next conduct an fMRI experiment to investigate whether the same medial temporal regions involved in conscious encoding and retrieval of episodically associated visual stimuli are also involved in their unconscious encoding and retrieval.

## 2.6 References

- Benwell, C. S., G. Thut, A. Grant and M. Harvey (2014). "A rightward shift in the visuospatial attention vector with healthy aging." Front Aging Neurosci **6**: 113.
- Binda, P., M. Pereverzeva and S. O. Murray (2013). "Attention to bright surfaces enhances the pupillary light reflex." J Neurosci **33**(5): 2199-2204.
- Brocher, A., R. Harbecke, T. Graf, D. Memmert and S. Huttermann (2018). "Using task effort and pupil size to track covert shifts of visual attention independently of a pupillary light reflex." Behav Res Methods **50**(6): 2551-2567.
- Bultitude, J. H. and A. M. Aimola Davies (2006). "Putting attention on the line: investigating the activation-orientation hypothesis of pseudoneglect." Neuropsychologia **44**(10): 1849-1858.
- Cabeza, R., E. Ciaramelli, I. R. Olson and M. Moscovitch (2008). "The parietal cortex and episodic memory: an attentional account." Nature reviews. Neuroscience **9**(8): 613-625.

Cabeza, R., F. Dolcos, R. Graham and L. Nyberg (2002). "Similarities and differences in the neural correlates of episodic memory retrieval and working memory." Neuroimage **16**(2): 317-330.

Cattaneo, Z., J. Silvanto, A. Pascual-Leone and L. Battelli (2009). "The role of the angular gyrus in the modulation of visuospatial attention by the mental number line." Neuroimage **44**(2): 563-568.

Cousineau, D. (2005). "Confidence intervals in within-subject designs: A simpler solution to Loftus and Masson's method." Tutorials in Quantitative Methods for Psychology **1**: 42–45.

Crane, J. and B. Milner (2002). "Do I know you? Face perception and memory in patients with selective amygdalo-hippocampectomy." Neuropsychologia **40**(5): 530-538.

Crutcher, M. D., R. Calhoun-Haney, C. M. Manzanares, J. J. Lah, A. I. Levey and S. M. Zola (2009). "Eye tracking during a visual paired comparison task as a predictor of early dementia." Am J Alzheimers Dis Other Demen **24**(3): 258-266.

Daselaar, S. M., M. S. Fleck, S. E. Prince and R. Cabeza (2006). "The medial temporal lobe distinguishes old from new independently of consciousness." J Neurosci **26**(21): 5835-5839.

de Schotten, M. T., F. Dell'Acqua, S. J. Forkel, A. Simmons, F. Vergani, D. G. M. Murphy and M. Catani (2011). "A lateralized brain network for visuospatial attention." Nature Neuroscience **14**(10): 1245-1246.

Degonda, N., C. R. Mondadori, S. Bosshardt, C. F. Schmidt, P. Boesiger, R. M. Nitsch, C. Hock and K. Henke (2005). "Implicit associative learning engages the hippocampus and interacts with explicit associative learning." Neuron **46**(3): 505-520.

Duss, S. B., T. P. Reber, J. Hanggi, S. Schwab, R. Wiest, R. M. Muri, P. Brugger, K. Gutbrod and K. Henke (2014). "Unconscious relational encoding depends on hippocampus." Brain **137**(Pt 12): 3355-3370.

Gainotti, G. (2013). "Laterality effects in normal subjects' recognition of familiar faces, voices and names. Perceptual and representational components." Neuropsychologia **51**(7): 1151-1160.

Gomes, C. A., D. Montaldi and A. Mayes (2015). "The pupil as an indicator of unconscious memory: Introducing the pupil priming effect." Psychophysiology **52**(6): 754-769.

Hannula, D. E. (2018). Chapter Nine - Attention and long-term memory: Bidirectional interactions and their effects on behavior. Psychology of Learning and Motivation. K. D. Federmeier, Academic Press. **69**: 285-323.

Hannula, D. E., R. R. Althoff, D. E. Warren, L. Riggs, N. J. Cohen and J. D. Ryan (2010). "Worth a glance: using eye movements to investigate the cognitive neuroscience of memory." Front Hum Neurosci **4**: 166.

Hannula, D. E. and C. Ranganath (2009). "The eyes have it: hippocampal activity predicts expression of memory in eye movements." Neuron **63**(5): 592-599.

Hannula, D. E., J. D. Ryan, D. Tranel and N. J. Cohen (2007). "Rapid onset relational memory effects are evident in eye movement behavior, but not in hippocampal amnesia." J Cogn Neurosci **19**(10): 1690-1705.

Heaver, B. and S. B. Hutton (2011). "Keeping an eye on the truth? Pupil size changes associated with recognition memory." Memory **19**(4): 398-405.

Henderson, J. M. (2007). "Regarding Scenes." Current Directions in Psychological Science **16**(4): 219-222.

Henke, K. (2010). "A model for memory systems based on processing modes rather than consciousness." Nat Rev Neurosci **11**(7): 523-532.

Henke, K., C. R. Mondadori, V. Treyer, R. M. Nitsch, A. Buck and C. Hock (2003). "Nonconscious formation and reactivation of semantic associations by way of the medial temporal lobe." Neuropsychologia **41**(8): 863-876.



Higuchi, S., K. Ishibashi, S. Aritake, M. Enomoto, A. Hida, M. Tamura, T. Kozaki, Y. Motohashi and K. Mishima (2008). "Inter-individual difference in pupil size correlates to suppression of melatonin by exposure to light." Neurosci Lett **440**(1): 23-26.

Hilliard, R. D. (1973). "Hemispheric Laterality Effects on a Facial Recognition Task in Normal Subjects." Cortex **9**(3): 246-258.

Jeneson, A., K. N. Mauldin, R. O. Hopkins and L. R. Squire (2011). "The role of the hippocampus in retaining relational information across short delays: the importance of memory load." Learning & memory (Cold Spring Harbor, N.Y.) **18**(5): 301-305.

Kafkas, A. and D. Montaldi (2011). "Recognition memory strength is predicted by pupillary responses at encoding while fixation patterns distinguish recollection from familiarity." Q J Exp Psychol (Hove) **64**(10): 1971-1989.

Kahneman, D. and J. Beatty (1966). "Pupil diameter and load on memory." Science **154**(3756): 1583-1585.

Kim, J. J., N. C. Andreasen, D. S. O'Leary, A. K. Wiser, L. L. B. Ponto, G. L. Watkins and R. D. Hichwa (1999). "Direct comparison of the neural substrates of recognition memory for words and faces." Brain **122**(6): 1069-1083.

Kirwan, C. B., Y. Shrager and L. R. Squire (2009). "Medial temporal lobe activity can distinguish between old and new stimuli independently of overt behavioral choice." Proc Natl Acad Sci U S A **106**(34): 14617-14621.

Kloth, N., C. Dobel, S. R. Schweinberger, P. Zwitterlood, J. Bolte and M. Junghofer (2006). "Effects of personal familiarity on early neuromagnetic correlates of face perception." Eur J Neurosci **24**(11): 3317-3321.

Kucewicz, M. T., J. Dolezal, V. Kremen, B. M. Berry, L. R. Miller, A. L. Magee, V. Fabian and G. A. Worrell (2018). "Pupil size reflects successful encoding and recall of memory in humans." Scientific Reports **8**(1): 4949.

Leehey, S. C. and A. Cahn (1979). "Lateral asymmetries in the recognition of words, familiar faces and unfamiliar faces." Neuropsychologia **17**(6): 619-628.

Liu, Z. X., K. Shen, R. K. Olsen and J. D. Ryan (2017). "Visual Sampling Predicts Hippocampal Activity." J Neurosci **37**(3): 599-609.

Lobato-Rincón, L.-L., M. D. C. Cabanillas-Campos, C. Bonnin-Arias, E. Chamorro-Gutiérrez, A. Murciano-Cespedosa and C. Sánchez-Ramos Roda (2014). "Pupillary behavior in relation to wavelength and age." Frontiers in human neuroscience **8**: 221-221.

Loftus, G. R. (1972). "Eye fixations and recognition memory for pictures." Cognitive Psychology **3**(4): 525-551.

Mathot, S., J. Fabius, E. Van Heusden and S. Van der Stigchel (2018). "Safe and sensible preprocessing and baseline correction of pupil-size data." Behav Res Methods **50**(1): 94-106.

McCourt, M. E., M. Garlinghouse and J. Butler (2001). "The influence of viewing eye on pseudoneglect magnitude." J Int Neuropsychol Soc **7**(3): 391-395.

Meghanathan, R. N., C. van Leeuwen and A. R. Nikolaev (2014). "Fixation duration surpasses pupil size as a measure of memory load in free viewing." Front Hum Neurosci **8**: 1063.

Meister, M. L. R. and E. A. Buffalo (2016). "Getting directions from the hippocampus: The neural connection between looking and memory." Neurobiol Learn Mem **134 Pt A**: 135-144.

Milner, B. (2003). "Visual recognition and recall after right temporal-lobe excision in man." Epilepsy Behav **4**(6): 799-812.

Molitor, R. J., P. C. Ko, E. P. Hussey and B. A. Ally (2014). "Memory-related eye movements challenge behavioral measures of pattern completion and pattern separation." Hippocampus **24**(6): 666-672.

Morad, Y., H. Lemberg, N. Yofe and Y. Dagan (2000). "Pupillography as an objective indicator of fatigue." Curr Eye Res **21**(1): 535-542.

Morey, R. (2008). "Confidence Intervals from Normalized Data: A correction to Cousineau." Tutorials in Quantitative Methods for Psychology **4**(61-4).

Naber, M., S. Frassle, U. Rutishauser and W. Einhauser (2013). "Pupil size signals novelty and predicts later retrieval success for declarative memories of natural scenes." J Vis **13**(2): 11.

Nakamura, K., R. Kawashima, N. Sato, A. Nakamura, M. Sugiura, T. Kato, K. Hatano, K. Ito, H. Fukuda, T. Schormann and K. Zilles (2000). "Functional delineation of the human occipito-temporal areas related to face and scene processing. A PET study." Brain **123** ( Pt 9): 1903-1912.

Newman, D. P., G. M. Loughnane, S. P. Kelly, R. G. O'Connell and M. A. Bellgrove (2017). "Visuospatial Asymmetries Arise from Differences in the Onset Time of Perceptual Evidence Accumulation." J Neurosci **37**(12): 3378-3385.

Nicholls, M. E., J. L. Bradshaw and J. B. Mattingley (1999). "Free-viewing perceptual asymmetries for the judgement of brightness, numerosity and size." Neuropsychologia **37**(3): 307-314.

Nicholls, M. E., A. Hobson, J. Petty, O. Churches and N. A. Thomas (2017). "The effect of cerebral asymmetries and eye scanning on pseudoneglect for a visual search task." Brain Cogn **111**: 134-143.

Nichols, E. A., Y.-C. Kao, M. Verfaellie and J. D. E. Gabrieli (2006). "Working memory and long-term memory for faces: Evidence from fMRI and global amnesia for involvement of the medial temporal lobes." Hippocampus **16**(7): 604-616.

Otero, S. C., B. S. Weekes and S. B. Hutton (2011). "Pupil size changes during recognition memory." Psychophysiology **48**(10): 1346-1353.

Petitot, P., M. P. Noonan, H. Bridge, J. X. O'Reilly and J. O'Shea (2015). "Testing the inter-hemispheric competition account of visual extinction with combined TMS/fMRI." Neuropsychologia **74**: 63-73.

Phillips, P. J., M. Hyeonjoon, S. A. Rizvi and P. J. Rauss (2000). "The FERET evaluation methodology for face-recognition algorithms." IEEE Transactions on Pattern Analysis and Machine Intelligence **22**(10): 1090-1104.

Phillips, P. J., H. Wechsler, J. Huang and P. J. Rauss (1998). "The FERET database and evaluation procedure for face-recognition algorithms." Image and Vision Computing **16**(5): 295-306.

Ranganath, C. and M. D'Esposito (2001). "Medial temporal lobe activity associated with active maintenance of novel information." Neuron **31**(5): 865-873.

Reber, T. P., R. Luechinger, P. Boesiger and K. Henke (2012). "Unconscious relational inference recruits the hippocampus." J Neurosci **32**(18): 6138-6148.

Rissman, J., A. Gazzaley and M. D'Esposito (2008). "Dynamic adjustments in prefrontal, hippocampal, and inferior temporal interactions with increasing visual working memory load." Cereb Cortex **18**(7): 1618-1629.

Rizzolatti, G., C. Umiltà and G. Berlucchi (1971). "Opposite superiorities of the right and left cerebral hemispheres in discriminative reaction time to physiognomical and alphabetical material." Brain **94**(3): 431-442.

Ryan, J. D., R. R. Althoff, S. Whitlow and N. J. Cohen (2000). "Amnesia is a deficit in relational memory." Psychol Sci **11**(6): 454-461.

Ryan, J. D. and N. J. Cohen (2004). "The nature of change detection and online representations of scenes." J Exp Psychol Hum Percept Perform **30**(5): 988-1015.

Sampaio, E. and S. Chokron (1992). "Pseudoneglect and reversed pseudoneglect among left-handers and right-handers." Neuropsychologia **30**(9): 797-805.

Schweinberger, S. R., V. Huddy and A. M. Burton (2004). "N250r: a face-selective brain response to stimulus repetitions." Neuroreport **15**(9): 1501-1505.

Siman-Tov, T., A. Mendelsohn, T. Schonberg, G. Avidan, I. Podlipsky, L. Pessoa, N. Gadoth, L. G. Ungerleider and T. Hendler (2007). "Bihemispheric Leftward Bias in a Visuospatial Attention-Related Network." The Journal of Neuroscience **27**(42): 11271-11278.

Smith, C. N., R. O. Hopkins and L. R. Squire (2006). "Experience-Dependent Eye Movements, Awareness, and Hippocampus-Dependent Memory." The Journal of neuroscience : the official journal of the Society for Neuroscience **26**(44): 11304-11312.

Smith, C. N. and L. R. Squire (2008). "Experience-dependent eye movements reflect hippocampus-dependent (aware) memory." The Journal of neuroscience : the official journal of the Society for Neuroscience **28**(48): 12825-12833.

Steiner, H., S. Sporrer, A. Kolb and N. Jung (2016). "Design of an Active Multispectral SWIR Camera System for Skin Detection and Face Verification." Journal of Sensors **2016**: 16.

Szczepanski, S. M. and S. Kastner (2013). "Shifting attentional priorities: control of spatial attention through hemispheric competition." J Neurosci **33**(12): 5411-5421.

Taylor, M. J., T. Mills and E. W. Pang (2011). "The development of face recognition; hippocampal and frontal lobe contributions determined with MEG." Brain Topogr **24**(3-4): 261-270.

Von Der Heide, R. J., L. M. Skipper and I. R. Olson (2013). "Anterior temporal face patches: a meta-analysis and empirical study." Front Hum Neurosci **7**: 17.

Wuethrich, S., D. E. Hannula, F. W. Mast and K. Henke (2018). "Subliminal encoding and flexible retrieval of objects in scenes." Hippocampus **28**(9): 633-643.

Yovel, G., A. Tambini and T. Brandman (2008). "The asymmetry of the fusiform face area is a stable individual characteristic that underlies the left-visual-field superiority for faces." Neuropsychologia **46**(13): 3061-3068.

Zust, M. A., P. Colella, T. P. Reber, P. Vuilleumier, M. Hauf, S. Ruch and K. Henke (2015).

"Hippocampus is place of interaction between unconscious and conscious memories." PLoS

One **10**(3): e0122459.